2025年北京市高等教育教学成果奖
支撑材料目录

成果名称：基于筑牢基础、创新引领、思政融合教学理念的《生态系统生态学》（课程）

成果完成人：白永飞、黄建辉、王艳芬

成果完成单位：中国科学院大学

支撑材料目录

论文

论文 01_PNAS_2025 ---------- 3
论文 02_Ecology Letters_2004 ---------- 11
论文 03_Communications Earth & Environment_2025 ---------- 22
论文 04_New Phytologist_2023 ---------- 33
论文 05_Science_2022 ---------- 45
论文 06_PNAS_2018 ---------- 52
论文 07_Journal of Ecology_2015 ---------- 58
论文 08_Journal of Applied Ecology_2012 ---------- 69
论文 09_PTRSB_2012 ---------- 81
论文 10_Global Change Biology_2010 ---------- 92
论文 11_Ecology_2008 ---------- 107
论文 12_Journal of Applied Ecology_2007 ---------- 121
论文 13_Nature_2004 ---------- 133
论文 14_科学通报_2023 ---------- 137
论文 15_中国科学院院刊_2020 ---------- 150
论文 16_科学通报_2020 ---------- 165
论文 17_科学通报_2018 ---------- 179

论文 18_科学通报_2016 ---------- 189
论文 19_植物生态学报_2014 ---------- 201
论文 20_生物多样性_2013 ---------- 211
专著
专著 01：国家野外科学观测研究站观测技术规范-第一卷生态系统与生物多样性 草地生态系统册.北京：科学出版社 ---------- 230
专著 02：第一章 内蒙古典型草原生态系统过程与变化. 韩兴国 主编. 2019. 草地与荒漠生态系统过程与变化. 北京：高等教育出版社 ---------- 248
标准
标准 01：草原生态修复技术规程（LY/T 3323-2022） ---------- 302
标准 02：草地固碳潜力核算技术指南（DB15/T 3761-2024） ----- 311
标准 03：草地固碳速率监测技术规程（DB15/T 3769-2024） ----- 317
标准 04：草地碳汇监测与核算技术规程（DB15/T 3765-2024） -- 326
奖励
奖励 01：2022 年度内蒙古自治区科学技术进步一等奖---------- 335
奖励 02：2020 年校级“研究生优秀课程”奖 ---------- 336
奖励 03：2020 年院级“研究生优秀课程”奖 ---------- 337
奖励 04：2017 年度中国科学院“朱李月华优秀教师奖” ---------- 338
奖励 05：2016 年被评为中国科学院优秀研究生导师---------- 339
奖励 06：2013 年度中国科学院大学 BHPB 导师科研奖 ---------- 340
报道
报道 01：2021 年白永飞接受中国国际电视台（CGTN）采访----- 341
课程讲义
讲义 01：生态系统生态学 ---------- 343

PNAS RESEARCH ARTICLE | ECOLOGY

Mycorrhiza increases plant diversity and soil carbon storage in grasslands

Entao Zhang[a,b,1], Yang Wang[a,1], Thomas W. Crowther[c], Weicheng Sun[a,b], Shiping Chen[a], Daowei Zhou[d], Zhouping Shangguan[e], Jianhui Huang[a,f], Jin-Sheng He[g,h], Yanfen Wang[f], Jiandong Sheng[i], Lisong Tang[j], Xinrong Li[k], Ming Dong[l], Yan Wu[m], Shuijin Hu[n], Yongfei Bai[a,f,2], and Guirui Yu[o]

Affiliations are included on p. 7.

Edited by James Tiedje, Michigan State University, East Lansing, MI; received June 21, 2024; accepted January 7, 2025

Experimental studies have shown that symbiotic relationships between arbuscular mycorrhizal (AM) fungi and host plants can regulate soil organic carbon (SOC) storage. Although the impacts of mycorrhiza are highly context-dependent, it remains unclear how these effects vary across broad spatial scales. Based on data from 2296 field sites across grassland ecosystems of China, here we show that mycorrhizal fungi symbiosis enhances SOC storage in the topsoil and subsoil through increasing plant diversity and elevating biomass allocation to belowground. SOC storage is significantly higher in both the topsoil and subsoil in systems dominated by obligate mycorrhizal (OM) and facultative mycorrhizal (FM) plants than those dominated by nonmycorrhizal (NM) plants. Also, the relative abundance of OM plants increases at the expense of FM plants as temperature and precipitation increase. These findings provide valuable insights into the potential mechanisms by which mycorrhizal fungi may influence grassland plant diversity and SOC storage in the context of global change.

arbuscular mycorrhizal fungi | soil organic carbon storage | plant diversity | biomass allocation

The soil organic carbon (SOC) pool is the largest component of carbon stocks in terrestrial ecosystems. The size of this pool is influenced by climate, plant carbon inputs, and the activities of soil microbes including mycorrhizal fungi (1, 2). Climate change and human activities have substantially increased carbon release in terrestrial ecosystems through accelerating the microbial decomposition of SOC in recent decades (2, 3). Therefore, understanding the role of microbes (e.g., mycorrhizal fungi) in regulating the plant carbon inputs and SOC storage is critical for mitigating the soil carbon loss (4, 5).

Plants form symbiotic relationships with two major types of mycorrhizal fungi, i.e., arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi (6). AM fungi acquire the carbon they need for growth entirely from their host plants because they cannot directly obtain carbon through decomposing litter, whereas many ECM fungi can decompose residues themselves (7). Both groups deposit much of the carbon into soil in the form of extraradical hyphae residues, fungal chitin, and glomalin-related soil protein, which form a rich microbial source of carbon input that contributes directly to SOC accumulation (8, 9). In addition, they impact SOC formation through a range of physical mechanisms including soil aggregate formation (10, 11) and by altering the diversity and composition of host plants (12, 13). However, the effect of mycorrhizal fungi on plant diversity varies significantly among ecosystems. For instance, studies conducted in grasslands and forests have yielded inconsistent or even contrasting results (14, 15). As a result, it remains unclear how the contribution of mycorrhizal fungi to plant diversity and SOC varies across large spatial scales (16).

The classical theory proposes that climate is the main driver controlling the large-scale distribution of mycorrhizal types; that is, with increasing latitude, ecosystems dominated by AM fungi tend to shift toward systems dominated by ECM fungi (17). Several studies have reported the distribution of the mycorrhizal types and their links to SOC at global and regional scales (18, 19). However, in ecosystems such as grasslands and deserts, plants often have a single mycorrhizal type (i.e., AM fungi) but variable mycorrhizal status (20). Mycorrhizal status can be classified as constantly colonized (i.e., obligately mycorrhizal, OM), sometimes colonized (facultatively mycorrhizal, FM), or never colonized (nonmycorrhizal, NM) based on the consistency of mycorrhizal symbiosis occurring among different individuals of a mycorrhizal plant species (21). Therefore, the broad-scale patterns of mycorrhizal status of plants, as a fundamental property of plant symbionts, may indicate the potential influence of mycorrhizal colonization on plant community structure, primary productivity, and SOC storage under different climatic conditions (19, 21). Yet, it remains unclear how changes in the relative abundance of OM, FM, and NM plants affect SOC storage across various ecosystems, such as natural grasslands.

Significance

Climate change and human activities have substantially increased carbon release from terrestrial ecosystems by accelerating the microbial decomposition of soil organic carbon (SOC) in recent decades. Investigating the role of microbes, such as mycorrhizal fungi, in regulating plant carbon inputs and SOC storage is essential for addressing soil carbon loss. Our findings suggest that mycorrhizal fungi symbiosis may enhance SOC storage in both the topsoil and subsoil by promoting plant diversity and enhancing belowground biomass allocation. SOC storage tends to be higher in ecosystems dominated by obligate and facultative mycorrhizal plants compared to those dominated by nonmycorrhizal plants. These results provide important insights into how mycorrhizal fungi influence plant diversity and SOC storage in the context of global environmental changes.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2025 the Author(s). Published by PNAS. This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

[1]E.Z. and Yang Wang contributed equally to this work.

[2]To whom correspondence may be addressed. Email: yfbai@ibcas.ac.cn.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2412556122/-/DCSupplemental.

Published February 12, 2025.

Downloaded from https://www.pnas.org by CAS INSTITUTE OF BOTANY on March 6, 2025 from IP address 159.226.232.223.

Here, we explore the patterns of plant mycorrhizal status and the potential influence of mycorrhiza on SOC storage across a broad range of climate conditions based on the intensive field survey conducted at 2296 grassland sites throughout China (*SI Appendix*, Fig. S1 and Table S1). We employed a plant community mycorrhizal index (MI) to reflect the degree of mycorrhization in the community and mycorrhizal symbiosis potential across various grassland ecosystems. The MI was calculated by summing the symbiotic potential of plants with different mycorrhizal status, weighted by their relative abundance within the community. To further elucidate the predominant symbiotic tendencies within the community, we categorized the plant communities into those dominated by OM, FM, NM plants, and mixed communities, based on the relative abundance of plants exhibiting different mycorrhizal status. Specifically, our study addresses three questions: i) how do the broad-scale patterns of plant mycorrhizal status vary across various grassland ecosystems? ii) how do the OM, FM, and NM plants differ in their relationships with SOC storage? iii) what are the major mechanisms associated with the influence of mycorrhiza on SOC storage in the topsoil and subsoil? Untangling these questions can provide mechanistic insights into the variation in SOC formation and stability across broad spatial scales, which are critical for projecting global carbon dynamics under future climate scenarios.

Results

Geographical Distribution of Plant Mycorrhizal Status. The MI differed significantly among grassland types and vegetation types, suggesting the diverse mycorrhizal colonization potential of plant species in these systems (Fig. 1*A*). The predictive power of climate variables (i.e., precipitation and temperature) on plant community MI enhanced significantly when grassland type was included in the general linear model (*SI Appendix*, Table S2). At the regional scale, MI generally increased along the humidity gradient, with grasslands in humid and warm regions showing the highest MI (Fig. 1*A* and *SI Appendix*, Table S3 and S4). MI also varied among grassland types within a vegetation type, caused mainly by water availability (Fig. 1*A* and *SI Appendix*, Table S1). In general, MI was significantly higher in mountain meadow than in lowland meadow and alpine meadow regions, and tropical shrubland exhibited a greater MI than warm shrubland (Fig. 1*A*). In addition, the relative abundance of OM plants increased with increasing mean annual temperature and mean annual precipitation, whereas the relative abundance of FM plants decreased, with NM plants showing the least variation in their relative abundance (Fig. 1*B*). For a given grassland type, the relative abundance of OM plants was higher than that of FM plants, with NM plants exhibiting the least abundance (Fig. 1*B*). Our general linear models further confirmed that precipitation and temperature were key climatic factors regulating the relative abundance of OM, FM, and NM plants across all grassland sites (*SI Appendix*, Table S5).

Effects of Climate, Mycorrhiza, Productivity, and Nitrogen Deposition on SOC Storage. Structural equation models (SEMs) showed that mean annual precipitation had a direct positive effect while mean annual temperature had a direct negative effect on topsoil and subsoil SOC storage (Fig. 2 *A*–*D*). The effects of precipitation and temperature on SOC storage were mediated by mycorrhiza, aboveground net primary productivity, belowground biomass, plant species richness (SR), and nitrogen deposition rate (Fig. 2 *A* and *B*). Belowground biomass exhibited consistently positive effects on SOC storage in both the topsoil and subsoil (Fig. 2 *A*–*D*). Aboveground primary productivity also exhibited direct positive effects on belowground biomass and SOC storage (only subsoil) (Fig. 2 *A* and *B*). The direct effect of plant SR on SOC storage was positive in the topsoil but not significant in the subsoil. Nitrogen deposition, in contrast, showed consistently direct negative effects on SOC storage (Fig. 2 *A*–*D*). In addition, mycorrhiza showed indirect positive effects on SOC through enhancing plant SR and belowground biomass, and aboveground primary productivity had indirect positive effect on SOC storage through a positive effect on belowground biomass (Fig. 2 *A*–*D*). Nitrogen deposition also indirectly affected SOC through its effect on aboveground primary productivity, plant SR, and belowground biomass (Fig. 2 *A* and *B*). The effects of temperature, precipitation, nitrogen deposition, MI, and plant SR on belowground biomass and SOC were quite consistent, even when the sample points were well matched between the topsoil and subsoil models (*SI Appendix*, Fig. S2).

Moreover, MI exhibited a significant positive effect on SOC storage in topsoil and subsoil (*SI Appendix*, Table S8). In both the topsoil and subsoil, the SOC storage was significantly higher in grasslands dominated by OM, FM, and mixed-type (MIX) plants compared to grasslands dominated by NM plants (*SI Appendix*, Fig. S3).

Effect of Mycorrhiza on Plant SR and Community Biomass Allocation. Across the study region, plant SR was positively correlated with both MI and mycorrhizal plant evenness (Fig. 3 *A* and *B*). However, the relationship between MI and plant SR was not linear, but rather hump-shaped (Fig. 3*A*). The relationships of plant SR with biotic and abiotic factors were qualitatively similar among the eight grassland types (*SI Appendix*, Fig. S4). Specifically, plant SR was significantly higher in communities dominated by OM and MIX plants than in communities dominated by FM and NM plants (Fig. 3*C* and *SI Appendix*, Fig. S5).

OM, FM, and MIX communities exhibited significantly greater belowground biomass and higher root-to-shoot ratios compared to NM communities. In contrast, the differences in aboveground primary productivity among various mycorrhizal status communities were minimal (Fig. 4*A* and *SI Appendix*, Table S9 and Fig. S5). The MI and mycorrhizal plant evenness showed positive effects whereas mean annual precipitation and mean annual temperature exhibited negative effects on root-to-shoot ratio across all grassland sites (*SI Appendix*, Table S10). Moreover, the type of dominant mycorrhizal status mediated the effect of temperature rather than precipitation on root-to-shoot ratio (Fig. 4*B*).

Discussion

Our study systematically investigated the relationship between plant-mycorrhizal associations and grassland SOC storage across extensive spatial scales in China, spanning 58 degrees of longitude (74.92°E to 132.94°E) and 32 degrees of latitude (18.76°N to 51.03°N). Our results demonstrate that SOC storage is significantly greater in both the topsoil and subsoil of ecosystems dominated by obligate mycorrhizal (OM) and facultative mycorrhizal (FM) plants compared to those dominated by NM plants. Mycorrhizal fungi symbiosis enhances SOC storage through promoting plant diversity and elevating the allocation of biomass belowground. These findings provide valuable insights into the role of plant–fungal symbiosis in regulating SOC dynamics and have important implications for understanding SOC balance under changing climatic conditions.

First, our results suggest that AM fungi may contribute to increased SOC storage in both the topsoil and subsoil by promoting plant diversity and enhancing the allocation of plant photosynthetic

Downloaded from https://www.pnas.org by CAS INSTITUTE OF BOTANY on March 6, 2025 from IP address 159.226.232.223.

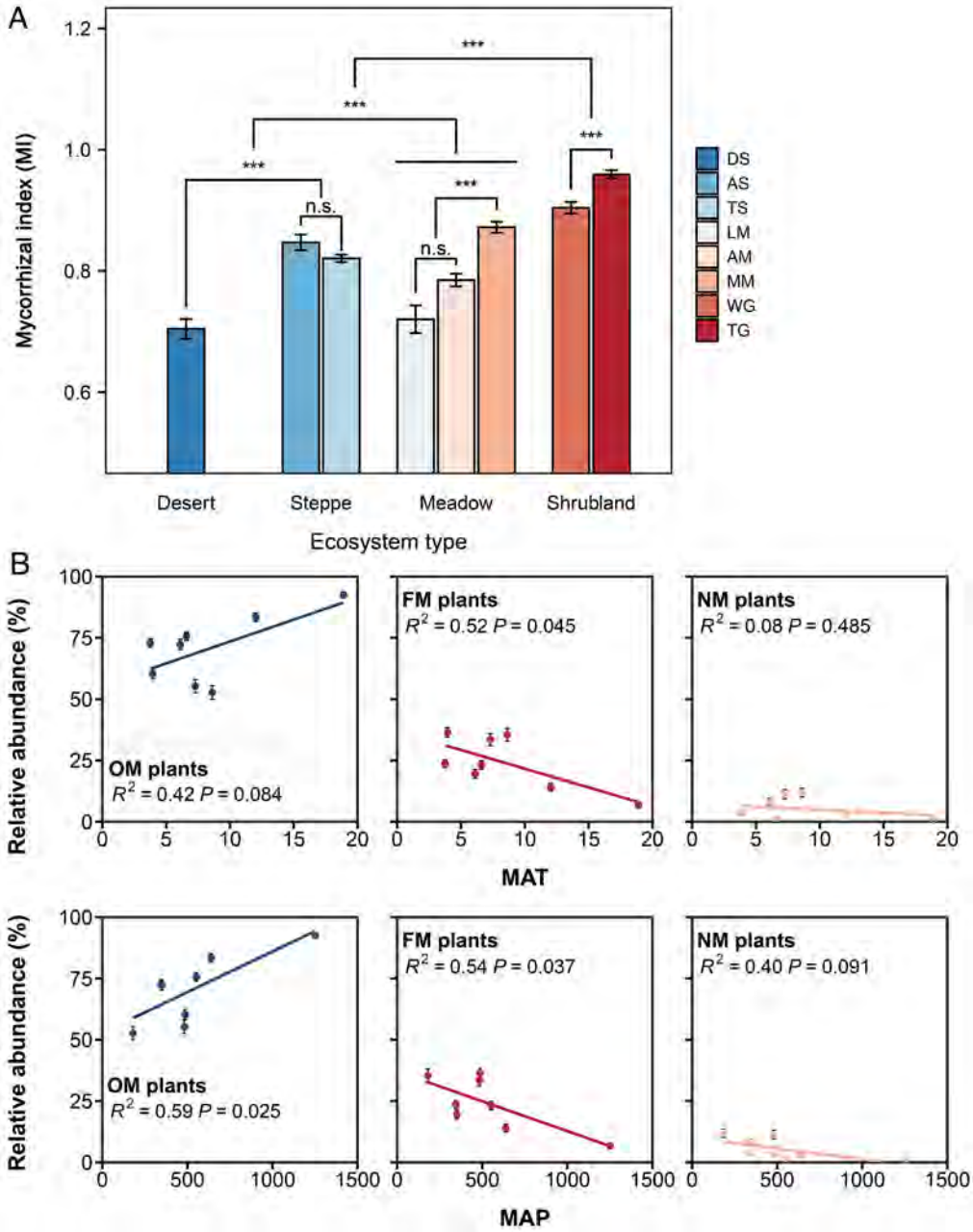


Fig. 1. Plant mycorrhizal status in different grassland types and effects of temperature and precipitation on the relative abundance of different mycorrhizal status species in the community. (*A*) Wilcoxon test was used for comparison of the community mycorrhizal index (MI) among various grasslands. Abbreviations: desert, desert grassland (n = 240); steppe, temperate steppe, and alpine steppe (n = 1233); meadow, lowland meadow, mountain meadow, and alpine meadow (n = 460); shrubland, warm shrubland, and tropical shrubland (n = 363). Significance level: ***P < 0.001; and n.s., not significant. (*B*) each point represents a grassland type. Abbreviations: AM, alpine meadow; AS, alpine steppe; MM, mountain meadow; TS, temperate steppe; LM, lowland meadow; DS, desert; WG, warm shrubland; TG, tropical shrubland. MAP, mean annual precipitation; and MAT, mean annual temperature. OM, obligately mycorrhizal; FM, facultatively mycorrhizal; NM, nonmycorrhizal.

products belowground. Plant carbon input is the primary source of SOC (22). Previous studies have attributed mycorrhizal facilitation of plant C input to belowground to plant C allocation to mycelium and associated structure, which accounts for 3 to 20% of the root dry weight (6). Our results showed that the increase in mycorrhizal symbiosis potential and mycorrhizal status evenness of the plant community strongly related to both the belowground biomass and root-to-shoot ratio of plants, thereby increasing the source of SOC. Contrary to the classical paradigm that mycorrhizal fungi generally enhance plant growth (23), we found no overall relationship between mycorrhizal symbiosis potential and aboveground primary productivity. In fact, experimental studies have reported positive (13), neutral (24), and negative effect of mycorrhiza on plant biomass in different contexts (25, 26). This inconsistency may be related to variations in AMF colonization rate under different soil nutrient conditions, which are difficult to capture using the MI. Our results show that the effect of mycorrhizal symbiosis potential on plant belowground biomass allocation is highly context-dependent, varying strongly with climate, plant diversity, and status of mycorrhizal plants.

Second, our results showed that different status of mycorrhizal plants is significantly related to SOC, providing additional context to previous research that has primarily examined the relationship between community-dominant mycorrhizal types and SOC storage (19). Across our study region, SOC storage was considerably higher in OM and FM plant-dominated communities

Downloaded from https://www.pnas.org by CAS INSTITUTE OF BOTANY on March 6, 2025 from IP address 159.226.232.223.

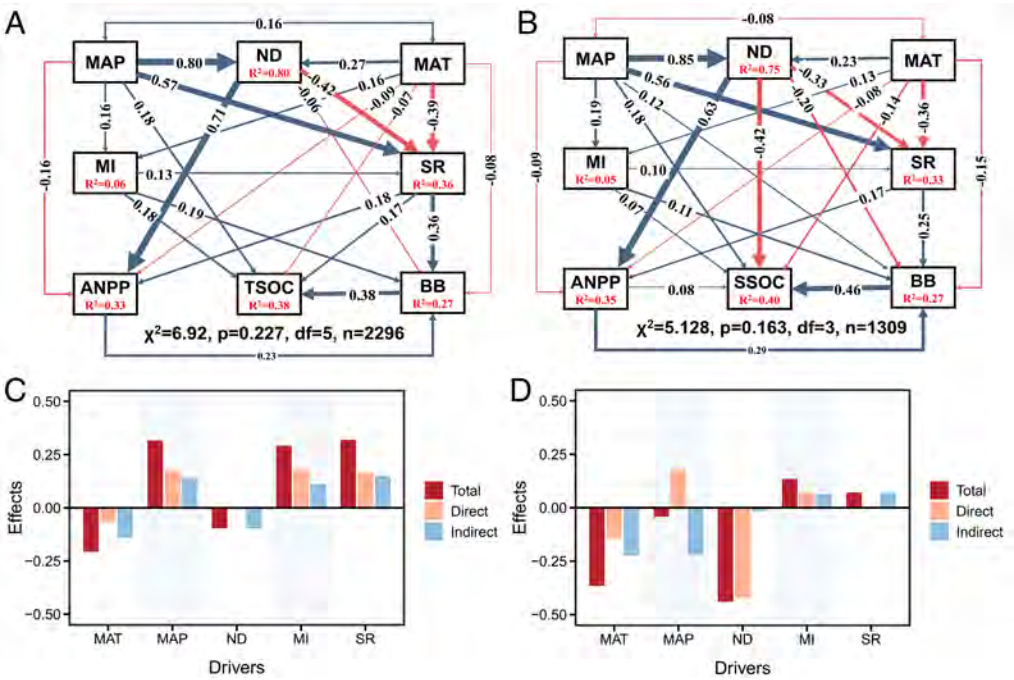


Fig. 2. Strucure equation models (SEMs) of the effects of abiotic and biotic factors on soil organic carbon (SOC) storage. (*A*) the topsoil. (*B*) the subsoil. (*C*) the direct, indirect, and total effects of drivers to topsoil SOC. (*D*) the direct, indirect, and total effects of drivers to subsoil SOC. For each SEM, blue and red arrows represent significant positive and negative pathways, respectively. Bold numbers indicate the standard path coefficients. The thickness of the line segment represents the magnitude of the effect. R^2 represents the proportion of variance explained for each dependent variable in the model. Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature; ND, nitrogen deposition; MI, plant community mycorrhizal index; SR, plant species richness; ANPP, aboveground net primary productivity; BB, belowground biomass; TSOC, topsoil SOC storage; and SSOC, subsoil SOC storage.

compared to those dominated by NM plants. This pattern was consistent in both the topsoil and subsoil, highlighting the influence of plant functional types on SOC storage across different soil depths. In particular, the root-to-shoot ratio was 2 to 4 times greater in ecosystems dominated by OM and FM plants than those dominated by NM plants. Numerous field experiments have previously shown that AM mycorrhiza increased glomalin-related soil protein and soil aggregates, thereby promoting SOC storage (27). Our results further indicate that the high relative abundance of OM and FM plants in the community may be associated with increased SOC storage, whereas the high relative abundance of NM plants may be linked to reduced SOC storage. A recent study in an Estonia calcareous grassland also reported that the composition of plant mycorrhizal status in community could reflect the closeness of the interconnection between plants and AM fungi (28). These findings indicate that plant community composition and its dominant mycorrhizal status may play a significant role influencing SOC storage through affecting plant species diversity and biomass allocation to belowground (29).

Third, our results suggest that climate is an important factor determining the large-scale distribution of mycorrhizal plants, which have direct implications for SOC storage. At the regional scale, we found that the mycorrhizal colonization potential varied considerably among different grassland types (Fig. 1*A* and *SI Appendix*, Table S3 and Table S4). Specifically, mycorrhization potential increased from desert to steppes and to hot and warm shrublands along the gradient of increasing climate favorability. The distinction between grassland types mainly stems from differences in plant species composition (30), as well as varying symbiotic potential of these plant taxa with AM fungi (31). In addition, the biogeographical patterns of mycorrhizal status of plants are predominantly controlled by precipitation and temperature, with OM plants increasing in warm, moist regions at the expense of FM plants (Fig. 1*B* and *SI Appendix*, Table S5). Several studies have reported that the distribution of mycorrhizal status of plants in Europe is mainly driven by temperature, whereas high precipitation has a neutral or negative effect on the proportion of OM plants (21, 32). Our results showed that precipitation exerts a significantly stronger positive effect on both the mycorrhizal symbiosis potential and the relative abundance of OM plants compared to the effect of temperature (Figs. 1*A* and 2). This suggests that water availability may be a more critical environmental factor than temperature in promoting mycorrhizal associations. The difference between our results and previous findings may be explained by two major reasons. First, plant diversity and community structure are predominantly influenced by water availability in grassland ecosystems (33). Hence, precipitation may have a greater effect on mycorrhizal colonization potential in grasslands although temperature is an important factor influencing AM mycelial growth (34). Second, most previous models have overestimated the proportion of OM plants at low latitudes and underestimated the proportion of FM plants at middle and high latitudes (35, 36). Our results suggest that vegetation type may not be negligible when considering the influence of climate on the distribution of plant mycorrhizal status. More importantly, we show that high mycorrhizal symbiosis potential and greater mycorrhizal status evenness enhance plant diversity and the root-to-shoot ratio of plants across all grassland types. These findings suggest that mycorrhiza may mediate the direct effect of climate favorability (high temperature and high precipitation) on SOC storage and indirectly contribute to the increase in SOC through positive mycorrhiza-species richness and mycorrhiza-belowground biomass pathways.

In conclusion, our findings suggest that the potential for mycorrhizal symbiosis and the prevailing mycorrhizal status of plant communities may play key roles in regulating SOC storage across large spatial scales. The distribution of different mycorrhizal types is influenced strongly by variations in climate conditions, which simultaneously affect the diversity and composition of plant host species. These interconnected mechanisms likely regulate SOC storage in

Downloaded from https://www.pnas.org by CAS INSTITUTE OF BOTANY on March 6, 2025 from IP address 159.226.232.223.

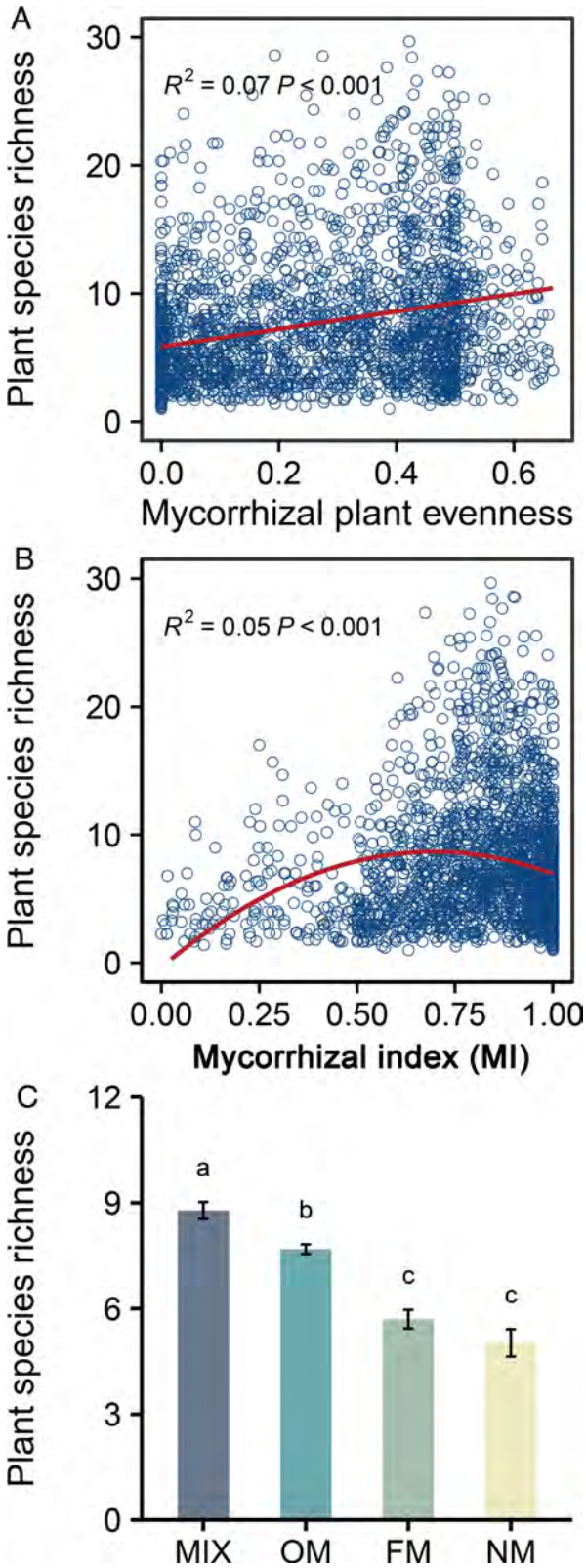


Fig. 3. Relationships of plant species richness (SR) with MI, mycorrhizal plant evenness, and dominant mycorrhizal status. The generalized linear models (GLM) were used to explore the relationships of SR with MI (*A*) and mycorrhizal plant evenness (*B*) (n = 2,296), with quasi-Poisson family model. A paired Wilcoxon test was performed to compare the differences in SR among different mycorrhizal status communities (*C*). The number of sampling sites is 1,469 for OM, 213 for FM, 542 for mixed-type (MIX), and 72 for NM plants dominated communities. Bars with different letters identify significant differences between means (Wilcoxon test, $P < 0.05$).

the topsoil and subsoil and provide mechanistic insights that may be critical for model projections of terrestrial carbon storage under current and future climate scenarios. It is important to note that the MI primarily reflects the degree of mycorrhization potential between plants and AM fungi. However, significant variability exists in the colonization potential of AM fungi, particularly under complex environmental conditions such as changing soil nutrient levels. To deepen our understanding of this relationship, future research should focus on directly examining how the extent of mycorrhizal symbiosis of the plant community affects SOC dynamics and balance in field settings. Furthermore, it is essential to accurately assess the role of mycorrhiza in soil carbon sequestration under projected climate change scenarios and varying land use conditions.

Materials and Methods

Field Investigation and Data Acquisition. In this study, we used field survey data from 2,296 sites representing various types of grasslands across China (*SI Appendix*, Fig. S1) (37). Field sampling and measurement were conducted during the annual peak-standing biomass period, which occurs from mid-July to August in the middle and high latitudes and Qinghai–Tibetan areas, and from August to September in desert, subtropical, and tropical regions. At each site, we measured aboveground biomass and belowground biomass of herbaceous plants using ten 1 m × 1 m plots (0.5 m × 0.5 m for meadow and alpine meadow) located along a 100 m transect (37). For shrubs, aboveground and belowground biomass were measured by collecting leaves and current-year twigs of each species and all roots, using five 5 m × 5 m plots randomly located within a 100 m × 100 m area. The aboveground and belowground biomass over all plots for each site were averaged to represent site-level aboveground and belowground biomass. This averaged total aboveground biomass was then used to estimate aboveground net primary productivity for each site. Five of the ten plots (three of the five plots for shrubs) at each site were selected randomly to estimate plant SR, species relative abundance, belowground biomass, soil bulk density, and SOC storage. The number of plant species recorded in five 1 × 1 m plots was averaged to quantify SR. For meadow, alpine meadow, and shrubland sites, the number of plant species within each plot was recorded, scaled to 1 × 1 m a plot using species–area curve specific to each grassland type, and then averaged over the five plots. Soil samples were collected from each plot using soil core methods. After removing residues and impurities from the soil surface, soil cores were taken sequentially with a 5-cm diameter auger at seven depths: 0 to 5, 5 to 10, 10 to 20, 20 to 30, 30 to 50, 50 to 70, and 70 to 100 cm. Three to six samples were collected from each soil layer for mixing within each plot. These soil samples were analyzed for gravel content (>2 mm), bulk density (g cm^{-3}), and SOC concentration. SOC storage for each soil layer was calculated by multiplying soil bulk density by SOC concentration, adjusting for gravel content. The total SOC from the 0 to 20 cm and 20 to 100 cm depths was used to represent SOC storage in the topsoil and subsoil, respectively (37). Additionally, soil classification data for each of sampling site were extracted from the Harmonized World Soil Database v1.2 (https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/). This database offers a resolution of 1 km (30 arc seconds by 30 arc seconds), which is finer than the distance between our sampling sites (38).

To facilitate our analysis and interpretations, the 2,296 field sites were classified into eight grassland types, including lowland meadows, mountain meadows, alpine meadows, temperate steppe, alpine steppe, warm shrubland, tropical shrubland, and desert, based on plant community composition, climate, and environmental conditions (37).

Mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) for each site were obtained from the Worldly data layers (i.e., bio_1 and bio_12) with a resolution of 30 s × 30 s (c.a. 1 × 1 km at the equator) (http://www.worldclim.org/). Nitrogen (N) deposition rate (kg N ha^{-1} yr^{-1}) for each site was obtained from the gridded long-term N deposition database (39).

Plant Mycorrhizal Status and MI. We utilized the MI as a measure to assess the extent of mycorrhization within the community at each site (20). First, the mycorrhizal status of plants was assigned to plant species across all sites according to the

Downloaded from https://www.pnas.org by CAS INSTITUTE OF BOTANY on March 6, 2025 from IP address 159.226.232.223.

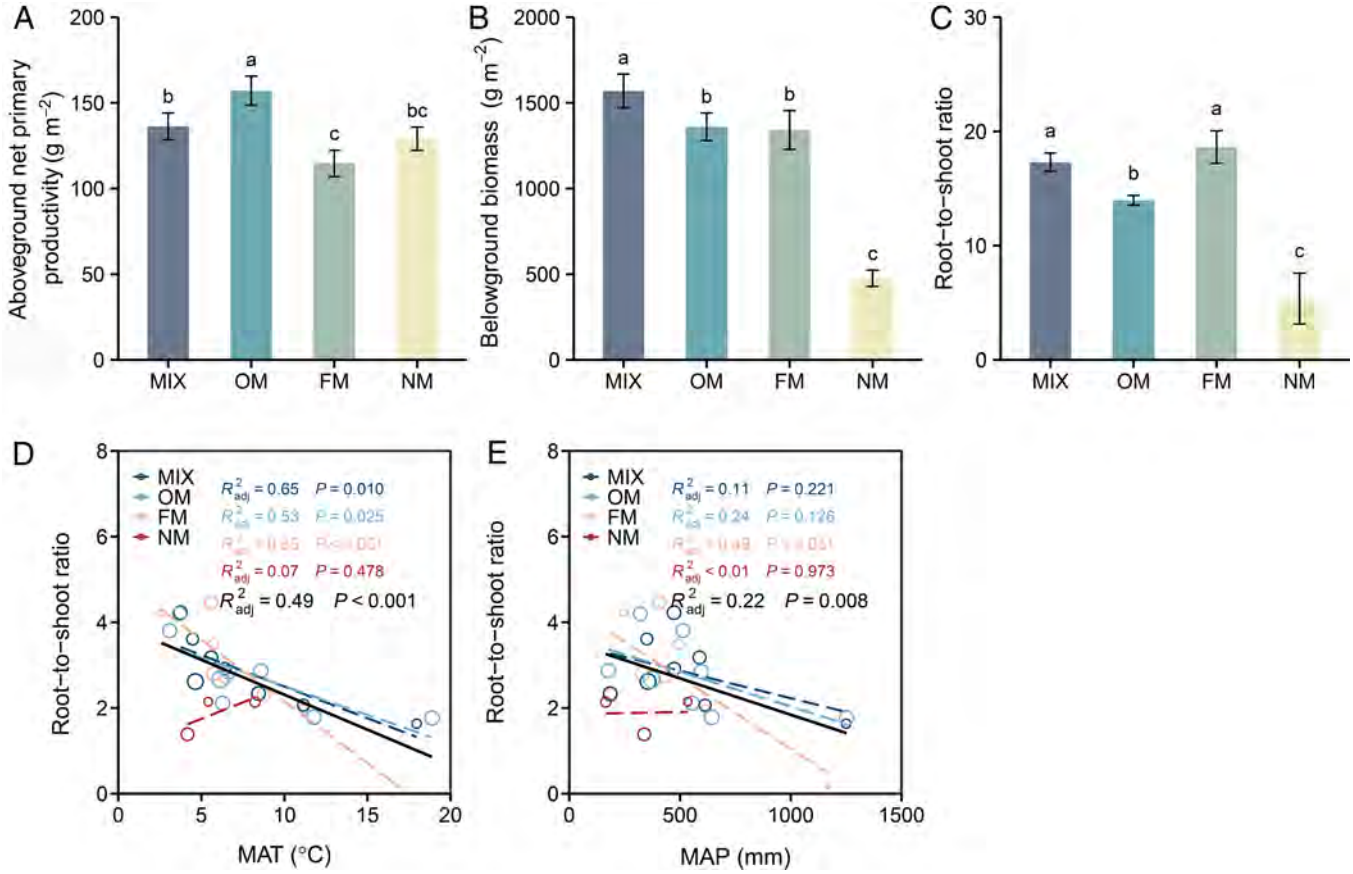


Fig. 4. Effect of community dominant mycorrhizal status on plant community above- and below-ground biomass and root-to-shoot ratio. (*A*–*C*) variance in the aboveground net primary productivity, belowground biomass, and root-to-shoot ratio of different mycorrhizal status communities. The number of sampling sites is 542 for MIX, 1,469 for OM, 213 for FM, and 72 for NM plants-dominated communities. Bars with different letters identify significant differences between means (Wilcoxon test, $P < 0.05$). (*D*–*F*) Relationships of root-to-shoot ratio in communities with different mycorrhizal status with MAT and MAP. Each point represents a grassland type, and the size of the points indicates the relative number of data points for each grassland type. The solid line represents the overall regression, the dashed line represents the different mycorrhizal status.

existing plant mycorrhizal information database- FungalRoot (20). To reduce and avoid fallacies in data usage, we performed plant mycorrhizal status matching based on the genus level of each species (40). Since there are only arbuscular mycorrhiza and very little orchid mycorrhiza in grassland ecosystems, we characterized each plant by the level of its mycorrhizal status: OM, facultative mycorrhizal (FM), and NM plants. The relative abundance OM, FM, and NM plants varied substantially at the genus level, and they did not autocorrelate with MAT and MAP (*SI Appendix*, Table S11 and Fig. S8). To quantify the contribution of each mycorrhizal status to community mycorrhization, we assigned numerical values (i.e., mycorrhization coefficient) to each category: 0 for NM plants, 0.5 for FM plants, and 1 for OM plants (41). The MI of each plant community was calculated using following formula:

$$\mathrm{MI} = \sum (Pi * Mi),$$

where MI is the community MI, *Pi* is the relative abundance of plant species *i* in the community, and *Mi* is the numerical value of mycorrhizal status of species *i*.

To measure the evenness of plants in different mycorrhizal status within the community, we used the following equation:

$$E = 1 - \sum (n/N)^2,$$

where n represents the number of individuals in different mycorrhizal status and *N* represents the total number of individuals in the community.

We also distinguished between communities in which plants of different mycorrhizal status were dominant. According to the classification (42), OM communities were those with a relative abundance of OM plants greater than 66.6%, FM communities with a relative abundance of FM plants greater than 66.6%, NM communities with a relative abundance of NM plants greater than 66.6%, and others were mixed communities.

Statistical Analyses. To examine the large-scale patterns of climate on the distribution and composition of plants with varying mycorrhizal status, we used general linear models to analyze mycorrhization in the community and the relative abundance of plants with different mycorrhizal status across various climate gradients. We used the Wilcoxon test to compare differences in MI across eight grassland types as well as four vegetation types. The relative abundance of species in the community was used in the form of percentages. The relationship between climate (MAP and MAT) and the plant relative abundance in three mycorrhizal status was analyzed using general linear model. We simultaneously ran general linear models to verify the effects of temperature and precipitation and their interactions on the relative abundance of plants with different mycorrhizal status in the community, with the temperature, precipitation, and grassland types as fixed effects.

To investigate how mycorrhizal plants composition mediates the effects of environmental factors on SOC accumulation, we used SEMs. For variables involved in the model, such as MAT, MAP, N deposition, MI, plant SR, aboveground primary productivity, belowground biomass, and SOC, we first established a correlation matrix to analyze the correlation of each factor (*SI Appendix*, Fig. S6). Second, we developed a null model of the SEM based on existing research and theory (16, 37, 43). All selected variables were transformed to natural logarithm values before the SEM analysis to mitigate departures from normality and linearity. To investigate the effects of climate and mycorrhiza on SOC storage at different depths, we also divided the soil into shallow layer (topsoil, 0 to 20 cm) and deep layer (subsoil, 20 to 100 cm). Based on Amos, all unimportant paths ($P > 0.05$) in the model refinement process were gradually eliminated until all paths were significant. To address the discrepancy in sample sizes between the topsoil model (n = 2,296) and the subsoil model (n = 1,309), we further standardized both models to the same number of data points (n = 1309). This approach was implemented to minimize errors arising from differences in sample size. All models calculated the total effect as well as the direct and indirect effect values of MAT, MAP, N deposition, MI, and plant SR on SOC. To further analyze the effect of the MI and climate

Downloaded from https://www.pnas.org by CAS INSTITUTE OF BOTANY on March 6, 2025 from IP address 159.226.232.223.

on SOC among different soil types, we used a mixed linear model to incorporate the above variables, using MAP and MAT as fixed terms and grassland type and soil type as random factors. The variables of SOC, MI, and climate were standardized to z-scores following a natural logarithm transformation before mixed linear model analysis.

To investigate the effects of MI and mycorrhizal plant evenness on plant species diversity, we ran generalized linear models (GLMs). In these models, we chose a quasi-Poisson distribution because the SR as response variable is count data. For MI, we also ran separate linear and quadratic term models. We further analyzed the effects of environmental factors and mycorrhiza on plant SR using a mixed linear model with MI, mycorrhizal plant evenness, MAP, MAT, and N deposition as fixed effects and grassland type as a random factor. We also used Wilcoxon test to compare differences in SR of communities dominated by different mycorrhizal status plants (OM, FM, NM, and mixed types).

To investigate differences in aboveground primary productivity and belowground biomass among communities with different mycorrhizal status, we conducted GLMs with aboveground primary productivity and belowground biomass as response variables and community mycorrhizal status as a predictor. Sequential orthogonal comparisons were then used to make pairwise comparisons between the different community mycorrhizal status. To investigate the effect of mycorrhiza on plant community biomass allocation between the aboveground and belowground parts, we ran general linear models in which MI, mycorrhizal plant evenness, MAP, and MAT were used as fixed factors. To reduce the autocorrelation of MI and mycorrhizal plant evenness, we ran separate models for MI and mycorrhizal plant evenness. The allocation of community biomass was defined as the ratio of belowground biomass to aboveground biomass of the whole community (root-to-shoot ratio), rather than individual species or individuals, to match the mycorrhiza symbiotic potential at the community level.

All statistical analyses except SEM were conducted in R, and the following packages: argicolae v.1.3-5, lme4 v.1.1-30, ggtext v.0.1.1, ggplot2 v.3.3.5, ggpubr v.0.4.0, tidyr v.1.1.4, and vegan v.2.5-7 were used. SEM was calculated in AMOS 24 (Amos Development Corporation, Chicago, IL, USA).

Data, Materials, and Software Availability. Excel data have been deposited in Dryad digital repository (https://doi.org/10.5061/dryad.ncjsxkt5z) (44).

ACKNOWLEDGMENTS. We are very grateful to all participants of the Grassland Carbon Sequestration Project for their contributions to the field work and laboratory analysis. This study was supported by the National Key Research and Development Program of China (2023YFF1304105) and National Natural Science Foundation of China (32192464).

Author affiliations: [a]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China; [b]College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China; [c]Department of Environmental Systems Science, Swiss Federal Institute of Technology, 8001 Zurich, Switzerland; [d]Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130012, China; [e]State Key Laboratory of Soil Erosion and Dryland Farming in the Loess Plateau, Northwest A&F University, Yangling 712100, China; [f]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China; [g]State Key Laboratory of Herbage Improvement and Grassland Agro-ecosystems, College of Pastoral Agriculture Science and Technology, and College of Ecology, Lanzhou University, Lanzhou 730000, China; [h]Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China; [i]Xinjiang Key Laboratory of Soil and Plant Ecological Processes, College of Grassland and Environment Sciences, Xinjiang Agricultural University, Urumqi 830052, China; [j]State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China; [k]Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China; [l]Key Laboratory of Hangzhou City for Ecosystem Protection and Restoration, College of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou 310036, China; [m]Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China; [n]Department of Entomology & Plant Pathology, North Carolina State University, Raleigh, NC 27695; and [o]Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

Author contributions: Y.B. designed research; E.Z., Yang Wang, D.Z., Z.S., J.H., J.-S.H., Yanfen Wang, J.S., L.T., X.L., M.D., Y. Wu, and Y.B. performed research; E.Z., Yang Wang, S.C., S.H., Y.B., and G.Y. analyzed data; and E.Z., Yang Wang, T.W.C., W.S., S.C., D.Z., Z.S., J.H., J.-S.H., Yanfen Wang, J.S., L.T., X.L., M.D., Y. Wu, S.H., Y.B., and G.Y. wrote the paper.

1. U. Stockmann *et al.*, The knowns, known unknowns and unknowns of sequestration of soil organic carbon. *Agric. Ecosyst. Environ.* **164**, 80–99 (2013).
2. Y. Bai, M. F. Cotrufo, Grassland soil carbon sequestration: Current understanding, challenges, and solutions. *Science* **377**, 603–608 (2022).
3. C. Terrer *et al.*, A trade-off between plant and soil carbon storage under elevated CO2. *Nature* **591**, 599–603 (2021).
4. M. A. Anthony, T. W. Crowther, D. S. Maynard, J. van den Hoogen, C. Averill, Distinct assembly processes and microbial communities constrain soil organic carbon formation. *One Earth* **2**, 349–360 (2020).
5. C. Liang, W. Amelung, J. Lehmann, M. Kastner, Quantitative assessment of microbial necromass contribution to soil organic matter. *Glob. Change Biol.* **25**, 3578–3590 (2019).
6. S. E. Smith, D. J. Read, Mycorrhizal symbiosis. *Q. Rev. Biol.* **3**, 273–281 (2008).
7. S. E. Smith, F. A. Smith, Roles of arbuscular mycorrhizas in plant nutrition and growth: New paradigms from cellular to ecosystem scales. *Annu. Rev. Plant Biol.* **62**, 227–250 (2011).
8. K. E. Clemmensen *et al.*, Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. *New Phytol.* **205**, 1525–1536 (2015).
9. P. H. Jeewani *et al.*, Arbuscular mycorrhizal fungi and goethite promote carbon sequestration via hyphal-aggregate mineral interactions. *Soil Biol. Biochem.* **162**, 108417 (2021).
10. C. Averill, B. L. Turner, A. C. Finzi, Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* **505**, 543–545 (2014).
11. S. E. Hannula, E. Morriën, Will fungi solve the carbon dilemma? *Geoderma* **413**, 115767 (2022).
12. L. Tedersoo, M. Bahram, M. Zobel, How mycorrhizal associations drive plant population and community biology. *Science* **367**, eaba1223 (2020).
13. M. G. A. van der Heijden *et al.*, Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72 (1998).
14. C. Urcelay, S. Diaz, The mycorrhizal dependence of subordinates determines the effect of arbuscular mycorrhizal fungi on plant diversity. *Ecol. Lett.* **6**, 388–391 (2003).
15. A. Carteron, M. Vellend, E. Laliberte, Mycorrhizal dominance reduces local tree species diversity across US forests. *Nat. Ecol. Evol.* **6**, 370–374 (2022).
16. D. Leon *et al.*, Plant diversity but not productivity is associated with community mycorrhization in temperate grasslands. *J. Veg. Sci.* **33**, e13107 (2022).
17. D. J. Read, J. Perez-Moreno, Mycorrhizas and nutrient cycling in ecosystems–a journey towards relevance? *New Phytol.* **157**, 475–492 (2003).
18. A. Menzel *et al.*, Distribution patterns of arbuscular mycorrhizal and non-mycorrhizal plant species in Germany. *Perspect. Plant Ecol. Evol. Syst.* **21**, 78–88 (2016).
19. N. A. Soudzilovskaia *et al.*, Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nat. Commun.* **10**, 5077 (2019).
20. N. A. Soudzilovskaia *et al.*, FungalRoot: Global online database of plant mycorrhizal associations. *New Phytol.* **227**, 955–966 (2020).
21. C. G. Bueno *et al.*, Plant mycorrhizal status, but not type, shifts with latitude and elevation in Europe. *Glob. Ecol. Biogeogr.* **26**, 690–699 (2017).
22. D. P. Rasse, C. Rumpel, M.-F. Dignac, Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation *Plant Soil* **269**, 341–356 (2005).
23. S. E. Smith, I. Jakobsen, M. Gronlund, F. A. Smith, Roles of arbuscular mycorrhizas in plant phosphorus nutrition: Interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiol.* **156**, 1050–1057 (2011).
24. C. M. Hack, M. Porta, R. Schäufele, A. A. Grimoldi, Arbuscular mycorrhiza mediated effects on growth, mineral nutrition and biological nitrogen fixation of Melilotus alba Med. in a subtropical grassland soil. *Appl. Soil Ecol.* **134**, 38–44 (2019).
25. S. Dassen, W. H. Putten, G. B. De Deyn, Severance of arbuscular mycorrhizal fungal mycelial networks in restoration grasslands enhances seedling biomass. *New Phytol.* **232**, 753–761 (2021).
26. B. Tang, J. Man, G. Xiang, Y. Wang, Y. Bai, Heavy grazing disrupts positive effects of arbuscular mycorrhizae symbiosis on community productivity and stability under low and high phosphorus conditions. *Plant Soil* **457**, 375–387 (2020).
27. J. S. Huang *et al.*, Plant carbon inputs through shoot, root, and mycorrhizal pathways affect soil organic carbon turnover differently. *Soil Biol. Biochem.* **160**, 108322 (2021).
28. L. Neuenkamp *et al.*, The role of plant mycorrhizal type and status in modulating the relationship between plant and arbuscular mycorrhizal fungal communities. *New Phytol.* **220**, 1236–1247 (2018).
29. N. A. Soudzilovskaia *et al.*, Quantitative assessment of the differential impacts of arbuscular and ectomycorrhiza on soil carbon cycling. *New Phytol.* **208**, 280–293 (2015).
30. D. J. Gibson, *Grasses and Grassland Ecology* (Oxford University Press, Oxford, 2009).
31. S. E. Smith, D. J. Read, in *Mycorrhizal Symbiosis*, (Academic Press, Amsterdam, 3 ed., 2008).
32. S. Hempel *et al.*, Mycorrhizas in the Central European flora: Relationships with plant life history traits and ecology. *Ecology* **94**, 1389–1399 (2013).
33. Y. F. Bai *et al.*, Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. *Ecology* **89**, 2140–2153 (2008).
34. C. Gao *et al.*, Increased precipitation, rather than warming, exerts a strong influence on arbuscular mycorrhizal fungal community in a semiarid steppe ecosystem. *Botany* **94**, 459–469 (2016).
35. C. G. Bueno *et al.*, Distribution of plant mycorrhizal traits along an elevational gradient does not fully mirror the latitudinal gradient. *Mycorrhiza* **31**, 149–159 (2021).
36. M. Zobel *et al.*, Ancient environmental DNA reveals shifts in dominant mutualisms during the late Quaternary. *Nat. Commun.* **9**, 139 (2018).
37. S. Chen *et al.*, Plant diversity enhances productivity and soil carbon storage. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 4027–4032 (2018).
38. F. Nachtergaele *et al.*, *Harmonized World Soil Database* (version 1.2, FAO, Rome/Laxenburg, 2010).
39. C. Q. Lu, H. Q. Tian, Half-century nitrogen deposition increase across China: A gridded time-series data set for regional environmental assessments. *Atmos. Environ.* **97**, 68–74 (2014).
40. C. G. Bueno *et al.*, Towards a consistent benchmark for plant mycorrhizal association databases. *New Phytol.* **231**, 913–916 (2021).
41. M. Moora, A. Helm, Mycorrhizal traits and plant communities: Perspectives for integration. *J. Veg. Sci.* **25**, 1126–1132 (2014).
42. I. Jo, K. M. Potter, G. M. Domke, S. Fei, Dominant forest tree mycorrhizal type mediates understory plant invasions. *Ecol. Lett.* **21**, 217–224 (2018).
43. M. Lange *et al.*, Plant diversity increases soil microbial activity and soil carbon storage. *Nat. Commun.* **6**, 6707 (2015).
44. E. Zhang *et al.*, Data from: Mycorrhizal symbiosis increases plant phylogenetic diversity and regulate community assembly [Dataset]. Dryad. https://doi.org/10.5061/dryad.rbnzs7hm4. Deposited 6 December 2024.

Downloaded from https://www.pnas.org by CAS INSTITUTE OF BOTANY on March 6, 2025 from IP address 159.226.232.223.

Ecology Letters

WILEY

ECOLOGY LETTERS

LETTER

Mycorrhizal Symbiosis Increases Plant Phylogenetic Diversity and Regulates Community Assembly in Grasslands

Entao Zhang[1,2] | Yang Wang[1] | Shiping Chen[1] | Daowei Zhou[3] | Zhouping Shangguan[4] | Jianhui Huang[1] | Jin-Sheng He[5,6] | Yanfen Wang[7] | Jiandong Sheng[8] | Lisong Tang[9] | Xinrong Li[10] | Ming Dong[11] | Yan Wu[12] | Shuijin Hu[13] | Yongfei Bai[1,7]

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China | [2]College of Life Sciences, University of Chinese Academy of Sciences, Beijing, China | [3]Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, China | [4]State Key Laboratory of Soil Erosion and Dryland Farming in the Loess Plateau, Northwest A&F University, Yangling, China | [5]State Key Laboratory of Herbage Improvement and Grassland Agro-Ecosystems, College of Pastoral Agriculture Science and Technology, and College of Ecology, Lanzhou University, Lanzhou, China | [6]Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing, China | [7]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China | [8]Xinjiang Key Laboratory of Soil and Plant Ecological Processes, College of Resources and Environment, Xinjiang Agricultural University, Urumqi, China | [9]State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, China | [10]Key Laboratory of Stress Physiology and Ecology in Cold and Arid Regions, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou, China | [11]Key Laboratory of Hangzhou City for Ecosystem Protection and Restoration, College of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou, China | [12]Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu, China | [13]Department of Entomology & Plant Pathology, North Carolina State University, Raleigh, North Carolina, USA

Correspondence: Yongfei Bai (yfbai@ibcas.ac.cn)

Received: 31 May 2024 | **Revised:** 29 July 2024 | **Accepted:** 1 September 2024

Editor: Edith Bai

Funding: This work was supported by National Key Research and Development Program of China (2023YFF1304105) and National Natural Science Foundation of China (332192464).

Keywords: community assembly | community composition | deterministic processes vs. stochastic processes | grassland | phylogenetic dispersion | phylogenetic diversity

ABSTRACT

The intricate mechanisms controlling plant diversity and community composition are cornerstone of ecological understanding. Yet, the role of mycorrhizal symbiosis in influencing community composition has often been underestimated. Here, we use extensive species survey data from 1315 grassland sites in China to elucidate the influence of mycorrhizal symbiosis on plant phylogenetic diversity and community assembly. We show that increasing mycorrhizal symbiotic potential leads to greater phylogenetic dispersion within plant communities. Mycorrhizal species predominantly influence deterministic processes, suggesting a role in niche-based community assembly. Conversely, non-mycorrhizal species exert a stronger influence on stochastic processes, highlighting the importance of random events in shaping community structure. These results underscore the crucial but often hidden role of mycorrhizal symbiosis in driving plant community diversity and assembly. This study provides valuable insights into the mechanisms shaping ecological communities and the way for more informed conservation that acknowledges the complex interplay between symbiosis and community dynamics.

Entao Zhang and Yang Wang contributed equally to this work.

© 2024 John Wiley & Sons Ltd.

1 | Introduction

Ecologists have long been fascinated by the intricate relationships among species within communities and how these relationships contribute to the assembly of communities. This curiosity traces back to Darwin, who posited that competition intensifies among closely related species, a hypothesis that has since guided numerous ecological studies (Darwin 1859). These studies, particularly following the development of the community phylogenetic framework (Webb et al. 2002), have sought to understand the mechanisms of community assembly through the lens of evolutionary relationships (Cahill Jr. et al. 2008). Among the myriad factors influencing community composition, the role of mycorrhizal fungi as symbiotic partners has emerged as a significant area of interest, because these fungi play a crucial role in mediating nutrients and water competition and disease resistance among plants of varying phylogenetic backgrounds (Tedersoo et al. 2013; Crawford et al. 2019). Nevertheless, the recent research has also raised questions about the impact of mycorrhiza on the phylogenetic dynamics within plant communities and the overarching process of community assembly—a topic that remains ripe for further exploration (Montesinos-Navarro et al. 2015; Wang et al. 2023).

The significance of mycorrhizal fungi in shaping community composition has been acknowledged due to their symbiotic exchange with host plants—obtaining carbon for survival in return for aiding nutrient absorption and providing pathogen resistance (Peay, Garbelotto, and Bruns 2010; Smith and Smith 2011; Bennett and Groten 2022). The extent of these mycorrhizal benefits varies with the phylogenetic relationships among plants (Montesinos-Navarro, Valiente-Banuet, and Verdú 2019), influencing interspecific resource competition and the likelihood of encountering shared pathogens (Parker and Gilbert 2004; Gilbert and Webb 2007). For instance, closely related species can establish a common mycorrhizal network (CMN), facilitating nutrient exchange and mutual benefits (Pickles et al. 2017; Shi, Wang, and Wang 2023). Field studies across various ecosystems, from tropical and temperate forests to grasslands, have illustrated how mycorrhizal associations can regulate community structure and diversity through plant–soil feedbacks (PSFs) (Bennett et al. 2017; Chen et al. 2019). However, most of these studies have focused on the taxonomic rather than the phylogenetic structure of communities (Wilson and Hartnett 1998; Bennett, Cahill, and van der Heijden 2016), which represents the evolutionary relationships among coexisting species (Webb et al. 2002), highlighting a gap in our understanding of mycorrhizal impacts on phylogenetic assembly processes.

Given the influence of mycorrhizae on community structure, recent research has pivoted towards examining their role in community assembly (Peay, Garbelotto, and Bruns 2010; Peay 2016; Davison et al. 2023). This assembly is governed by a balance of deterministic processes (Vellend 2010) and stochastic processes (Hubbell 2001). Mycorrhizae influence these processes in two primary ways: by modulating species' environmental tolerances and resource acquisition (Bennett and Groten 2022), thereby affecting niche differentiation (Peay 2016), and by enhancing plant pathogen resistance, contributing to deterministic assembly processes (Parker and Gilbert 2004). Despite these insights, the distribution of facultatively mycorrhizal plants across various environments indicates that mycorrhizal associations are not solely determined by soil nutrient conditions (Bueno et al. 2017; Zobel et al. 2018). This suggests that the role of deterministic processes (e.g., environmental screening) in the involvement of mycorrhizal plants in community assembly may vary from site to site. Additionally, the role of mycorrhizae, particularly arbuscular mycorrhizae (Kennedy 2010; Bennett et al. 2017), in plant–soil feedback processes presents mixed results, from positive feedbacks to neutral and negative feedbacks (Hartnett and Wilson 2002; van der Putten et al. 2007), likely due to variations in mycorrhizal status among plants and dominance of symbiotic plants in the community (Mariotte et al. 2018; Neuenkamp et al. 2018). Addressing these complexities requires a comprehensive framework that delineates the role of mycorrhizal symbiosis in both stochastic and deterministic processes of community assembly and clarifies the contributions of plants with different mycorrhizal status to these processes (Chase 2010; Chase and Myers 2011).

Grassland ecosystems, dominated by arbuscular mycorrhizal fungi, provide a unique opportunity to investigate the role of mycorrhizal status in community assembly. Plant species in these ecosystems exhibit varying degrees of dependence on mycorrhizal associations, ranging from obligate (OM) to facultative (FM) and non-mycorrhizal (NM) strategies (Gerz et al. 2016). The strength of mycorrhizal-plant interactions may affect community assembly processes. For example, OM and FM strategies are often expected to promote plant performance (e.g., drought tolerance, nutrient acquisition, pathogen resistance) and species coexistence (Bennett and Groten 2022), and thereby contributing to deterministic processes of plant community assembly. Non-mycorrhizal plants, in contrast, can succeed in conditions that are favourable for organic compound mineralisation, contributing to stochastic processes of community assembly (Gerz et al. 2016). This study utilises extensive field survey data from 1315 grassland sites across China to examine the effects of mycorrhizal colonisation on community phylogenetic diversity and assembly processes. We address three key questions: (1) How does species composition vary across grassland ecosystems (i.e., desert, steppe, meadow and shrubland) dominated by different mycorrhizal types in terms of OM, FM and NM plants? (2) How does mycorrhizal symbiosis influence the phylogenetic diversity of plant communities? (3) How do plants with different mycorrhizal statuses contribute to deterministic and stochastic processes in community assembly? To answer these questions, we test the following hypotheses: (1) Changes in dominant mycorrhizal status of plants are predictably related to variations in species composition of grassland communities; (2) Plant communities with higher mycorrhisation exhibit greater overall phylogenetic diversity; and (3) OM and FM plants primarily influence deterministic processes, while NM plants contribute to stochastic processes in community assembly.

2 | Materials and Methods

2.1 | Field Survey and Data Collection

The grassland survey data used in this study were obtained from the datasets of the 'Strategic Priority Research Program-Climate Change: Carbon Budget and Relevant Issues' of the Chinese Academy of Sciences (Fang et al. 2018). We excluded sites that had incomplete plant species survey data or been

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

heavily grazed. Finally, this study utilised field survey data collected from 1315 sites across various grassland ecosystems in China. Vegetation surveys were conducted during the peak plant growth season, specifically from mid-July to August in middle and high latitude regions and from August to September in desert, subtropical and tropical regions (Chen et al. 2018). At each site, plant community data were collected using ten 1 × 1 m quadrats (reduced to 0.5 × 0.5 m for meadow and alpine meadow) located randomly within a 100 × 100 m area. For shrubland ecosystems, five 5 × 5 m quadrats were randomly placed within the same 100 × 100 m area. Five of the ten quadrats (or all five quadrats in shrublands) were randomly selected for detailed vegetation analysis. Within these selected quadrats, plant species richness (SR) and species relative abundance were recorded. Soil samples were collected from each quadrat using a soil core method at a depth of 20 cm. Soil organic carbon content (SOC) was measured for each sample. Total phosphorus (TP), total nitrogen (TN) and soil pH were interpolated from the basic soil property dataset of high-resolution China Soil Information Grids (2010–2018).

To facilitate analysis and interpretation, the 1315 field sites were classified into four distinct ecosystem types: meadow (further categorised into lowland meadows (LM), mountain meadows (MM) and alpine meadows (AM)), steppe (divided into temperate steppe (TS) and alpine steppe (AS)), shrubland (classified as warm shrubland (WG) and tropical shrubland (TG)) and desert (DS). This classification was based on plant community composition, climate and prevailing environmental conditions.

Mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm) and mean diurnal range (mean of monthly maximum temperature—minimum temperature, °C) for each site were obtained from the CHELSA V2.1 dataset (Philipp et al. 2022).

Remote sensing data, including Fraction of Photosynthetically Active Radiation (Fpar) were obtained from MOD15A2H Version 6 data product; slope and elevation data were extracted from the STRM 90 m dataset 171 in China, based on the SRTM V4.1 database (https://www.resdc.cn/data.aspx?DATAID=123). Fpar is defined as the fraction of incident photosynthetically active radiation, 400–700 nm (nm), absorbed by the green elements of a vegetation canopy.

2.2 | Plant Mycorrhizal Status and Community Mycorrhizal Index

To quantify the mycorrhizal status of each plant community, we calculated a mycorrhisation index representing the degree of potential mycorrhizal colonisation within the community. The mycorrhizal status of each plant species was determined using an established database of mycorrhizal associations. To minimise potential errors during the matching process, species were matched based on their genus level (Brundrett and Tedersoo 2019).

Orchid mycorrhizal associations were excluded from the analysis due to their extremely low prevalence in our dataset (< 1% of species richness and < 0.1% of total abundance). Consequently, plants were categorised into three mycorrhizal statuses: obligate mycorrhizal (OM), facultatively mycorrhizal (FM) and non-mycorrhizal (NM). To quantify the contribution of each mycorrhisal status to community mycorrhisation, numerical values were assigned: 0 for NM species, 0.5 for FM species and 1 for OM species (Moora and Helm 2014). The mycorrhisation index of each plant community was calculated using the following formula:

$$\mathbf{MI} = \sum (Pi * Mi)$$

where MI is the community mycorrhisation index, Pi is the relative abundance of plant species i in the community, and Mi is the numerical value of mycorrhizal status of species i.

The dominant mycorrhizal status of each community was determined based on the mycorrhizal status exhibiting the highest abundance within that community. This approach allowed us to differentiate communities based on the predominant mycorrhizal association of their constituent plant species.

2.3 | Construction of Phylogenetic Relationships and Calculation of Phylogenetic Distances

Phylogenetic relationships and distances between plant species were determined using the V. PhyloMaker package and picante package in R. The V. PhyloMaker generated phylogenetic hypotheses for the 1235 plant species in our study by linking them to the 'GBOTB.extended' megatree. This megatree encompasses 74,531 species, representing all families of extant vascular plants, and serves as the largest dated phylogeny for vascular plants. Phylogenetic distances within each community were calculated using the picante package. We calculated two metrics: mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). To account for the relative abundance of each species within the community, species abundance was incorporated as a weighting factor in the phylogenetic distance calculations.

To mitigate the influence of species richness on community phylogenetic distances, standardised effect size metrics for MPD (SESMPD) and MNTD (SESMNTD) were calculated. This standardisation involved generating a null distribution by randomly shuffling the distance matrix labels across all taxa 999 times. The mean of the null distribution was then used to calculate the standardised effect size (SES). SES values less than 0 indicate phylogenetic clustering, where species within the community are more closely related than expected by chance. Conversely, SES values greater than 0 indicate phylogenetic overdispersion, where species are more distantly related than expected.

2.4 | Statistical Analyses

2.4.1 | Comparison of Plant Community Composition

To compare plant community composition across different dominant mycorrhizal statuses, we first examined the relative abundance of different plant families within each of the community types. We then performed non-metric multidimensional scaling (NMDS) using the metaMDS function in the vegan package, based on a Bray–Curtis distance matrix. The stress function

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

value was assessed to ensure model reliability. Significant differences between groups were determined using Adonis.

2.4.2 | Assessing the Influence of Mycorrhizae on Species Richness and Phylogenetic Diversity

To evaluate the role of mycorrhizae in shaping community species richness and phylogenetic diversity, we constructed a set of predictor variables encompassing climate (MAT, MAP, MDR and Fpar), geographic factors (longitude, latitude, elevation, slope), mycorrhizal status (MI) and soil properties (TN, TP, SOC and pH).

Multiple regression models were developed using the MuMIn package in R to assess the effects of these predictors on species richness and phylogenetic diversity. A full set of models incorporating all predictors was generated and ranked based on the Akaike information criterion (AIC) using maximum likelihood estimation. Models with $\Delta AIC < 2$ were retained, and model averaging was employed to calculate parameter estimates and p-values. The relative effect of each predictor was determined by calculating the ratio of its parameter estimate to the sum of all parameter estimates. To further emphasise the importance of mycorrhizae in predicting species richness and phylogenetic diversity, we constructed comparative models excluding the mycorrhizal index while retaining all other predictors. These reduced models were compared to their corresponding full models using AICc values, with lower AICc values indicating superior model performance.

2.4.3 | Quantifying the Relative Importance of Stochastic and Deterministic Processes in Community Assembly

To assess the influence of mycorrhizae on community assembly processes, we utilised normalised stochasticity ratio (NST) analysis. NST, an extension of the beta-diversity metric, quantifies the relative contribution of stochastic and deterministic processes in community assembly. NST values range from 0 to 1, with 0.5 representing an equal contribution of both processes. NST values predominantly above 0.5 indicate a dominance of stochastic processes, while values below 0.5 suggest a greater influence of deterministic processes. We used weighted Unifrac-based distances to test the effect of geographic distance on the dissimilarity of communities with different dominant mycorrhizal statuses.

We further investigated the impact of different mycorrhizal plant types on community assembly using phylogenetic bin-based null model analysis (iCAMP) (Ning et al. 2020). This method, implemented using the iCAMP package in R, divides plant species into phylogenetic bins with significant phylogenetic signals and quantifies the contribution of each bin to deterministic (homogeneous selection (HoS), heterogeneous selection (HeS)) and stochastic (dispersal limitation (DL), homogenising dispersal (HD) and drift (DR)) processes. We selected the 300 most abundant plant species (representing 91.6% of total individuals), assigned them to phylogenetic bins, and determined the dominant mycorrhizal status within each bin. The relative contribution of each bin to different assembly processes was then assessed to quantify the influence of different mycorrhizal plant types on ecological processes.

3 | Results

3.1 | Influence of Mycorrhizal Status on Plant Community Composition

Our results revealed significant differences in plant community composition among communities dominated by different mycorrhizal statuses. The dominant plant families varied across community types, with Poaceae and Asteraceae dominating OM communities, Cyperaceae and Poaceae prevailing in FM communities, and Amaranthaceae and Poaceae dominating NM communities (Figure S1). Non-metric multidimensional scaling (NMDS) analysis confirmed significant differences in plant composition among communities with different dominant mycorrhizal statuses (Figure 1).

3.2 | Influence of Mycorrhizal Symbiosis on Plant Community Species Richness and Phylogenetic Diversity

Mycorrhizal symbiosis significantly influenced both plant community species richness and phylogenetic diversity. The best-fitting linear models for predicting species richness (Model 1), mean pairwise distance (MPD; Model 2), and mean nearest taxon distance (MNTD; Model 3) all included mycorrhizal index (MI) as a significant predictor (Figure 2, Table S1). This highlights the importance of mycorrhizal associations in shaping both the number and phylogenetic relatedness of species within plant communities.

Along the latitudinal gradient, standardised MPD (SESMPD) and MNTD (SESMNTD) exhibited similar patterns, with values greater than 0 at low latitudes and less than 0 at middle and high latitudes (Figure 3). A significant positive correlation was observed between community mycorrhizal index and SESMPD, indicating that communities with higher mycorrhizal potential tend to exhibit greater phylogenetic overdispersion. However, no significant correlation was found between mycorrhizal index and SESMNTD (Figure 4a,b).

Examining phylogenetic diversity across ecosystem types and dominant mycorrhizal status revealed that SESMPD was significantly higher in OM communities compared to NM communities, while FM communities exhibited intermediate values (Figure 4a). Notably, SESMPD was significantly greater than 0 in OM-dominated shrubland communities, indicating strong phylogenetic overdispersion. In contrast, SESMNTD values were consistently less than 0 across all community types and did not exhibit significant differences among dominant mycorrhizal status (Figure 4b–d).

3.3 | Influence of Mycorrhizal Status on Community Assembly Processes

Analysis of normalised stochasticity ratio (NST) revealed that deterministic processes dominated community assembly across all three dominant mycorrhizal status types, as indicated by NST values predominantly below 0.5 (Supplementary Figure 3). Further investigation into the contributions of different plant

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

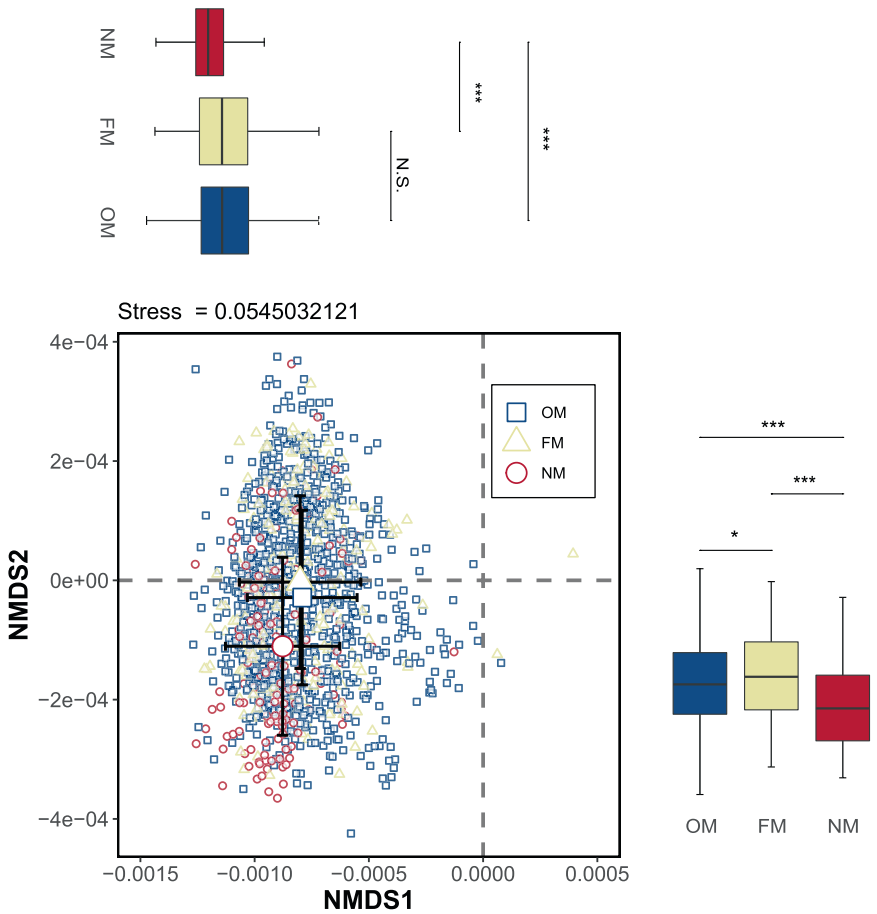


FIGURE 1 | Species composition variability among communities with different dominant mycorrhizal status. Non-metric multidimensional scaling (NMDS) based on Bray–Curtis distances illustrates the variation in species composition among communities dominated by different mycorrhizal status. NMDS1 and NMDS2 axes represent the ordination of sample plots based on species composition. Adonis tests were used to assess significant differences between groups along each NMDS axis. Significance levels: n.s., not significant; $^{*}p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$.

taxa to deterministic and stochastic processes revealed distinct patterns. Typical OM plant families, such as Asteraceae (Bin 2), Fabaceae (Bin 12), Rosaceae (Bin 13) and Amaryllidaceae (Bin 17), primarily influenced deterministic processes, suggesting their involvement in niche-based assembly. Conversely, taxa containing a higher proportion of FM and NM plants, such as Amaranthaceae (Bin 10) and Cyperaceae (Bin 22), played a more significant role in stochastic processes. Poaceae, encompassing both OM and FM species (mainly in Bins 18, 19, 20 and 21), influenced both deterministic and stochastic processes (Figure 5, Table S2).

Interestingly, the relative abundance of certain taxa did not always correspond to their contribution to assembly processes. For example, Amaryllidaceae (Bin 17) exhibited low relative abundance (4%) in desert ecosystems but exerted a strong influence on deterministic selection. Similarly, FM and NM plants (primarily Cyperaceae and Amaranthaceae in Bins 10 and 22) exhibited relatively low abundance (approximately 9% in steppe and 25% in meadow) but exerted a substantial influence on the drift process (Table S3). These results underscore the complex and nuanced role of mycorrhizal status in shaping community assembly processes.

4 | Discussion

This study presents the first effort in quantitatively assessing the impact of mycorrhizal symbiosis on plant community composition, phylogenetic diversity, and the mechanisms of community assembly. Our findings reveal that mycorrhizal associations significantly influence the phylogenetic structure of grassland communities, with OM-dominated communities exhibiting greater phylogenetic overdispersion compared to those dominated by FM or NM plants. This pattern aligns with the observation that shrublands, characterised by a predominance of OM plants, exhibiting higher phylogenetic overdispersion than desert grasslands and steppes, where FM and NM plants are more prevalent. Previous research has hinted at the role of mycorrhizal symbiosis in community structure, noting how mycorrhizal plants in forests may experience negative plant–soil feedbacks due to the accumulation of host-specific pathogenic fungi (Bever et al. 2010; Bennett et al. 2017; Chen et al. 2019), thus contributing to community-level plant diversity. However, these studies largely focused on taxonomic diversity, leaving the phylogenetic dimensions less explored (Horn et al. 2017). Phylogenetically, the trait that plants and mycorrhizal fungi form a stable symbiotic

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

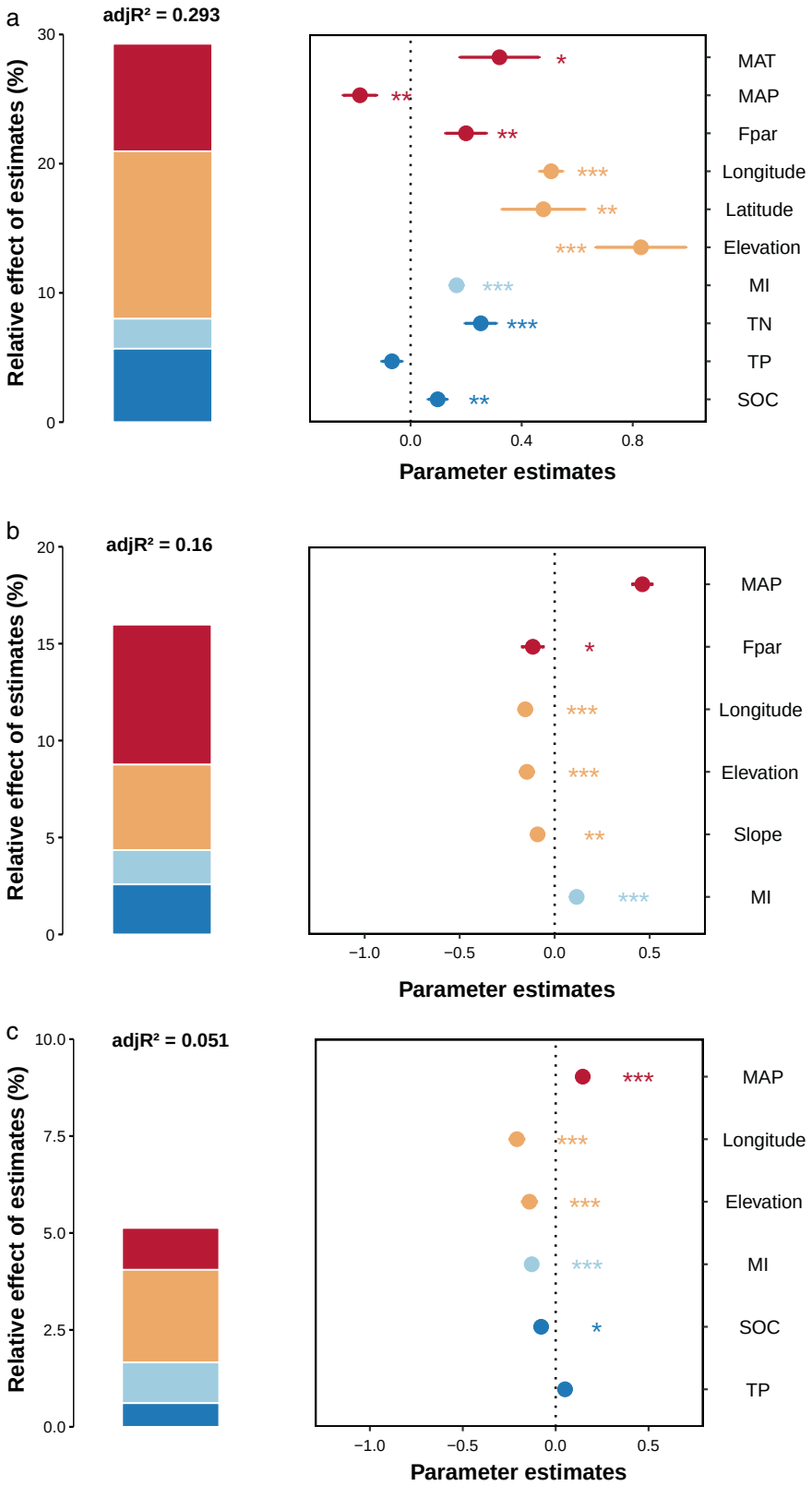


FIGURE 2 | Effects of predictors on plant species richness, phylogenetic diversity, and mean nearest taxon distance. (a) Plant species richness (SR), (b) mean pairwise distance (MPD) and (c) mean nearest taxon distance (MNTD). The left panels depict the relative importance of each predictor category, expressed as a percentage of explained variance. The right panels display mean standardised regression coefficients and their associated 95% confidence intervals for each predictor. Predictor categories include climate (MAT, MAP and MDR), geographic factors (longitude, latitude, elevation and slope), mycorrhizal index (MI) and soil factors (TN, TP, SOC and pH). Significance levels: n.s., not significant; *$p < 0.05$; **$p < 0.01$; and ***$p < 0.001$. MAT, mean annual temperature; MAP, mean annual precipitation; MDR, mean diurnal range; Fpar, fraction of photosynthetically active radiation; Lon, longitude; Lat, latitude; TN, soil total nitrogen content; and SOC, soil organic carbon content.

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

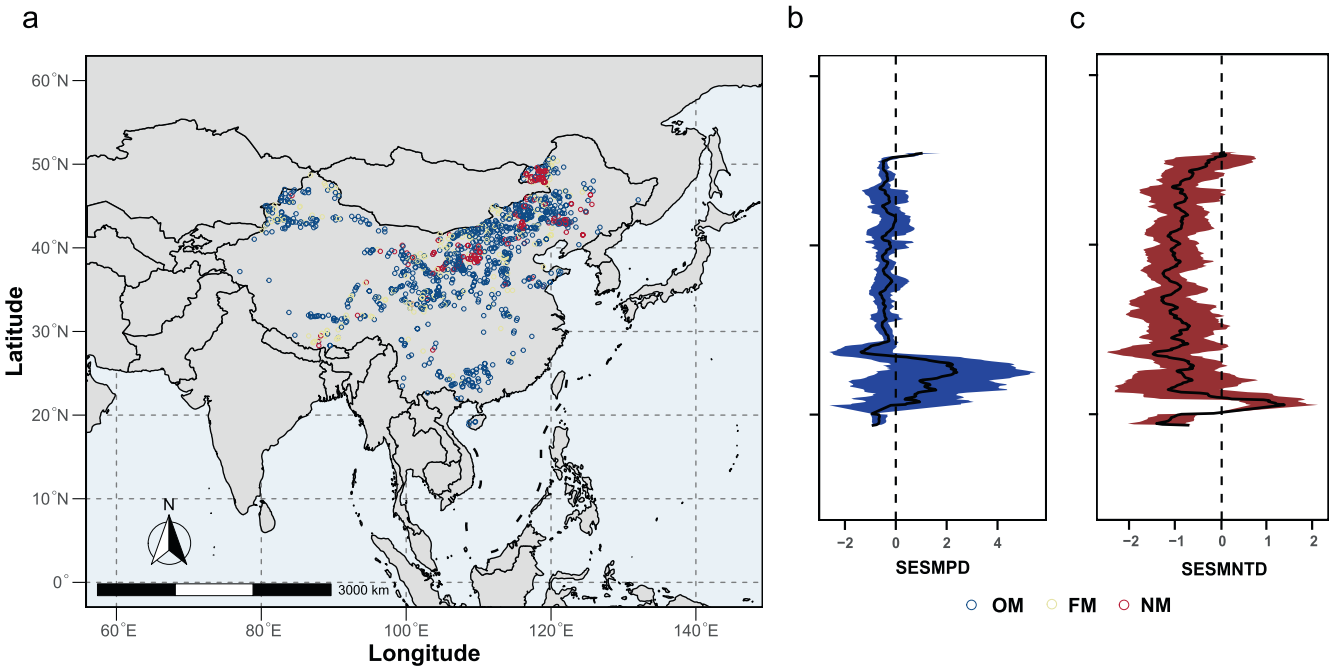


FIGURE 3 | Geographical distribution of sampling sites and latitudinal trends in community phylogenetic diversity. (a) Distribution of sampling sites across China, colour-coded by dominant mycorrhizal status. (b) Latitudinal variation in standardised mean pairwise distance (SESMPD). (c) Latitudinal variation in standardised mean nearest taxon distance (SESMNTD). Black lines represent mean phylogenetic diversity, and shaded areas represent standard deviation.

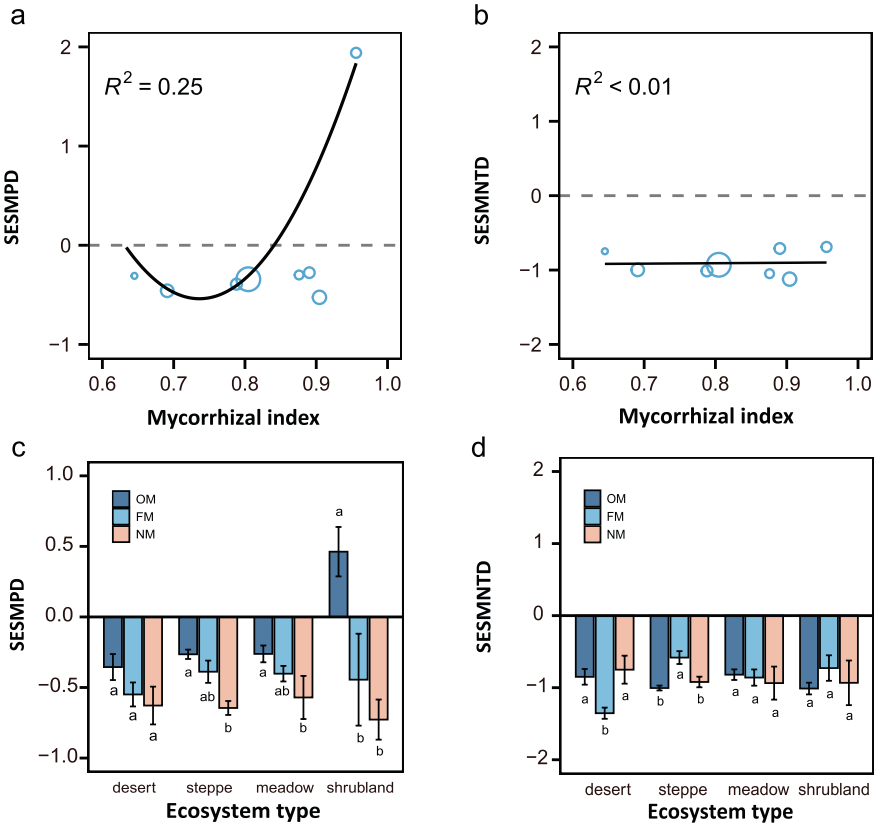


FIGURE 4 | Influence of mycorrhizal symbiosis on phylogenetic diversity across grassland types. (a) Relationship between mycorrhizal index and latitudinal variation in standardised mean pairwise distance (SESMPD) in eight grassland types, assessed using general linear model. Circle size represents the number of sample plots. (b) Relationship between mycorrhizal index and latitudinal variation in standardised mean nearest taxon distance (SESMNTD) in eight grassland types. (c) Differences in SESMPD among communities with different dominant mycorrhizal status within four ecosystem types, assessed using Wilcoxon tests. Error bars represent standard deviations. Letters indicate significant differences between groups. (d) Differences in SESMNTD among communities with different dominant mycorrhizal status within four ecosystem types.

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

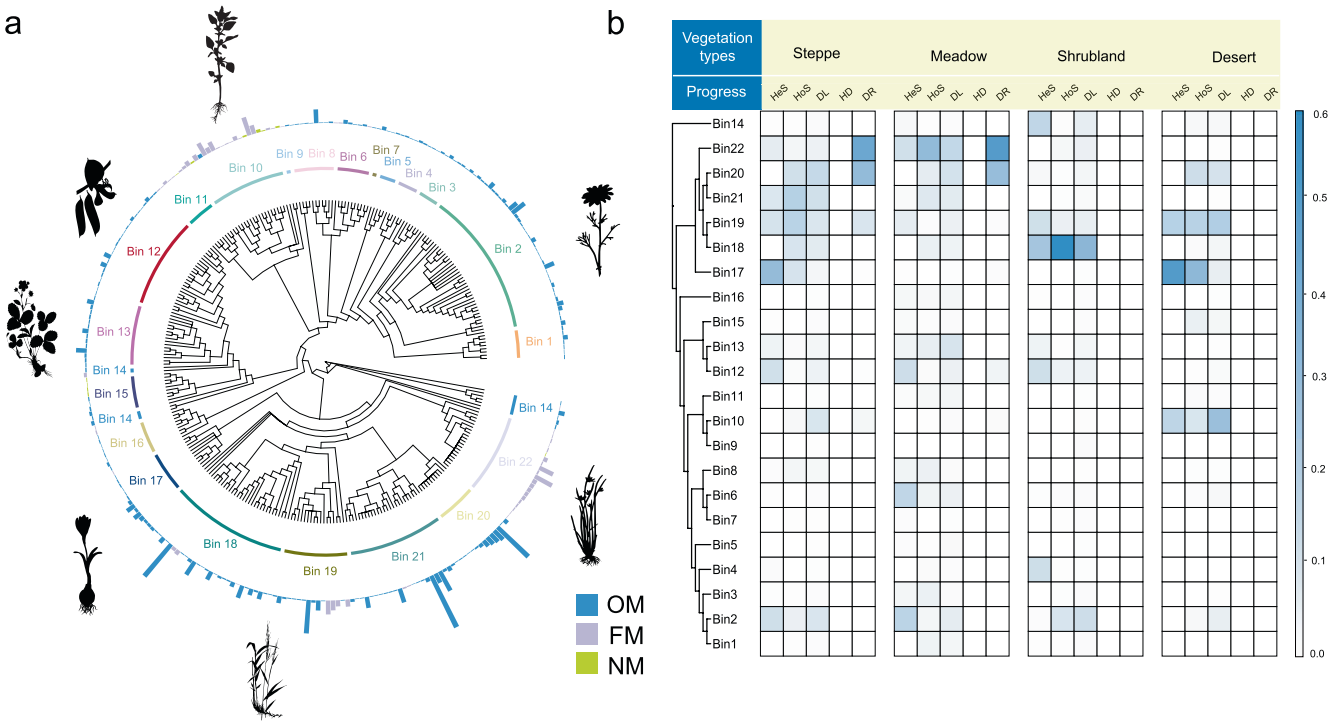


FIGURE 5 | Contribution of plant taxa with varied mycorrhizal status to community assembly processes. (a) Phylogenetic tree of the 300 most abundant plant species. The innermost ring represents phylogenetic relationships, the middle ring depicts phylogenetic bins, and the outermost ring represents species abundance, colour-coded by mycorrhizal status. (b) Contribution of each phylogenetic bin to five community assembly processes (homogeneous selection (HoS), heterogeneous selection (HeS), dispersal limitation (DL), homogenising dispersal (HD) and drift (DR)) within each ecosystem type. The left side displays the phylogenetic relationships of bins, with square colour intensity representing the magnitude of contribution.

relationship is relatively conserved in the evolutionary history of both (van der Heijden et al. 2015), and thus serves as a guarantee that mycorrhizal fungi could symbiosis with plants with close phylogenetic relations (Montesinos-Navarro et al. 2015; Kokkoris et al. 2020). Our research extends these insights, applying a phylogenetic perspective to demonstrate consistent patterns across diverse ecosystems at a continental scale.

Interestingly, our results did not support previous findings that mycorrhizal factors are key predictors of phylogenetic diversity when considering mean nearest taxon distance as a phylogenetic indicator. This discrepancy suggests that communities with closely related species may be more influenced by environmental factors, such as nutrient or water availability, rather than mycorrhizal symbiosis. Our observation supports the concept of niche overlap, where closely related species with similar resource requirements tend to compete more intensely, potentially diminishing the benefits of mycorrhizal symbiosis (Maherali and Klironomos 2007). In contrast, greater phylogenetic distances among co-occurring species may facilitate niche partitioning and enhance the positive effects of mycorrhizal associations on resource acquisition and competitive outcomes (Burns and Strauss 2011; Liu et al. 2019). Our findings underscore the complexity of ecological niches and the diminishing role of mycorrhizal symbiosis in similar ecological niches, highlighting the importance of phylogenetic distance in understanding community structure beyond mere species richness (Valiente-Banuet and Verdú 2007; Peay 2016).

The results of our study consistently indicate that deterministic processes predominantly govern community assembly in grasslands, despite variations in mycorrhizal plant compositions. However, stochastic processes also play a significant, though less dominant role. For example, an experimental study in a floodplain grassland in the Netherlands found that herbivore exclusion promoted a more stochastic plant community assembly, whereas grazing by large herbivores acted as a strong deterministic force in plant community assembly (Alberti et al. 2017). This finding aligns with previous research suggesting that deterministic processes increasingly overshadow stochastic processes in mature, climax communities (Maren et al. 2018). It also aligns with the traditional ecological niche theory, which posits that species coexistence is primarily driven by deterministic processes such as niche differentiation, habitat filtering and biotic interactions (Silvertown 2004; Harpole and Tilman 2007). Notably, our study reveals distinct contributions of different mycorrhizal plant types to community assembly in grassland ecosystems. OM plants primarily influence deterministic processes, such as selection, while FM and NM plants exert a greater influence on stochastic processes, including dispersal limitation and drift. An experimental study in a subtropical forest in China also reveals that the phylogenetic patterns of plant and arbuscular mycorrhizal fungi communities are nonrandom but conserved and interdependent (Chen et al. 2017). This differentiation underscores the unique contributions of plants with varying mycorrhizal status to community assembly, driven by distinct ecological processes including environmental tolerance and strategies for nutrient and water acquisition (Veresoglou et al. 2018).

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Previous studies have highlighted the role of mycorrhizal symbiosis in differentiating resource-based ecological niches, suggesting that resource competition exerts a stronger influence on community assembly than habitat filtering at local scales (Douma et al. 2012; Davison et al. 2023). This finding is particularly intriguing given the evidence that OM plants have evolved greater drought tolerance compared to FM and NM plants (Cosme 2023). Moreover, research has shown that specific plant-mycorrhizal fungi combinations can influence plant coexistence by enhancing the uptake of limiting resources and exerting pressure on non-limiting resources (Jiang et al. 2017). In contrast, NM plants have evolved alternative strategies, such as elongated root hairs and increased root surface area (Smith and Read 2008), to reduce their reliance on mycorrhizal partners for resource acquisition and exhibit a broad distribution across diverse habitats (Collins and Foster 2009; Zobel et al. 2018), highlighting their role in stochastic community assembly processes.

In conclusion, our study provides a pioneering framework for quantifying the influence of mycorrhizae on plant phylogenetic diversity and community assembly at a large scale. By emphasising the significance of phylogenetic diversity in plant-mycorrhizal symbioses, our work contributes to a deeper understanding of the intricate relationships governing plant competition and coexistence, offering new perspectives on the ecological dynamics of plant communities. Findings from this study have important implications for biodiversity conservation and restoration of degraded grasslands. First, protecting the phylogenetic diversity of plant community is critical for maintaining the provision of goods and services in grassland ecosystems because greater phylogenetic diversity can facilitate niche partitioning and promote the positive effects of mycorrhizal associations on plants drought tolerance, nutrient acquisition and pathogen resistance. Second, management approaches that facilitate the successful establishment of OM plants can accelerate the restoration processes of degraded grasslands because OM plants primarily influence deterministic processes of community assembly, although FM and NM plants also play an important role in structuring plant community diversity, particularly in the early stage of ecological restoration, through regulating stochastic processes of community assembly. In addition, given that our findings are built on OM, FM and NM plants in grassland ecosystems, future studies should further explore how other types of symbiotic relationships, such as ectomycorrhizal fungi, regulate plant community assembly processes across a variety of natural ecosystems.

Author Contributions

Y.B. conceived the study. Y.B., Yang Wang, S.C., D.Z., Z.S., J.H., J.-S.H., Yanfen Wang., J.S., L.T., X.L., M.D., and Yan Wu contributed to data collection. E.Z., Yang Wang, S.C., S.H., and Y.B. conducted data analysis and drafted the manuscript. All authors contributed to the revision of the manuscript.

Data Availability Statement

The data used in this study are available in the Dryad digital repository https://doi.org/10.5061/dryad.rbnzs7hm4. The raw survey data are not provided due to regulatory restrictions, but the processed data are available.

References

Alberti, J., E. S. Bakker, R. van Klink, H. Olff, and C. Smit. 2017. "Herbivore Exclusion Promotes a More Stochastic Plant Community Assembly in a Natural Grassland." *Ecology* 98: 961–970.

Bennett, A. E., and K. Groten. 2022. "The Costs and Benefits of Plant-Arbuscular Mycorrhizal Fungal Interactions." *Annual Review of Plant Biology* 73: 649–672.

Bennett, J. A., J. F. Cahill, and M. van der Heijden. 2016. "Fungal Effects on Plant-Plant Interactions Contribute to Grassland Plant Abundances: Evidence From the Field." *Journal of Ecology* 104: 755–764.

Bennett, J. A., H. Maherali, K. O. Reinhart, Y. Lekberg, M. M. Hart, and J. Klironomos. 2017. "Plant-Soil Feedbacks and Mycorrhizal Type Influence Temperate Forest Population Dynamics." *Science* 355: 181–184.

Bever, J. D., I. A. Dickie, E. Facelli, et al. 2010. "Rooting Theories of Plant Community Ecology in Microbial Interactions." *Trends in Ecology & Evolution* 25: 468–478.

Brundrett, M. C., and L. Tedersoo. 2019. "Misdiagnosis of Mycorrhizas and Inappropriate Recycling of Data can Lead to False Conclusions." *New Phytologist* 221: 18–24.

Bueno, C. G., M. Moora, M. Gerz, et al. 2017. "Plant Mycorrhizal Status, but Not Type, Shifts With Latitude and Elevation in Europe." *Global Ecology and Biogeography* 26: 690–699.

Burns, J. H., and S. Y. Strauss. 2011. "More Closely Related Species Are More Ecologically Similar in an Experimental Test." *Proceedings of the National Academy of Sciences of the United States of America* 108: 5302–5307.

Cahill, J. F., Jr., S. W. Kembel, E. G. Lamb, and P. A. Keddy. 2008. "Does Phylogenetic Relatedness Influence the Strength of Competition Among Vascular Plants?" *Perspectives in Plant Ecology, Evolution and Systematics* 10: 41–50.

Chase, J. M. 2010. "Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments." *Science* 328: 1388–1391.

Chase, J. M., and J. A. Myers. 2011. "Disentangling the Importance of Ecological Niches From Stochastic Processes Across Scales." *Philosophical Transactions of the Royal Society Biology Science* 366: 2351–2363.

Chen, L., N. G. Swenson, N. Ji, et al. 2019. "Differential Soil Fungus Accumulation and Density Dependence of Trees in a Subtropical Forest." *Science* 366: 124–128.

Chen, L., Y. Zheng, C. Gao, et al. 2017. "Phylogenetic Relatedness Explains Highly Interconnected and Nested Symbiotic Networks of Woody Plants and Arbuscular Mycorrhizal Fungi in a Chinese Subtropical Forest." *Molecular Ecology* 26: 2563–2575.

Chen, S. P., W. T. Wang, W. T. Xu, et al. 2018. "Plant Diversity Enhances Productivity and Soil Carbon Storage." *Proceedings of the National Academy of Sciences of the United States of America* 115: 4027–4032.

Collins, C. D., and B. L. Foster. 2009. "Community-Level Consequences of Mycorrhizae Depend on Phosphorus Availability." *Ecology* 90: 2567–2576.

Cosme, M. 2023. "Mycorrhizas Drive the Evolution of Plant Adaptation to Drought." *Communications Biology* 6: 346.

Crawford, K. M., J. T. Bauer, L. S. Comita, et al. 2019. "When and Where Plant-Soil Feedback May Promote Plant Coexistence: A Meta-Analysis." *Ecology Letters* 22: 1274–1284.

Darwin, C. 1859. *On the Origin of Species*. London, UK: John Murray.

Davison, J., M. Gerz, I. Hiiesalu, M. Moora, M. Semchenko, and M. Zobel. 2023. "Niche Types and Community Assembly." *Ecology Letters* 27: e14327.

Douma, J. C., B. Shipley, J. P. M. Witte, R. Aerts, and P. M. van Bodegom. 2012. "Disturbance and Resource Availability act Differently on the Same Suite of Plant Traits: Revisiting Assembly Hypotheses." *Ecology* 93: 825–835.

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Fang, J., G. Yu, L. Liu, S. Hu, and F. S. Chapin III. 2018. "Climate Change, Human Impacts, and Carbon Sequestration in China." *Proceedings of the National Academy of Sciences of the United States of America* 115: 4015–4020.

Gerz, M., C. G. Bueno, M. Zobel, M. Moora, and F. Pugnaire. 2016. "Plant Community Mycorrhization in Temperate Forests and Grasslands: Relations With Edaphic Properties and Plant Diversity." *Journal of Vegetation Science* 27: 89–99.

Gilbert, G. S., and C. O. Webb. 2007. "Phylogenetic Signal in Plant Pathogen-Host Range." *Proceedings of the National Academy of Sciences of the United States of America* 104: 4979–4983.

Harpole, W. S., and D. Tilman. 2007. "Grassland Species Loss Resulting From Reduced Niche Dimension." *Nature* 446: 791–793.

Hartnett, D. C., and G. W. T. Wilson. 2002. "The Role of Mycorrhizas in Plant Community Structure and Dynamics: Lessons From Grasslands." *Plant and Soil* 244: 319–331.

Horn, S., S. Hempel, E. Verbruggen, M. C. Rillig, and T. Caruso. 2017. "Linking the Community Structure of Arbuscular Mycorrhizal Fungi and Plants: A Story of Interdependence?" *ISME Journal* 11: 1400–1411.

Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton: Princeton University Press.

Jiang, J., J. A. Moore, A. Priyadarshi, and A. T. Classen. 2017. "Plant-Mycorrhizal Interactions Mediate Plant Community Coexistence by Altering Resource Demand." *Ecology* 98: 187–197.

Kennedy, P. 2010. "Ectomycorrhizal Fungi and Interspecific Competition: Species Interactions, Community Structure, Coexistence Mechanisms, and Future Research Directions." *New Phytologist* 187: 895–910.

Kokkoris, V., Y. Lekberg, P. M. Antunes, et al. 2020. "Codependency Between Plant and Arbuscular Mycorrhizal Fungal Communities: What Is the Evidence?" *New Phytologist* 228: 828–838.

Liu, M., Y. Che, J. Jiao, L. Li, and X. Jiang. 2019. "Exploring the Community Phylogenetic Structure Along the Slope Aspect of Subalpine Meadows in the Eastern Qinghai-Tibetan Plateau, China." *Ecology and Evolution* 9: 5270–5280.

Maherali, H., and J. N. Klironomos. 2007. "Influence of Phylogeny on Fungal Community Assembly and Ecosystem Functioning." *Science* 316: 1746–1748.

Maren, I. E., J. Kapfer, P. A. Aarrestad, J.-A. Grytnes, and V. Vandvik. 2018. "Changing Contributions of Stochastic and Deterministic Processes in Community Assembly Over a Successional Gradient." *Ecology* 99: 148–157.

Mariotte, P., Z. Mehrabi, T. M. Bezemer, et al. 2018. "Plant-Soil Feedback: Bridging Natural and Agricultural Sciences." *Trends in Ecology & Evolution* 33: 129–142.

Montesinos-Navarro, A., J. G. Segarra-Moragues, A. Valiente-Banuet, and M. Verdú. 2015. "Evidence for Phylogenetic Correlation of Plant-AMF Assemblages?" *Annals of Botany* 115: 171–177.

Montesinos-Navarro, A., A. Valiente-Banuet, and M. Verdú. 2019. "Plant Facilitation Through Mycorrhizal Symbiosis Is Stronger Between Distantly Related Plant Species." *New Phytologist* 224: 928–935.

Moora, M., and A. Helm. 2014. "Mycorrhizal Traits and Plant Communities: Perspectives for Integration." *Journal of Vegetation Science* 25: 1126–1132.

Neuenkamp, L., M. Moora, M. Opik, et al. 2018. "The Role of Plant Mycorrhizal Type and Status in Modulating the Relationship Between Plant and Arbuscular Mycorrhizal Fungal Communities." *New Phytologist* 220: 1236–1247.

Ning, D., M. Yuan, L. Wu, et al. 2020. "A Quantitative Framework Reveals Ecological Drivers of Grassland Microbial Community Assembly in Response to Warming." *Nature Communications* 11: 4717.

Parker, I. M., and G. S. Gilbert. 2004. "The Evolutionary Ecology of Novel Plant-Pathogen Interactions." *Annual Review of Ecology, Evolution, and Systematics* 35: 675–700.

Peay, K. G. 2016. "The Mutualistic Niche: Mycorrhizal Symbiosis and Community Dynamics." *Annual Review of Ecology, Evolution, and Systematics* 47: 143–164.

Peay, K. G., M. Garbelotto, and T. D. Bruns. 2010. "Evidence of Dispersal Limitation in Soil Microorganisms: Isolation Reduces Species Richness on Mycorrhizal Tree Islands." *Ecology* 91: 3631–3640.

Philipp, B., E. Z. Niklaus, H. Chantal, P. Loïc, and K. Dirk Nikolaus. 2022. "CHELSA-BIOCLIM+ A Novel set of Global Climate-Related Predictors at Kilometre-Resolution." *EnviDat*. https://doi.org/10.16904/envidat.332.

Pickles, B. J., R. Wilhelm, A. K. Asay, A. S. Hahn, S. W. Simard, and W. W. Mohn. 2017. "Transfer of (13)C Between Paired Douglas-Fir Seedlings Reveals Plant Kinship Effects and Uptake of Exudates by Ectomycorrhizas." *New Phytologist* 214: 400–411.

Shi, J., X. Wang, and E. Wang. 2023. "Mycorrhizal Symbiosis in Plant Growth and Stress Adaptation: From Genes to Ecosystems." *Annual Review of Plant Biology* 74: 569–607.

Silvertown, J. 2004. "Plant Coexistence and the Niche." *Trends in Ecology & Evolution* 19: 605–611.

Smith, S. E., and D. J. Read. 2008. *Mycorrhizal Symbiosis*. Amsterdam, Netherlands: Academic Press.

Smith, S. E., and F. A. Smith. 2011. "Roles of Arbuscular Mycorrhizas in Plant Nutrition and Growth: New Paradigms From Cellular to Ecosystem Scales." *Annual Review of Plant Biology* 62: 227–250.

Tedersoo, L., M. Mett, T. A. Ishida, and M. Bahram. 2013. "Phylogenetic Relationships Among Host Plants Explain Differences in Fungal Species Richness and Community Composition in Ectomycorrhizal Symbiosis." *New Phytologist* 199: 822–831.

Valiente-Banuet, A., and M. Verdú. 2007. "Facilitation can Increase the Phylogenetic Diversity of Plant Communities." *Ecology Letters* 10: 1029–1036.

van der Heijden, M. G. A., F. M. Martin, M. A. Selosse, and I. R. Sanders. 2015. "Mycorrhizal Ecology and Evolution: The Past, the Present, and the Future." *New Phytologist* 205: 1406–1423.

van der Putten, W. H., G. A. Kowalchuk, E. P. Brinkman, et al. 2007. "Soil Feedback of Exotic Savanna Grass Relates to Pathogen Absence and Mycorrhizal Selectivity." *Ecology* 88: 978–988.

Vellend, M. 2010. "Conceptual Synthesis in Community Ecology." *Quarterly Review of Biology* 85: 183–206.

Veresoglou, S. D., M. C. Rillig, D. Johnson, and O. Godoy. 2018. "Responsiveness of Plants to Mycorrhiza Regulates Coexistence." *Journal of Ecology* 106: 1864–1875.

Wang, J., S.-P. Li, Y. Ge, et al. 2023. "Darwin's Naturalization Conundrum Reconciled by Changes of Species Interactions." *Ecology* 104: e3850.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. "Phylogenies and Community Ecology." *Annual Review of Ecology and Systematics* 33: 475–505.

Wilson, G. W. T., and D. C. Hartnett. 1998. "Interspecific Variation in Plant Responses to Mycorrhizal Colonization in Tallgrass Prairie." *American Journal of Botany* 85: 1732–1738.

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Zobel, M., J. Davison, M. E. Edwards, et al. 2018. "Ancient Environmental DNA Reveals Shifts in Dominant Mutualisms During the Late Quaternary." *Nature Communications* 9: 139.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

14610248, 2024, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ele.14516 by - Institute Of Botany , Wiley Online Library on [02/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

communications earth & environment

Article

https://doi.org/10.1038/s43247-024-01458-9

Current national nature reserves are insufficient to safeguard the long-term survival of birds and mammals in China

Check for updates

Weicheng Sun[1,2,4], Yujin Zhao[1,4], Wenhe Chen[1,2] & Yongfei Bai[1,3]

Enhancing the connectivity of protected areas is a global consensus for conserving biodiversity. Yet, it is unclear whether habitats are sufficiently connected within protected areas to efficiently protect wildlife populations for long-term survival. Here we show that, in general, China's national nature reserves can effectively protect about one-half of the bird and mammal populations within protected areas for long-term survival. However, they can only protect 25% of birds and 13% of terrestrial mammals with high motility. Areas of low conservation effectiveness are highly overlapped with protected areas of small size and high intensity of human activity. Artificial landscapes (arable land and built-up land), which account for less than 2% area of the protected areas, disproportionately cause nearly 40% of the connectivity loss. The results suggest that maintaining high levels of functional connectivity within protected areas is as important as maintaining high connectivity in the national or global protected area networks. Our findings have important implications for improving the management of protected areas in China and beyond.

Protected areas (PAs) are a key tool in the effort to spearhead nature conservation[1,2]. The effectiveness of PAs is impacted through a multi-dimensional approach of design, location, functional connectivity, and management[3]. Assessing their effectiveness in perpetuating the future of biodiversity becomes extraordinarily important, yet challenging[3]. Previous studies on the effectiveness of PAs have often focused on the total extent, representativeness, and governance components of PAs[3,4]. Nevertheless, functional connectivity, an indicator used to evaluate the difficulty of animal movement within habitat networks[5], has been frequently ignored, although it represents a fundamental dimension that directly regulates ecological effectiveness. Moreover, fewer studies have quantified the impact of PAs on the health and persistence of wildlife populations, particularly at national and regional scales[6,7]. Therefore, the Kunming-Montreal Global biodiversity framework, adopted at the 15th meeting of the Conference of Parties to the UN Convention on Biological Diversity (CBD COP15), reiterates the call to maintain, enhance or restore, and significantly increase functional connectivity of wildlife habitats[8].

Most analyses of PA effectiveness that focus on conservation tools such as total area, representation, and management have overlooked the impact of habitat quality on wildlife, assuming that the areas designated as PAs provide high-quality, suitable habitats for wildlife populations[9]. In reality, however, the potential movement of wildlife populations is limited by habitat quality[10]. Natural landscape heterogeneity and changes in landscape patterns due to human activities within PAs may diminish functional connectivity and change habitat circulation patterns for wildlife species[11,12]. Recently, there has been a growing consensus that maintaining well-connected habitats within and among PAs can safeguard wildlife's long-term survival[8,13] and efficiently reduce the risk of population extinction caused by habitat fragmentation[2,7,14]. Hence, functional connectivity is pivotal for many ecological processes at various spatial-temporal scales, for instance, from daily foraging movements to inter-population dispersal[15]. Several studies have explored functional connectivity within PA networks and within individual PAs, emphasizing the necessity to establish and increase new PAs to improve functional connectivity[12,16,17]. However, most studies regarding functional connectivity are often organized and analyzed at a single scale[12], lacking comprehensive and inter-regional comparability in extension to biological taxa[15,18,19]. Therefore, integrating spatial-temporal scales in evaluating the functional connectivity of PAs is crucial to understanding the effects of specific life cycles on the movements of different species[15].

Habitat availability and habitat type diversity are the main factors regulating functional connectivity in natural scenarios, whereas human-

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China. [2]College of Life Sciences, University of Chinese Academy of Sciences, No. 19A Yuquan Road, Beijing 100049, China. [3]College of Resources and Environment, University of Chinese Academy of Sciences, No. 19A Yuquan Road, Beijing 100049, China. [4]These authors contributed equally: Weicheng Sun, Yujin Zhao.
e-mail: yfbai@ibcas.ac.cn

dominated habitat loss and fragmentation are severe challenges to sustaining well connectedness of wildlife habitats[20]. Most PAs are located in human-dominated, fragmented land-use scenarios where wildlife populations are frequently isolated by human-modified landscapes[21]. Several studies have reported that declines in habitat amounts and habitat heterogeneity of natural landscapes can substantially reduce the population flow and gene exchange of wildlife species, further increasing the risk of extinction[10–12]. For example, habitat fragmentation caused by transportation infrastructure has become one of the serious threats to biodiversity[22,23], especially the impact of roads on intact natural ecosystems such as PAs[24–26]. Hence, there is an urgent need for research that focuses on the key factors that impact the functional connectivity of PAs. National nature reserves (NNRs), which form the key body of PAs and occupy 10% of the country's land surface in China, with the strictest management[27]. However, the NNRs are often established based on province or even county boundaries rather than on gaps in biodiversity conservation. There are significant geographical and regional variations in the amount and/or size distributed. In particular, conservation investments at the national level are disproportionately invested in remote areas that are less likely to be threatened by agriculture or human activities. Because the expansion of NNRs extent in these regions is more easily achieved[28,29]. Therefore, assessing how effective they are in achieving a sustainable biodiversity future is not trivial[9].

Numerous methods have been developed to model functional connectivity and explore how habitats impact the sustainability of wildlife populations[30,31]. Graph theory is widely used in conservation and landscape planning, which requires less data input to provide reliable visualization of ecological networks[32,33]. The ecological network, a set of habitat patch nodes connected by potential links between populations, is frequently used to model the functional connectivity of wildlife populations[15]. By using these approaches, we conducted a robust evaluation of the impact of PAs on population connectivity at the national scale. Our study is designed to assess how China's NNRs (474 in total number) affect the wildlife populations of 11,424 birds and terrestrial mammals with different habitat preferences within each individual NNR, where populations were defined as virtual species groups characterized by their ecological niches[34–36]. We focused on "landscape species" or "umbrella species" whose viable populations are restricted within a single NNR. The population life histories were combined with a nested scale approach at both intra- and inter-population scales (Fig. S1 in Supporting Information). The effectiveness of NNRs in terms of their ability to sustain bird and mammal populations maintains a minimum threshold of inter-population genetic exchange connectivity for long-term survival. Specifically, we address three questions: First, how do China's NNRs affect the effectiveness of conserving inner populations for long-term survival? Second, what are the natural and anthropogenic factors that regulate the effectiveness of the NNRs? Third, to what degree do the artificial landscapes (e.g., roads) modify the effectiveness of the NNRs?

Results

Patterns of functional connectivity and effectiveness of NNRs

NNRs are widely distributed across the geographic and climatic gradients in China (Fig. S2 in Supporting Information). The functional connectivity of wildlife populations (including birds and terrestrial mammals) in NNRs was highly diverse between habitat types within each biome and among different biomes (Fig. 1 and Fig. S4). For forest habitats, the functional connectivity, on average, was the highest in temperate coniferous forests and temperate broadleaf and mixed forests in China's NNRs. For grassland habitats, the functional connectivity was the highest in temperate grasslands, savannas, and shrublands. For wetland habitats, flooded grasslands and savannas exhibited the highest functional connectivity in China's NNRs (Fig. 1 and Fig. S5).

China's NNRs effectively protected 57% of bird populations and 42% of terrestrial mammal populations for long-term survival, and a total of 50% for both birds and mammals (Table S3 in Supporting Information). However, for birds and mammals with high motility, the proportions of effectively protected populations were less than 25% and 13%, respectively. Further, we mapped the distribution extent and effectiveness patterns of birds and mammals using the distribution extent of real species matched to our virtual species (Fig. S9). The results showed that PAs in eastern China provide poor protection for high-mobility birds and terrestrial mammals (Table S5). The habitat area of effective NNRs is, on average, 5.6 times larger for birds and 13.5 times larger for mammals than that of ineffective NNRs for high movement ability species. Our results also showed that about 48% of NNRs exhibited a sufficiently large (>50%) proportion of habitat area (HA), yet NNRs area is too small to effectively protect potentially viable populations (Fig. 2f). Similarly, high overlap occurred between small PAs, high human pressure, and low conservation effectiveness areas (Fig. 2). Specifically, the two biomes, temperate coniferous forests and temperate broadleaf and mixed forests, exhibited the lowest NNR effectiveness (10.8% and 15.9%, respectively) for high motility species (Table S3). In addition, the two biomes showed less than 3% of the NNRs coverage (the global average is 10% and 16%, respectively) (Fig. 2e), and the average area of individual NNRs was less than 4% of the national average PA size (Table S4). More importantly, the two biomes have the second and fifth-highest global average conversion rates of natural vegetation to other land uses (Fig. 2e) and the most densely populated and economically developed regions in China[37].

Impact of habitat characteristics on functional connectivity

The random forest importance analysis for natural and anthropogenic factors influencing the functional connectivity of NNRs showed that the proportion of HA contributed more than other factors in determining the variation of functional connectivity of NNRs (Fig. 3). For NNRs located in the eastern part of the Hu-line, the dividing line between population development and the social economic pattern in China[38], functional connectivity was more likely to be regulated by artificial landscape intensity (ALI). For NNRs near the Hu-line, functional connectivity was more easily constrained by NNRs area (AREA), whereas it was more vulnerable to ecosystem diversity (ED) for NNRs located in the western part of the Hu-line (Fig. 3). The best-fitting generalized additive model (GAM) analysis showed that functional connectivity was influenced by the interactions of HA, ALI, AREA, and ED. Functional connectivity increased with an increasing proportion of HA. However, functional connectivity decreased with increasing ALI (Fig. S13a) and exhibited a significant quadratic relationship with ED, peaking at the medium levels of ED (Fig. S13b). In addition, functional connectivity decreased with increasing protected area for small PAs and increased with increasing protected area for large PAs. The effect of the protected area on functional connectivity increased with an increasing proportion of HA and ED (Fig. S13c, d).

Impact of human activities on functional connectivity and NNR effectiveness

Artificial landscapes, which account for less than 2% of the total NNR areas, disproportionately reduced nearly 40% of the functional connectivity for highly mobile terrestrial mammals (Fig. 4a and Table S6). Terrestrial mammals with stronger median daily and dispersal movement capacity were generally more vulnerable to the impacts of human activities. However, birds with weaker median daily and dispersal movement capacity were more sensitive to the impacts of artificial landscapes (Fig. S6). The effectiveness of NNRs decreased with increasing intensity of human activities (Fig. S11). In addition, non-human dominated NNRs (HF > 4 is often used as a threshold to measure whether dominated by humans; see Table S7) provided great effectiveness for wildlife populations. For high-mobility birds and terrestrial mammals, the proportion of effectively protected populations in NNRs with HF < 4 increased up to 50%; whereas the proportion of effectively protected populations decreased to less than 30% with increasing intensity of human activities (Fig. 4b). In the scenario of removing artificial landscapes, we found that barrier effect-induced decreases in functional connectivity reduced the conservation effectiveness of the population. However, this does not make a complete reversal of whether the population can be effectively conserved.

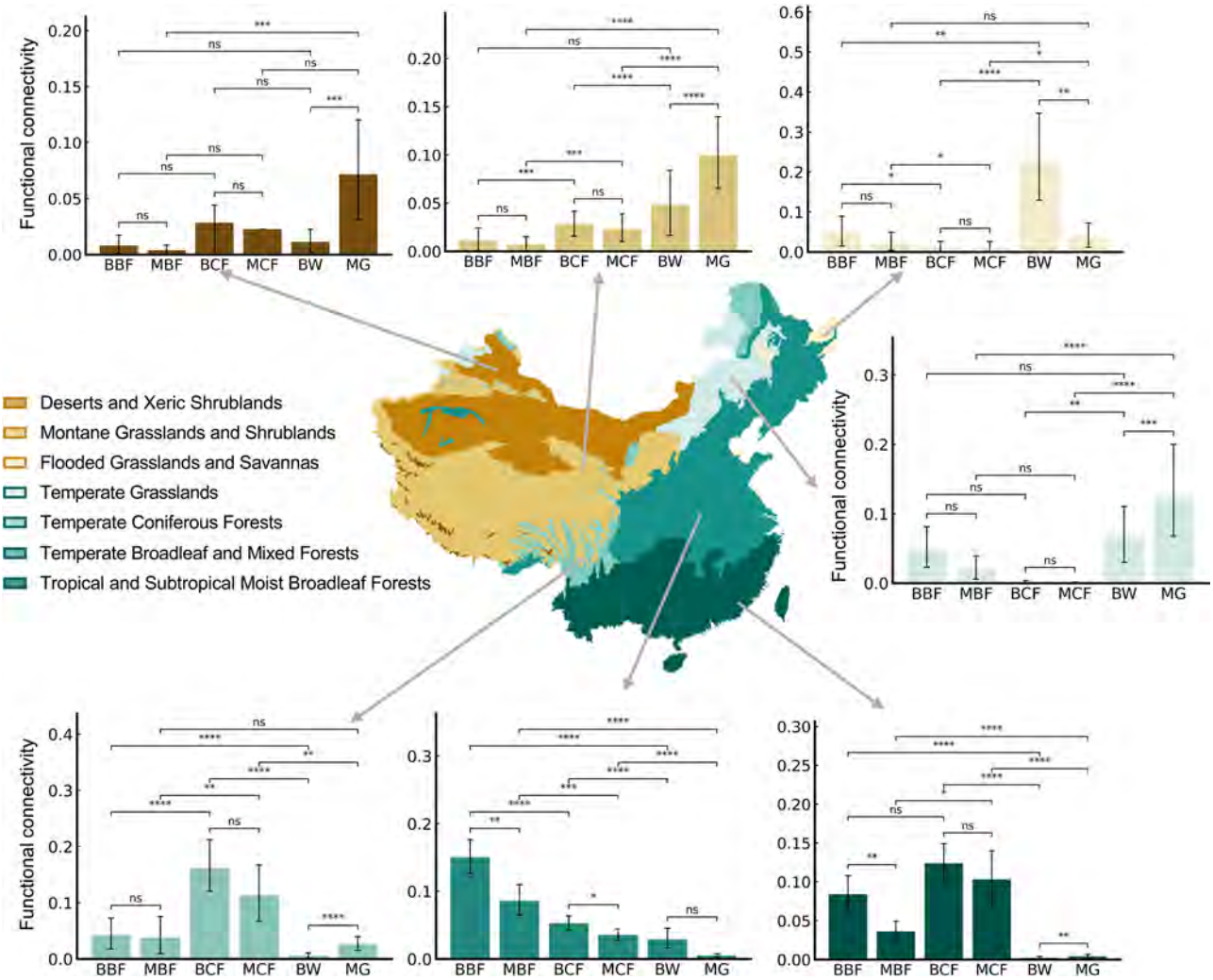


Fig. 1 | Map of the functional connectivity. The gradation of colors from green to yellow represents seven different biomes. The horizontal axis labels of the histogram represent the following: BBF, birds living in broadleaf forest habitats; MBF, terrestrial mammals living in broadleaf forest habitats; BCF, birds living in coniferous forest habitats; MCF, terrestrial mammals living in coniferous forest habitats; BW, birds living in wetland habitats; MG, terrestrial mammals in grassland habitats. The vertical lines denote the 95% confidence interval. Significance levels are as follows: *, $<p \le 0.05$; **, $0.001 <p \le 0.01$; ***, $0.0001<p \le 0.001$; ****, $p \le 0.0001$. Statistical methods using the Mann–Whitney *U* non-parametric test.

Discussion

Small-sized NNRs limit the effectiveness of safeguarding wildlife

Our results demonstrate that nearly one-half of NNRs in China face risks of being too small for the long-term survival of bird and mammal populations. These findings highlight the importance of PAs size for safeguarding biodiversity, especially for sustaining the long-term survival of high-motility and large-body-size species[2]. Our findings suggest that the smaller size of PAs in eastern China limits their effectiveness in safeguarding wildlife, although most species with high movement ability are mainly distributed in western China. However, a considerable portion of threatened species were historically widespread in eastern China through our analysis of the list of Chinese terrestrial wildlife important habitats. Inadequate PA sizes result in higher exposure to human activities for these threatened species and, thus, higher risk of extinction. Moreover, from the lens of functional connectivity, we found a high degree of overlap between PAs of small size and high human activity intensity and areas of low conservation effectiveness. Global anthropogenic pressure assessment also shows that small PAs have higher anthropogenic intensity and undermine conservation effectiveness[39]. Our study adds new considerations to the debate on "single large or several small PAs". Previous studies have shown that several small PAs generally support higher species richness than single larger ones but that larger PAs are critical for the long-term survival of larger species[6,40,41]. The functional connectivity lens in this study differs from those of biodiversity and endangered species in conservation studies. First, biodiversity-focused studies are often based on the potential range of species, while ignoring the viable populations. Our study shows that sufficiently large PAs are critical for the long-term survival of populations. Second, we combined population life-history traits to define long-term survival using the concept of "metapatches" that were nested at different scales such as population foraging and dispersal. Although the species we defined are virtual species constructed based on ecological niches, they can represent the vast majority of scenarios and provide inter-regionally comparable analyses.

Multiple natural and anthropogenic factors regulate the functional connectivity of NNRs

Numerous studies have shown that human activities[16,42–47] and natural landscapes (e.g., habitat area size[48] and ecosystem type diversity)[49] have different degrees of impact on functional connectivity[42,45]. Yet, few studies have investigated the complex influences of these natural and anthropogenic factors on functional connectivity and how these influences vary across regions. Our abundant modeling data provide strong evidence for the complexity of factors influencing functional connectivity. First, habitat loss

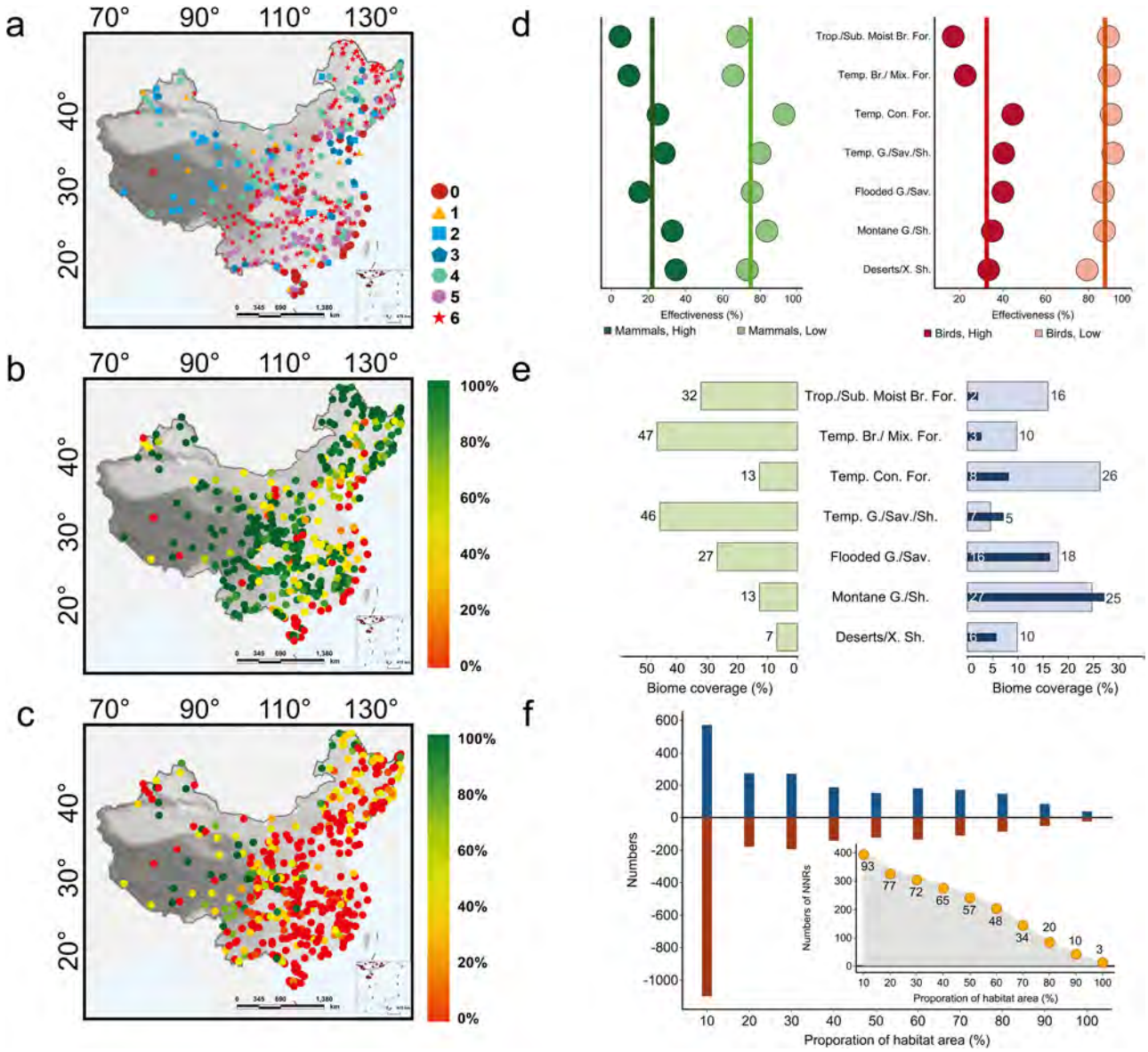


Fig. 2 | Proportion of effectively protected by National Nature Reserves (NNRs). **a** The number of potentially resident species categories in NNRs. **b** and **c** The effectiveness of NNRs under low and high motility, respectively (for detailed information, refer to Fig. S7). **d** The effectiveness patterns of species within NNRs in various biomes. The green and red dots represent low and high-motility species, respectively. The colored lines parallel to the column axis represent the average proportion of effectiveness protected for various movement ability species, respectively (for detailed information, refer to Table S3). **e** Habitat conversion and protection in the world's 14 terrestrial biomes (following Watson et al. 2016). The light blue bars in the habitat protection proportions represent the global scale, whereas the dark blue bars represent the China scale. **f** The relationship between the proportion of habitat area (HA) and effectiveness. The horizontal axis of the bar graph represents HA, and the vertical axis represents the number of populations that can/cannot be effectively conserved. Blue and positive values represent effective conservation, and red and negative values represent cannot be effectively conserved. The horizontal coordinate of the scatter plot represents HA, and the vertical coordinate represents the number of NNRs in which populations cannot be effectively conserved. The numbers near the dots represent the proportion of NNRs that cannot be effectively protected among all NNRs.

should be considered in all regions as the most coherent and critical threat to the functional connectivity and effectiveness of biodiversity conservation. Second, the impacts of NNR area, ecosystem diversity, and artificial landscape intensity on functional connectivity vary across different geographic areas. Hence, it is necessary to distinguish the degree of potential threats to functional connectivity and effectiveness of NNRs in different regions. We propose a framework of common but differentiated management strategies to enhance the role of NNRs in different geographic regions of China for safeguarding the long-term survival of bird and mammal populations. Moreover, decisions should be made with reference to the setting of relevant priority management strategies, maximizing functional connectivity benefits[12].

Infrastructure offsets conservation gains

Our study suggests that the construction of artificial hard-surface landscapes, such as roads and settlements, can substantially reduce functional connectivity and change the flow patterns of species in NNRs. Reducing the proportion of artificial landscapes in NNRs with high human footprints can improve functional connectivity more than increasing the proportion of habitat. Such findings support the current calls that merely expanding the size of existing NNRs probably did not improve conservation effectiveness to the high level expected[29,50]. Our study distinguished two important biota taxa, i.e., birds and terrestrial mammals, in the absence of current research on the conservation effectiveness of birds[6,44,51–53]. For terrestrial mammals, we found that the greater the movement capacity, the greater the loss of

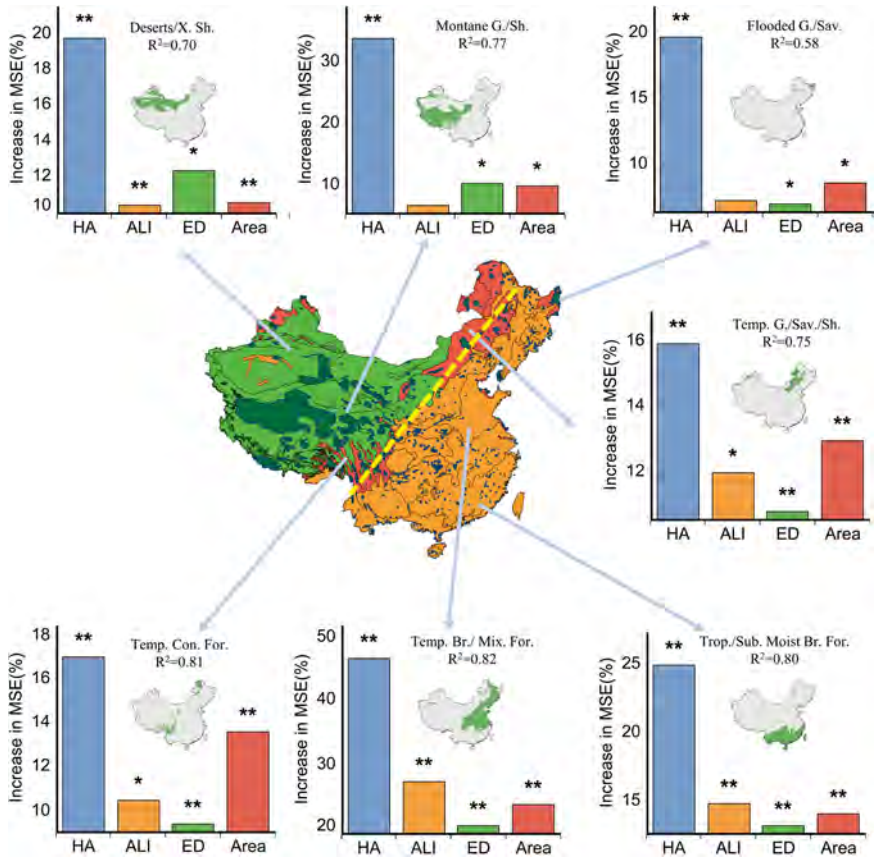


Fig. 3 | Potential drivers of functional connectivity in various biomes. Random forest (RF) mean predictor importance (percentage of increase of mean square error) of proportion of habitat area (HA), artificial landscape intensity (ALI), ecosystem diversity (ED), and NNRs area (AREA) as drivers for functional connectivity. The accuracy importance measure was computed for each tree and averaged over the forest (500 trees). Percentage increases in the MSE (mean squared error) of variables were used to estimate the importance of these predictors, and higher MSE% values imply more important predictors. Significance levels are as follows: $^{*}P < 0.05$ and $^{**}P < 0.01$. MSE, mean squared error.

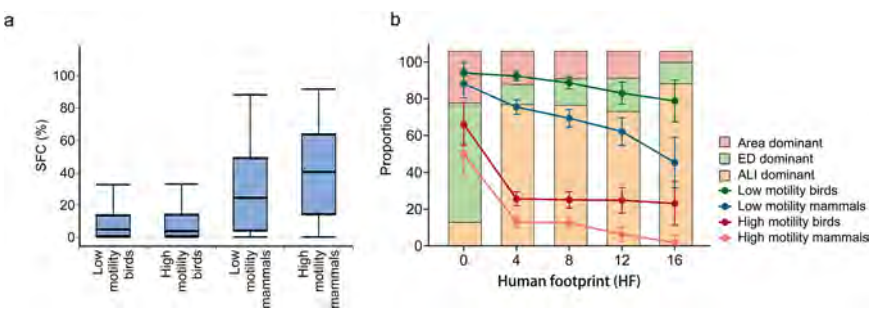


Fig. 4 | Effects of artificial landscape intensity (ALI) and human footprint (HF) on functional connectivity. a Relative gain (sensitivity) of functional connectivity with different mobility in modeled scenarios without artificial landscapes. Error bars indicate the 95% credible intervals. **b** The impact of the human footprint on the effectiveness of NNRs. Colored dots represent the mean effectiveness ratios of birds or terrestrial mammals with various motility abilities. Error bars indicate the 95% credible intervals. Colored blocks represent the proportion of effectiveness of NNRs in various driver-dominated biomes.

functional connectivity caused by human activities, which is corroborated by findings from a previous study[34]. For birds, however, we show that the weaker the movement ability, the higher the vulnerability of functional connectivity to the impact of infrastructure. Because highly mobile birds tend to rely more on flight than surface movement, linear infrastructure such as roads tend to have less impact on their movements. Migratory birds, for example, usually suffer from the risk of population extinction due to the loss of stepping-stone habitat[54]. Nonetheless, non-flying birds, such as the white-tailed ground chough, *Podoces biddulphi*[55], and the Chinese srouse, *Tetrastes sewerzowi*[56,57], are often threatened by habitat fragmentation due to human activities.

Importantly, we show that the conservation effectiveness of birds is less vulnerable to landscape fragmentation than terrestrial mammals with the same dispersal ability. This might be explained by the fact that birds of the same dispersal ability are generally less sensitive to roads than terrestrial mammals when only road isolation effects are considered[58]. Agricultural fields within PAs may also provide a potential source of food and habitat for them[59]. It is worth noting that it does not imply that birds have a lower risk of extinction than terrestrial mammals - in fact, just the opposite[52,60,61]. Our study compares the difference of conservation effectiveness between birds and terrestrial mammals at the same dispersal distance. Their body size differs by tens or even hundreds of folds. The requirements for habitat patch size and food quantity are much lower than the needs of terrestrial mammals with the same movement abilities. Therefore, appropriate agricultural activities in non-core zones of PAs might be beneficial for some birds. However, the accompanying transportation infrastructure construction and other human activities such as noise from roads, vehicle crashes, and even the increase in tourism and poaching activities caused by road accessibility will undoubtedly undermine the overall conservation effectiveness[62,63]. Future conservation efforts should continue to focus on protecting the

agricultural field biodiversity out of NNRs to supplement the lack of conservation for vulnerable birds by NNRs alone[64].

Implications for management of PAs

Our study has important implications for improving the management of PAs in China and beyond. First, previous studies regarding the establishment and management of PAs are often discussed at the global or national scale, yet some important social and environmental issues need to be considered at a much more detailed scale due to intra-country and intra-regional heterogeneities. We propose a common but differentiated management framework to facilitate sub-regional priority implementation. Strategies of increasing the number/area of PAs and reducing the intensity of human activities in PAs combine to maximize benefits[12]. However, different conservation strategies should be prioritized in geographical areas with different socioeconomic conditions. Our findings suggest that increasing habitat diversity will be beneficial for improving the functional connectivity of NNRs because low ecosystem diversity limits the availability of suitable habitats for mammals and birds, such as water sources and wetlands. Second, we demonstrate that reducing human activity within PAs may improve functional connectivity and, thus, the degree of effective conservation. Nearly half of the PAs might suffer from being too small for viable populations for long-term survival. Merely restricting human activities in these PAs cannot effectively safeguard viable populations. We suggest that conservation investments that priority in size should be made for PAs that are too small to be effectively protected. Optimize and integrate previously established PAs based on administrative boundaries such as provinces and counties to create larger and more separated ownership and responsibility for PAs. For example, the establishment of large national parks as prioritized conservation investments[65]. Finally, given that most PAs are small in China, expanding PAs to the extent necessary to provide sufficient conservation for species may be politically, economically, and socially difficult due to its large population[66]. Therefore, it is critical to improve functional connectivity among PAs and link the PA nodes into national networks for maintaining and conserving high levels of biodiversity. Under the impact of climate change or increased human activity, viable populations may become less resilient, increasing the long-term extinction risk[2]. The establishment of cross-border PA networks, ecological corridors, and inter-regional cooperative efforts all enhance the migration of wildlife species and the connectedness of PAs.

Methods

We modeled functional connectivity using Graphab, a software application for modeling ecological networks[67], which is widely used in ecology, conservation, and landscape planning[32] that based on a graph theoretic method for simplified representation of visualizing ecological networks (Fig. S1 in Supporting Information). The nodes of ecological networks are habitat patches and the links represent the potential flow between them to simulate habitat connectivity of wildlife populations[33]. This approach is based on the theory of least-cost path (LCP) analysis, which designates a landscape resistance surface based on the hypothetical "cost" imposed by landscape components on species movement and identifies pathways that minimize the cumulative cost between locations[68]. Two inputs are required for this analysis: landscape resistance surface and the potential movement ability of wildlife.

Landscape resistence surface. The resistance of each landscape unit is calculated to reflect the "high" or "low" suitability of different landscape factors (e.g., land cover, topography, and human activities) and is intended to represent the sum of the assumed energy expenditures, mortality risks, or facilitative (or hindering) effects of landscape elements on wildlife movement. The resistance values for each factor were weighted according to their relative importance and combined to produce a movement resistance surface. The path cost between habitat patches for species is the resistance distance weighted by the cumulative resistance value of all crossed cells[32]. LCP analysis identifies paths that minimize the cumulative cost between habitat patches and that minimize the cumulative resistance of movement[68]. We defined resistance values for each ecosystem type and artificial landscape (land cover/use type) based on various species taxa and their habitat preferences (Table S1 in Supporting Information). In particular, we set the resistance values for terrestrial mammals crossing the artificial hard-surface landscape as high as possible, especially for main roads, highways, and railroads. These linear infrastructures would often be separated on both sides by iron fences and barbed wire. Despite the design of corridors or culverts, these linear infrastructures still severely impede the movement of most terrestrial mammals[69–72]. We also set a high resistance value for birds to cross the artificial hard-surface landscape. The study has found that roads are not only a physical barrier to birds but include other impacts such as traffic accidents, chemical pollution, noise disturbance, poaching, etc[22]. To ensure the accurate evaluation of the long-term survival of bird populations, the impact of roads on birds is estimated to be large enough to avoid underestimation. Furthermore, it is important to note that the distribution of roads may be underestimated due to limited data accessibility, and the fences enclosing the roads are usually much wider than the vector data[34]. Therefore, it may be reasonable to consider the greater impact of roads on mammals and birds. We further revised the value of the resistance surface weighted by slope in terms of reflecting the cost of resistance to movement in steep topography (see subsequent DEM for calculation details).

Potential movement ability of wildlife. A distance needs to be defined when exploring the graph theory modeling of functional connectivity based on a resistance model approach to characterize the mobility of each species. Concurrently, the research target is oriented to the species, which could either refer to one or more realistic and specific biotic species[73], as well as based on virtual species characterized by an ecological niche in a broader spatial and temporal scale and more widespread scenarios[34,36]. For the purpose of comparison among national nature reserves (NNRs) of different geographical regions and ecosystem types across China, we used a virtual species approach to provide a standardized and comparable protocol for all species[34,74]. We constructed six virtual species groups (birds for coniferous, broadleaf, and wetland habitat types; terrestrial mammals corresponding to coniferous, broadleaf, and grassland habitat types; abbreviated respectively as BCF, BBF, BW, MCF, MBF, and MG) based on two biological taxa and four habitat preferences. Since the dispersal process is a key factor in population viability[35], each virtual species group is characterized by its dispersal distance. To fit the scale of movement within a single NNR, we used the 25th and 75th percentiles of the minimum enclosing circle diameter of NNRs vector boundary as the median dispersal distance for low and high motility virtual species groups, the distance is 10 km and 50 km respectively. To ensure a realistic match, we verified the reasonableness of the virtual species dispersal distance set by collecting the real species dispersal distance in literature and documents. We also examined other models with different dispersal distances and confirmed the high correlation between all models (see Reasonableness and sensitivity analysis for details). Moreover, we obtained three ecological variables, including median daily movement distance within populations, key patch area for meta-populations, and species geographic range area of isolated populations, based on the allometric relationships that allowed these ecological traits to be derived from dispersal distance among populations and diet (see The definition of NNR effectiveness for details). Given the lack of references on average daily movement distances for birds and terrestrial mammals, we adopted an allometric relationship model that calculates the home range of species[75,76]. The radius of a circle with the same home range area is used to approximately represent the average daily movement distance. In this study, we used herbivorous allotropic relationships to model the ecological traits of low movement ability species and carnivorous allotropic relationships to model the ecological traits of high movement ability species (Table S2). Our research focuses on these short-distance, long-timescale movements as they are more representative of the scale of movement occurring within each PAs and thus represent movements that promote gene flow, rescue effects, or climate adaptation[12].

Nature reserve data. We used the robust polygon data collected from multiple data sources revised and integrated for the boundaries of NNRs in China. Up to 2024, there are 474 NNRs in China. Due to differences in data availability and management systems, Taiwan Province, Hong Kong, and Macau Special Administrative Regions are excluded. These NNRs account for 10.4% of China's total territorial surface area and 58% of the total area of various nature reserves in China. The distribution of the NNRs on the climatic gradient and NNRs' basic information are detailed in Figs. S2 and S3. For some watershed NNRs that are too small in size and have linear boundaries, we extended a buffer zone of 10 km outward from the known boundaries as the study area. For NNRs with marine ecosystems and marine creatures as conservation targets, the conservation effectiveness is only shown in Fig. 2a–c for the proportion of single NNR effectively protected. These NNRs are not included in the subsequent calculation of the proportion of effectively protected biomes and national scales.

Resistance surface. The landscape data used for the resistance surface is based on the ChinaCover 2010 (30 × 30 m resolution) land cover dataset[77], and the 2020 land cover changes are monitored by visual interpretation of 2010 and 2020 Landsat satellite images and further overlayed with the OpenStreetMap dataset to refine the information on roads, waters, farmlands, and settlements to obtain the 30 m resolution 2020 land cover dataset specifically built for the study of NNRs. Finally, the digital elevation model (DEM) is used to deduce the slope, which is overlaid with the land cover map to define the resistance surface.

ChinaCover. ChinaCover 2010 is based on remote sensing data as the main data source, supplemented by the vegetation map of the People's Republic of China (1:1,000,000), land use maps of 2000 and 2005, and slope and slope direction data, etc., produced by ASTERDEM, and adopts object-oriented technology to realize the interpretation. The primary classes of the classification system are consistent with the IPCC for 6 categories, and the secondary classes adopt 38 types with global unified code generated by FAO's LCCS. At present, the accuracy of ChinaCover2010 is 91% for primary classes and about 82% for secondary classes.

Open Street Map. Based on the updated ChinaCover for 2020 land cover, we overlaid the land cover categories that need to be focused on, especially the linear artificial landscape. We mainly used the Open Street Map (OSM) data (OpenStreetMap contributors, https://www.openstreetmap.org) to update the line features data for roads and paths, railways, and waterways, as well as the polygon features data for bodies of water and some buildings. A more detailed process is to divide the roads into major roads and minor roads. For linear road data, a width of 90 m is set for major roads, and a width of 30 m is set for minor roads. The rivers are divided into major rivers and minor rivers (stream, canal, and drain), and widths of 90 m and 30 m are set for these linear water bodies, respectively. However, in OSM, larger waters, rivers, and reservoirs are often used as polygonal geometries. The line geometries will then run through the middle of the polygon geometries in the direction of the water flow. We superimpose linear and polygonal geometric data during data processing related to water. In addition, we also overlaid the built-up and related land (residential, industrial, quarry, and farmland) layer data. Given the pace of road construction and data limitations, our results underestimate the intensity of artificial landscapes and the magnitude of human impacts.

DEM. We use a digital elevation model (DEM) to calculate the slope that is used together with the land cover map to define the resistance surface and to calculate the cost distance[18]. The DEM dataset was used with ASTER GDEM v2 (30 m), which was obtained from the Geospatial Data Cloud (http://www.gscloud.cn), and slope layers in percent were extracted using ArcGIS 10.2. Resistance values previously defined can be weighted by slope with the parameter coef (c), which can adjust the importance of the slope (p) weighting. For a given pixel, the resulting resistance value (r_{final})is calculated with the following formula:

$$r_{\text{final}} = r * \left(1 + c.p\right) \tag{1}$$

$p = 0$ if the slope is flat, $p = 1$ for a slope of 100%.

We defined $c = 10$, which means the resistance value is doubled for a slope of 10%[18].

Functional connectivity and sensitivity of functional connectivity (SFC). In this study, we used functional connectivity to quantify the conservation effectiveness of their viable populations. The analysis of functional connectivity is based on The Probability of Connectivity (PC) index[5]. This index provides the probability that two points randomly placed in the study area are connected. It is the most widely used index to quantify the functional connectivity efficiency of ecological networks. Functional connectivity has different distribution patterns among vegetation types and biomes (see Figs. S4 and S5). The PC index is given by the following expression:

$$\text{PC} = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^*}{A_L^2} \tag{2}$$

where a_i and a_j are the areas of the habitat patches i and j, and A_L is the total studied area (both habitat and non-habitat patches). p^*_{ij} is defined as the maximum product probability of all possible paths between patches i and j[67].

p_{ij} is determined with an exponential function such that:

$$p_{ij} = e^{-\alpha d_{ij}} \tag{3}$$

where d_{ij} is the least-cost distance between patches i and j, and α expresses the intensity of decreasing the dispersal probability p resulting from the exponential function[67].

Different movement ability species have different sensitivity of functional connectivity after infrastructure (artificial landscape intensity) removal (see Fig. S6 and Table S6). The connectivity gain due to the removal of infrastructure (D) is evaluated using the following expression to represent the sensitivity of functional connectivity (SFC):

$$\text{SFC} = \frac{\left(\text{PC}_D - \text{PC}\right) \times 100}{\text{PC}} \tag{4}$$

Nested spatial and temporal scales of ecological processes. We used the concept of metapatches, a concept that considers a nested scale from the interactions of individuals within populations to the interactions between separate populations[15,34,73]. Individuals within populations living and interacting on small spatial and temporal scales. Daily or seasonal movements connected a continuous habitat patch or several discontinuous habitat patches into a metapatch. This metapatch may include several home ranges of overlapping or non-overlapping individuals, and these collections of individuals are defined as a (local) population. The spatial and temporal scales of inter-population interactions are much larger, and usually exist several dispersal or genetic pathways linking several (local) populations to form a meta-population (Fig. S1).

The definition of NNR effectiveness. We measure the effectiveness of NNRs in terms of their ability to sustain wildlife populations over the long term. Populations must be large enough to maintain long-term survival in NNRs, or to maintain periodic genetic exchange by keeping well-connected with nearby populations. We used a trait-based criterion of survival, using the relationship between life history traits and movement ability to estimate the minimum meta-population size that could maintain NNR effectiveness. We refer the criteria of related literature and combine with the allometric relationship[2,52,78–81], it is estimated that the minimum meta-population size is about 60 individuals for herbivorous mammals with interpopulation dispersal movement ability less than 10 km, and about 20 individuals for carnivorous mammals with interpopulation dispersal close to 50 km. For birds, both herbivorous birds with an interpopulation dispersal distance of about 10 km and carnivorous birds with an interpopulation dispersal distance close to 50 km have a minimum meta-population size of about 400 individuals. Particular emphasis must be placed on the fact that this is the least strict standard, preferring PAs as refugees rather than as solutions to biodiversity loss. We obtained the minimum key patch area for meta-

populations ($MinA_k$) to maintain the above meta-population size based on allometric relationships similarly. The NNR effectiveness is defined by evaluating whether $MinA_k$ in NNRs is sufficient to support the minimum meta-population size.

For species with relatively low movement ability, we define PAs as effective for conservation if the NNR is large enough to contain several populations and the habitat area occupied by the meta-population is up to $MinA_k$. For species with relatively high motility, the outer boundary of wildlife population survival has exceeded the extent of NNR. Single NNRs are unable to sustain any individual (local) populations, so we define them as NNRs that cannot be effectively protected. However, given that the habitats of some wildlife populations occupied a large part of the PA and that the habitats were geographically contiguously distributed, it is not possible to build the above scale-nested connectivity model. We considered species with habitat patches connected by daily distances larger than the species geographic range area of isolated populations (Ag, also obtained based on the above-mentioned allometric relationship) as effectively protected (Table S2). The minimum isolated population size is about 500 individuals for herbivorous mammals with a median daily movement distance of less than 1 km and about 60 individuals for carnivorous mammals with a median daily distance of 5 km. For birds, both herbivorous birds with a median daily distance of about 0.5 km and carnivorous birds with a median daily movement distance close to 2.4 km have a minimum meta-population size of about 10,000 individuals.

Proportion of NNR effectively protected. An individual proportion of NNR effectively protected is the ratio of the number of population types of virtual species that can be effectively protected over the number of potentially viable population types (the existence of ecosystems within NNR that are preferred by several of the six types of populations). For example, there are four types of ecosystems in NNR: coniferous forest, broadleaf forest, grassland, and wetland, but only the populations that live in the coniferous forest and broadleaf forest ecosystems are evaluated as being effectively protected. Then the proportion of effectively protected is 50%.

The proportion of effectively protected at biome or national scales is the sum of the number of population types that can be effectively protected in each NNRs over the total number of potentially viable population types.

Human footprint. For the dataset of human footprint intensity within the reserve, we used HumanFootprint, v2 (2009) (https://wcshumanfootprint.org/v2/). We analyzed the human footprint intensity within different biomes and the intensity of human footprint in different functional areas of the reserve under different biome gradients (see Tables S4 and S7; and Fig. S10). Furthermore, the relationship between human footprint intensity and conservation effectiveness was analyzed (Fig. S11). To ensure the analysis is robust, we also used Global Human Modification of Terrestrial Systems, v1 (2016)[82], for comparison to show the consistency pattern of the two datasets (Fig. S10).

Reasonableness and sensitivity analysis. To ensure the reasonableness of the virtual species we defined could match with the real species. We used the list of Chinese terrestrial wildlife important habitats for important protected species (https://www.forestry.gov.cn/search/538542). In total, 122 important protected species were selected by weight, movement ability, and other allotropic relationships to match with the virtual species. Moreover, we obtained the distribution extent of the 122 species from the IUCN Red List of threatened species (https://www.iucnredlist.org/). Their distribution extent was merged to obtain the distribution extent of the virtual species group classified by various gradients of movement ability. It is important to note that the merged distribution extent is only used to analyze the reasonableness of the virtual species group. Matched real species are probably distributed outside the merged ranges since our samples are only parts of the important protected species.

We conducted a series of tests to evaluate (a) the sensitivity of functional connectivity to movement distances of various taxa and (b) the sensitivity of effectiveness of conservation to different ecological characteristics of various taxa, such as dispersal distances and diet. First, to ensure our results have the consistency to be generalized to more common species with different dispersal abilities, we calculated and compared the functional connectivity values between our main model and the sensitivity test model using the same methodology. We approximated the allometric relationship equation for birds and terrestrial mammals with dispersal distances less than 20 km as low movement ability and used the allometric relationship equation for low movement ability species in Table S2. Birds and terrestrial mammals with dispersal distances of more than 30 km were considered as high movement ability, and the allometric relationship equation for high motility species was used. Functional connectivity values for birds and terrestrial mammals were highly correlated between the models (Pearson's $R^2 > 0.97$; Fig. S12). Second, we examined the relationship between dispersal distance and diet and conservation effectiveness and compared the effectiveness between our main model and the sensitivity test model. Conservation effectiveness was highly correlated between the models (Pearson's $R^2 > 0.85$; Fig. S8).

Statistical analyses of prediction variables. We used GAMs with negative binomial distribution to determine complex nonlinear relations of functional connectivity and prediction variables (Fig. S13). We used habitat characteristic variables (i.e., PAs area, proportion of habitat area, ecosystem type diversity, and artificial landscape intensity) as predictors and fitted their interactions to functional connectivity. We implemented GAMs models on R (version 4.2.2) using the "mgcv" package. We used restricted maximum likelihood as the method for estimating the smoothing parameters and applied tensor product smoothing as the smoothing function when fitting the interactions[17]. We restrict the maximum degrees of freedom of the smoother to 2. To determine the most suitable model, we performed a stepwise backward selection using the Akaike Information Criterion (AIC) (see Tables S8 and S9).

We also applied random forest analysis with a tenfold cross-validation approach[83] to estimate the significance of habitat characteristic variables to explain the limiting factors affecting functional connectivity. The "rfPermute" package was used to assess the significance of each predictor on the response variable[84].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data used in this manuscript is openly available online. The ChinaCover land cover dataset is available from: The land cover atlas of the People's Republic of China (1:1,000,000), Beijing: SinoMaps Press, 2017. Road data are available from: https://www.openstreetmap.org. ASTER GDEM v2 (30 m) is available from: http://www.gscloud.cn. Dataset of human footprint intensity are available from https://wcshumanfootprint.org/v2/, and Global Human Modification of Terrestrial Systems, v1 (2016) available from: https://sedac.ciesin.columbia.edu/data/set/lulc-human-modification-terrestrial-systems. The main data analyzed are the connectivity model outputs, for the data used to plot the main graphs used in this study can be accessed at https://doi.org/10.6084/m9.figshare.25928938.v1.

Code availability

All statistical analyses were performed using Graphab (version 2.6), ArcMap (version 10.2), and R (version 4.2.2). We used the following R packages for analyses: mgcv(version 4.2.2), randomForest (version 4.7-1.1), rfPermute (version 2.5.1). The connectivity model building parameters in Graphab refer to the user manual[67], and there is no code for the operating interface. The data analyses in R software are basic calculations of each package, with no custom code used in this study.

Received: 7 October 2023; Accepted: 21 May 2024;
Published online: 07 June 2024

References

1. Cazalis, V. et al. Effectiveness of protected areas in conserving tropical forest birds. *Nat. Commun.* **11**, 4461 (2020).
2. Williams, D. R., Rondinini, C. & Tilman, D. Global protected areas seem insufficient to safeguard half of the world's mammals from human-induced extinction. *Proc. Natl Acad. Sci. USA* **119**, e2200118119 (2022).
3. Rodrigues, A. S. L. & Cazalis, V. The multifaceted challenge of evaluating protected area effectiveness. *Nat. Commun.* **11**, 5147 (2020).
4. Visconti, P. et al. Protected area targets post-2020. *Science* **364**, 239–241 (2019).
5. Saura, S. & Pascual-Hortal, L. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landsc. Urban Plan.* **83**, 91–103 (2007).
6. Wauchope, H. S. et al. Protected areas have a mixed impact on waterbirds, but management helps. *Nature* **605**, 103–107 (2022).
7. Terraube, J., Van Doninck, J., Helle, P. & Cabeza, M. Assessing the effectiveness of a national protected area network for carnivore conservation. *Nat. Commun.* **11**, 2957 (2020).
8. SCBD. Kunming-Montreal Global Biodiversity Framework. *Secr. Conv. Biol. Divers.* (2022).
9. Eklund, J. & Cabeza, M. Quality of governance and effectiveness of protected areas: crucial concepts for conservation planning. *Ann. N. Y. Acad. Sci.* **1399**, 27–41 (2017).
10. Tucker, M. A. et al. Moving in the anthropocene: global reductions in terrestrial mammalian movements. *Science* **359**, 466–469 (2018).
11. Watson, J. E. M. et al. Persistent disparities between recent rates of habitat conversion and protection and implications for future global conservation targets. *Conserv. Lett.* **9**, 413–421 (2016).
12. Brennan, A. et al. Functional connectivity of the world's protected areas. *Science* **376**, 1101–1104 (2022).
13. SCBD. Zero Draft of the Post-2020 Global Biodiversity Framework. *Secr. Conv. Biol. Divers.*1–14 (2020).
14. Ashrafzadeh, M. R. et al. A multi-scale, multi-species approach for assessing effectiveness of habitat and connectivity conservation for endangered felids. *Biol. Conserv.* **245**, 108523 (2020).
15. Zetterberg, A., Mortberg, U. M. & Balfors, B. Making graph theory operational for landscape ecological assessments, planning, and design. *Landsc. Urban Plan* **95**, 181–191 (2010).
16. Roever, C. L., van Aarde, R. J. & Leggett, K. Functional connectivity within conservation networks: delineating corridors for African elephants. *Biol. Conserv.* **157**, 128–135 (2013).
17. Xu, Y. et al. Landscape-scale giant panda conservation based on metapopulations within China's national park system. *Sci. Adv.* **8**, eabl8637 (2022).
18. Clauzel, C., Deng, X., Wu, G., Giraudoux, P. & Li, L. Assessing the impact of road developments on connectivity across multiple scales: application to Yunnan snub-nosed monkey conservation. *Biol. Conserv.* **192**, 207–217 (2015).
19. Tarabon, S., Dutoit, T. & Isselin-Nondedeu, F. Pooling biodiversity offsets to improve habitat connectivity and species conservation. *J. Environ. Manag.* **277**, 111425 (2021).
20. Haddad, N. M. et al. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).
21. Ibisch, P. L. et al. A global map of roadless areas and their conservation status. *Science* **354**, 1423–1427 (2016).
22. Laurance, W. F., Goosem, M. & Laurance, S. G. W. Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* **24**, 659–669 (2009).
23. Allan, B. F., Keesing, F. & Ostfeld, R. S. Effect of forest fragmentation on Lyme disease risk. *Conserv. Biol.* **17**, 267–272 (2003).
24. Boakes, E. H., Mace, G. M., McGowan, P. J. K. & Fuller, R. A. Extreme contagion in global habitat clearance. *Proc. R. Soc. B Biol. Sci.* **277**, 1081–1085 (2010).
25. Caro, T., Dobson, A., Marshall, A. J. & Peres, C. A. Compromise solutions between conservation and road building in the tropics. *Curr. Biol.* **24**, R722–R725 (2014).
26. Hoffmann, S., Irl, S. D. H. & Beierkuhnlein, C. Predicted climate shifts within terrestrial protected areas worldwide. *Nat. Commun.* **10**, 4787 (2019).
27. Liu, F. et al. Effectiveness of functional zones in National Nature Reserves for the protection of forest ecosystems in China. *J. Environ. Manag.* **308**, 114593 (2022).
28. Joppa, L. N. & Pfaff, A. High and far: biases in the location of protected areas. *Plos ONE* **4**, e8273 (2009).
29. Pimm, S. L., Jenkins, C. N. & Li, B. V. How to protect half of Earth to ensure it protects sufficient biodiversity. *Sci. Adv.* **4**, eaat2616 (2018).
30. Saura, S. & Torne, J. Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. *Environ. Model. Softw.* **24**, 135–139 (2009).
31. Hall, K. R. et al. Circuitscape in Julia: empowering dynamic approaches to connectivity assessment. *Land* **10**, 301–301 (2021).
32. Foltête, J.-C. et al. Graphab: an application for modeling and managing ecological habitat networks. *Softw. Impacts* **8**, 100065 (2021).
33. Savary, P., Foltete, J.-C., Moal, H., Vuidel, G. & Garnier, S. graph4lg: A package for constructing and analysing graphs for landscape genetics in R. *Methods Ecol. Evolut.* **12**, 539–547 (2021).
34. Mimet, A., Clauzel, C. & Foltete, J.-C. Locating wildlife crossings for multispecies connectivity across linear infrastructures. *Landsc. Ecol.* **31**, 1955–1973 (2016).
35. Sahraoui, Y., Foltete, J.-C. & Clauzel, C. A multi-species approach for assessing the impact of land-cover changes on landscape connectivity. *Landsc. Ecol.* **32**, 1819–1835 (2017).
36. Hirzel, A. H., Helfer, V. & Metral, F. Assessing habitat-suitability models with a virtual species. *Ecol. Model.* **145**, 111–121 (2001).
37. Xu, W. et al. Strengthening protected areas for biodiversity and ecosystem services in China. *Proc. Natl Acad. Sci. USA* **114**, 1601–1606 (2017).
38. Li J, Lu D, Xu C, Li Y, Chen M. Spatial heterogeneity and its changes of population on the two sides of Hu Line. *Acta Geogr. Sin.* **72**, 148–160 (2017).
39. Jones, K. R. et al. One-third of global protected land is under intense human pressure. *Science* **360**, 788 (2018).
40. Fahrig, L. Why do several small patches hold more species than few large patches? *Glob. Ecol. Biogeogr.* **29**, 615–628 (2020).
41. Newmark, W. D. Extinction of mammal populations in western North-American national parks. *Conserv. Biol.* **9**, 512–526 (1995).
42. Carlier, J., Moran, J., Aughney, T. & Roche, N. Effects of greenway development on functional connectivity for bats. *Glob. Ecol. Conserv.* **18**, e00613 (2019).
43. Mimet, A., Houet, T., Julliard, R. & Simon, L. Assessing functional connectivity: a landscape approach for handling multiple ecological requirements. *Methods Ecol. Evolut.* **4**, 453–463 (2013).
44. Burge, O. R. et al. Assessing the habitat and functional connectivity around fenced ecosanctuaries in New Zealand. *Biol. Conserv.* **253**, 108896 (2021).
45. Magioli, M. et al. Connectivity maintain mammal assemblages functional diversity within agricultural and fragmented landscapes. *Eur. J. Wildl. Res.* **62**, 431–446 (2016).
46. Pardo, J. M. et al. Much more than forest loss: four decades of habitat connectivity decline for Atlantic Forest jaguars. *Landsc. Ecol.* **38**, 41–57 (2023).

47. Valerio F, et al. Integrating remote sensing data on habitat suitability and functional connectivity to inform multitaxa roadkill mitigation plans. *Landsc. Ecol.* **38**, 3335–3352 (2023).
48. Niculae, M.-I., Nita, M. R., Vanau, G. O. & Patroescu, M. In *25th International Conference on Environment at Crossroads—SMART Approaches for a Sustainable Future*. 28–37 (2016).
49. Carvalho, F., Carvalho, R., Mira, A. & Beja, P. Assessing landscape functional connectivity in a forest carnivore using path selection functions. *Landsc. Ecol.* **31**, 1021–1036 (2016).
50. Yang, R. et al. Cost-effective priorities for the expansion of global terrestrial protected areas: setting post-2020 global and national targets. *Sci. Adv.* **6**, eabc3436 (2020).
51. Salgueiro, P. A. et al. Multispecies landscape functional connectivity enhances local bird species' diversity in a highly fragmented landscape. *J. Environ. Manag.* **284**, 112066 (2021).
52. Hilbers, J. P. et al. An allometric approach to quantify the extinction vulnerability of birds and mammals. *Ecology* **97**, 615–626 (2016).
53. Fagan, M. E., DeFries, R. S., Sesnie, S. E., Arroyo-Mora, J. P. & Chazdon, R. L. Targeted reforestation could reverse declines in connectivity for understory birds in a tropical habitat corridor. *Ecol. Appl.* **26**, 1456–1474 (2016).
54. Xu, Y. et al. Loss of functional connectivity in migration networks induces population decline in migratory birds. *Ecol. Appl.* **29**, e01960 (2019).
55. Tong, Y., Xu, F., Li, X. & Yang, W. Nest-site selection of the Xinjiang Ground-Jay (*Podoces bidduphi*). *Chin. J. Zool.* **53**, 790–796 (2018).
56. Sun, Y.-H. Patch occupancy by the Chinese Grouse (Tetrastes sewerzowi) in a fragmented landscape. *Chin. Birds* **4**, 232–239 (2013).
57. Siegfried, K., Winfried, V., Yun, F., Peter, S. & Yuehua, S. Patch occupancy by the Chinese Grouse (*Tetrastes sewerzowi*) in a fragmented landscape. *Chin. Birds* **4**, 232–239 (2013).
58. Rytwinski, T. & Fahrig, L. In *Handbook of Road Ecology* 237–246 (2015).
59. Martin-Velez, V. et al. Functional connectivity network between terrestrial and aquatic habitats by a generalist waterbird, and implications for biovectoring. *Sci. Total Environ.* **705**, 135886 (2020).
60. Pe'er, G. et al. Toward better application of minimum area requirements in conservation planning. *Biol. Conserv.* **170**, 92–102 (2014).
61. Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. Predicting extinction risk in declining species. *Proc. R. Soc. B Biol. Sci.* **267**, 1947–1952 (2000).
62. Teixeira, F. Z., Rytwinski, T. & Fahrig, L. Inference in road ecology research: what we know versus what we think we know. *Biol. Lett.* **16**, 20200140 (2020).
63. Barthelmess, E. L. & Brooks, M. S. The influence of body-size and diet on road-kill trends in mammals. *Biodivers. Conserv.* **19**, 1611–1629 (2010).
64. Li, L. et al. A farmland biodiversity strategy is needed for China. *Nat. Ecol. Evol.* **4**, 772–774 (2020).
65. Wilson, K. A. et al. Prioritizing conservation investments for mammal species globally. *Philos. Trans. R. Soc. B Biol. Sci.* **366**, 2670–2680 (2011).
66. Shen X, et al. Countries' differentiated responsibilities to fulfill area-based conservation targets of the Kunming-Montreal Global Biodiversity Framework. *One Earth* **6**, 548–559 (2023).
67. Foltete, J. C., Clauzel, C. & Vuidel, G. A software tool dedicated to the modelling of landscape networks. *Environ. Model. Softw.* **38**, 316–327 (2012).
68. Sawyer, S. C., Epps, C. W. & Brashares, J. S. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? *J. Appl. Ecol.* **48**, 668–678 (2011).
69. Rytwinski, T. & Fahrig, L. Why are some animal populations unaffected or positively affected by roads? *Oecologia* **173**, 1143–1156 (2013).
70. Holderegger, R. & Di Giulio, M. The genetic effects of roads: a review of empirical evidence. *Basic Appl. Ecol.* **11**, 522–531 (2010).
71. Rytwinski, T. & Fahrig, L. Do species life history traits explain population responses to roads? A meta-analysis. *Biol. Conserv.* **147**, 87–98 (2012).
72. Jack, J., Rytwinski, T., Fahrig, L. & Francis, C. M. Influence of traffic mortality on forest bird abundance. *Biodivers. Conserv.* **24**, 1507–1529 (2015).
73. Girardet, X., Foltete, J.-C. & Clauzel, C. Designing a graph-based approach to landscape ecological assessment of linear infrastructures. *Environ. Impact Assess. Rev.* **42**, 10–17 (2013).
74. Bissonette, J. A. & Adair, W. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biol. Conserv.* **141**, 482–488 (2008).
75. Bowman, J. Is dispersal distance of birds proportional to territory size? *Can. J. Zool.* **81**, 195–202 (2003).
76. Santini, L. et al. Ecological correlates of dispersal distance in terrestrial mammals. *Hystrix-Ital. J. Mammal.* **24**, 181–186 (2013).
77. Wu BF, Q. J., Zeng Y. *Land Cover Atlas of the People's Republic of China (1:1,000,000)*. (Beijing: SinoMaps Press, 2017).
78. Hendriks, A. J., Willers, B. J. C., Lenders, H. J. R. & Leuven, R. S. E. W. Towards a coherent allometric framework for individual home ranges, key population patches and geographic ranges. *Ecography* **32**, 929–942 (2009).
79. Carbone, C., Cowlishaw, G., Isaac, N. & Rowcliffe, M. How Far Do Animals Go? Determinants of Day Range in Mammals. *Am. Nat.* **165**, 290–297 (2005).
80. Sutherland GD, Harestad AS, Price K, Lertzman KP. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conserv. Ecol.* **4** (2000).
81. Hendriks, A. J. The power of size: a meta-analysis reveals consistency of allometric regressions. *Ecol. Model.* **205**, 196–208 (2007).
82. Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S. & Kiesecker, J. Managing the middle: a shift in conservation priorities based on the global human modification gradient. *Glob. Change Biol.* **25**, 811–826 (2019).
83. Cai, L. et al. Global models and predictions of plant diversity based on advanced machine learning techniques. *N. Phytol.* **237**, 1432–1445 (2023).
84. Jiao S, Chen W, Wang J, Du N, Li Q, Wei G. Soil microbiomes with distinct assemblies through vertical soil profiles drive the cycling of multiple nutrients in reforested ecosystems. *Microbiome* **6,** 146 (2018).

Acknowledgements

This study was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (Grant No. XDA23080000).

Author contributions

Y.B. conceived the study. W.S., Y.Z., W.C., and Y.B. conducted data analysis and drafted the manuscript. All authors contributed to the revision of the paper, and Y.B. edited the paper.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s43247-024-01458-9.

Correspondence and requests for materials should be addressed to Yongfei Bai.

Peer review information *Communications Earth & Environment* thanks the anonymous reviewers for their contribution to the peer review of this work. Primary Handling Editors: Huai Chen, Clare Davis, Heike Langenberg, Alienor Lavergne. A peer review file is available.

Reprints and permissions information is available at http://www.nature.com/reprints

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2024

New Phytologist

Research

Plant litter loss exacerbates drought influences on grasslands

Wanjie Chen[1,2], Lin Jiang[3], Ruoyu Jia[1,2], Bo Tang[1], Hongzhi Jiang[1], Yang Wang[1], Xiaoming Lu[1], Jishuai Su[1] and Yongfei Bai[1,4]

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, 100093, China; [2]College of Life Sciences, University of Chinese Academy of Sciences, No. 19A Yuquan Road, Beijing, 100049, China; [3]School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332, USA; [4]College of Resources and Environment, University of Chinese Academy of Sciences, No. 19A Yuquan Road, Beijing, 100049, China

Author for correspondence:
Yongfei Bai
Email: yfbai@ibcas.ac.cn

Received: *5 June 2023*
Accepted: *25 September 2023*

New Phytologist (2023)
doi: 10.1111/nph.19374

Key words: anthropogenic disturbance, community compositional stability, plant litter removal, primary productivity, semiarid grassland, soil warming, species and functional group asynchrony.

Summary

- Plant litter is known to affect soil, community, and ecosystem properties. However, we know little about the capacity of litter to modulate grassland responses to climate change.
- Using a 7-yr litter removal experiment in a semiarid grassland, here we examined how litter removal interacts with a 2-yr drought to affect soil environments, plant community composition, and ecosystem function.
- Litter loss exacerbates the negative impacts of drought on grasslands. Litter removal increased soil temperature but reduced soil moisture and nitrogen mineralization, which substantially increased the negative impacts of drought on primary productivity and the abundance of perennial rhizomatous graminoids. Moreover, complete litter removal shifted plant community composition from grass-dominated to forb-dominated and reduced species and functional group asynchrony, resulting in lower ecosystem temporal stability.
- Our results suggest that ecological processes that lead to reduction in litter, such as burning, grazing, and haying, may render ecosystems more vulnerable and impair the capacity of grasslands to withstand drought events.

Introduction

Droughts, which impose large and long-lasting negative impacts on ecological systems, are projected to become more frequent and severe in the future (Dai, 2013; Kröel-Dulay *et al.*, 2022; Vilonen *et al.*, 2022; Xi *et al.*, 2022; Yuan *et al.*, 2023). This is particularly true in water-limited ecosystems, such as grasslands, which are known to experience major reductions in primary production in response to droughts (Bai *et al.*, 2004; Gao *et al.*, 2019; Luo *et al.*, 2023). Previous studies have demonstrated that plant litter can modulate soil temperature, moisture, and nutrient retention and help to regulate grassland community structure and dynamics (Redmann, 1978; Knapp & Seastedt, 1986; Facelli & Pickett, 1991; Wang *et al.*, 2011; Hou *et al.*, 2019; Ma *et al.*, 2022). This suggests that anthropogenic disturbances and climate change, such as fire, grazing, and drought (Blair, 1997; Li *et al.*, 2018; Luo *et al.*, 2021), can substantially reduce plant litter production and thereby exacerbate the negative effects of droughts. However, the effects of reductions in plant litter on ecosystem function are often confounded with many other effects of these disturbances. Therefore, it is critical to understand how plant litter loss influences the ability of grasslands to respond to droughts.

Although many studies have shown that grassland ecosystems are often sensitive to droughts (Mackie *et al.*, 2019; Luo *et al.*, 2021; Bai & Cotrufo, 2022; Kröel-Dulay *et al.*, 2022), postdrought ecosystem performance and recovery have been inconsistent across studies in terms of recovery time of ecosystem structural and functional properties (Schwalm *et al.*, 2017; Jiao *et al.*, 2021). These inconsistencies may be caused by drought intensity or duration (Meng *et al.*, 2019), soil nutrient availability (Bharath *et al.*, 2020), and climate conditions (e.g. mean annual precipitation) and plant community composition (Knapp *et al.*, 2015). Previous studies have shown that ecosystem production can completely recover 1 yr after drought in some of the world's grasslands, driven largely by dominant species recovery (Hoover *et al.*, 2014; Isbell *et al.*, 2015; Wilcox *et al.*, 2020; Xu *et al.*, 2022). Nevertheless, most of these studies have neglected postdrought community structure, which hinders our ability to examine ecosystem-wide recovery (Hoover *et al.*, 2014; Xu *et al.*, 2022). More importantly, predicting the trajectory of ecosystem recovery may not be straightforward because the postdrought recovery of community composition is often species-specific (Deutsch *et al.*, 2010; Hoover *et al.*, 2014; Xu *et al.*, 2022) and regulated by plant litter-induced changes in soil environment (e.g. soil temperature, moisture, and nutrient availability; Facelli & Pickett, 1991; Hou *et al.*, 2019). For example, litter loss-created open areas may favor the recruitment of annual forb (AF) species (Wilcox *et al.*, 2020). Moreover, litter loss-induced warmer and drier conditions may benefit perennial forbs (PFs) and bunchgrasses rather than rhizomatous species because of their deep roots and/or conservative lifestyle strategy (Chen *et al.*, 2005; Hou *et al.*, 2019; Li *et al.*, 2020).

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

Ecosystem temporal stability, defined as the degree of constancy of ecosystem functions and/or processes (Bai *et al.*, 2004; Tilman *et al.*, 2006; Isbell *et al.*, 2015), has received much recent attention. Understanding the drivers of ecosystem stability has emerged as a pressing issue in a period when many ecosystems are experiencing climate change and anthropogenic disturbance (Ma *et al.*, 2017; Wu *et al.*, 2019; Li *et al.*, 2020). Previous studies have demonstrated that the temporal stability of ecosystem production is mainly governed by the stability of dominant species or functional groups (Wu *et al.*, 2019; Ma *et al.*, 2022) and species or functional group asynchrony (Ma *et al.*, 2017; Valencia *et al.*, 2020; He *et al.*, 2022). Furthermore, community composition may also influence functional stability (Hillebrand & Kunze, 2020; Li *et al.*, 2020). In particular, higher community composition stability during and after disturbances could favor ecosystem temporal functional stability (Xu *et al.*, 2022). Results from litter manipulation experiments suggest that shifts in community composition under drought are likely modulated by plant litter through biophysical interactions at the ground surface or via changing soil environments (Wang *et al.*, 2011; Hou *et al.*, 2019), which may have consequences for ecosystem temporal stability. It is thus critical to understand how plant litter will mediate drought impact on temporal stability.

In this study, we established a long-term plant litter removal experiment in October 2014 to simulate moderate and heavy levels of litter loss in the semiarid grassland of Inner Mongolia, China. During two growing seasons (2016 and 2017), the study area experienced two consecutive droughts (Supporting Information Fig. S1), providing a unique opportunity to examine how litter removal interacts with a 2-yr drought to affect soil environments, plant community composition, and ecosystem function. Specifically, we address two questions: First, how does plant litter removal affect soil environments (i.e. soil temperature, moisture, and nitrogen availability) and mediate plant community responses (i.e. species and functional group composition and aboveground primary production) to consecutive droughts? Second, how does plant litter removal affect the postdrought recovery of community composition and ecosystem temporal stability? We hypothesize that: (1) plant litter removal would exacerbate the negative effects of drought on plant growth and aboveground primary production by increasing soil temperature, decreasing soil moisture, and reducing soil nitrogen availability; (2) the extent of recovery of primary production and community composition from drought would differ under litter removal because plant functional groups (PFGs) have distinct performance in response to litter removal under drought; (3) long-term litter removal-induced changes in soil environments and community compositional stability weaken ecosystem temporal stability.

Materials and Methods

Study site and experimental treatments

The field experiment was conducted in a semiarid steppe at the Inner Mongolia Grassland Ecosystem Research Station (116°42′E, 43°38′N, and 1250 m asl) of the Chinese Academy of Sciences, located in Inner Mongolia, northern China. This area has a semiarid temperate continental climate with mean annual precipitation (1982–2021) of 333.1 mm, of which 60–80% falls from May to August. Mean winter precipitation that falls as snow is 27.8 mm (November to April), accounting for 8.3% of the total annual precipitation (1982–2021). The mean annual temperature is 1.0°C, with mean monthly temperatures ranging from −21.2°C in January to 19.7°C in July. The soil at the study site is dark chestnut with loamy sand texture. The plant community in the study area is dominated by perennial herbaceous plants, including *Leymus chinensis* (Trin.) Tzvel., *Stipa grandis* P. Smirn., *Agropyron cristatum* (L.) Gaertn., *Cleistogenes squarrosa* (Trin.) Keng, and *Carex korshinskyi* Kom. (Bai *et al.*, 2010).

The plant litter removal experiment was conducted in a grassland enclosure that had been protected from grazing since 1999. A randomized complete block experiment was established in October 2014 (Fig. S2), including three plant litter removal treatments and six replicates for each treatment. Three 3 × 3 m plots were randomly laid out in each of six blocks (18 total plots) and then assigned to the three treatments: partial litter removal (−50%), complete litter removal (−100%), and no litter removal (control). Before the litter removal, there were no differences in plant community and soil properties among treatments (Table S1). The litter removal treatments were applied annually at the end of October after plant natural senescence from 2014 to 2021. In each complete litter removal plot, all standing litter was removed by cutting with scissors and fallen plant litter was cleared by raking. In each partial litter removal plot, half of the standing and fallen litter were returned to the community in the first year and only the standing litter was manipulated in the following years. The amount of litter removed each year is provided in Table S2.

Soil moisture, temperature, and nitrogen mineralization

Soil temperature was continuously measured every 60 min at a depth of 10 cm from November 2014 to September 2021. Measurements were recorded automatically with a Datalogger (iButton DS1922L; Wdsen Electronic Technology Co. Ltd, Shenzhen, China). Based on the daily average temperature data, we calculated the mean soil temperature in the growing season (ST) from May to September and in the nongrowing season (NGST) from October to April. Soil moisture was measured three times per month within the depth interval of 0–12 cm in each plot from June to August, using manual time domain reflectometry (TDR) equipment (Soil Moisture Equipment Corp., Santa Barbara, CA, USA).

Soil net N mineralization rate was measured using the *in situ* soil core incubation method from mid-July to mid-August each year from 2015 to 2021, corresponding to the peak growing season. For each plot, two sharp-edged PVC tubes (5 cm in diameter and 12 cm in length) were inserted into the soil at 10 cm depth to extract soil cores. One core was sealed by a parafilm membrane to prevent water penetration while allowing gas exchange and was then incubated in the field for *c.* 28 d (Shan *et al.*, 2011). The other core was taken back to the laboratory and stored in a

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

refrigerator at 4°C for measuring the initial inorganic N contents. Soil inorganic N (NH_4^+-N and NO_3^--N) was extracted with a 2 mol L^{-1} KCl solution and subsequently measured using a continuous flow injection analyzer (AA3 HR; SEAL Analytical GmbH, Boston, MA, USA).

After harvesting the plant biomass, three soil cores (3 cm diameter, 0–10 cm depth) were randomly collected and mixed into one sample in each plot in mid-August 2021. Soil total nitrogen (STN) and soil organic carbon (SOC) were measured after soil samples were air-dried, ground, and passed through a 2 mm sieve. Soil total nitrogen was determined following Kjeldahl digestion by a Nitrogen Analyzer System (Kjeltec 2300 Auto System II; Foss Tecator AB, Höganäs, Sweden). Soil organic carbon was analyzed by the Walkley–Black modified acid-dichromate $FeSO_4$ titration method (Sparks *et al.*, 1996). Roots and stones were removed before all soil sample processing.

Plant species composition and biomass

A permanent 1 × 1 m quadrat was randomly established in each of the 18 plots. Species richness was measured by the number of species in the 1 × 1 m quadrat in mid-August at the peak of aboveground biomass of the plant community from 2015 to 2021. The species abundance was determined in the 1 × 1 m quadrat by individual counts, and the community abundance was quantified by the total number of plants in each quadrat. We randomly selected five individuals for each species present in the plot to measure plant height. If there were fewer than five individuals, all of them were measured. We then calculated the weighted average of plant height at the functional group level. Plant species were classified into four functional groups based on their life forms, including perennial bunchgrasses (PBs), perennial rhizomatous graminoids (PRs), PFs, and AFs (Bai *et al.*, 2004). The four groups consisted of 7, 2, 26, and 8 species, respectively (Table S3). To estimate the biomass of the entire community and individual species, one 0.25 m × 1 m rectangular quadrat was randomly chosen within each plot in mid-August from 2015 to 2021, away from the 1 × 1 m quadrats. All plants in each rectangular quadrat were clipped and sorted by species and then weighed for biomass after drying at 65°C to a consistent weight for at least 48 h. Aboveground primary productivity (ANPP) was estimated using the peak aboveground biomass of the plant community (Bai *et al.*, 2004).

Statistical analysis

Growing season (May–August) Standardized Precipitation-Evapotranspiration Index (SPEI) was calculated with the SPEI R package (Beguería *et al.*, 2017) using monthly precipitation and potential evapotranspiration data, with the 1982–2012 climatic data as a reference period. Years with SPEI values below −1 are considered drought years (Slette *et al.*, 2019). All climatic data were obtained from the Inner Mongolia Grassland Ecosystem Research Station of the Chinese Academy of Sciences.

The resistance and recovery of ANPP were calculated as the log response ratio of ANPP during drought and postdrought, respectively, to predrought ANPP in each plot (Xu *et al.*, 2022). A value of 0 indicates no changes under drought or complete recovery postdrought, while values below 0 indicate decreases under drought or incomplete recovery postdrought. Community compositional similarity was measured as quantitative similarity between drought or postdrought year and predrought year for each plot (Xu *et al.*, 2022), which was calculated based on Bray–Curtis similarity matrix (Bray & Curtis, 1957) using the Hellinger-transformed plant species relative abundance matrix. Values range between 0 and 1, with a value of 1 indicating 100% similar to predrought communities. Community compositional dynamics were quantified and visualized by principal coordinate analysis (PCoA; Anderson, 2001). The two-way permutational multivariate analysis of variance (PERMANOVA) was used to measure the effect of litter removal treatments, year, and their interaction with the VEGAN in R package (Oksanen *et al.*, 2020). Pseudo-*F*- and *P*-values were calculated based on 999 permutations of the data using the *adonis* function. Community compositional stability was calculated with 1 minus the mean Euclidean distance from each plot to its 7-yr (2015–2021) plot centroid, based on the cross-year Bray–Curtis dissimilarity matrix (Xu *et al.*, 2022).

The temporal stability of the community and each PFG and each species was calculated as the ratio of temporal mean biomass (2015–2021) to its temporal standard deviation in each plot (Tilman *et al.*, 2006). For each organization level (i.e. community, functional group, and species), one-way ANOVA with Duncan's Test was used to compare stability across treatments. Species and functional group asynchrony were calculated as the community-wide asynchrony index (Loreau & de Mazancourt, 2008):

$$1-\phi_x = 1-\sigma^2/\left(\sum_{i=1}^{S}\sigma_i\right)^2$$

where ϕ_x is the species or functional group synchrony; σ^2 is the variance of community biomass and σ_i is the standard deviation of the biomass of species or functional group i in a given plot with S species or functional groups. The asynchrony index equals 1 when species fluctuations are perfectly asynchronized and equals 0 when they are perfectly synchronized.

Linear mixed effect models were used to assess the influence of plant litter removal on ANPP and changes in ANPP, abundance, community similarity, vegetation height, and species richness using the *lmer* function of the LME4 package (Bates *et al.*, 2015). Treatment and year were considered a fixed effect, and the block was considered a random factor. One-way ANOVA with Duncan's test was also performed to evaluate how the species asynchrony, functional group asynchrony, and community compositional stability differ across treatments. Paired-sample *t*-tests were used to compare the ANPP and abundance of community and each functional group between predrought years and drought or postdrought years for each treatment. Spearman's rank correlation was performed to analyze relationships of species abundance, vegetation height, biomass, and stability of functional groups and communities with soil environment (soil temperature, soil moisture, and soil inorganic nitrogen). All statistical analyses were conducted in R v.4.0.5 (R Foundation for Statistical Computing, Vienna, Austria).

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Structural equation modeling (SEM) was used to investigate the direct and indirect effects of litter removal treatments on plant community ANPP and stability. The principal component analysis (PCA) was used to create integrated variables representative of changes in the soil environment. Because of the high correlations among soil environmental variables ($r = 0.42$–1) except for soil inorganic nitrogen, we performed PCA and used the score of the first axis to indicate the soil environment (Fig. S3a). The first principle component (PC1) accounted for 70.35% of the total variances. A positive value of soil environment means an increase in soil moisture, nongrowing season soil temperature, soil nitrogen mineralization, and STN, but a decrease in growing season soil temperature, and vice versa (Fig. S3b). Based on the results of the ANOVA and Spearman correlation analysis, we first considered a model that included all possible pathways and established a model of hypothesized relationships (Fig. S4). We then sequentially eliminated nonsignificant pathways until we obtained the final model. Path coefficients were obtained using a maximum likelihood estimation technique. We employed chi-squared (χ^2) tests, *P*-values, the root mean square error of approximation (RMSEA), and the Akaike information criterion (AIC) to evaluate the goodness of fit of the model (Grace *et al.*, 2012). The SEM analyses were performed with AMOS 21.0 (Amos Development Co., New York, NY, USA).

Results

Soil temperature, moisture, nitrogen availability

The experiment had three plant litter removal treatments: 50% litter removal (partial removal, −50%), 100% litter removal (complete removal, −100%), and no litter removal (control). Over the 7 yr from 2015 to 2021, litter removal increased soil temperature on average by 1.6°C for −50% and 2.1°C for −100% during the growing season (Fig. 1a). Furthermore, complete litter removal elevated soil temperature more under drought years (2.9°C for 2016–2017) than in postdrought years (1.6 for 2018–2021; Fig. S5a). However, litter removal decreased soil temperature by 0.9°C for −50% and 1.1°C for −100% during the nongrowing season (Fig. 1b). Overall, litter removal on average reduced soil moisture by 16% for −50% and 21.2% for −100% during the growing season (Fig. 1c); the effect of litter removal on soil moisture also varied significantly among years (Fig. S6a). Soil inorganic nitrogen concentration did not show a significant response to litter removal during the growing season (Fig. 1d), but it varied substantially among years (Fig. S6b). Complete litter removal significantly reduced the overall soil net N mineralization (Fig. 1e), which also varied across years (Fig. S6c). After the 7-yr litter removal, complete removal treatment substantially reduced STN concentration (Fig. 1f).

Primary productivity, community composition, and plant functional group abundance and height

Aboveground net primary productivity (ANPP) decreased during two drought years (2016 and 2017) in all litter removal treatments (Fig. 2a; Table S4). Specifically, ANPP was reduced by 11.7% for the control, 31.0% for −50%, and 28.8% for −100% in the first drought year (2016); ANPP was reduced by 41.6% for the control, 44.7% for −50%, and 54.0% for −100% in the second drought year (2017; Fig. S7a). Overall, ANPP increased 1 yr after the drought and recovered to *c.* 70% of the predrought year level, and completely recovered 2 yr after the drought regardless of litter removal (Fig. 2a; Table S4). At the PFG level, litter removal decreased the biomass of PRs and PBs, while not affecting the biomass of PFs and AFs in two drought years (Fig. S7b–e; Table S5). The biomass of PRs remains low but the biomass of PFs and AFs increased with litter removal in postdrought years (Fig. S7; Table S4).

Litter removal altered plant community structure in postdrought years (Fig. 2b; Table S5). In general, postdrought communities differed substantially from predrought communities under litter removal treatments (Fig. S8). Principal coordinate analysis showed that no significant change in community composition was observed in control plots over the 7-yr experiment ($P = 0.551$), but that community composition dramatically shifted in litter removal plots (all $P < 0.001$; Fig. S8). Specifically, compared with the control plots, the relative abundance of PRs decreased, AFs increased after two postdrought years, and PFs increased in the latter 2 yr in the two litter removal treatments (Fig. S9). Moreover, the abundances of PBs and PRs did not return to their predrought abundances in four postdrought years under litter removal treatments (Table S6; Fig. S10). Despite the shift in abundance, the height of each functional group had recovered to predrought (Fig. S11). In the control plots, however, the abundance of each functional group changed slightly during drought and after drought periods, while the height prominently increased post-drought (Table S6; Figs S10, S11).

Species richness and asynchrony and stability of community and functional groups

At both the community and functional group levels, species richness did not differ across treatments before the start of the experiment (Table S1). Litter removal decreased both species and functional group asynchrony (Fig. 3a,b), although total species richness on average increased by 2.2 species for −50% and 1.7 species m^{-2} for −100% litter treatments over 7 yr (Fig. S12a). At the functional group level, species richness of PRs showed little change during drought years, but decreased in postdrought years for −100% (Fig. S12c). Species richness of AFs on average increased by 1.7 for −50% and 2.0 species m^{-2} for −100%, while no significant changes in the richness of PBs and PFs were observed over 7 yr (Fig. S12b–e).

Community compositional stability and biomass stability significantly decreased in all removal treatments (Fig. 3c,d), while the average stability of both plant species and functional groups was not affected by litter removal manipulations ($P > 0.05$). Spearman's rank correlation analysis showed that community stability was positively related to PC1 of the soil environment

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

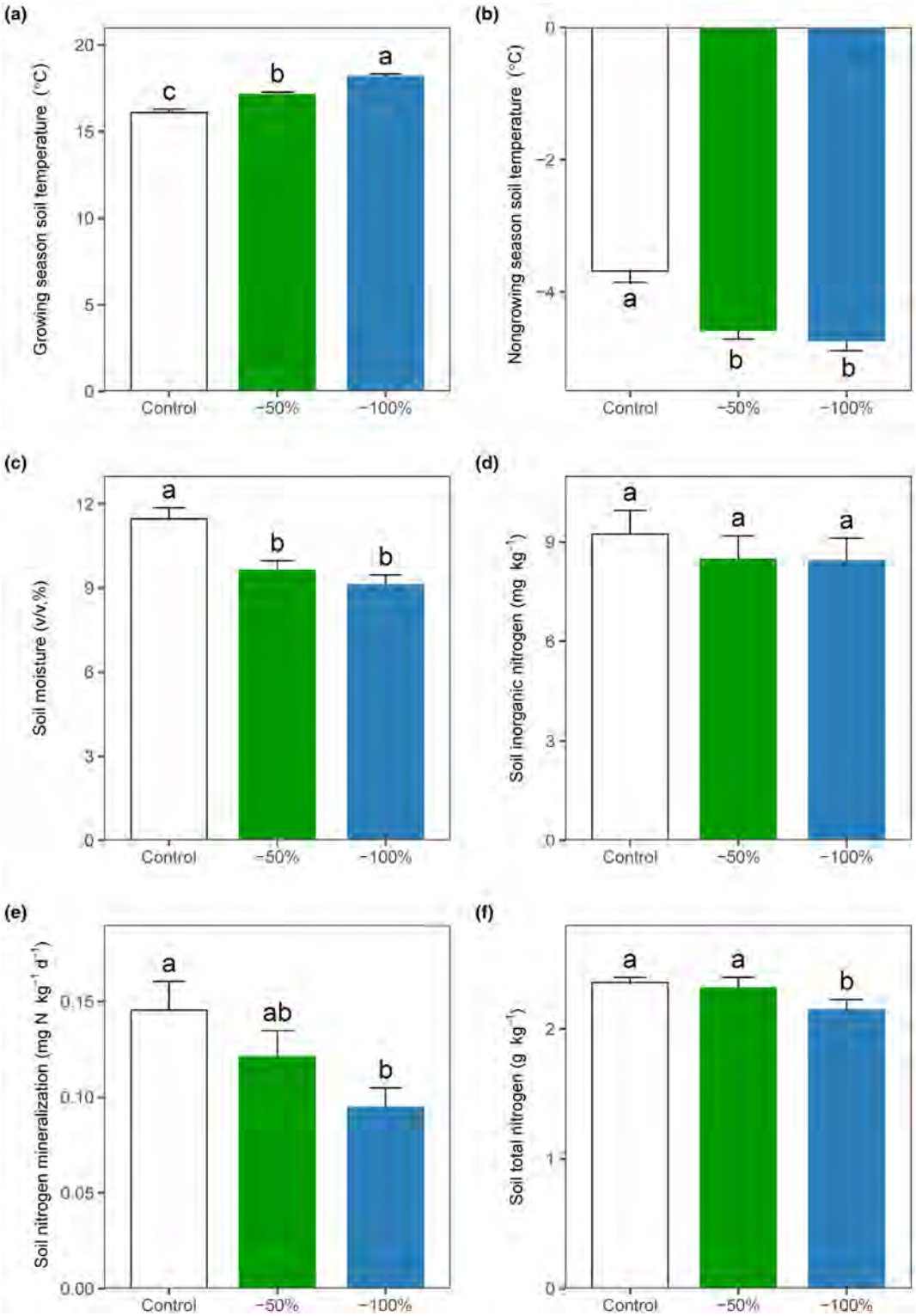


Fig. 1 Changes in soil environments under different litter removal manipulations. Shown are average values over 7 yr (2015–2021) for (a) growing season soil temperature at 0–10 cm, (b) nongrowing season soil temperature at 0–10 cm, (c) growing season soil moisture at 0–12 cm, (d) soil inorganic nitrogen content (growing season), and (e) soil inorganic nitrogen mineralization (growing season), and (f) soil total nitrogen (only in 2021). The average values for the period covered in each year are shown in Supporting Information Figs S5 and S6. Error bars indicate 1 SE ($n = 6$). Different letters close to the bars indicate significant differences between treatments at $\alpha = 0.05$ based on one-way ANOVA with Duncan's Test. Control = no litter removal; −50% = 50% litter removal; and −100% = 100% litter removal.

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

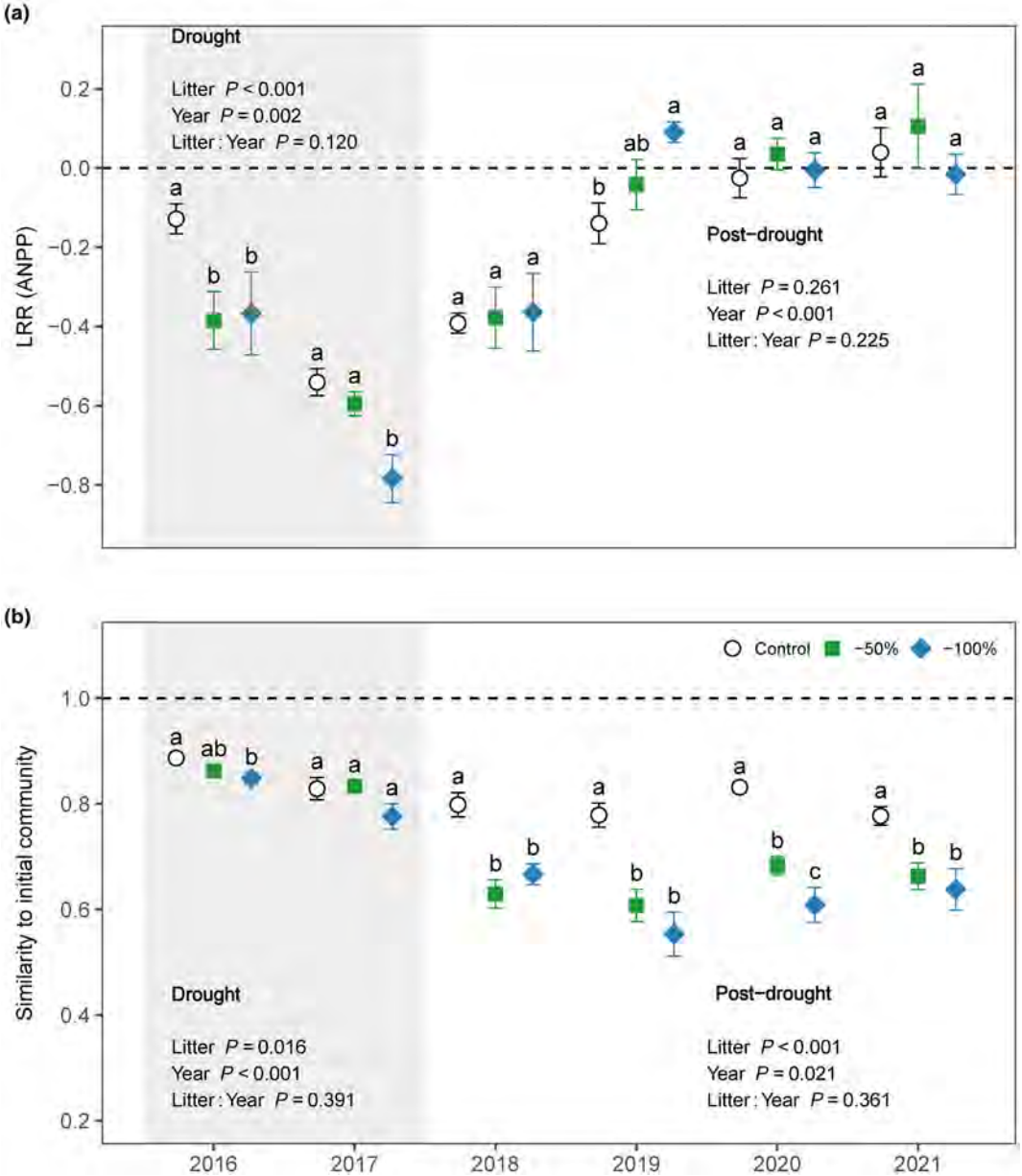


Fig. 2 Changes in aboveground net primary productivity (ANPP) and abundance under different litter removal manipulations. Shown are (a) changes in ANPP and (b) community compositional similarity over drought years (2016–2017) and postdrought years (2018–2021) compared with the predrought year (2015). Error bars indicate 1 SE ($n = 6$). For each year, different letters close to the bars indicate significant differences between treatments at $\alpha = 0.05$ based on one-way ANOVA with Duncan's Test. Control, no litter removal; −50%, 50% litter removal; −100%, 100% litter removal.

(Fig. S13). For biotic factors, community stability was positively related to the asynchrony of species and functional groups and community compositional stability but negatively related to species richness (Fig. S13). Structural equation modeling (SEM) further showed that plant litter removal decreased the community compositional stability through altering the soil environment, which decreased the mean of ANPP, and consequently, community stability (Fig. 3). Moreover, litter removal increased the variation of ANPP via decreasing species asynchrony and functional group asynchrony (Fig. 3; Table S7), which in turn decreased community stability (Fig. 4).

Discussion

Litter removal impairs soil environment and exacerbates the negative impact of drought on ecosystem productivity

Based on a 7-yr field manipulation experiment, we show that plant litter removal, which is a common result of human activities (e.g. burning, grazing, and haying) in grasslands (Blair, 1997; Bai *et al.*, 2012; Gao *et al.*, 2019), exacerbated the negative effect of droughts on primary productivity by elevating soil temperature and intensifying water limitation. For example, complete litter

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

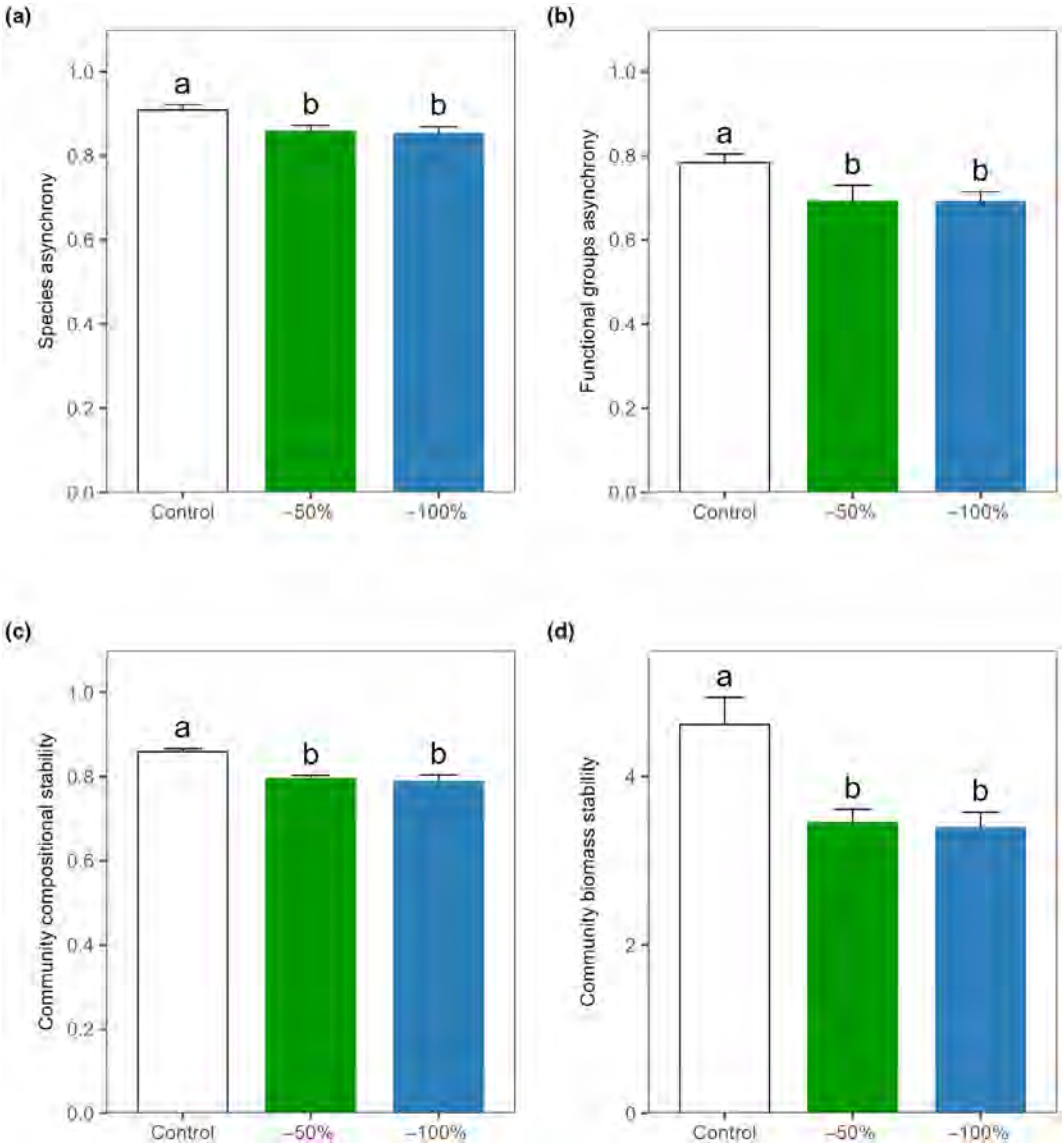


Fig. 3 Effects of litter removal on species and functional group asynchrony and community stability. Shown are (a) species asynchrony, (b) functional groups asynchrony, (c) compositional stability, and (d) community biomass stability over the 7-yr experiment from 2015 to 2021. Error bars indicate 1 SE ($n = 6$). Different letters close to the bars indicate significant differences between treatments at $\alpha = 0.05$ based on one-way ANOVA with Duncan's Test. Control, no litter removal; −50%, 50% litter removal; −100%, 100% litter removal.

removal increased soil temperature by > 2°C during the growing season, which is greater than both the climate warming of the past several decades and the projected climate warming by 2040 (IPCC, 2021). In the nongrowing season, litter removal decreased soil temperature, which is similar to the grazing effect (Yan *et al.*, 2018). The contrasting effects of litter removal on soil temperature across seasons provide strong evidence that plant litter can mitigate the negative impacts of climate warming because it acts as an insulating layer buffering heat exchange between soil and atmosphere (Facelli & Pickett, 1991). In addition, litter removal substantially reduced soil moisture and soil N mineralization, thereby intensifying the strength of plant water and N limitation. However, we did not find that litter removal decreased soil inorganic N, probably because the water deficit may have suppressed the soil N uptake (He & Dijkstra, 2014). Consequently, productivity reduction in drought years was 1.2–2.6 times greater in litter removal treatments than that in control plots, supporting our first hypothesis. Surprisingly, we found that the effects of litter removal and drought were additive, rather than synergistic (Stampfli *et al.*, 2018; Komatsu *et al.*, 2019). This is likely because the negative impacts of litter removal and drought on soil moisture and ecosystem function are qualitatively similar.

More importantly, the reduction of community production under litter removal was much greater in the second drought year than that in the first drought year, which may be explained by several reasons. First, the positive effect of plant litter on plant growth is greater in the first drought year than in the second drought year; because sustained drought cumulatively eroded the

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

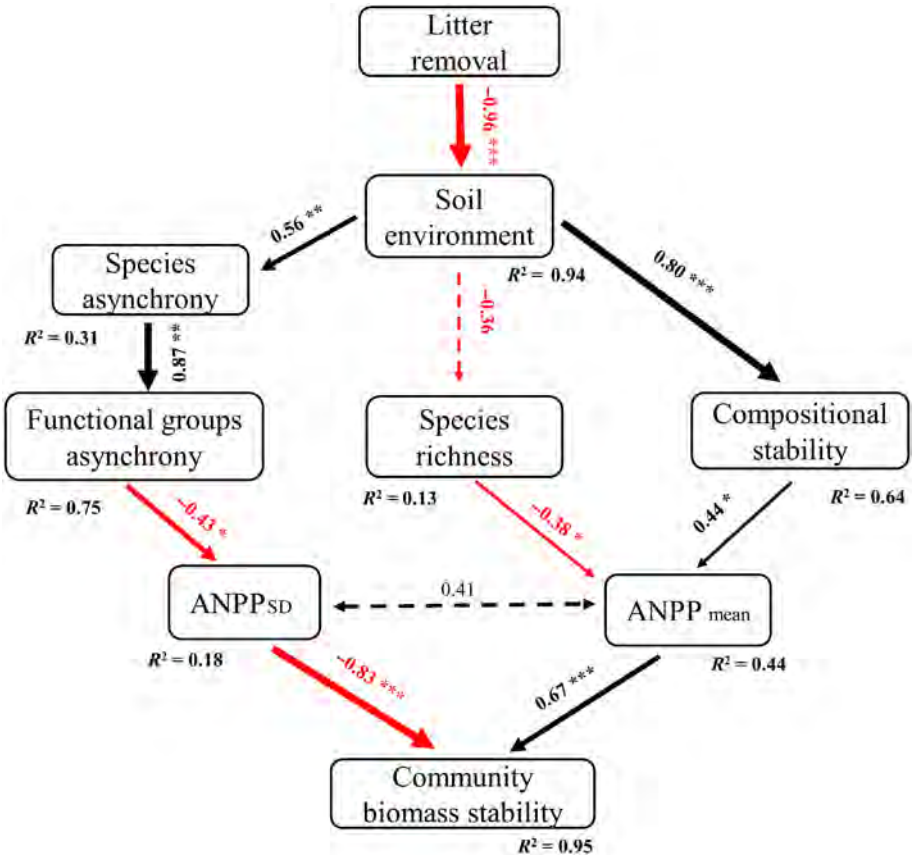


Fig. 4 Structural equation model of litter removal effects on community temporal stability. The structural equation model illustrates the direct and indirect effects of litter removal on the community biomass stability ($\chi^2 = 26.776$, df = 25, $P = 0.367$; root mean square error of approximation = 0.065; Akaike information criteria = 66.776). Red and black arrows represent significant negative and positive pathways, respectively, and dashed arrows indicate nonsignificant pathways. The arrow width is proportional to the strength of the relationship, and numbers adjacent to arrows are standardized path coefficients, calculated by the partial correlation analysis after controlling the effect of other variables. R^2 represents the proportion of variance explained for each dependent variable in the model. Significance level: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

positive effect of plant litter on soil moisture due to persistent low precipitation (Fig. S6), thereby intensifying water limitation to primary production (Fig. S7). Second, the first-year drought may have had carryover effects on plant community structure and ecosystem processes, which could have constrained plant performance in the second-year drought (Sala *et al.*, 2012; Xi *et al.*, 2022). Indeed, the total plant community aboveground biomass and the biomass of PBs and PRs in the second-year drought were lowest during the 7-yr experiment (Fig. S7). Finally, the second consecutive drought event occurred in the early growing season, which may have had more severe impacts on plant productivity than middle-season and later-season droughts (Meng *et al.*, 2019). Water inputs in the early growing season are more essential for plant growth, especially for PBs and perennial rhizomatous grasses (Sun *et al.*, 2022), which contribute > 70% of the total aboveground biomass in this semiarid grassland (Bai *et al.*, 2004). Previous studies have reported that more precipitation in the early growing season could offset the negative effect of drought in the middle stage (Sala *et al.*, 2012; Li *et al.*, 2020).

Litter removal weakens postdrought recovery of plant community composition

Our results show that litter loss drives the shift in plant community composition from grass-dominated to forb-dominated after drought because litter loss-induced changes in the soil environment are species-specific in semiarid grasslands. Under litter removal, the biomass of both AFs and PFs increased after drought. Annual forbs (AFs) have aggressive resource-use strategies as well as high dispersal ability because of their high seed densities in soil seed banks, high seed germination rates, and high seedling recruitment into open areas (Wilcox *et al.*, 2020; Li *et al.*, 2021). In addition, drought decreased nutrient supplies and plant nutrient uptake, which caused an initial spike in the abundance of AFs in the first 2-yr postdrought due to the increased availability of soil nitrogen (Sala *et al.*, 2012; Stampfli *et al.*, 2018; Sun *et al.*, 2022). Additionally, deep-rooted PFs have a competitive advantage over shallow-rooted grasses under litter loss-induced warmer and drier conditions (Li *et al.*, 2020). The increase in PFs in litter removal plots 3 yr after the drought reflects the inherent differences between perennial grasses and PFs in adapting to warmer and drier soil conditions caused by long-term litter removal. On one hand, litter removal-induced soil warming consistently reduced seedling recruitment of grasses during and after drought. On the other hand, diminished recovery of grass abundance may be due to nitrogen limitation because litter removal not only reduces nutrient input (Xu *et al.*, 2013) but also intensifies competition between grasses and forbs, with the latter having the competitive advantage in nitrogen absorption efficiency (Bai *et al.*, 2010). After a 4-yr postdrought recovery, the biomass of community as well as each functional group fully recovered to their predrought biomass while PBs and rhizomatous graminoids did not return to their

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

predrought abundances despite above-average growing season precipitation. The results revealed that the biomass recovery of PBs and PRs is primarily governed by the increase in plant height (i.e. plants grow larger) rather than the increase in plant abundance, which exhibited rather slow recovery.

In control plots, the reductions in biomass and abundance of PBs were only observed in the 7th yr (2021; Table S4; Fig. S10) because litter accumulation may impede plant tillering and colonization of PBs (Wang *et al.*, 2011; Hou *et al.*, 2019). However, the reduction in the abundance of PBs was fully compensated by gains in the abundance of PRs. Clearly, the increased soil moisture associated with plant litter is more preferred for PRs with acquisitive resource-use strategies than for PBs, which exhibit conservative resource-use strategies (Chen *et al.*, 2005; Bai *et al.*, 2010; Hou *et al.*, 2019). For perennial and AFs, no discernable changes in their abundances were observed in control plots throughout the 7-yr experiment. Together, the results from litter removal and control plots indicate that plant litter plays an important role for maintaining the compensatory dynamics and mitigating the unreversible shift in plant community composition under environmental changes in semiarid grasslands.

Litter removal reduces ecosystem temporal stability

Our results demonstrate that long-term litter removal decreased the temporal stability of community biomass during and after drought, suggesting that plant litter could help maintain the temporal stability of primary productivity in grasslands. First, litter loss diminishes compensation between PRs and PBs and decreases species and functional group asynchrony, which in turn increases the variation of community primary productivity under climate fluctuations (Bai *et al.*, 2004; Ma *et al.*, 2017; Valencia *et al.*, 2020). This is consistent with previous findings that compensatory effects among major functional groups maintain ecosystem stability in temperature steppes (Bai *et al.*, 2004) and alpine grasslands (Liu *et al.*, 2018). Second, plant litter removal decreased community temporal stability through decreases in compositional stability and primary productivity. Plant litter loss aggravates the soil environment by elevating soil temperatures and intensifying water and nitrogen limitation, which in turn shift community structure. In particular, deep-rooted forbs have been predicted to dominate many grassland ecosystems at the expense of grass species under future drought (Li *et al.*, 2020; Wilcox *et al.*, 2020). Given that plant litter is effective at buffering the soil environment and thereby mitigating the reduction in cover/abundance of grasses caused by changes in plant size and tiller density during drought, litter loss can trigger the shift of communities from grass-dominated to forb-dominated and therefore reduce ecosystem temporal stability (Hou *et al.*, 2019; Li *et al.*, 2020). Third, although litter removal increased species richness, changes in species diversity explained little variation in plant community temporal stability under drought, which contradicts the oft-cited theory that species diversity tends to increase community stability (Tilman *et al.*, 2006; Isbell *et al.*, 2015). This discrepancy is possibly attributed to the fact that the increased species richness in our experiment was mainly due to the addition of several annual species, which contributed little to community biomass compared with perennial species. Nevertheless, our findings indicate that the effects of species richness on ecosystem stability are often weak, which is confirmed by studies in both temperate and alpine grasslands (Ma *et al.*, 2017; Wu *et al.*, 2019).

Our study presents the first empirical evidence that the effects of plant litter loss and the consecutive drought climate are additive, leading to greater reductions in ecosystem stability than drought alone. This suggests that human activities that lead to reduction in plant litter input can be detrimental to the structure and stability of semiarid grasslands. The negative effects of plant litter loss are ultimately attributable to changes in the soil environment and community composition. In addition to ameliorating the soil environment in the growing season (i.e. through buffered soil temperatures and retention of soil moisture and nitrogen), plant litter appears to trap and retain snow in the non-growing season, which reduces cold exposure in winter and increases soil moisture in the early or even the whole growing season, increasing perennial grasses and stabilizing community processes (Bai *et al.*, 2010; Li *et al.*, 2020). Our results suggest that the negative effects of litter reduction on semiarid grassland ecosystem stability may be limited if human activities and climate change are mitigated, particularly in the context of droughts.

Conclusions

Our 7-yr study provides novel experimental evidence that plant litter loss has profound influences on ecosystem processes in semiarid grasslands, especially in the face of consecutive drought. We show that plant litter removal exacerbates the negative influence of drought on ecosystem functions through litter loss-induced soil warming and reductions in soil moisture and nitrogen mineralization. Although community production can recover from consecutive droughts, predrought community composition may not necessarily return due to species-specific responses to plant litter removal, particularly following total litter removal. Therefore, more broadly, the combined negative effects of consecutive drought and human activity-induced changes in plant litter mass (e.g. burning, grazing, and haying) can strongly modify long-term ecosystem composition and stability (Redmann, 1978; Blair, 1997; Knapp *et al.*, 2015; Meyer *et al.*, 2023). These findings highlight the indispensable role of plant litter in stabilizing ecosystem functions and services by buffering the negative impacts of environmental change and maintaining ecosystem stability in semiarid grasslands and beyond.

Acknowledgements

We are grateful to the editor (Dr Amy Austin) and four anonymous reviewers for their extremely valuable comments on our manuscript. We are grateful to staff at the IMGERS for their help with field sampling and laboratory work. This study was funded by the National Natural Science Foundation of China (32192464) and the Strategic Priority Research Program of Chinese Academy of Sciences (grant no. XDA23080000).

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Competing interests

None declared.

Author contributions

YB designed the study. WC, RJ, BT and HJ performed the field sampling and measurements. WC, RJ, YW, XL, JS, LJ and YB conducted data analysis and drafted the manuscript. All authors contributed to the revision of the manuscript, and YB edited the manuscript.

ORCID

Yongfei Bai https://orcid.org/0000-0001-6656-4501
Wanjie Chen https://orcid.org/0000-0002-9697-818X
Ruoyu Jia https://orcid.org/0000-0003-2661-2104
Hongzhi Jiang https://orcid.org/0009-0009-6863-2497
Lin Jiang https://orcid.org/0000-0002-7114-0794
Xiaoming Lu https://orcid.org/0000-0001-7380-0699
Jishuai Su https://orcid.org/0000-0001-7263-2654
Bo Tang https://orcid.org/0000-0002-0508-5467
Yang Wang https://orcid.org/0000-0002-6953-3935

Data availability

The data used in this study are available at Dryad Digital Repository (https://doi.org/10.5061/dryad.sf7m0cgcb).

References

Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**: 32–46.

Bai YF, Cotrufo MF. 2022. Grassland soil carbon sequestration: current understanding, challenges, and solutions. *Science* **377**: 603–608.

Bai YF, Han XG, Wu JG, Chen ZZ, Li LH. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature* **431**: 181–184.

Bai YF, Wu JG, Clark CM, Naeem S, Pan QM, Huang JH, Zhang LX, Han XG. 2010. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from Inner Mongolia grasslands. *Global Change Biology* **16**: 358–372.

Bai YF, Wu JG, Clark CM, Pan QM, Zhang LX, Chen SP, Wang QB, Han XG. 2012. Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. *Journal of Applied Ecology* **49**: 1204–1215.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using LME4. *Journal of Statistical Software* **67**: 1–48.

Beguería S, Vicente-Serrano SM, Beguería MS. 2017. *SPEI: calculation of the Standardised Precipitation-Evapotranspiration Index*. R package v.1.7. [WWW document] URL https://github.com/sbegueria/SPEI [accessed 20 June 2022].

Bharath S, Borer ET, Biederman LA, Blumenthal DM, Fay PA, Gherardi LA, Knops JMH, Leakey ADB, Yahdjian L, Seabloom EW. 2020. Nutrient addition increases grassland sensitivity to droughts. *Ecology* **101**: e02981.

Blair JM. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology* **78**: 2359–2368.

Bray JR, Curtis JT. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* **27**: 326–349.

Chen SP, Bai YF, Zhang LX, Han XG. 2005. Comparing physiological responses of two dominant grass species to nitrogen addition in Xilin River Basin of China. *Environmental and Experimental Botany* **53**: 65–75.

Dai AG. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change* **3**: 52–58.

Deutsch ES, Bork EW, Willms WD. 2010. Soil moisture and plant growth responses to litter and defoliation impacts in Parkland grasslands. *Agriculture Ecosystems and Environment* **135**: 1–9.

Facelli JM, Pickett STA. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* **57**: 1–32.

Gao JB, Zhang LL, Tang Z, Wu SH. 2019. A synthesis of ecosystem aboveground productivity and its process variables under simulated drought stress. *Journal of Ecology* **107**: 2519–2531.

Grace JB, Schoolmaster DR Jr, Guntenspergen GR, Little AM, Mitchell BR, Miller KM, Schweiger EW. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. *Ecosphere* **3**: art73.

He MZ, Dijkstra FA. 2014. Drought effect on plant nitrogen and phosphorus: a meta-analysis. *New Phytologist* **204**: 924–931.

He YL, Wang JS, Tian DS, Quan Q, Jiang L, Ma FF, Yang L, Zhang FY, Zhou QP, Niu SL. 2022. Long-term drought aggravates instability of alpine grassland productivity to extreme climatic event. *Ecology* **103**: e3792.

Hillebrand H, Kunze C. 2020. Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. *Ecology Letters* **23**: 575–585.

Hoover DL, Knapp AK, Smith MD. 2014. Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* **95**: 2646–2656.

Hou DJ, He WM, Liu CC, Qiao XG, Guo K. 2019. Litter accumulation alters the abiotic environment and drives community successional changes in two fenced grasslands in Inner Mongolia. *Ecology and Evolution* **9**: 9214–9224.

IPCC. 2021. *Climate change 2021: the physical science basis: working group I contribution to the sixth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Isbell F, Craven D, Connolly J, Loreau M, Schmid B, Beierkuhnlein C, Bezemer TM, Bonin C, Bruelheide H, De Luca E. 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* **526**: 574–577.

Jiao T, Williams CA, De Kauwe MG, Schwalm CR, Medlyn BE. 2021. Patterns of post-drought recovery are strongly influenced by drought duration, frequency, post-drought wetness, and bioclimatic setting. *Global Change Biology* **27**: 4630–4643.

Knapp AK, Carroll CJW, Denton EM, La Pierre KJ, Collins SL, Smith MD. 2015. Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia* **177**: 949–957.

Knapp AK, Seastedt TR. 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* **36**: 662–668.

Komatsu KJ, Avolio ML, Lemoine NP, Isbell F, Grman E, Houseman GR, Koerner SE, Johnson DS, Wilcox KR, Alatalo JM *et al.* 2019. Global change effects on plant communities are magnified by time and the number of global change factors imposed. *Proceedings of the National Academy of Sciences, USA* **116**: 17867–17873.

Kröel-Dulay G, Mojzes A, Szitár K, Bahn M, Batáry P, Beier C, Bilton M, De Boeck HJ, Dukes JS, Estiarte M *et al.* 2022. Field experiments underestimate aboveground biomass response to drought. *Nature Ecology and Evolution* **6**: 540–545.

Li P, Sayer EJ, Jia Z, Liu WX, Wu YT, Yang S, Wang CZ, Yang L, Chen DM, Bai YF. 2020. Deepened winter snow cover enhances net ecosystem exchange and stabilizes plant community composition and productivity in a temperate grassland. *Global Change Biology* **26**: 3015–3027.

Li WH, Li X, Zhao YJ, Zheng SX, Bai YF. 2018. Ecosystem structure, functioning and stability under climate change and grazing in grasslands: current status and future prospects. *Current Opinion in Environmental Sustainability* **33**: 124–135.

Li ZM, Wu JF, Han Q, Nie KY, Xie JN, Li YF, Wang XY, Du HB, Wang DL, Liu JS. 2021. Nitrogen and litter addition decreased sexual reproduction and increased clonal propagation in grasslands. *Oecologia* **195**: 131–144.

Liu HY, Mi ZR, Lin L, Wang YH, Zhang ZH, Zhang FW, Wang H, Liu LL, Zhu B, Cao GM *et al.* 2018. Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proceedings of the National Academy of Sciences, USA* **115**: 4051–4056.

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Loreau M, de Mazancourt C. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist* **172**: E48–E66.

Luo W, Muraina TO, Griffin-Nolan RJ, Ma W, Song L, Fu W, Yu Q, Knapp AK, Wang Z, Han X *et al.* 2023. Responses of a semiarid grassland to recurrent drought are linked to community functional composition. *Ecology* **104**: e3920.

Luo WT, Griffin-Nolan R, Ma W, Zuo XA, Xu C, Yu Q, Mariotte P, Collins SL, Knapp A, Wang ZW *et al.* 2021. Plant traits and soil fertility mediate productivity losses under extreme drought in C_3 grasslands. *Ecology* **102**: e03465.

Ma ZW, Zeng YF, Wu J, Zhou QP, Hou FJ. 2022. Plant litter influences the temporal stability of plant community biomass in an alpine meadow by altering the stability and asynchrony of plant functional groups. *Functional Ecology* **36**: 148–158.

Ma ZY, Liu HY, Mi ZR, Zhang ZH, Wang YH, Xu W, Jiang L, He JS. 2017. Climate warming reduces the temporal stability of plant community biomass production. *Nature Communications* **8**: 15378.

Mackie KA, Zeiter M, Bloor JMG, Stampfli A. 2019. Plant functional groups mediate drought resistance and recovery in a multisite grassland experiment. *Journal of Ecology* **107**: 937–949.

Meng B, Shi BK, Zhong SZ, Chai H, Li SX, Wang YB, Henry HAL, Ma JY, Sun W. 2019. Drought sensitivity of aboveground productivity in *Leymus chinensis* meadow steppe depends on drought timing. *Oecologia* **191**: 685–696.

Meyer K, Broda J, Brettin A, Muñiz MS, Gorman S, Isbell F, Hobbie SE, Zeeman ML, McGehee R. 2023. Nitrogen-induced hysteresis in grassland biodiversity: a theoretical test of litter-mediated mechanisms. *The American Naturalist* **201**: E153–E167.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2020. *VEGAN: community ecology package*. R package v.2.5-7.

Redmann RE. 1978. Plant and soil water potentials following fire in a northern mixed grassland. *Rangeland Ecology & Management/Journal of Range Management Archives* **31**: 443–445.

Sala OE, Gherardi LA, Reichmann L, Jobbagy E, Peters D. 2012. Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **367**: 3135–3144.

Schwalm CR, Anderegg WRL, Michalak AM, Fisher JB, Biondi F, Koch G, Litvak M, Ogle K, Shaw JD, Wolf A *et al.* 2017. Global patterns of drought recovery. *Nature* **548**: 202–205.

Shan YM, Chen DM, Guan XX, Zheng SX, Chen HJ, Wang MJ, Bai YF. 2011. Seasonally dependent impacts of grazing on soil nitrogen mineralization and linkages to ecosystem functioning in Inner Mongolia grassland. *Soil Biology and Biochemistry* **43**: 1943–1954.

Slette IJ, Post AK, Awad M, Even T, Punzalan A, Williams S, Smith MD, Knapp AK. 2019. How ecologists define drought, and why we should do better. *Global Change Biology* **25**: 3193–3200.

Sparks DL, Page AL, Helmke PA, Loeppert RH, Soltanpour PN, Tabatabai MA, Johnston CT, Sumner ME. 1996. *Methods of soil analysis. Part 3 – Chemical methods*. Madison, WI, USA: Soil Science Society of America and American Society of Agronomy.

Stampfli A, Bloor JMG, Fischer M, Zeiter M. 2018. High land-use intensity exacerbates shifts in grassland vegetation composition after severe experimental drought. *Global Change Biology* **24**: 2021–2034.

Sun JM, Liu W, Pan QM, Zhang B, Lv YX, Huang JH, Han XG. 2022. Positive legacies of severe droughts in the Inner Mongolia grassland. *Science Advances* **8**: eadd6249.

Tilman D, Reich PB, Knops JMH. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**: 629–632.

Valencia E, de Bello F, Galland T, Adler PB, Lepš J, Anna E, van Klink R, Carmona CP, Danihelka J, Dengler J. 2020. Synchrony matters more than species richness in plant community stability at a global scale. *Proceedings of the National Academy of Sciences, USA* **117**: 24345–24351.

Vilonen L, Ross M, Smith MD. 2022. What happens after drought ends: synthesizing terms and definitions. *New Phytologist* **235**: 420–431.

Wang J, Zhao ML, Willms WD, Han GD, Wang ZW, Bai YF. 2011. Can plant litter affect net primary production of a typical steppe in Inner Mongolia? *Journal of Vegetation Science* **22**: 367–376.

Wilcox KR, Koerner SE, Hoover DL, Borkenhagen AK, Burkepile DE, Collins SL, Hoffman AM, Kirkman KP, Knapp AK, Strydom T. 2020. Rapid recovery of ecosystem function following extreme drought in a South African savanna grassland. *Ecology* **101**: e02983.

Wu Q, Ren HY, Wang ZW, Li ZG, Liu YH, Wang Z, Li YH, Zhang RY, Zhao ML, Chang SX. 2019. Additive negative effects of decadal warming and nitrogen addition on grassland community stability. *Journal of Ecology* **108**: 1442–1452.

Xi NX, Chen DX, Bahn M, Wu HY, Chu CJ, Cadotte MW, Bloor JMG. 2022. Drought soil legacy alters drivers of plant diversity-productivity relationships in oldfield systems. *Science Advances* **8**: eabn3368.

Xu QN, Yang X, Song J, Ru JY, Xia JY, Wang SP, Wan SQ, Jiang L. 2022. Nitrogen enrichment alters multiple dimensions of grassland functional stability via changing compositional stability. *Ecology Letters* **25**: 2713–2725.

Xu S, Liu LL, Sayer EJ. 2013. Variability of above-ground litter inputs alters soil physicochemical and biological processes: a meta-analysis of litterfall-manipulation experiments. *Biogeosciences* **10**: 7423–7433.

Yan YC, Yan RR, Chen JQ, Xin XP, Eldridge DJ, Shao CL, Wang X, Lv SJ, Jin DY, Chen JQ. 2018. Grazing modulates soil temperature and moisture in a Eurasian steppe. *Agricultural and Forest Meteorology* **262**: 157–165.

Yuan X, Wang Y, Ji P, Wu P, Sheffield J, Otkin JA. 2023. A global transition to flash droughts under climate change. *Science* **380**: 187–191.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Standardized Precipitation-Evapotranspiration Index and growing season precipitation at the study site during 2014–2021.

Fig. S2 Experimental design of the litter removal experiment.

Fig. S3 Relationship among soil variables and results of the principal component analysis.

Fig. S4 *A priori* conceptual structural equation model of litter removal manipulation on temporal biomass stability.

Fig. S5 Effects of plant litter removal on soil temperature from 2015 to 2021.

Fig. S6 Effects of plant litter removal on soil moisture, soil inorganic nitrogen, and soil N mineralization under different litter removal manipulations from 2015 to 2021.

Fig. S7 Effects of plant litter removal on aboveground net primary productivity of plant community and functional groups.

Fig. S8 Principal coordinate analysis of community composition over the 7-yr experiment based on Bray–Curtis similarities.

Fig. S9 Effects of plant litter removal on the relative abundance of functional groups.

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Fig. S10 Effects of plant litter removal on the abundance of different functional groups.

Fig. S11 Effects of plant litter removal on plant height of different functional groups.

Fig. S12 Effects of plant litter removal on species richness of community and functional groups.

Fig. S13 Spearman's correlation coefficients between plant and soil variables.

Table S1 Soil nutrients and plant community variables before the experiment.

Table S2 Amount of plant litter removed in each manipulation from 2014 to 2020 (g m^{-2}).

Table S3 List of plant species and plant functional groups included in the litter manipulation experiment.

Table S4 Pairwise *t*-test analysis (*P*-values) on aboveground net primary production and biomass of each functional group in the predrought year (2015) compared with individual litter manipulation years (2016–2021).

Table S5 Permutation analysis (*P*-values) on Bray–Curtis plant community composition in the predrought year (2015) compared with individual litter manipulation years (2016–2021).

Table S6 Pairwise *t*-test analysis (*P*-values) on the abundance of each functional group in the predrought year (2015) compared with individual litter manipulation years (2016–2021).

Table S7 Spearman's rank correlation coefficients between plant functional groups in terms of abundance and biomass.

Please note: Wiley is not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.

© 2023 The Authors
New Phytologist © 2023 New Phytologist Foundation

14698137, 0, Downloaded from https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.19374 by Institute Of Botany, Wiley Online Library on [07/11/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

REVIEW

Grassland soil carbon sequestration: Current understanding, challenges, and solutions

Yongfei Bai[1,2]* and M. Francesca Cotrufo[3]

Grasslands store approximately one third of the global terrestrial carbon stocks and can act as an important soil carbon sink. Recent studies show that plant diversity increases soil organic carbon (SOC) storage by elevating carbon inputs to belowground biomass and promoting microbial necromass contribution to SOC storage. Climate change affects grassland SOC storage by modifying the processes of plant carbon inputs and microbial catabolism and anabolism. Improved grazing management and biodiversity restoration can provide low-cost and/or high-carbon-gain options for natural climate solutions in global grasslands. The achievable SOC sequestration potential in global grasslands is 2.3 to 7.3 billion tons of carbon dioxide equivalents per year (CO_2e year^{-1}) for biodiversity restoration, 148 to 699 megatons of CO_2e year^{-1} for improved grazing management, and 147 megatons of CO_2e year^{-1} for sown legumes in pasturelands.

Grassland ecosystems cover an area of 52.5 million km^2, accounting for ~40.5% of the Earth's land surface excluding Greenland and Antarctica (*1*). Grasslands provide habitats for biodiversity, contribute to food production, and deliver many cultural services (*1*). They also store ~34% of the terrestrial carbon stock (*1*), with ~90% of their carbon stored belowground as root biomass and soil organic carbon (SOC), thus playing a vital role in soil carbon sequestration (*1*, *2*). However, grasslands are highly vulnerable to human disturbance (e.g., overgrazing and land-use conversion to agriculture) and climate change (*1*–*3*). Worldwide, grasslands have undergone severe decreases in biodiversity and ecosystem functions, leading to reductions in SOC storage (*2*, *4*, *5*). Here, we review the recent advances in our understanding of SOC dynamics, current challenges, and possible solutions to enhance SOC sequestration in global grassland ecosystems. We address three questions: (i) How do key biotic and abiotic factors regulate grassland SOC formation, turnover, and stability?; (ii) how do climate warming, alterations in precipitation, and fire affect SOC storage?; and (iii) how does grazing management affect SOC and how can improved practices result in SOC sequestration?

Mechanisms and drivers of SOC sequestration

In grassland ecosystems, ~60% of net primary productivity is allocated belowground (*6*). Belowground carbon inputs are more often incorporated into SOC than aboveground inputs because of their chemical composition (e.g., aliphatic compounds and root exudates) and their presence in the soil (Fig. 1) (*6*). On average, root carbon inputs have a SOC stabilization efficiency that is five times greater than aboveground carbon inputs (*6*).

Organic carbon in soil is distributed between particulate organic matter (POM) and mineral-associated organic matter (MAOM) fractions, with only a minor portion (1 to 2%) present as dissolved organic matter. POM and MAOM differ in their formation, physical and chemical properties, and mean residence times in soil (*7*, *8*). POM is formed from the fragmentation of plant and microbial residues, and therefore is composed of lightweight fragments made of large polymers (Fig. 1). MAOM, by contrast, is formed from single small molecules that are leached from plant residues or exuded from plant roots, which associate to minerals directly (ex vivo) or after microbial assimilation (in vivo) as microbial necromass (*7*, *8*). MAOM on average has a lower carbon:nitrogen ratio because of its proportionally higher microbial origin, its longer mean residence time in soils (from decades to centuries) compared with POM (<10 years to decades), and its strong chemical bonding to minerals and physical protection in fine aggregates (*7*, *8*). Therefore, MAOM contributes to longer-term carbon sequestration in soil. Root exudates such as dissolved sugars, amino acids, and organic acids are the key pathway to MAOM formation largely through microbial in vivo transformations (Fig. 1) (*8*, *9*). Plant aboveground, root, and rhizodeposition inputs exhibit different

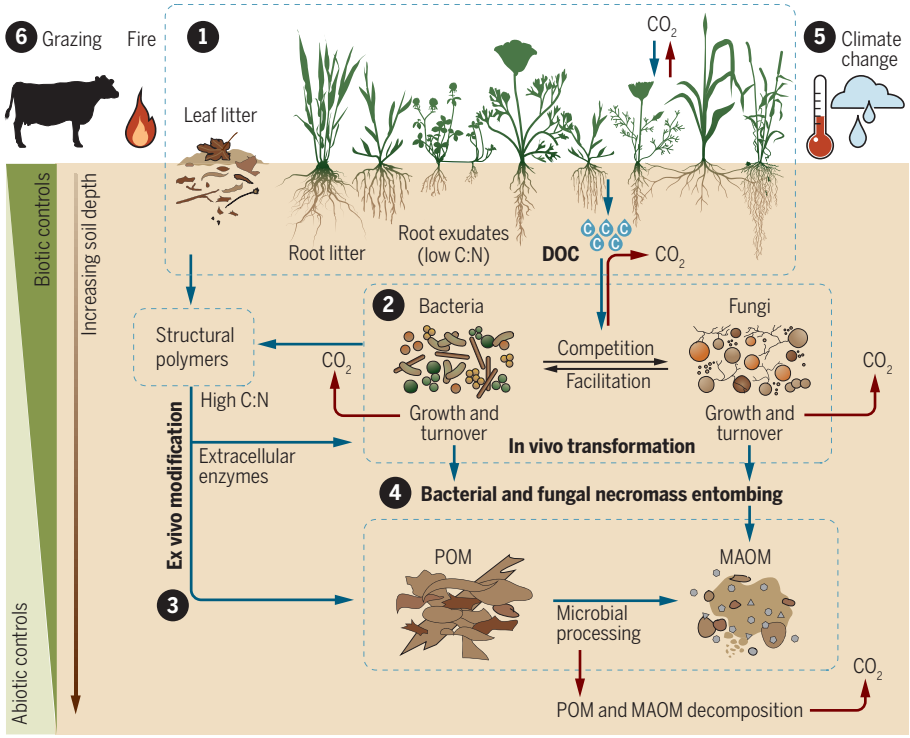


Fig. 1. Conceptual framework for key factors and mechanisms controlling SOC sequestration in grassland ecosystems. (**1**) Plant diversity controls on productivity, biomass allocation, and SOC inputs through litter and root exudates (*6*, *13*, *14*). (**2**) Key pathway of MAOM formation through microbial in vivo transformation (*8*, *17*). (**3**) Pathway of POM formation through microbial ex vivo modification (*8*, *17*). (**4**) Microbial necromass carbon (C) accumulation in MAOM (*9*, *11*). (**5**) Climate change impacts on SOC sequestration through plant and microbial pathways (*26*, *28*). (**6**) Grazing and fire impacts on SOC storage through pathways of plant and animal waste C inputs, compaction, and bioturbation (e.g., trampling and wallowing), microbial in vivo transformation, and microbial ex vivo modification (*33*, *36*, *38*, *46*). C:N, carbon: nitrogen ratio; DOC, dissolved organic carbon.

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China. [2]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China. [3]Department of Soil and Crop Science and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, USA.
*Corresponding author. Email: yfbai@ibcas.ac.cn

Downloaded from https://www.science.org at Institute of Botany, Cas on August 04, 2022

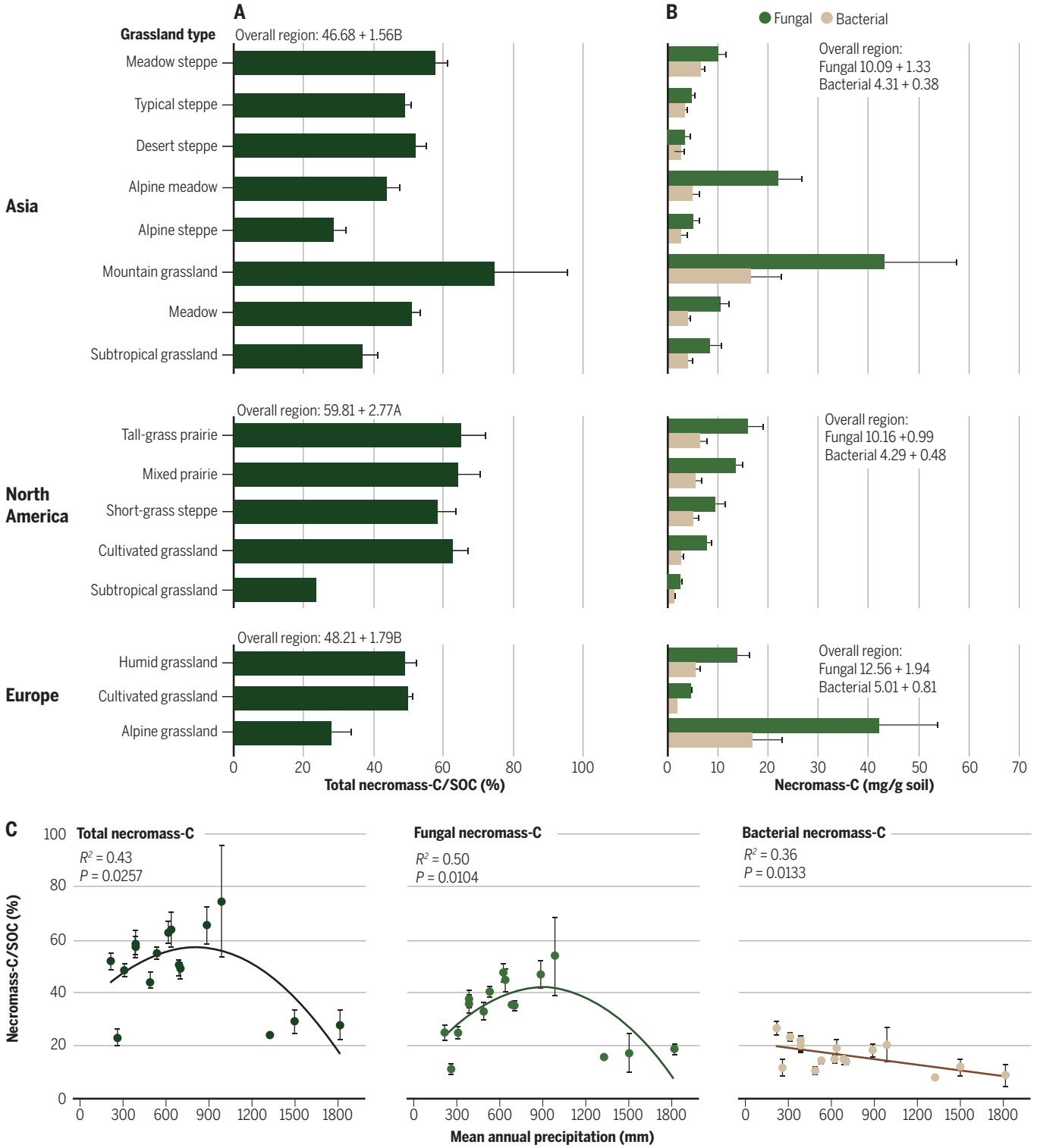


Fig. 2. Patterns and climatic drivers of microbial necromass contribution to SOC. (**A**) Microbial necromass C contribution to SOC. (**B**) Fungal and bacterial necromass C concentrations. (**C**) Relationships of total microbial, fungal, and bacterial necromass C contributions to SOC with mean annual precipitation in the topsoil of grassland systems in Asia, North America, and Europe. Data are from Liang *et al*. (*17*) and Wang *et al*. (*18*). Only the topsoil microbial necromass C and corresponding SOC data (n = 223) were used for global and regional synthesis. All data were classified into different grassland types within regions on the basis of sampling site information from the original study, Asia (eight grassland types, n = 122), North America (five grassland types, n = 47), and Europe (three grassland types, n = 54). Within each grassland type, mean and standard error for each variable were calculated across different sampling sites. General linear model analyses were performed to explore whether the total microbial necromass C contribution to SOC and fungal and bacterial necromass C concentrations differ among different regions. Values with different letters are significantly different at the $P < 0.05$ level. Simple linear regression was used to analyze to the relationship of mean annual precipitation with fungal, bacterial, and total microbial necromass C contributions to SOC across all grassland types on the global scale.

Downloaded from https://www.science.org at Institute of Botany, Cas on August 04, 2022

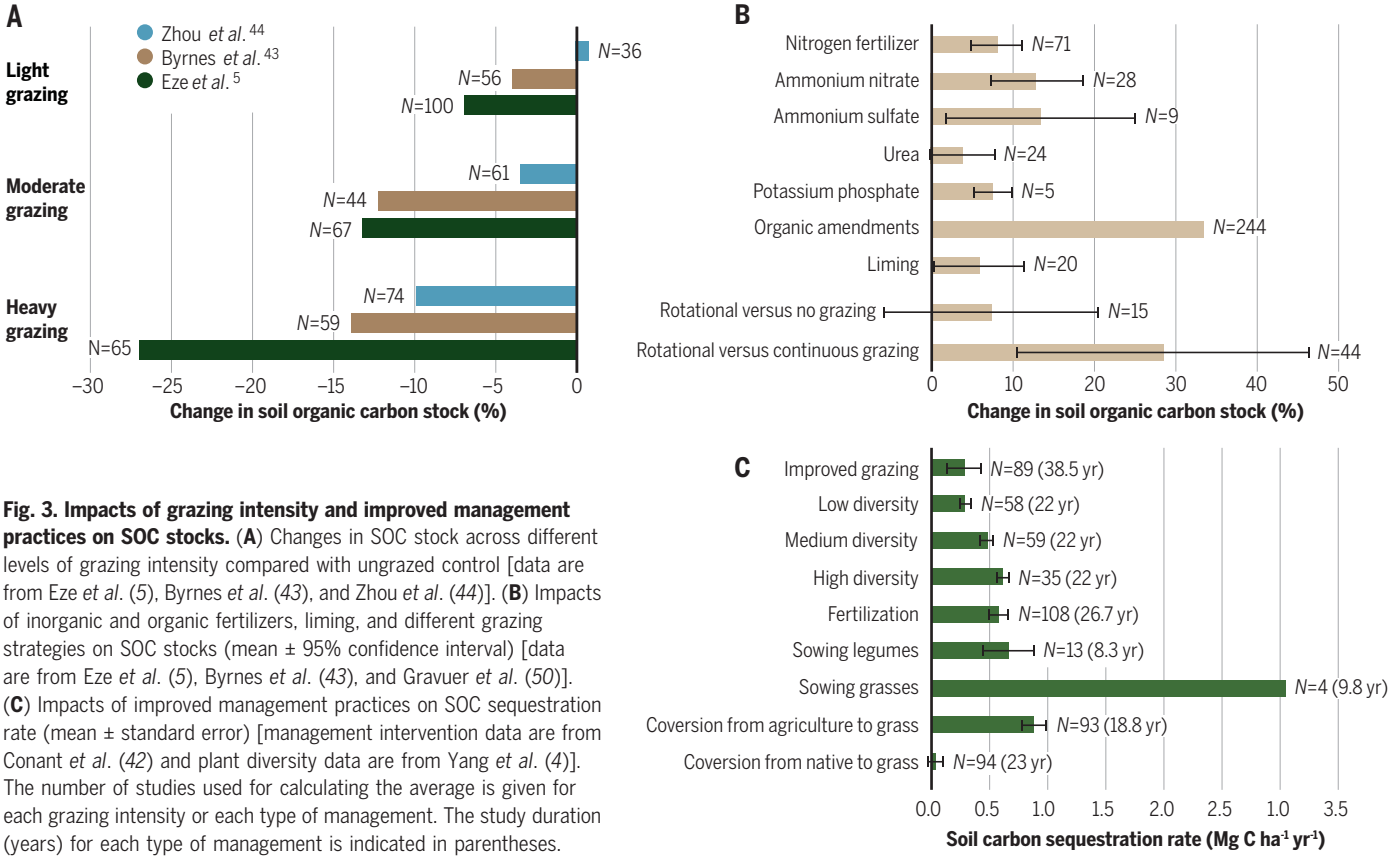


Fig. 3. Impacts of grazing intensity and improved management practices on SOC stocks. (**A**) Changes in SOC stock across different levels of grazing intensity compared with ungrazed control [data are from Eze *et al*. (*5*), Byrnes *et al*. (*43*), and Zhou *et al*. (*44*)]. (**B**) Impacts of inorganic and organic fertilizers, liming, and different grazing strategies on SOC stocks (mean ± 95% confidence interval) [data are from Eze *et al*. (*5*), Byrnes *et al*. (*43*), and Gravuer *et al*. (*50*)]. (**C**) Impacts of improved management practices on SOC sequestration rate (mean ± standard error) [management intervention data are from Conant *et al*. (*42*) and plant diversity data are from Yang *et al*. (*4*)]. The number of studies used for calculating the average is given for each grazing intensity or each type of management. The study duration (years) for each type of management is indicated in parentheses.

POM and MAOM formation efficiencies. Approximately 46% of root exudates, 9% of root tissues, and 7% of aboveground carbon residues are transformed into MAOM, whereas 19% of root litter is transformed into POM across crops, grasses, and trees growing in the field and under controlled laboratory conditions (*10*). Thus, plants with greater carbon allocation to roots contribute more to soil carbon sequestration, particularly the formation of MAOM. However, it remains largely unclear how the contributions of roots (root exudates and root litter) and aboveground inputs to SOC accumulation (POM and MAOM) change with grassland types, soil properties, and climate conditions.

In grassland topsoils, 50 to 75% of SOC is found in MAOM. The average carbon:nitrogen varies from ~10 to ~12 for MAOM and from ~16 to ~18 for POM (*3*); therefore, the accrual of SOC in MAOM requires substantially greater nitrogen than the equivalent accrual in POM (*11*). The formation of POM is primarily driven by climate (temperature and precipitation). By contrast, the accumulation of MAOM is controlled by soil properties such as silt and clay content, cation-exchange capacity, and microbial nitrogen availability, which means that it may saturate (*8*, *12*). In European grasslands, topsoil carbon storage in MAOM saturates at ~50 g C kg^{-1} soil, beyond which the additional increase in SOC storage completely depends upon accrual in POM (*11*). Currently, most European grasslands (80%) are below saturation, indicating a large capacity for SOC sequestration in their topsoils (*11*).

Plant diversity is a key driver of SOC formation and storage (*4*). High plant diversity enhances SOC storage by elevating belowground carbon (i.e., root biomass and root exudates) inputs (*13*, *14*) and promoting microbial growth, turnover, and entombment of necromass (*15*). Maintaining consistently high levels of biodiversity and root carbon inputs is essential for enhancing SOC storage and persistence in grasslands (Fig. 1).

Fungi and bacteria have a strong influence on SOC accumulation, stabilization, and turnover in grasslands (Fig. 1), as in other terrestrial ecosystems (*6*, *16*). Microbial necromass plays an important role in SOC accumulation and stabilization (*9*, *17*). In the topsoil of global grasslands, the contribution of the microbial necromass to total SOC ranges from 23 to 74%, with an average of 50% (Fig. 2A), which is greater than its contribution in agricultural and temperate forest soils (*17*, *18*). The contribution of necromass to SOC changes with soil depth (*18*) and is typically dominated by fungal necromass, with the fungi-to-bacteria necromass carbon ratio ranging from 1.2 to 4.1 across global grasslands (Fig. 2B). This is likely because fungi produce more chemically recalcitrant structural compounds and have greater carbon use efficiency than bacteria (*6*, *16*). Moreover, mycorrhizal fungi, which live in association with plant roots and derive their carbon directly from the plant, can regulate the carbon sequestration capacity in soil. Carbon sequestration capacity per unit nitrogen in soil is 1.7 times greater in ecosystems dominated by ectomycorrhizal fungi–associated plants (e.g., savannas, shrublands, and forests) than in systems dominated by arbuscular mycorrhizal fungi–associated plants (e.g., nonwoody grasslands) because ectomycorrhizal fungi can produce enzymes to degrade organic nitrogen from plant litter (*19*). However, MAOM is relatively higher in ecosystems that are dominated by arbuscular mycorrhizal fungi (*13*), such as grasslands.

Climate regulates the metabolic activity of microbes and thus controls large-scale patterns of microbial necromass and SOC storage (*18*, *20*). At the global scale, cold, moist soils promote the accumulation of microbial necromass carbon. The maximum microbial necromass carbon occurs at a mean annual precipitation of 900 to 1000 mm with a mean annual temperature <0°C (Fig. 2C), indicating high priorities for preserving the current stocks in these systems. Few studies have measured the contribution of microbial necromass carbon to SOC in grassland soils, and data are lacking from

Downloaded from https://www.science.org at Institute of Botany, Cas on August 04, 2022

Africa, South America, and Australia (*17*, *18*, *20*). Microbial diversity may also affect SOC storage by regulating the efficiency of microbial assimilation of carbon and the production of organo-mineral associations in soils (*21*). Recently, microbial diversity was found to promote the stabilization efficiency of grass litter–derived POM but to reduce that of MAOM (*22*).

Climate change impacts on SOC sequestration

Sixty-seven percent of the world's grasslands are distributed in semiarid, arid, and cold climates, with only 23% occurring in humid climates (*1*). Thus, carbon sequestration in most grasslands is highly sensitive to climate change, which can exert strong and diverse impacts on SOC accrual and stability through plant- and microbial-mediated mechanisms (*8*). The impacts of climate change on soil carbon sequestration often vary with grassland type, climate, and soil conditions. In semiarid steppe, warming may enhance root-derived carbon input but inhibit the decomposition of MAOM by suppressing fungal growth and soil respiration, resulting in an increase in the MAOM pool (*23*). In humid tallgrass prairies, warming may increase C_4 grass cover and C_4-derived carbon input into soil organic matter, but it also increases the decay rate of these fractions, resulting in a negligible change in soil carbon sequestration (*24*). In alpine grasslands, warming-induced permafrost degradation reduces active-layer SOC storage by decreasing the stability of microbial networks and accelerating SOC (and specifically POM) decay (*25*). A recent meta-analysis demonstrated that long-term (≥5 years) warming increases the ratios of ligninase to cellulase activity and enhances microbial utilization of recalcitrant carbon, leading to a 14% reduction in the topsoil recalcitrant carbon pool (*26*). However, warming may increase the accumulation of root-derived carbon in the subsoil MAOM pool (*27*). POM is much more climate sensitive than MAOM (*3*, *11*). The percent change in POM (−12.2%) with climate warming is on average three times greater than that in MAOM (−3.8%) in global grasslands (*28*). This suggests that grasslands with a high proportion of MAOM will contribute less to soil carbon-climate feedbacks.

Future projected precipitation anomalies and long-lasting droughts (*29*, *30*) will likely influence soil carbon sequestration of grassland ecosystems by altering plant community composition, productivity and carbon allocation, and microbial processes. In the semiarid steppe, increased precipitation promotes soil aggregation by stimulating fungal growth and increasing soil-exchangeable magnesium (*23*). Precipitation anomalies (increases and decreases) can substantially alter root-to-shoot ratios and vertical root distribution in grasslands (*31*), thus regulating soil microbial growth and SOC storage. Reduced precipitation strongly suppresses oxidase activity, whereas higher precipitation stimulates the activity of nitrogen-acquisition extracellular enzymes (*32*). However, on the global scale, only a negative tendency for POM and a positive tendency for MAOM and total SOC concentrations with increased precipitation were observed in grasslands because of the limited data availability (*28*).

Climate change–induced increases in fire frequency can substantially modify long-term SOC storage in grasslands, particularly in savanna grasslands, by intensifying nutrient limitation, which suppresses plant growth and carbon inputs. Elevated fire frequencies reduce soil carbon stocks on average by 0.21 megagrams of carbon per hectare per year (Mg C ha^{-1} $year^{-1}$) in the upper soil layer (0 to 20 cm) in global savanna grasslands (*33*). However, a recent study showed that fire suppression (i.e., >60 years of fire exclusion) has little effect on total SOC storage (0 to 60 cm) in tropical savannas because C_4 grass–derived carbon dominates the SOC, particularly in deeper soil layers, where soil carbon is less affected by changes in fire frequencies (*34*). It remains unclear to what extent different fire regimes regulate plant diversity, above- and belowground biomass allocation, microbial-mediated processes, and SOC storage in shallower and deeper soil profiles.

Impacts of grazing pressure on grassland soil carbon

Natural grasslands are grazed by wild ungulates, which can enhance SOC storage because they graze for short periods of time and move across the landscape. This results in maintained plant cover, diversity and productivity, promotion of species with deep roots, microbial processing with the formation of both POM and MAOM, and soil-mixing processing by soil fauna (*35*, *36*). Increases in ecosystem metabolism and plant labile carbon inputs (e.g., root exudates) are expected to increase both the ex vivo and in vivo formation of MAOM (*9*, *10*, *37*). Conversely, increased root inputs and allocation to depth result in higher POM in the subsoil (*6*, *38*). In addition, large herbivores create habitats for many bioturbators (e.g., fossorial mammals and soil macrofauna) to loosen up soil and expose larger aggregates of soil organic matter to organo-mineral interaction by vertical soil mixing (*36*). However, both the direction and magnitude of effects of large wild herbivores on soil carbon storage can vary strongly with soil nutrient availability, across grasslands, and under different levels of herbivore density. For example, a recent short-term study suggested that nutrient availability strongly moderates the impact of herbivore grazing on soil carbon sequestration in herbaceous grasslands (*39*). Large herbivore grazing increases the upper-layer soil carbon storage under elevated nutrient (fertilization) conditions but has no effect on soil carbon storage under ambient nutrient conditions (*39*). Sandhage-Hofmann *et al.* (*40*) report that elevated elephant densities enhance SOC stocks [4.7 tons (t) ha^{-1}] despite losses of woody biomass in moist, semiarid, wood-encroached savannas of south-central Africa. However, a synthesis of 174 experiments showed that large herbivore exclusion generally increases SOC storage across different biomes (grassland, forest, shrubland, tundra, woodland, etc.), suggesting an overall negative impact of large wild herbivores on soil carbon storage (*41*).

Livestock grazing is the most common use of grasslands worldwide. Some grasslands are managed to improve forage quantity and quality, thereby increasing livestock production and/or SOC storage (*1*, *2*, *42*). In livestock-dominated systems, these pathways are strongly controlled by grazing intensity and rest periods. Continuous livestock grazing reduces plant cover, diversity, and productivity, and thus root inputs and plant- and microbial-mediated SOC formation, while stimulating losses through microbial turnover and erosion caused by increased compaction and reduced cover (*1*, *2*, *43*). Eze *et al.* (*5*) demonstrated that livestock grazing on average decreases SOC stock by 15% across five continents, with the greatest reduction (−22.4%) in SOC stock in the tropics and the least reduction (−4.5%) in temperate grasslands. At the global scale, light grazing (e.g., seasonal and rotational grazing) shows the least negative effects or even promotes soil carbon storage, whereas moderate and heavy (continuous) grazing consistently reduces soil carbon stocks (Fig. 3A) (*5*, *43*, *44*). For a given category of grazing intensity, the discrepancy in magnitude of changes in SOC stocks between these studies may partly arise from the lack of quantitative measures of grazing intensity and the difference in data sources (*5*, *43*, *44*). Nevertheless, the magnitude and directions of grazing impacts on soil carbon sequestration are context dependent and vary with climate and soil conditions, vegetation properties, livestock type, herbivore diversity, grazing strategies (e.g., continuous versus rotational grazing), and grazing intensity and duration (*5*, *38*, *43*–*45*). The negative impact of increasing grazing intensity on SOC is lessened with greater water availability (*5*, *44*) but is more severe with warmer temperatures and longer grazing duration in temperate grasslands (*44*). With moderate and heavy grazing, SOC increases in grasslands dominated by C_4 species and decreases in grasslands dominated by C_3 species (*45*). Sheep grazing generally has a greater negative impact on SOC than cattle grazing, and the reduction in SOC with grazing is substantially greater in topsoil than that in subsoil (*44*). A mixed cattle and megaherbivore system was shown to be a sustainable management strategy in African savanna ecosystems with high

Downloaded from https://www.science.org at Institute of Botany, Cas on August 04, 2022

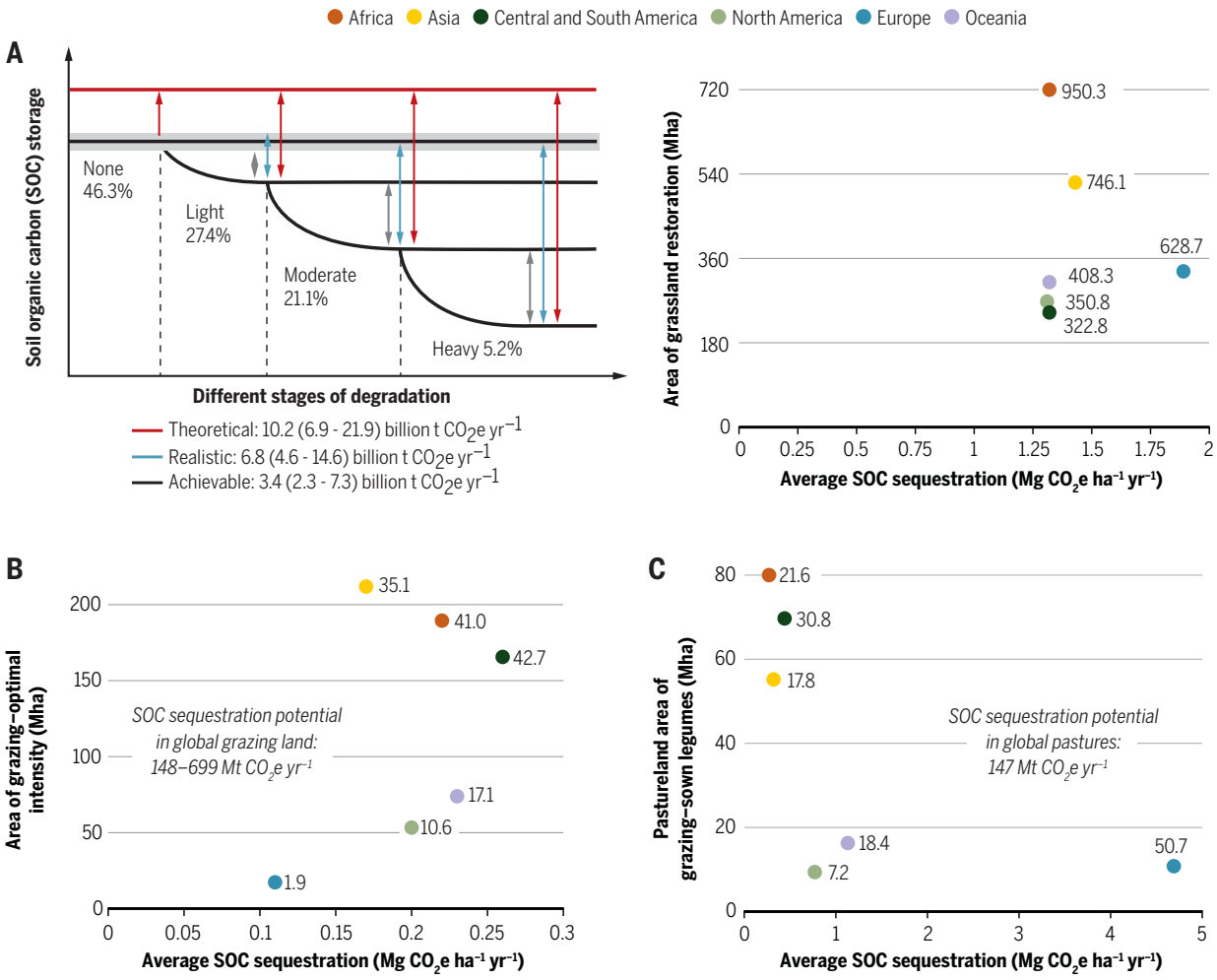


Fig. 4. Soil C sequestration potential of grassland ecosystems at the regional and global scales. SOC sequestration potentials are arranged according to average SOC sequestration rates and area of each management strategy for denoting their relative contributions. (**A**) Capacity and attainability of SOC sequestration by restoring degraded grasslands [data are from White *et al*. (*1*), De Deyn *et al*. (*52*), Deng *et al*. (*54*), and Fargione *et al*. (*53*)]. At the global scale, SOC sequestration potential is presented as theoretical, realistic, and achievable, respectively, based on Chapman (*55*). Means and the 95% confidence intervals (parentheses) are given (left panel). At the regional scale, only achievable SOC sequestration potential are estimated because of the large uncertainties for estimating the theoretical and realistic SOC sequestration potentials in each region. For each region, the mean achievable SOC sequestration potential (Mt CO_2e year^{-1}) is given (right panel). (**B** and **C**) Global SOC sequestration potential (Mt CO_2e year^{-1}) through optimizing grazing intensity in grazing lands and sowing legumes in pasturelands [data are from Griscom *et al*. (*51*)]. Only maximum climate mitigation potential with safeguards for reference year 2030 is shown.

herbivore diversity (*46*). Moreover, rotational grazing consistently shows higher SOC stocks compared with continuous grazing (or free grazing) (*43*), with gains observed specifically in the mineral associated fraction (*47*).

Managing for soil carbon storage in grasslands

Empirical and experimental studies have indicated that improving grassland management can increase SOC storage, thus mitigating carbon losses caused by climate change, long-term overgrazing, and grassland degradation (*2*, *42*, *48*). Management improvements may result in soil carbon accrual through several interrelated mechanisms (Fig. 1). Conversion from croplands to grasslands removes disturbance from tillage and increases root carbon inputs to soil (*6*, *42*). Restoring the biodiversity of degraded grasslands may increase plant production and promote microbial turnover and necromass entombment (*4*, *13*, *15*). Grazing improvement can increase higher-quality root carbon (lower carbon:nitrogen ratios) inputs (*38*) and/or nitrogen retention, thus promoting the formation and persistence of MAOM in soils (*47*). Sowing legumes increases soil carbon and nitrogen inputs by elevating root biomass, root exudates, and fine root turnover (*42*, *49*). Applications of inorganic and organic fertilizers may stimulate primary productivity and high-quality plant carbon inputs to soil, resulting in more efficient microbial carbon use (*5*, *28*, *50*).

A number of management interventions have been adopted to restore grasslands (Fig. 3, B and C). On the global scale, the improved grassland managements increase SOC stocks on average by 0.47 Mg C ha^{-1} year^{-1} (*42*). This suggests that the world's grazing lands, which occupy an area of ~34 million km^2, have substantial potential to increase SOC storage (Fig. 4). Among all improved management practices, conversion from cultivation to grasslands, increasing plant diversity, sowing legumes and grasses, and fertilization are associated with the highest soil carbon sequestration rates (Fig. 3C) (*4*, *42*). Under moderate grazing intensity, the average SOC stock increase (28.4%) is substantially greater with rotational grazing than that with continuous grazing (Fig. 3B). In the southeast United States, grassland soils managed with adaptive multi-paddock grazing that used a high-density-short-duration rotational grazing had more carbon (72.49 Mg C ha^{-1}) and nitrogen (9.26 Mg N ha^{-1}) stocks compared with continuous grazing (64.02 Mg C ha^{-1} and 8.52 Mg N ha^{-1}) in the 0 to 100 cm soil layer (*47*). However, the

Downloaded from https://www.science.org at Institute of Botany, Cas on August 04, 2022

direction and magnitude of management effects on soil carbon stocks are context specific, depending on factors such as climate, plant community composition, and soil properties (*5*, *43*, *50*). Therefore, grazing practices need to be implemented with an understanding of context. Moreover, further studies are required to examine the synergy and trade-offs among grassland biodiversity, primary productivity, and soil carbon sequestration under management interventions.

Soil carbon sequestration potential varies in both quantity and attainability among grasslands with different degrees of degradation and across different regions (Fig. 4). Given that ~50% of the global grassland area has been degraded (*1*, *2*), restoration of grassland cover and biodiversity is an effective strategy for promoting SOC storage and mitigating the negative impacts of global climate change (*4*, *15*, *51*–*53*). For example, the SOC accrual rate with grazing exclusion is on average 0.68 Mg C ha^{-1} $year^{-1}$ in topsoil (0 to 30 cm) and 0.62 Mg C ha^{-1} $year^{-1}$ in subsoil (30 to 100 cm) across 145 degraded grassland sites in China (*54*), indicating that it has not reached saturation over the 27-year period of grassland restoration.

Potential soil carbon sequestration capacities can be categorized as theoretical, realistic, or achievable (*55*). Theoretical soil carbon sequestration capacity refers to the estimate of restoring all soils to their natural capacity or even enhancing it through management interventions, realistic soil carbon sequestration capacity refers to the optimistic value accounting for social and economic constraints, and achievable capacity is the value of a pragmatic scenario based on the current trends (*55*). At the global scale, the mean theoretical, realistic, and achievable capacities of SOC sequestration with grassland restoration are estimated to be 10.2, 6.8, and 3.4 billion t CO_2 equivalents per year (CO_2e $year^{-1}$), respectively (Fig. 4A). At the regional scale, Africa, Asia, and Europe are projected to have the largest achievable capacity of soil carbon sequestration with grassland restoration, with Oceania and North and South America exhibiting the least SOC sequestration potential (Fig. 4A). These global patterns of SOC sequestration potential are primarily caused by the differences in average soil carbon sequestration rate and the area of degraded grassland in different regions. The greater SOC sequestration potential with grassland restoration in Africa and Asia is due to the larger areas of degraded grasslands in these continents, whereas European grasslands have a higher average soil carbon sequestration rate (Fig. 4A). In addition, optimizing grazing intensity (e.g., rotational grazing) is projected to increase soil carbon sequestration potential by 148 to 699 megatons (Mt) CO_2e $year^{-1}$ in global grazing lands (Fig. 4B), with the greatest SOC sequestration potential occurring in Central and South America, Africa, and Asia (*51*). Moreover, sowing legumes is projected to enhance SOC storage by 147 Mt CO_2e $year^{-1}$ in global pasturelands (*51*), with Europe exhibiting the greatest soil carbon sequestration potential caused by both the largest pastureland areas and the highest average soil carbon sequestration rate (Fig. 4C). At both the regional and global scales, large uncertainties exist regarding the projected soil carbon sequestration potential and rate of accrual. These uncertainties are caused by the complex interactions among climate change, human activities, and spatial and temporal variations in ecosystem and soil responses (*51*, *53*, *56*). Scientific research and management innovations are required in the future to maximize the attainable SOC storage in global grasslands.

Conclusion

Recent studies have made considerable progress toward addressing major challenges associated with identifying the capacity and key mechanisms of various grasslands to sequester and preserve carbon in soils and developing knowledge-based strategies to restore biodiversity, preserve current SOC stocks, and promote additional sequestration for climate change mitigation and sustainable management in grasslands. These advances highlight the important roles of plant and soil biodiversity in regulating the formation of microbial necromass carbon, MAOM, and POM, mediating the impacts of climate change, and promoting SOC storage through management improvements and restoration in global grasslands. They also demonstrate that the impacts of climate change, grazing, fire, grassland restoration, and mitigation solutions on soil carbon sequestration are moderated by multiple context-dependent factors. Future research is needed to address the uncertainty and context dependency of the proposed mitigation solutions and their carbon sequestration potentials and to consider their possible synergies and trade-offs for biodiversity conservation, climate mitigation, and food production.

REFERENCES AND NOTES

1. R. P. White, S. Murray, M. Rohweder, *Pilot Analysis of Global Ecosystems: Grassland Ecosystems* (World Resources Institute, 2000).
2. R. D. Bardgett *et al*., *Nat. Rev. Earth Environ.* **2**, 720–735 (2021).
3. E. Lugato, J. M. Lavallee, M. L. Haddix, P. Panagos, M. F. Cotrufo, *Nat. Geosci.* **14**, 295–300 (2021).
4. Y. Yang, D. Tilman, G. Furey, C. Lehman, *Nat. Commun.* **10**, 718 (2019).
5. S. Eze, S. M. Palmer, P. J. Chapman, *J. Environ. Manage.* **223**, 74–84 (2018).
6. R. B. Jackson *et al*., *Annu. Rev. Ecol. Evol. Syst.* **48**, 419–445 (2017).
7. J. M. Lavallee, J. L. Soong, M. F. Cotrufo, *Glob. Chang. Biol.* **26**, 261–273 (2020).
8. M. F. Cotrufo, J. M. Lavallee, *Adv. Agron.* **172**, 1–66 (2022).
9. C. Liang, J. P. Schimel, J. D. Jastrow, *Nat. Microbiol.* **2**, 17105 (2017).
10. S. H. Villarino, P. Pinto, R. B. Jackson, G. Piñeiro, *Sci. Adv.* **7**, eabd3176 (2021).
11. M. F. Cotrufo, M. G. Ranalli, M. L. Haddix, J. Six, E. Lugato, *Nat. Geosci.* **12**, 989–994 (2019).
12. E. Mitchell *et al*., *Glob. Chang. Biol.* **27**, 5383–5391 (2021).
13. S. Chen *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **115**, 4027–4032 (2018).
14. M. Lange *et al*., *Nat. Commun.* **6**, 6707 (2015).
15. J. Prommer *et al*., *Glob. Chang. Biol.* **26**, 669–681 (2020).
16. S. D. Frey, *Annu. Rev. Ecol. Evol. Syst.* **50**, 237–259 (2019).
17. C. Liang, W. Amelung, J. Lehmann, M. Kästner, *Glob. Chang. Biol.* **25**, 3578–3590 (2019).
18. B. Wang, S. An, C. Liang, Y. Liu, Y. Kuzyakov, *Soil Biol. Biochem.* **162**, 108422 (2021).
19. C. Averill, B. L. Turner, A. C. Finzi, *Nature* **505**, 543–545 (2014).
20. T. Ma *et al*., *Nat. Commun.* **9**, 3480 (2018).
21. J. G. Ernakovich *et al*., *Biogeochemistry* **153**, 1–15 (2021).
22. M. F. Cotrufo, M. L. Haddix, M. E. Kroeger, C. E. Stewart, *Soil Biol. Biochem.* **168**, 108648 (2022).
23. T. Bai *et al*., *Glob. Chang. Biol.* **26**, 5320–5332 (2020).
24. X. Cheng, Y. Luo, X. Xu, R. Sherry, Q. Zhang, *Biogeosciences* **8**, 1487–1498 (2011).
25. M.-H. Wu *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2025321118 (2021).
26. J. Chen *et al*., *Glob. Chang. Biol.* **26**, 1944–1952 (2020).
27. J. Jia *et al*., *Glob. Chang. Biol.* **25**, 4383–4393 (2019).
28. K. S. Rocci, J. M. Lavallee, C. E. Stewart, M. F. Cotrufo, *Sci. Total Environ.* **793**, 148569 (2021).
29. A. J. Felton, A. K. Knapp, M. D. Smith, *Glob. Chang. Biol.* **27**, 1127–1140 (2021).
30. V. Humphrey *et al*., *Nature* **592**, 65–69 (2021).
31. B. Zhang *et al*., *Ecology* **100**, e02828 (2019).
32. W. Xiao, X. Chen, X. Jing, B. Zhu, *Soil Biol. Biochem.* **123**, 21–32 (2018).
33. A. F. A. Pellegrini *et al*., *Nature* **553**, 194–198 (2018).
34. Y. Zhou *et al*., *Nature* **603**, 445–449 (2022).
35. O. J. Schmitz *et al*., *Science* **362**, eaar3213 (2018).
36. J. A. Kristensen, J.-C. Svenning, K. Georgiou, Y. Malhi, *Trends Ecol. Evol.* **37**, 117–128 (2022).
37. N. W. Sokol, M. A. Bradford, *Nat. Geosci.* **12**, 46–53 (2019).
38. C. H. Wilson, M. S. Strickland, J. A. Hutchings, T. S. Bianchi, S. L. Flory, *Glob. Chang. Biol.* **24**, 2997–3009 (2018).
39. J. Sitters *et al*., *Glob. Chang. Biol.* **26**, 2060–2071 (2020).
40. A. Sandhage-Hofmann, A. Linstädter, L. Kindermann, S. Angombe, W. Amelung, *Glob. Chang. Biol.* **27**, 4601–4614 (2021).
41. E. S. Forbes *et al*., *Funct. Ecol.* **33**, 1597–1610 (2019).
42. R. T. Conant, C. E. P. Cerri, B. B. Osborne, K. Paustian, *Ecol. Appl.* **27**, 662–668 (2017).
43. R. C. Byrnes, D. J. Eastburn, K. W. Tate, L. M. Roche, *J. Environ. Qual.* **47**, 758–765 (2018).
44. G. Zhou *et al*., *Glob. Chang. Biol.* **23**, 1167–1179 (2017).
45. M. E. McSherry, M. E. Ritchie, *Glob. Chang. Biol.* **19**, 1347–1357 (2013).
46. J. Sitters, D. M. Kimuyu, T. P. Young, P. Claeys, H. Olde Venterink, *Nat. Sustain.* **3**, 360–366 (2020).
47. S. Mosier *et al*., *J. Environ. Manage.* **288**, 112409 (2021).
48. Y. F. Bai, Q. M. Pan, Q. Xing, *Chin. Sci. Bull.* **61**, 201–212 (2016).
49. G.-L. Wu, Y. Liu, F.-P. Tian, Z.-H. Shi, *Land Degrad. Dev.* **28**, 1336–1344 (2017).
50. K. Gravuer, S. Gennet, H. L. Throop, *Glob. Chang. Biol.* **25**, 1152–1170 (2019).
51. B. W. Griscom *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **114**, 11645–11650 (2017).
52. G. B. De Deyn *et al*., *J. Appl. Ecol.* **48**, 600–608 (2011).
53. J. E. Fargione *et al*., *Sci. Adv.* **4**, eaat1869 (2018).
54. L. Deng, Z.-P. Shangguan, G.-L. Wu, X.-F. Chang, *Earth Sci. Rev.* **173**, 84–95 (2017).
55. S. J. Chapman, in *Carbon Capture: Sequestration and Storage*, R. E. Hester, R. M. Harrison, Eds. (RSC Publishing, 2010), pp. 179–202.
56. F. Lu *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **115**, 4039–4044 (2018).

ACKNOWLEDGMENTS

We thank S. P. Chen, J. Q. Tian, Y. J. Zhao, S. X. Zheng, Y. Wang, X. M. Lu, B. Tang, J. Man, and J. S. Su for discussion on the topic of grassland carbon sequestration. **Funding:** This work was supported by the National Natural Science Foundation of China (grant no. 32192464) and the Strategic Priority Research Program of the Chinese Academy of Sciences (grant no. XDA23080000). **Author contributions:** Y.F.B. conceived the concept, structure, and writing of the manuscript. M.F.C. contributed to the development of ideas and writing of the manuscript. **Competing interests:** M.F.C. provides consulting services for C quester Analytics. Services are provided to a number of companies invested in soil carbon sequestration, including by the adoption of regenerative grazing management. The remaining authors declare no competing interests.

License information: Copyright © 2022 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. https://www.science.org/about/science-licenses-journal-article-reuse

Submitted 13 April 2022; accepted 15 June 2022
10.1126/science.abo2380

Downloaded from https://www.science.org at Institute of Botany, Cas on August 04, 2022

Science

Grassland soil carbon sequestration: Current understanding, challenges, and solutions

Yongfei BaiM. Francesca Cotrufo

Science, 377 (6606), • DOI: 10.1126/science.abo2380

View the article online
https://www.science.org/doi/10.1126/science.abo2380
Permissions
https://www.science.org/help/reprints-and-permissions

Downloaded from https://www.science.org at Institute of Botany, Cas on August 04, 2022

Use of this article is subject to the Terms of service

Science (ISSN) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.
Copyright © 2022 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works

SPECIAL FEATURE

Plant diversity enhances productivity and soil carbon storage

Shiping Chen[a,1], Wantong Wang[b,1], Wenting Xu[a,1], Yang Wang[a,1], Hongwei Wan[a,1], Dima Chen[a], Zhiyao Tang[c], Xuli Tang[b], Guoyi Zhou[b], Zongqiang Xie[a], Daowei Zhou[d], Zhouping Shangguan[e], Jianhui Huang[a], Jin-Sheng He[c,f], Yanfen Wang[g], Jiandong Sheng[h], Lisong Tang[i], Xinrong Li[j], Ming Dong[k], Yan Wu[l], Qiufeng Wang[m], Zhiheng Wang[c], Jianguo Wu[n,o], F. Stuart Chapin III[p], and Yongfei Bai[a,2]

[a]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China; [b]South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China; [c]College of Urban and Environmental Sciences, Peking University, Beijing 100871, China; [d]Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130012, China; [e]State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling 712100, China; [f]Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China; [g]College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China; [h]Key Laboratory of Soil and Plant Ecological Processes, College of Grassland and Environment Sciences, Xinjiang Agricultural University, Urumqi 830052, China; [i]State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China; [j]Key Laboratory of Stress Physiology and Ecology in Cold and Arid Regions, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China; [k]Key Laboratory of Hangzhou City for Ecosystem Protection and Restoration, College of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou 310036, China; [l]Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China; [m]Synthesis Research Center of Chinese Ecosystem Research Network, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China; [n]School of Life Sciences and School of Sustainability, Arizona State University, Tempe, AZ 85287; [o]Center for Human-Environment System Sustainability, State Key Laboratory of Earth Surface Processes & Resource Ecology, Beijing Normal University, Beijing 100875, China; and [p]Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775

Edited by Susan E. Trumbore, Max Planck Institute for Biogeochemistry, Jena, Germany, and approved September 20, 2017 (received for review February 15, 2017)

Despite evidence from experimental grasslands that plant diversity increases biomass production and soil organic carbon (SOC) storage, it remains unclear whether this is true in natural ecosystems, especially under climatic variations and human disturbances. Based on field observations from 6,098 forest, shrubland, and grassland sites across China and predictions from an integrative model combining multiple theories, we systematically examined the direct effects of climate, soils, and human impacts on SOC storage versus the indirect effects mediated by species richness (SR), aboveground net primary productivity (ANPP), and belowground biomass (BB). We found that favorable climates (high temperature and precipitation) had a consistent negative effect on SOC storage in forests and shrublands, but not in grasslands. Climate favorability, particularly high precipitation, was associated with both higher SR and higher BB, which had consistent positive effects on SOC storage, thus offsetting the direct negative effect of favorable climate on SOC. The indirect effects of climate on SOC storage depended on the relationships of SR with ANPP and BB, which were consistently positive in all biome types. In addition, human disturbance and soil pH had both direct and indirect effects on SOC storage, with the indirect effects mediated by changes in SR, ANPP, and BB. High soil pH had a consistently negative effect on SOC storage. Our findings have important implications for improving global carbon cycling models and ecosystem management: Maintaining high levels of diversity can enhance soil carbon sequestration and help sustain the benefits of plant diversity and productivity.

soil carbon storage | species richness | aboveground net primary productivity | belowground biomass | human disturbance

Soils represent the largest carbon stocks in Earth's terrestrial ecosystems, and compelling evidence indicates that large amounts of soil carbon in natural ecosystems have been lost in recent decades because of the effects of climate change and human disturbance (1–3). Therefore, soil carbon sequestration plays an important role in mitigating the positive feedback between terrestrial carbon and climate (2, 4). A central issue to understanding the mechanisms controlling soil carbon sequestration and a much-debated subject is how plant diversity and productivity are related to soil carbon storage (5, 6). Soil organic carbon (SOC) storage, in general, represents the balance of two main processes: carbon inputs (e.g., net carbon gain by plants) and losses (e.g., microbial decomposition) (2, 5, 7). Theoretical and experimental studies suggest that biodiversity has the potential to influence ecosystem carbon sequestration by modifying both processes (7–9). Recent experimental studies at small spatial scales have shown that high plant diversity increases SOC storage by elevating carbon inputs (particularly belowground carbon inputs) and increasing soil microbial community diversity and activity, and/or by suppressing carbon losses from decomposition (6, 10). However, many studies at large spatial scales have reported that the patterns of SOC storage are controlled by climate, vegetation, and soil conditions (11–13). Thus, it remains unclear whether plant diversity has important positive effects on

Significance

Soil carbon sequestration plays an important role in mitigating anthropogenic increases in atmospheric CO_2 concentrations. Recent studies have shown that biodiversity increases soil organic carbon (SOC) storage in experimental grasslands. However, the effects of species diversity on SOC storage in natural ecosystems have rarely been studied, and the potential mechanisms are yet to be understood. The results presented here show that favorable climate conditions, particularly high precipitation, tend to increase both species richness and belowground biomass, which had a consistent positive effect on SOC storage in forests, shrublands, and grasslands. Nitrogen deposition and soil pH generally have a direct negative effect on SOC storage. Ecosystem management that maintains high levels of plant diversity can enhance SOC storage and other ecosystem services that depend on plant diversity.

Author contributions: Y.B. designed research; Y.B. served as principal investigator (PI) of the grassland ecosystem carbon project; S.C., Yang Wang, H.W., D.Z., Z.S., J.H., J.-S.H., Yanfen Wang, J.S., L.T., X.L., M.D., and Yan Wu contributed data collection for grassland ecosystems; G.Z. served as PI of the forest ecosystem carbon project, and provided data collection for forest ecosystems; Z.X. and Z.T. served as PIs of the shrubland ecosystem carbon project, and provided data collection for shrubland ecosystems; S.C., W.W., W.X., Yang Wang, H.W., D.C., Z.W., and Y.B. analyzed data; and S.C., J.W., F.S.C., and Y.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Published under the PNAS license.

[1]S.C., W.W., W.X., Yang Wang, and H.W. contributed equally to this work.

[2]To whom correspondence should be addressed. Email: yfbai@ibcas.ac.cn.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1700298114/-/DCSupplemental.

Published online April 16, 2018.

Downloaded at Institute of Botany,CAS on September 16, 2021

ECOLOGY

SOC storage in natural ecosystems (e.g., forests, shrublands, and grasslands) in which environmental factors, human disturbance, and plant-soil feedbacks affect diversity-soil carbon relationships. Further studies are needed to better understand species effects on SOC storage and predict the ecological consequences of global biodiversity loss and climate change on the biological sequestration of carbon.

Ecological theories suggest that the broad-scale patterns of SOC storage, plant diversity, and productivity are controlled predominantly by favorable climates (i.e., high temperature and precipitation), although a variety of mechanisms have been proposed to explain these patterns (11, 14). Specifically, SOC storage generally increases with increasing precipitation, and for a given level of precipitation, SOC storage decreases with increasing temperature due primarily to increased respiration (5, 11). Species richness and primary productivity increase with increasing climate favorability along ecological gradients (14–16). In addition, high SOC storage can impose a positive feedback on species richness and productivity by increasing soil water-holding capacity and sustaining soil fertility (17). There is abundant evidence that human disturbance (e.g., N deposition, road density) has substantially altered biodiversity and ecosystem functions across all terrestrial biomes (18, 19). N enrichment generally increases productivity, but reduces species richness (18, 20) and enhances SOC storage (21, 22). Soil pH also regulates the capacity for SOC storage and nutrient supplies and, thereby, regulates primary productivity (23). Recent studies have proposed that high soil acidity can inhibit soil microbial activities and increase SOC accumulation (24). Together, these studies suggest that SOC storage and the diversity-soil carbon relationship are controlled by multiple interrelated processes and complex plant-soil feedbacks.

Here, we examined the influences of environmental factors and human disturbance on SOC storage, plant diversity, productivity, and the interrelationships among these factors based on data from 6,098 field sites in China obtained using standardized sampling methods (*SI Appendix*, Fig. S1). Recognizing the multitude of factors and the effect of spatial scale on variables, we classified these field sites into 28 vegetation types that were grouped into three biome types: forests, shrublands, and grasslands. To facilitate our analysis, we also collected data on climate (temperature, precipitation, and photosynthetically active radiation), soil properties (soil pH), and human disturbance (N deposition rate and road density) for all sites. Specifically, our study was designed to address the following two questions: First, how do climate, soil properties, and human disturbance affect SOC storage via direct effects and indirect effects mediated by community properties, such as species richness (SR), aboveground net primary productivity (ANPP), and belowground biomass (BB)? Second, what role does plant diversity play in the plant-soil feedbacks among SOC storage, ANPP, and BB? To address the first question, we used structural equation models (SEMs) (25) to tease apart the direct effects of environmental and human factors on SOC storage and the indirect effects mediated by the community properties and test the predictions and hypotheses from multiple theories based on an integrative multivariate causal network in each biome type (Table 1 and *SI Appendix*, Fig. S2). To address the second question, we used general linear mixed-effects models

Table 1. Pathways and standardized partial effect size across three biomes and proposed interpretations based on structural equation models (SEMs)

Pathway	Forest	Shrubland	Grassland	Hypothesized mechanism
Climate → SOC	−0.512	−0.233	0.157	Climate favorability regulates soil C balance by stimulating C decomposition and increasing C losses from soils (1, 11, 12).
Human → SOC	−0.135	0.203	−0.198	N deposition inhibits decomposition of plant litter and SOC (21), while high road density leads to ecosystem degradation, diversity loss, and decreases SOC (45).
Soil pH → SOC	−0.184	−0.381	−0.164	High soil acidity inhibits soil microbial activities and increases SOC accumulation (24).
SR → SOC	0.157	0.116	0.167	High plant species richness increases SOC by increasing soil microbial diversity and activity and suppressing carbon losses (6).
ANPP → SOC	−0.097	−0.200	0.145	ANPP either increases or decreases SOC depending on the net result of plant-C inputs and C decomposition (11, 46).
BB → SOC	0.114	0.411	0.395	SOC increases with C inputs from root residues (6).
Climate → Soil pH	−0.764	−0.366	−0.500	Soil pH is controlled by climatic forcing, particularly water balance (23).
Human → Soil pH	0.166	−0.302	−0.139	High N deposition increases soil acidity (47).
Climate → SR	−0.404	0.562	−0.363	Water, energy, and their interaction control large-scale patterns of plant diversity (14).
Human → SR	0.612	−0.098	0.151	N deposition decreases plant diversity (18, 20). High road density increases both exotic species invasion and disturbance to native species (19).
Soil pH → SR	−0.492	−0.179	−0.299	High soil acidity affects plant diversity, but the underlying mechanisms are unclear (48).
Climate → ANPP	NS	0.248	0.092	Climate favorability regulates large-scale patterns of ANPP (49).
Human → ANPP	NS	0.124	0.441	N deposition generally increases ANPP (18, 20). High road density triggers ecosystem degradation and declines in productivity (45).
Soil pH → ANPP	−0.155	NS	NS	Soil pH affects primary productivity by regulating soil nutrient supply and uptake by plants (23).
SR → ANPP	0.314	0.243	0.221	High diversity increases primary productivity by complementary resource use (16, 30).
Climate → BB	−0.143	−0.776	−0.141	Climate regulates root growth and belowground biomass allocation (50).
Human → BB	−0.135	0.325	−0.164	N deposition alters belowground biomass allocation (21).
Soil pH → BB	−0.123	−0.266	−0.133	Soil acidity regulates root growth and belowground C allocation (51).
SR → BB	0.123	0.050	0.348	High species diversity increases rooting depth and belowground biomass (52).
ANPP → BB	0.552	0.724	0.346	Higher plant productivity provides more carbohydrate for roots (53).
Feedbacks*				
ANPP → SR	0.210	0.186	0.160	More productive ecosystems host more diverse plant species (54).
SOC → SR	0.130	0.111	0.326	High resource availability increases species diversity (55).
SOC → ANPP	NS	0.139	0.288	High water-holding capacity and nutrient supply increases plant productivity (49).
SOC → BB	0.098	0.271	0.376	Higher soil fertility enhances belowground biomass (56).

Magnitude of pathway is presented by standardized partial effect size fitted by the SEM shown in *SI Appendix*, Fig. S2. All significant pathways are shown ($P < 0.10$). NS means no significant effect ($P > 0.10$).

*Feedbacks are fitted separately based on the SEM shown in *SI Appendix*, Fig. S2*B*.

Downloaded at Institute of Botany,CAS on September 16, 2021

to determine the relationships of SR with ANPP, BB, and SOC storage. We also used SEMs to explore the feedbacks between SOC storage, SR, ANPP, and BB in each biome type.

Results

Patterns of SR, ANPP, BB, and SOC Storage Across Different Vegetation Types in China. Our study sites are distributed broadly across geographical and climate gradients in China, covering three biome types and 28 vegetation types (*SI Appendix*, Table S1 and Fig. S1). Plant SR, ANPP, BB, and SOC storage in the 0- to 30-cm soil layers varied substantially among the different vegetation types within each biome type and across different biome types in Chinese terrestrial ecosystems (Fig. 1). On average, SR was 10.2 tree species in the forests (plot size = 1,000 m^2), 5.0 shrub species in the shrublands (plot size = 100 m^2), and 6.7 herbaceous species in the grasslands (plot size = 1 m^2). ANPP averaged 12.8 $Mg{\cdot}ha^{-1}$ in forests, 3.7 $Mg{\cdot}ha^{-1}$ in shrublands, and only 1.3 $Mg{\cdot}ha^{-1}$ in grasslands. BB was 32.3 $Mg{\cdot}ha^{-1}$ in forests, 8.5 $Mg{\cdot}ha^{-1}$ in shrublands, and 12.5 $Mg{\cdot}ha^{-1}$ in grasslands. SOC storage averaged 73.8 Mg $C{\cdot}ha^{-1}$ in forests, 47.1 Mg $C{\cdot}ha^{-1}$ in shrublands, and 47.3 Mg $C{\cdot}ha^{-1}$ in grasslands (Fig. 1 and *SI Appendix*, Table S1). At the biome type level, SR, ANPP, BB, and SOC were strongly correlated with climate factors, including the mean annual temperature (MAT) and mean annual precipitation (MAP) (*SI Appendix*, Fig. S3). Generally, SR and ANPP were positively correlated with MAT and MAP in all biome types. BB and SOC were negatively correlated with MAT but positively correlated with MAP except in forests (*SI Appendix*, Fig. S3 and Table S2).

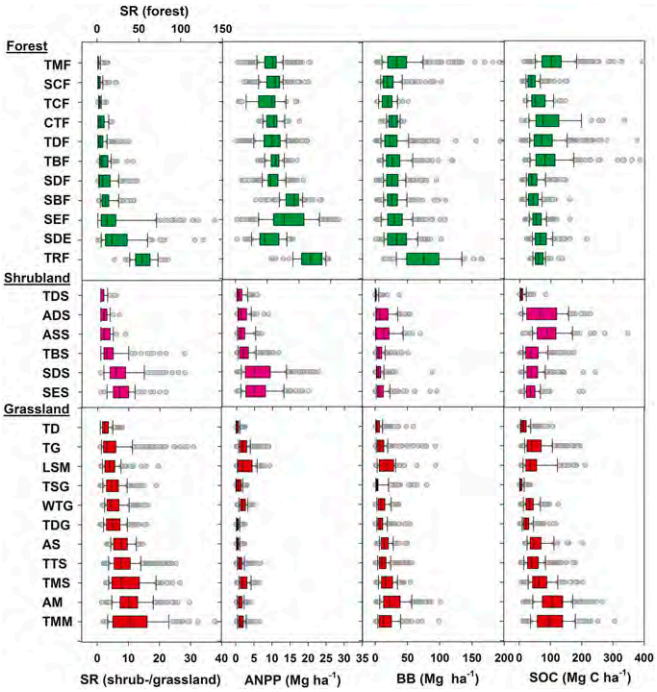


Fig. 1. Median and interquartile range of plant SR, ANPP, BB, and SOC storage in 0–30 cm soil depth across different vegetation and biome types. The boundary of the box indicates the 25th and 75th percentile. Error bars denote the 90th and 10th percentiles. Abbreviations of vegetation types: ADS, subalpine deciduous broadleaved shrubland; AM, alpine meadow; AS, alpine steppe; ASS, subalpine sclerophyllous evergreen broadleaved shrubland; CTF, cold temperate coniferous forest; LSM, lowland and saline meadow; SBF, subtropical coniferous-broadleaved forest; SCF, subtropical coniferous forest; SDE, subtropical deciduous-evergreen broadleaved forest; SDF, subtropical deciduous broadleaved forest; SDS, subtropical deciduous broadleaved shrubland; SEF, subtropical evergreen broadleaved forest; SES, subtropical evergreen broadleaved shrubland; TBF, temperate coniferous-broadleaved forest; TBS, temperate deciduous broadleaved shrubland; TCF, temperate coniferous forest; TD, temperate desert; TDF, temperate deciduous broadleaved forest; TDG, temperate desert steppe; TDS, temperate desert shrubland; TG, tropical grassland; TMF, temperate montane coniferous forest; TMM, temperate mountain meadow; TMS, temperate meadow steppe; TRF, tropical rainforest and monsoon forest; TSG, temperate sandy grassland; TTS, temperate typical steppe; WTG, warm temperate grassland.

Effects of Climate, Soil, and Human Disturbance on SOC Storage. Considering only the direct effects of drivers on SOC storage, climate favorability (high temperature and precipitation) showed a consistent negative relationship with SOC storage in all biome types except in grasslands, which mostly occurred in less climatically favorable sites (Fig. 2). With decreasing climate favorability, the magnitude of the negative partial effect (r_∂) of climate on SOC storage declined from forests ($r_\partial = -0.51$) to shrublands ($r_\partial = -0.23$) and shifted to positive in grasslands ($r_\partial = 0.16$; Table 1) because of the increasing relative importance of precipitation as a limiting factor (*SI Appendix*, Table S2). We further split the dataset of each biome type into two regions based on MAP of each sampling site. For forests and shrublands, sampling sites were classified into arid and subhumid region (MAP < 800 mm) and humid region (MAP > 800 mm). For grasslands, sampling sites were classified into arid and semiarid region (MAP < 400 mm) and subhumid and humid region (MAP > 400 mm). Again, the negative effects of climate favorability (e.g., high temperature) on SOC storage were consistently observed in each region, except in subhumid and humid grasslands (*SI Appendix*, Fig. S4). In addition, the effects of climate favorability on SOC storage were also mediated by SR and BB, both of which exhibited consistently positive effects on SOC storage in all biome types (Fig. 2). In forests, the indirect climate effects mediated by SR and BB were negative, reinforcing the direct climate effect on SOC storage. In shrublands, the strongest indirect effect was negative (through BB—reinforcing the direct effect of climate), and there was a positive indirect effect of climate acting through SR. In grasslands, the indirect effects through SR and BB were negative in contrast to the weak positive effects through climate (Fig. 2). Although the direct effect of ANPP on SOC storage was negative in forests and shrublands, the indirect effect of ANPP on SOC storage was consistently positive in all biome types, mediated by SR (through feedbacks) and BB (Table 1 and *SI Appendix*, Fig. S5). The SEMs further revealed that feedbacks of high SOC storage to SR, ANPP, and BB as well as high ANPP to SR were consistently positive in all biome types (Table 1 and *SI Appendix*, Fig. S5).

Human activity also had both direct and indirect effects on SOC storage, with the direct effects being negative in forests and grasslands and positive in shrublands (Fig. 2). The indirect effects of human activity on SOC storage were mediated by SR, ANPP, and BB. In forests and grasslands, intensified human activity, presumably N deposition, generally had positive effects on ANPP (grassland only) and SR, which were counterbalanced by decreased BB, leading to a relatively weak negative effect on SOC storage (Table 1 and *SI Appendix*, Table S2). However, intensified human activity was positively correlated with SOC storage in shrublands, and this relationship was further strengthened by the significant positive effect of SOC on BB (Fig. 2). High soil pH exhibited a negative effect on SOC storage in all biome types through its direct effects and the indirect effects mediated by SR and BB (Fig. 2). Both climate favorability and intensified human activity (e.g., N deposition) showed a consistent negative correlation with soil pH, and the reduced soil pH partly buffered the negative effects of climate favorability and/or intensified human activity on SOC storage through its effects on SR and BB. The indirect effects of climate on SOC were also mediated by soil pH, which declined with increasing climate favorability (Fig. 2 and Table 1). In addition, the negative effects of human activity on SOC storage were stronger in wet regions than in dry regions for all biome types, especially in grasslands (*SI Appendix*, Fig. S4). Collectively, the indirect pathways of climate, soil pH, and human activity resulted in consistently positive effects of SR and BB on SOC storage across different biome types (Table 1).

We further conducted partial regression analysis to assess the independent effect of each significant predictor variable (i.e., climate, human activity, soil pH) on SOC storage when the effects of other independent variables involved in the fitted SEM models were controlled. For each biome type, the partial regression coefficients

SPECIAL FEATURE
ECOLOGY
Downloaded at Institute of Botany,CAS on September 16, 2021

were extremely similar to those of the standardized effect sizes (path coefficients) from the SEM analysis (*SI Appendix*, Fig. S6).

Relationships of SR, ANPP, and BB to SOC Storage at Different Organizational Levels. At the vegetation-type level, significant positive-linear relationships of SR with ANPP, BB, and SOC storage were found for most of the vegetation types (Fig. 3). However, substantial variations in the slope and intercept of SR–ANPP, SR–BB, and SR–SOC relationships were observed among different vegetation types within each biome type, especially in shrublands and grasslands (Fig. 3). At the biome-type level, results of linear mixed-effects model (LMM) analysis showed that vegetation types generally had a significant random effect on both the intercept and slope of the SR–ANPP, SR–BB, and SR–SOC relationships in all biome types (*SI Appendix*, Tables S5 and S6). When the effect of vegetation types was considered as a random-effect factor, the relationships of SR–ANPP, SR–BB, and SR–SOC were predominantly positive linear across all sites in each biome type, except the SR–SOC relationship in forests (Fig. 3).

Discussion

Our study used extensive field sampling of forests, shrublands, and grasslands across China and combined the predictions from multiple theories into an integrative model to compare the direct effects of climate, soil, and human impacts on SOC storage and the indirect effects mediated by SR, ANPP, and BB in natural ecosystems. The findings from this study suggest three broad generalizations.

First, our results support the general theoretical predictions and empirical findings that broadscale patterns of SOC storage are regulated predominantly by climate favorability (1, 5, 11, 13). The strong negative effect of climate favorability (high temperature and precipitation) on forest SOC storage and the strong negative effect of high temperature on shrubland SOC storage indicate that carbon losses through heterotrophic respiration may play a predominant role in controlling the spatial patterns of soil carbon sequestration in these two biome types. This finding is consistent with regional-scale carbon flux observations (26). However, we found that climate favorability, particularly high precipitation, was associated with both higher SR and higher BB, which had consistent positive effects on SOC storage in all biome types, thus offsetting the direct negative effect of favorable climate on SOC. More importantly, our results suggest that the positive effects of SR and BB on SOC are likely reinforced by the positive feedbacks of high SOC storage to SR and BB. Findings from long-term experiments indicate that the feedbacks of high SOC to SR and BB can play important roles in governing the relationships between biodiversity and carbon and nutrient cycles in natural ecosystems (27). The consistent positive effects of SR and BB on SOC storage found in the current study are corroborated by recent experimental studies showing that high plant diversity increases belowground carbon inputs, enhances diversity and activity of soil microbial communities, and suppresses carbon losses from microbial decomposition, thereby increasing SOC storage (6, 10, 28). This study represents a test of the plant diversity-soil carbon storage hypothesis in natural ecosystems at broad spatial scales.

Second, our results indicate that the indirect effects of climate on SOC storage depend on the shape of the diversity-productivity relationships. At the biome-type level, the relationships of SR–ANPP and SR–BB were consistently positive in all biome types although the slope and intercept of SR–ANPP and SR–BB relationships differed substantially among different vegetation types within each biome type. This finding suggests that higher plant diversity leads to greater ANPP and BB, which enhances belowground carbon inputs and, thereby, SOC storage (29). Positive diversity-productivity relationships have also been reported by recent broad-scale studies in forests (16) and grasslands (15, 30). In addition, many experimental studies have proposed that high plant diversity increases ANPP and BB as well as the resistance of productivity to climate extremes (9, 31, 32). However, higher ANPP does not necessarily lead to greater carbon sequestration in soils, especially in warm and mesic ecosystems where carbon turnover and release processes may be major determinants of soil carbon stocks (26). In our study, the negative effect of ANPP on SOC in forests and shrublands indicates that the carbon losses associated with microbial respiration may offset the positive effect of BB on SOC storage (33). In contrast, the positive relationships of SR–ANPP and SR–BB in grasslands may further strengthen the positive effect of SR to SOC because most grasslands in China occur in climatically less favorable sites where carbon decomposition rate is relatively low (34).

Third, we found that human disturbance and soil pH had both direct and indirect effects on SOC storage. The direct effects of

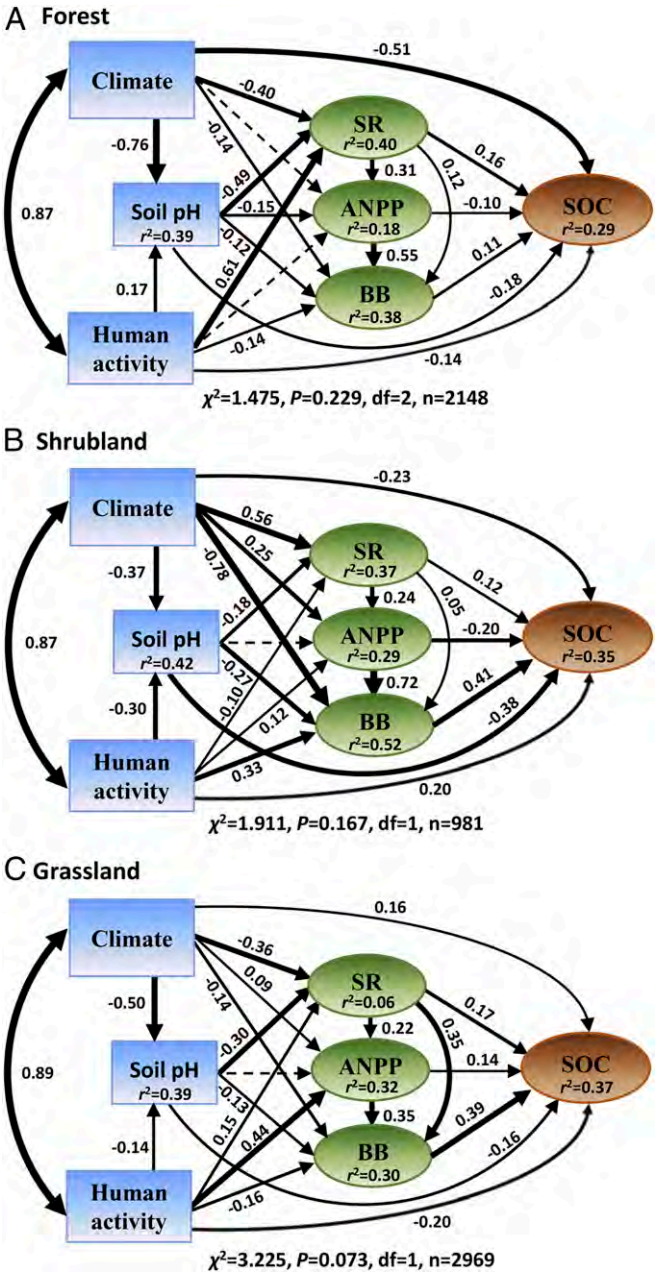


Fig. 2. SEMs fitted to connections among SR, ANPP, BB, and SOC storage and the effects of climate, soil, and human activity variables on SR, ANPP, BB, and SOC in forests (*A*), shrublands (*B*), and grasslands (*C*). Numbers adjacent to arrows represent the standardized path coefficients. Climate is PCA component 1 of mean annual precipitation, mean annual temperature, and photosynthetically active radiation. Human activities represent a composite variable including nitrogen deposition rate and road density. R^2 indicates the proportion of variance explained. Solid arrows represent significant paths ($P < 0.10$), and dashed arrows represent nonsignificant paths ($P > 0.10$).

Downloaded at Institute of Botany,CAS on September 16, 2021

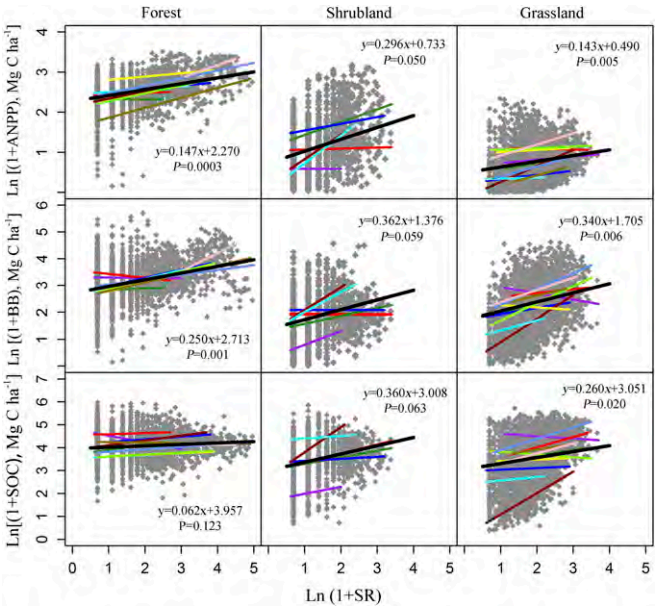


Fig. 3. Relationships of SR with ANPP, BB, and SOC storage at 0–30 cm soil depth in forests (*Left*), shrublands (*Center*), and grasslands (*Right*). Colored lines present regression plots of different vegetation types as indicated in Fig. 1. Bold black lines indicate SR–ANPP, SR–BB, and SR–SOC relationships at the biome-type level. The intercept and slope were the fixed effects of SR on response variables estimated by linear mixed-effects model (random slope model), with the effect of vegetation type as a random factor. All variables were natural logarithm transformed before regression analysis.

human disturbance on SOC storage were presumably caused by the impacts of N deposition on SOC, which were negative in forests and grasslands and positive in shrublands. The negative effects of N deposition on SOC may be caused by a reduction in microbial carbon contribution to stable soil carbon pools (35), whereas the positive effects may be attributable to the N-induced increase in root biomass (21, 22). Several studies have shown that elevated N inputs generally decrease the abundance of mycorrhizal fungi, which is an important source of recalcitrant soil carbon (36, 37). Greater N availability also decreases decomposition of SOC by regulating production and activity of microbial extracellular enzymes (38). In addition, high road density, an indicator of intense human disturbances, may cause habitat degradation and diversity loss and reduce SOC storage (19). Moreover, the consistently strong negative effects of high soil pH on SOC storage suggest that high soil pH may decrease the capacity for SOC storage and nutrient supply in all biome types (39). A recent study reported that high soil acidity increased SOC accumulation by inhibiting microbial activity and accelerating the leaching of dissolved organic carbon to subsoils (24). Finally, human disturbance and soil pH also affect SOC indirectly through changes in SR, ANPP, and BB. High levels of N deposition can also result in soil acidification and consequently lead to mobilization of heavy metals (e.g., Al^{3+} and Mn^{2+}) and loss of acid-intolerant species (40).

In general, by combining methods of SEM, partial regression, and linear mixed-effects model, our analysis presents strong evidence that SR, ANPP, and BB can be just as important as the direct effects of environmental drivers, although uncertainties exist because of the difficulties in disentangling the effects of MAT, MAP, and nitrogen deposition. These findings suggest that SOC storage can be substantially enhanced by fostering SR and BB. As SR only referred to tree species in forests and shrub species in shrublands, the role of plant diversity may be underestimated for these biome types. This strong positive species effect on carbon sequestration has not been well captured by global carbon-cycling models and is a potentially important mechanism that should be recognized. Our study also has important management implications because maintaining high levels of diversity can enhance soil carbon sequestration, while maintaining the benefits of plant diversity and productivity on other ecosystem services (9, 15, 16, 31, 41).

Materials and Methods

Study Sites. All site-level data for the forests, shrublands, and grasslands were obtained from the datasets of the "Strategic Priority Research Program-Climate Change: Carbon Budget and Relevant Issues" of the Chinese Academy of Sciences (42). In total, more than 13,000 sites were established for the field measurements (43). In this study, all artificial forest sites were excluded because most plantations are monocultures. Only sites with complete data on the SR, aboveground biomass (AGB), BB, and SOC storage were selected. In total, 6,098 sites were included in this study, including 2,148 sites for forests, 981 sites for shrublands, and 2,969 sites for grasslands. These sites represent 28 different vegetation types associated with different climate zones (i.e., cold temperate, temperate, subtropical, and tropical zones) and functional groups (e.g., coniferous vs. broadleaved, deciduous vs. evergreen) (*SI Appendix*, Table S1).

Vegetation and Soil Survey. Field inventories of all sites were conducted from 2011 to 2013. For detailed sampling protocols, please refer to Tang et al. (43). Specifically, standardized sampling and measurement protocols were applied in the vegetation and soil survey of each biome type. In forests, a plot with an area of 20 m × 50 m was investigated at each site. The number of tree species was recorded within each plot and used as the measure of SR of a particular site. The diameter at breast height (DBH) and height of each tree (DBH ≥ 5 cm) were measured to estimate the stand biomass and the aboveground and belowground proportions using allometric equations. In shrublands, three plots with areas of 5 m × 5 m (10 m × 10 m for desert shrublands) were sampled within each site. All shrub species in each plot were recorded, and the average number of shrub species over three plots was used as the measure of SR a particular site. Two different methods were used for evaluating the AGB and BB of the shrubs. For shrubs with a main stem, shrub height, diameter of basal stem, and crown were measured, and then AGB and BB of shrubs were calculated using allometric equations. For shrubs without main stems, all aboveground and belowground parts were harvested (1 m × 1 m) in each plot to evaluate the AGB and BB. In grasslands, 10 1 m × 1 m plots were sampled along a 100-m transect within each site. The aboveground and belowground parts of plants were harvested to estimate the AGB and BB of each plot. The number of herbaceous species in three to five plots was recorded as SR. The SR and the AGB and BB over all plots of each site were averaged and used as a measure of the site-level SR and the AGB and BB.

At least five soil samples were collected from each plot of forest, shrubland, and grassland sites using a soil auger. Air-dried soil samples were used to measure the gravel content (>2 mm) (GC), soil bulk density (BD), and SOC concentration. SOC storage was calculated by multiplying (1 − GC), BD, and SOC concentration in each soil layer. The sum of SOC in the 0- to 30-cm soil depth was used to represent SOC storage at a particular site.

To distinguish the role of dominant functional groups in ecosystem structure and function, only the SR, ANPP, and BB of the trees, shrubs, or herbaceous species were considered in the data analyses of forests, shrublands, and grasslands, respectively. Additional details for ANPP estimation are available in *SI Appendix, SI Materials and Methods*.

Climate, Soil and Human Activity Variables. For each site, MAT and MAP were calculated using the WorldClim data layers (www.worldclim.org/), and the average daily photosynthetically active radiation (PAR) was obtained from the National Earth System Science Data Sharing Infrastructure (www.geodata.cn/). Soil pH value for each site was obtained from SoilGrids1 km via www.isric.org/explore/soilgrids. N deposition rate (ND) for each site was obtained from the gridded long-term N deposition database (44). Data on the road density (RD) were obtained from the National Earth System Science Data Sharing Infrastructure (www.geodata.cn/). Additional details for MAT, MAP, PAR, soil pH, ND, and RD are available in *SI Appendix, SI Materials and Methods*.

Statistical Analyses. Details for statistical methods used in this study are available in *SI Appendix, SI Materials and Methods*.

ACKNOWLEDGMENTS. We thank all participants, a group of more than 1,000 scientists, for their contributions to the field work and laboratory analysis and Jingyun Fang, Guirui Yu, David Hooper, Shuijin Hu, Huifeng Hu, and Nianpeng He for their valuable comments and suggestions on an early version of this paper. This work was financially supported by the Strategic Priority Research Program of the Chinese Academy of Sciences Grant XDA05050000 and the National Natural Science Foundation of China Grants 31630010 and 31320103916.

Downloaded at Institute of Botany,CAS on September 16, 2021

1. Jenny H (1980) *The Soil Resource: Origin and Behavior* (Springer, New York).
2. Houghton RA (2007) Balancing the global carbon budget. *Annu Rev Earth Planet Sci* 35:313–347.
3. Crowther TW, et al. (2016) Quantifying global soil carbon losses in response to warming. *Nature* 540:104–108.
4. Paustian K, et al. (2016) Climate-smart soils. *Nature* 532:49–57.
5. De Deyn GB, Cornelissen JHC, Bardgett RD (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol Lett* 11:516–531.
6. Lange M, et al. (2015) Plant diversity increases soil microbial activity and soil carbon storage. *Nat Commun* 6:6707.
7. Diaz S, Hector A, Wardle DA (2009) Biodiversity in forest carbon sequestration initiatives: Not just a side benefit. *Curr Opin Environ Sustain* 1:55–60.
8. Chapin FS, III, et al. (2000) Consequences of changing biodiversity. *Nature* 405:234–242.
9. Hooper DU, et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108.
10. Fornara DA, Tilman D (2008) Plant functional composition influences rates of soil carbon and nitrogen accumulation. *J Ecol* 96:314–322.
11. Post WM, Emanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones. *Nature* 298:156–159.
12. Schimel DS, et al. (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochem Cycles* 8:279–293.
13. Yang Y, Mohammat A, Feng J, Zhou R, Fang J (2007) Storage, patterns and environmental controls of soil organic carbon in China. *Biogeochemistry* 84:131–141.
14. Hawkins BA, et al. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117.
15. Grace JB, et al. (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature* 529:390–393.
16. Liang J, et al. (2016) Positive biodiversity-productivity relationship predominant in global forests. *Science* 354:aaf8957.
17. Tiessen H, Cuevas E, Chacon P (1994) The role of soil organic matter in sustaining soil fertility. *Nature* 371:783–785.
18. Clark CM, Tilman D (2008) Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature* 451:712–715.
19. Ibisch PL, et al. (2016) A global map of roadless areas and their conservation status. *Science* 354:1423–1427.
20. Bobbink R, et al. (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecol Appl* 20:30–59.
21. Fornara DA, Tilman D (2012) Soil carbon sequestration in prairie grasslands increased by chronic nitrogen addition. *Ecology* 93:2030–2036.
22. De Vries W, Reinds GJ, Gundersen P, Sterba H (2006) The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. *Glob Change Biol* 12:1151–1173.
23. Slessarev EW, et al. (2016) Water balance creates a threshold in soil pH at the global scale. *Nature* 540:567–569.
24. Funakawa S, Fujii K, Kadono A, Watanabe T, Kosaki T (2014) Could soil acidity enhance sequestration of organic carbon in soils? *Soil Carbon*, eds Hartemink AE, McSweeney K (Springer, Cham), pp 209–216.
25. Grace JB (2006) *Structural Equation Modeling and Natural Systems* (Cambridge Univ Press, Cambridge, UK).
26. Valentini R, et al. (2000) Respiration as the main determinant of carbon balance in European forests. *Nature* 404:861–865.
27. Tilman D, Reich PB, Isbell F (2012) Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proc Natl Acad Sci USA* 109:10394–10397.
28. De Deyn GB, et al. (2011) Additional carbon sequestration benefits of grassland diversity restoration. *J Appl Ecol* 48:600–608.
29. Rasse DP, Rumpel C, Dignac MF (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil* 269:341–356.
30. Fraser LH, et al. (2015) Plant ecology. Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science* 349:302–305.
31. Isbell F, et al. (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526:574–577.
32. Tilman D, Reich PB, Knops JMH (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632.
33. Follett RF, Stewart CE, Pruessner EG, Kimble JM (2012) Effects of climate change on soil carbon and nitrogen storage in the US Great Plains. *J Soil Water Conserv* 67:331–342.
34. Yang Y, et al. (2010) Soil carbon stock and its changes in northern China's grasslands from 1980s to 2000s. *Glob Chang Biol* 16:3036–3047.
35. Liang C, Balser TC (2012) Warming and nitrogen deposition lessen microbial residue contribution to soil carbon pool. *Nat Commun* 3:1222.
36. Leff JW, et al. (2015) Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. *Proc Natl Acad Sci USA* 112:10967–10972.
37. Farrer EC, Suding KN (2016) Teasing apart plant community responses to N enrichment: The roles of resource limitation, competition and soil microbes. *Ecol Lett* 19: 1287–1296.
38. Waldrop MP, Zak DR, Sinsabaugh RL, Gallo M, Lauber C (2004) Nitrogen deposition modifies soil carbon storage through changes in microbial enzymatic activity. *Ecol Appl* 14:1172–1177.
39. Weil RR, Brady NC (2016) *The Nature and Properties of Soils* (Pearson, Columbus, OH), 15th Ed.
40. Stevens CJ, Thompson K, Grime JP, Long CJ, Gowing DJG (2010) Contribution of acidification and eutrophication to declines in species richness of calcifuge grasslands along a gradient of atmospheric nitrogen deposition. *Funct Ecol* 24:478–484.
41. Lu F, et al. (2018) Effects of national ecological restoration projects on carbon sequestration in China from 2001 to 2010. *Proc Natl Acad Sci USA* 115:4039–4044.
42. Fang J, Yu G, Liu L, Hu S, Chapin FSI (2018) Climate change, human impact, and carbon sequestration in China. *Proc Natl Acad Sci USA* 115:4015–4020.
43. Tang X, et al. (2018) Carbon pools in China's terrestrial ecosystems: New estimates based on an intensive field survey. *Proc Natl Acad Sci USA* 115:4015–4020.
44. Lu CQ, Tian HQ (2014) Half-century nitrogen deposition increase across China: A gridded time-series data set for regional environmental assessments. *Atmos Environ* 97:68–74.
45. Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv Biol* 14:18–30.
46. Bradford MA, et al. (2016) Managing uncertainty in soil carbon feedbacks to climate change. *Nat Clim Chang* 6:751–758.
47. Tian DS, Niu SL (2015) A global analysis of soil acidification caused by nitrogen addition. *Environ Res Lett* 10:024019.
48. Palpurina S, et al. (2017) The relationship between plant species richness and soil pH vanishes with increasing aridity across Eurasian dry grasslands. *Glob Ecol Biogeogr* 26: 425–434.
49. Chapin FS, Bloom AJ, Field CB, Waring RH (1987) Plant-responses to multiple environmental-factors. *Bioscience* 37:49–57.
50. Hui D, Jackson RB (2006) Geographical and interannual variability in biomass partitioning in grassland ecosystems: A synthesis of field data. *New Phytol* 169:85–93.
51. Högberg MN, Högberg P, Myrold DD (2007) Is microbial community composition in boreal forest soils determined by pH, C-to-N ratio, the trees, or all three? *Oecologia* 150:590–601.
52. Turnbull LA, Isbell F, Purves DW, Loreau M, Hector A (2016) Understanding the value of plant diversity for ecosystem functioning through niche theory. *Proc Biol Sci* 283: 20160536.
53. Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytol* 147:13–31.
54. Gillman LN, et al. (2015) Latitude, productivity and species richness. *Glob Ecol Biogeogr* 24:107–117.
55. Lewandowska AM, et al. (2016) The influence of balanced and imbalanced resource supply on biodiversity-functioning relationship across ecosystems. *Philos Trans R Soc Lond B Biol Sci* 371:20150283.
56. Yuan ZY, Chen HYH (2010) Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses. *Crit Rev Plant Sci* 29:204–221.

Downloaded at institute of Botany,CAS on September 16, 2021

100 YEARS Journal of Ecology
British Ecological Society

Journal of Ecology 2015, **103**, 750–760 doi: 10.1111/1365-2745.12395

Testing the scaling effects and mechanisms of N-induced biodiversity loss: evidence from a decade-long grassland experiment

Zhichun Lan[1,2], G. Darrel Jenerette[3], Shuxia Zhan[1,2], Wenhuai Li[1,2], Shuxia Zheng[1] and Yongfei Bai[1]*

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, China; [2]University of Chinese Academy of Sciences, Beijing 100049, China; and [3]Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124, USA

Summary

1. Although extensive studies demonstrate that nitrogen (N) enrichment frequently reduces plant diversity within small quadrats (0.5–4 m^2), only a few studies have evaluated N effects on biodiversity across different spatial scales.

2. We conducted the first experimental test of the scale dependence of N effects on species richness from a 10-year N treatment (1.75–28 g N m^{-2} $year^{-1}$) in a typical steppe. We used species–area relationship (SAR) to analyse the scale dependence of species loss with power model $S = cA^z$ (S is species number, A is area, c is intercept, and z is slope).

3. Absolute species loss decreased at sampling area > 8 m^2. Proportional species loss (compared to control) decreased and critical threshold (N_{crit}) for biodiversity losses increased with sampling areas.

4. These scale dependences were quantified as increasing slope (z-value) of SAR with N addition. Through SAR decomposition, we found that this overall positive effect was in response to positive effects of changes to the species abundance distribution over negative effects of overall species richness losses.

5. *Synthesis*. As nitrogen (N) enrichment typically occurs at scales much larger than individual plots, understanding how N enrichment affects the scaling patterns of biodiversity is necessary for biodiversity conservation and ecosystem management in response to anthropogenic N deposition.

Key-words: critical threshold, determinants of plant community diversity and structure, N enrichment, number of individuals, SAR decomposition, scaling effect, species abundance distribution, species aggregation, species–area relationship (SAR)

Introduction

While terrestrial primary production is widely limited by nitrogen (N) availability (Vitousek & Howarth 1991), the increasing rate of nitrogen pollution is changing biodiversity and ecosystem functioning world-wide (Vitousek *et al.* 1997; Phoenix *et al.* 2006; Galloway *et al.* 2008; Bobbink *et al.* 2010; Pardo *et al.* 2011). Decreases in biodiversity are commonly observed following N input (Suding *et al.* 2005; Clark & Tilman 2008; Hautier, Niklaus & Hector 2009; Clark *et al.* 2013), and N deposition is recognized as one of the major causes of biodiversity decline in terrestrial ecosystems (Sala *et al.* 2000; Stevens *et al.* 2004a). However, these findings are limited to quadrat scale responses and are not necessarily representative of the regional N deposition. Only a few studies have evaluated scaling relations of N-induced species loss (Crawley *et al.* 2005; Hillebrand *et al.* 2007; Chalcraft *et al.* 2008; Lepš 2014). These findings suggested that the patterns of N-induced biodiversity loss may be changed at larger scales, and few studies have tested mechanisms underlying these patterns (Chalcraft *et al.* 2008; Lepš 2014). The scale dependence of biodiversity change also suggests that a scale-dependent critical threshold (N_{crit}) for N enrichment may exist, below which N might have minimal effects on biodiversity (Clark & Tilman 2008; Bai *et al.* 2010; Lan & Bai 2012). It is still unclear how the sensitivity and magnitude of biodiversity loss after N addition vary with spatial scales. A mechanistic understanding of scale-dependent N-induced species loss is needed to extend findings from plot level and develop more efficient management strategies for biodiversity conservation (Chalcraft *et al.* 2008; Cleland & Harpole 2010).

*Correspondence author. E-mail: yfbai@ibcas.ac.cn

© 2015 The Authors. Journal of Ecology © 2015 British Ecological Society

Species–area relationship (SAR) is one of the most frequently used approaches to analyse scale dependence of biodiversity changes (Keil *et al.* 2011; Sandel & Corbin 2012; Powell, Chase & Knight 2013). The scale dependence of biodiversity is commonly modelled as a power function (Preston 1960; Tjørve 2003), $S = cA^z$, where S is species number, A is area, and *c* and *z* are constants (Arrhenius 1921). The slope (*z*-value) and intercept (*c*-value) of the SAR in log–log space are frequently used to quantify how species richness varies across multiple spatial scales (Tjørve 2003; Powell, Chase & Knight 2013). For example, the commonly observed reduction of species richness at the plot level with increased N may be associated with decreases in the intercept (*c*-value) and/or increases in the slope (*z*-value) of the SAR (Crawley *et al.* 2005; Chalcraft *et al.* 2008). If N increases the slope (*z*-value) of SAR, the rate of species loss would be smaller at broader scales, whereas if N decreases the slope of SAR, then species reduction will be larger at broader scales (Fig. 1). However, the majority of research into understanding variation in SARs has been observational and experimental approaches, though more challenging, are needed to directly test potential mechanisms (Jenerette & Shen 2012).

Recent SAR decomposition approaches provide an analytical framework to quantify changes in the *c*- and *z*-values as caused by a combination of changing species pool, number of individuals, species abundance distribution and/or species aggregation (spatial distributions) (He & Legendre 2002; Tjørve *et al.* 2008; Scheiner *et al.* 2011; Powell, Chase & Knight 2013). N addition may affect overall SAR and consequently regulate the scale dependence of biodiversity changes through its distinct influences on each of the four individual factors above. First, N addition may lead to decreased species pool through loss of rare species (H1: *reduced richness*) (Crawley *et al.* 2005; Chalcraft *et al.* 2008). Through the reduced richness hypothesis, we expect N additions to decrease both the *c*- and *z*- value of the SAR, and N-induced species loss would increase with sampling area. Secondly, N addition increases biomass production, causes assemblage-level thinning and thereby decreases the number of individuals because of increased plant size and intensified light competition (H2: *reduced individuals*) (Goldberg & Miller 1990; Oksanen 1996). Through reductions in the number of individuals, we expect N addition would decrease the *c*-value but increase the *z*-value of SAR (Oksanen 1997), and thus, the effects of N enrichment on species richness would diminish with increasing sampling area. Thirdly, N addition increases the abundance of a few N-favoured species at the expense of less favoured species (H3: *altered abundance distributions*) (Suding *et al.* 2005; Bai *et al.* 2010), which will decrease the evenness of community (Gilliam 2006; Hillebrand *et al.* 2007). Through decreased evenness of species abundance distribution, we expect N additions would decrease the *c*-value but increase the *z*-value, and thereby the N-induced reduction in species richness would become increasingly moderated with sampling area. Finally, N addition intensifies recruitment limitation (Stevens *et al.* 2004b), which will reduce immigration between different communities and increase species aggregations (H4: *species aggregation*). Through increases in species aggregation, we expect N addition would decrease the *c*-value but increase the *z*-value of SAR; hence, the effects of N enrichment on species richness would decrease with increasing sampling area (Table S1 in Supporting Information).

Our objective in this study was to experimentally quantify the scale dependence of N-induced species loss and test the underpinning mechanisms. We established a 10-year field

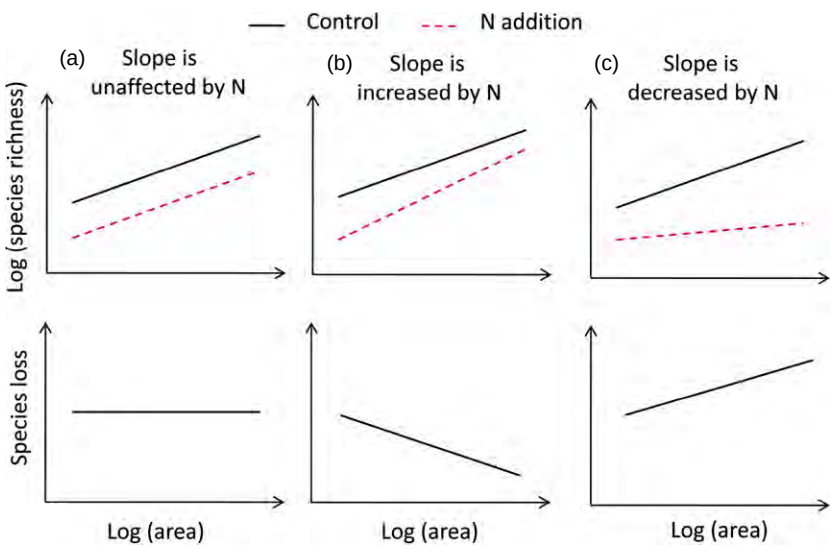


Fig. 1. Three scenarios of how N addition affects the slope of species–area relationship (SAR) and the corresponding scale effects on proportional species loss (PSL). In each scenario, the discrepancy between the two SARs represent N-induced species loss, that is $\Delta S = \log(S_{control}) - \log(S_N) = \log(S_{control}/S_N)$, or $\exp(\Delta S) = S_{control}/S_N$. Proportional species loss (PSL) was defined as proportion of species loss in N treatments compared to control, that is $PSL = 1 - S_N/S_{control} = 1 - 1/[\exp(\Delta S)]$. Therefore, PSL was positively correlated with ΔS. (a) N addition has no effects on the slope of SAR, and ΔS and PSL are independent of spatial scale; (b) N addition increases the slope of SAR, and ΔS and PSL decrease with increasing sampling area; (c) N addition decreases the slope of SAR, and ΔS and PSL increases with sampling area.

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

experiment with six levels of N addition rate in a semi-arid Inner Mongolia grassland, China. The Inner Mongolia grassland both historically and currently received little N deposition (Galloway *et al.* 2008) and has not yet experienced a rapid loss of plant species induced by chronic N input. This low N deposition background allows testing N effects on biodiversity. Specifically, we address two questions: first, how do the N-induced biodiversity loss (i.e. plant species richness, absolute and proportional species loss and critical threshold) change with spatial scales? Secondly, what are the relative contributions of alternative mechanisms in terms of species pool, number of individuals, species abundance distributions and species aggregation, mediating the scale dependence of N-induced species loss?

Materials and methods

STUDY SITE

The study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS; 116°42′ E, 43°38′ N and 1250 m a.s.l.), which is located in the Xilin River Basin, Inner Mongolia Autonomous Region of China (Bai *et al.* 2010). The mean annual temperature in the study area is 0.3 °C, with mean monthly temperature ranging from −21.6 °C in January to 19.0 °C in July. The mean annual precipitation is 346.1 mm, with about 80 per cent occurring in the growing season from May to September. The field experiment was carried out on a natural steppe community, which was fenced to prevent grazing since 1979. At the beginning of the experiment, there were 48 vascular plant species and 80% of them were rare species (relative abundance < 1%) (Lan & Bai 2012). The dominant and common species in plant community include *Leymus chinensis* (perennial rhizomatous grass, PR), *Stipa grandis* (perennial bunchgrass, PB), *Agropyron cristatum* (PB), *Achnatherum sibiricum* (PB), *Carex korshinskyi* (sedge), *Kochia prostrate* (perennial forbs, PF), *Allium tenuissimum* (PF), *Chenopodium glaucum* (annual forbs, AF), *Axyris amaranthoides* (AF) and *Salsola collina* (AF) (Bai *et al.* 2004).

N ADDITION EXPERIMENT

To explore the effects of N addition on plant species diversity and ecosystem functioning, an N addition experiment was initiated in 2000 and is still ongoing (Bai *et al.* 2010; Lan & Bai 2012). The experiment has six treatments and nine replicates for each treatment, with a total number of 54 5 m × 5 m plots. Experimental plots were arranged in a randomized block design, with 1-m-width walkways between plots. N treatments included six levels of N addition rate, 0, 1.75, 5.25, 10.5, 17.5 and 28.0 g N m^{-2} $year^{-1}$ as commercial granular NH_4NO_3 (Bai *et al.* 2010). The low N input rates (e.g. 0, 1.75 and 5.25 g N m^{-2} $year^{-1}$) allow us to approximate N deposition and estimate critical thresholds for species loss (Bobbink *et al.* 2010). The high N input rates (i.e. 10.50, 17.50, 28.00 g N m^{-2} $year^{-1}$) allow us to approximate management techniques (e.g. N fertilization) and assess the effects of N enrichment on plant diversity (Schellberg *et al.* 1999; Crawley *et al.* 2005; Socher *et al.* 2012). For all treatments, to ensure that N was the only limiting nutrient, based on the soil census data, we also added the same amount of P (10 g P_2O_5 m^{-2} $year^{-1}$), S (0.2 mg m^{-2} $year^{-1}$) and trace elements (Zn, 190 mg m^{-2} $year^{-1}$, Mn, 160 mg m^{-2} $year^{-1}$ and B, 31 mg m^{-2} $year^{-1}$). Each year, nutrients were uniformly applied to each treatment plot with manual broadcasting in the mid-growing season (July 1–5) coinciding with high temperature and precipitation, as in other N addition studies (Tilman 1987).

SPECIES–AREA RELATIONSHIP

To test the scale dependence of N effects on species richness, we collected species abundance data from fifty-four 5 m × 5 m plots for constructing species–area relationship (SAR). Each 25 m^2 plot was divided into twenty-five spatially explicit 1 m × 1 m quadrats. In each quadrat, we determined the abundance (number of individuals) for each species in August 2010. For non-clonal species with no physical connections among different stems (e.g. *C. glaucum*), an individual was defined as a separately rooted above-ground shoot. For caespitose species with densely packed ramets, such as bunchgrasses (i.e. *S. grandis*), an individual was defined as a basal. For rhizomatous species with widely spaced ramets (e.g. *L. chinensis*), an individual was defined as a ramet (Pérez-Harguindeguy *et al.* 2013).

Based on our data sets, the empirical SAR in each plot was constructed with type IIA design (Scheiner 2003), that is using a set of spatially explicit quadrats arrayed in a continuous grid (Fig. S1 in Supporting Information). The set of quadrat sizes in each 5 m × 5 m plot includes 1, 2, 3, 4, 5, 6, 8, 9, 10, 12, 15, 16, 20 and 25 m^2, respectively. For a given quadrat (sampling area), we aggregated contiguous 1 m^2 quadrats and counted the number of species. For a given quadrat size within each plot, the species richness was the average of number of species across all quadrats with the same size. For example, the species richness of 1 m^2 quadrats within each plot was the average of number of species across twenty-five 1 m × 1 m quadrats. In the same way, we determined the species richness of 2, 3, 4 m^2 and other quadrat sizes within each plot.

SARs were fitted and model parameters were estimated using MMSAR R-package (Guilhaumon, Mouillot & Gimenez 2010). Specifically, we fitted all the eight candidate models of SARs in the MMSAR R-package (Fig. S2). These models include power, exponential, negative exponential, Monod, rational function, logistic, Lomolino and cumulative Weibull functions of SAR (Guilhaumon, Mouillot & Gimenez 2010). The preliminary analysis indicated that, among the eight models, power, logistic and Monod functions were three best fit models with the highest R^2 value but lowest AIC, AICc and BIC values. However, based on the experimental design and sampling scheme of this study, the shape of the species–area curve is expected to be convex upward, which can be best fitted by the power model (Tjørve 2003). It can also be used to determine the predicted N_{crit} and extrapolate the results to larger scales. Therefore, we used the power model $S = cA^z$ (S, species; A, sampling area) to assess the scale dependence of N effects on species richness.

ESTIMATING EFFECTS OF N ADDITION ON SPECIES LOSS

Absolute species loss was calculated as the difference of species richness between control and each N treatment (i.e. $Richness_{control} - Richness_{treat}$). To allow direct comparison across sampling areas, proportional species loss was defined as loss proportion compared to control and calculated as one minus species richness response ratio (i.e. $1 - Richness_{treat}/Richness_{control}$). For each N treatment, the percentage of overall species richness was calculated as the ratio of species richness at a given sampling area to the overall species richness of the plot (25 m^2), with the values ranging from 0% to 100%.

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1. Parameters of 25 m^2 plots used for each simulation to partition mechanisms contributing to changes in the slope and intercept of species–area relationship (SAR). Parameters were calculated from control and N addition plot. Simulations 1 and 2 represent observed SAR of control and N addition plot, respectively. Simulations 3, 4 and 5 change parameters to test the contribution of each mechanism. The contribution of the four potential mechanisms to changes in the *z*- and c-value of SAR was calculated as follows: overall species richness = S_2–S_3; total number of individuals = S_3–S_4; species abundance distribution = S_4–S_5; species aggregation = S_5–S_1; and total effect = S_2–S_1 (S_1–S_5 represent the *z*-value of simulated SAR from simulations 1–5, respectively)

	Control community parameters				N addition community parameters			
Simulation	Overall species richness	Number of individuals	Species abundance distribution	Species aggregation	Overall species richness	Number of individuals	Species abundance distribution	Species aggregation
1	✓	✓	✓	✓				
2					✓	✓	✓	✓
3	✓					✓	✓	✓
4	✓	✓					✓	✓
5	✓	✓	✓					✓

For a given simulation, parameters with check marks ('✓') were included in the simulation, whereas parameters without check marks were not included in the simulation.

Based on the relationships between proportional species loss and N addition rate, we extrapolated our fitted curve and calculated the predicted critical threshold of N rate (N_{crit}), below which there are no reductions in species diversity (Clark & Tilman 2008). Therefore, for a given sampling area, when N addition rates < N_{crit}, species loss would not occur as the extant community is capable to sequester the added N; when N rates > N_{crit}, species richness would be decreased in response to N addition (Bai *et al.* 2010).

SAR DECOMPOSITION

To partition the relative contribution of the four potential mechanisms responsible for N-induced changes in the slope (*z*-value) and intercept (*c*-value) of SAR, we created a set of null models based on sampled data using methods of Collins & Simberloff (2009) and Powell, Chase & Knight (2013). For each 25 m^2 plot of each treatment, SARs were determined and simulated by four factors: species aggregation overall, species abundance distribution, total number of individuals and species richness (Table 1).

We used rarefaction bias to quantify the effect of species aggregation (i.e. inter- and intraspecies aggregation) on changes in the *z*- and *c*-values of SAR, and a greater bias indicated higher spatial aggregation (Collins & Simberloff 2009; Powell, Chase & Knight 2013). For each N treatment, the null model was constructed using spatially explicit species abundance data collected in nine 25 m^2 plot. For each 25 m^2 plot, we randomized individuals within and among the twenty-five 1 m^2 quadrats, determined species richness at each sampling area (quadrat size) and constructed the rarefaction curve based on the set of rarefaction species richness and sampling area (Powell, Chase & Knight 2013). The mean rarefaction curve for each plot was the average of 1000 simulated rarefaction curves, while the mean rarefaction curve for each treatment was the average of 9000 simulated rarefaction curves. These processes were performed using the software *EstimateS*. Rarefaction bias (RB) was calculated as the difference in area between the mean rarefaction curve (non-spatially explicit) and empirical SAR (spatially explicit) divided by the area under the empirical SAR, that is RB = $(Area_{rarefaction} - Area_{empirical})/Area_{empirical}$ (Collins & Simberloff 2009; Powell, Chase & Knight 2013). For a given sampling area, per cent rarefaction bias (PRB) was calculated as the difference of species richness between mean rarefaction and empirical SAR divided by the species richness of empirical SAR, that is PRB = $(SR_{rarefaction} - SR_{empirical})/SR_{empirical}$ (Collins & Simberloff 2009).

To examine the effect of species abundance distribution on shifts in the *z*- and *c*-values of SAR, we fitted the ranked species abundance distributions for each 25 m^2 plot by using a log-series model: $Y = (-1/\log(1-c)) * c^{X}/X$, where Y is species' relative abundance, X is rank of species' relative abundance, and *c* is coefficient (Powell, Chase & Knight 2013). In the null models, species abundance was calculated by multiplying total number of individuals collected in each 25 m^2 plot and the relative abundance of each species obtained from the log-series distribution of the same plot. We randomly filled twenty-five 1 m^2 quadrats based on the number of individuals in each plot and reassigned all individuals randomly in space for each 25 m^2 plot. We determined the average species richness at each sampling area (i.e. 1, 2, 3, 4, 5, 6, 8, 9, 10, 12, 15, 16, 20 and 25 m^2). Then, the average species richness was divided by (1+ per cent rarefaction bias) to get the simulated species richness at each sampling area (Collins & Simberloff 2009). By the set of simulated species richness and sampling areas, we constructed the simulated SAR using power model ($S = cA^z$). We replicated each simulation 1000 times and then calculated the mean simulated SAR. All simulations were conducted with R 2.14 (R Development Core Team).

As our experiment was a random block design with nine blocks, we compared simulated SARs between N treatment plots and control plot (zero N) from the same block for examining the N effects on the slopes and intercepts of SARs in log–slog space. For a given pair of N treatment and control plots, we generated five simulations using the parameters as shown in Table 1. Simulations 1 and 2 represent observed SARs. Simulations 3, 4 and 5 changed the parameters to test the contribution of each mechanism. The contribution of each mechanism was calculated by subtracting the *z*- or *c*-values of the simulations (Powell, Chase & Knight 2013). Specifically, the contribution of the four potential mechanisms to changes in the *z*-value of SAR was calculated as follows: overall species richness = S_2–S_3; total number of individuals = S_3–S_4; species abundance distribution = S_4–S_5; species aggregation = S_5–S_1; and total effect = S_2–S_1 (S_1–S_5 represent the *z*-value of simulated SAR from simulations 1–5, respectively). We repeated these processes to partition the mechanisms contributing to the changes in the *c*-value of SAR.

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

STATISTICAL ANALYSIS

Statistical analyses were performed using SAS v. 8.0 (SAS Institute, Cary, NC, USA). Two-way ANOVAS were performed on the effects of N treatment, sampling area and their interactions on species richness and proportional species loss. Regression models were used to determine the relationships between N addition rate and biodiversity responses (adjustments for nonlinearity were made as needed).

Results

N EFFECTS ON SPECIES RICHNESS ACROSS DIFFERENT SAMPLING AREAS

Two-way ANOVAS on the effects of N treatment (N), sampling area (A) and their interactions on species richness (SR) and absolute species loss (ASL) showed that the effects of N addition and sampling area on SR and ASL were highly significant ($P < 0.0001$), with their interactions being non-significant (Table 2). Effects of N treatment on proportional species loss were also highly significant ($P < 0.0001$), while the effects of sampling area were not significant ($P = 0.2375$; Table 2). After 10 years of treatment, N addition significantly ($P < 0.05$) decreased species richness at each sampling area for most treatments except the treatment of 1.75 g N m^{-2} $year^{-1}$ (Fig. 2a). There was no significant ($P > 0.10$) difference in species richness between control and treatment of 1.75 g N m^{-2} $year^{-1}$ across all sampling areas in our study (Fig. 2a; Table S2). At the treatment of 5.25 g N m^{-2} $year^{-1}$, species richness was not significantly different ($P > 0.10$) from that of control when sampling area ≥ 20 m^2 (Fig. 2a; Table S2).

Table 2. Results of two-way anovas on the effects of N treatment (N), sampling area (A) and their interactions on species richness, absolute species loss and proportional species loss

Response	Term	d.f.	*F*	*P* value
Species richness	N	5	201.92	< 0.0001
	A	13	89.24	< 0.0001
	N × A	65	0.54	0.9986
Absolute species loss	N	4	201.95	< 0.0001
	A	13	3.73	< 0.0001
	N × A	52	0.54	0.9986
Proportional species loss	N	4	214.86	< 0.0001
	A	13	1.25	0.2375
	N × A	52	0.07	1.0000

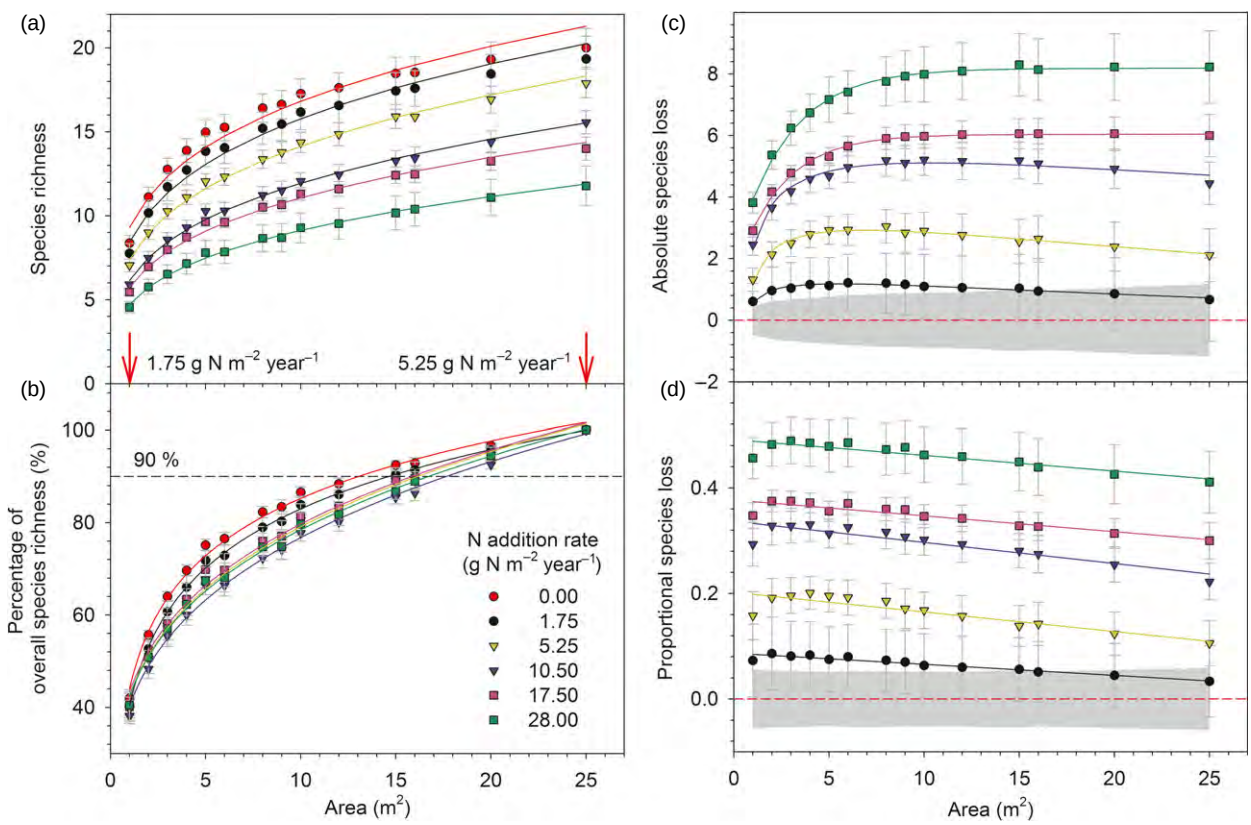


Fig. 2. Effects of N addition on (a) species richness, (b) percentage of overall species richness, (c) absolute species loss and (d) proportional species loss across different sampling areas. For a given sampling area, percentage of overall species richness was the ratio of species richness to overall species richness of 25 m^2 plot. Absolute species loss was calculated as the difference of species richness between control and each N treatment (i.e. $Richness_{control} - Richness_{treat}$). Proportional species loss was calculated as the ratio of species loss in each N treatment to the mean species richness in control (i.e. $1 - Richness_{treat}/Richness_{control}$). The values for each treatment were the average of nine replicates (error bars denote SEM). Error bands in Fig 1c and d were standard errors at each sampling area in control plots. Arrows indicated the least sampling area that species richness of N addition plots was not significantly different ($P > 0.10$) from control.

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

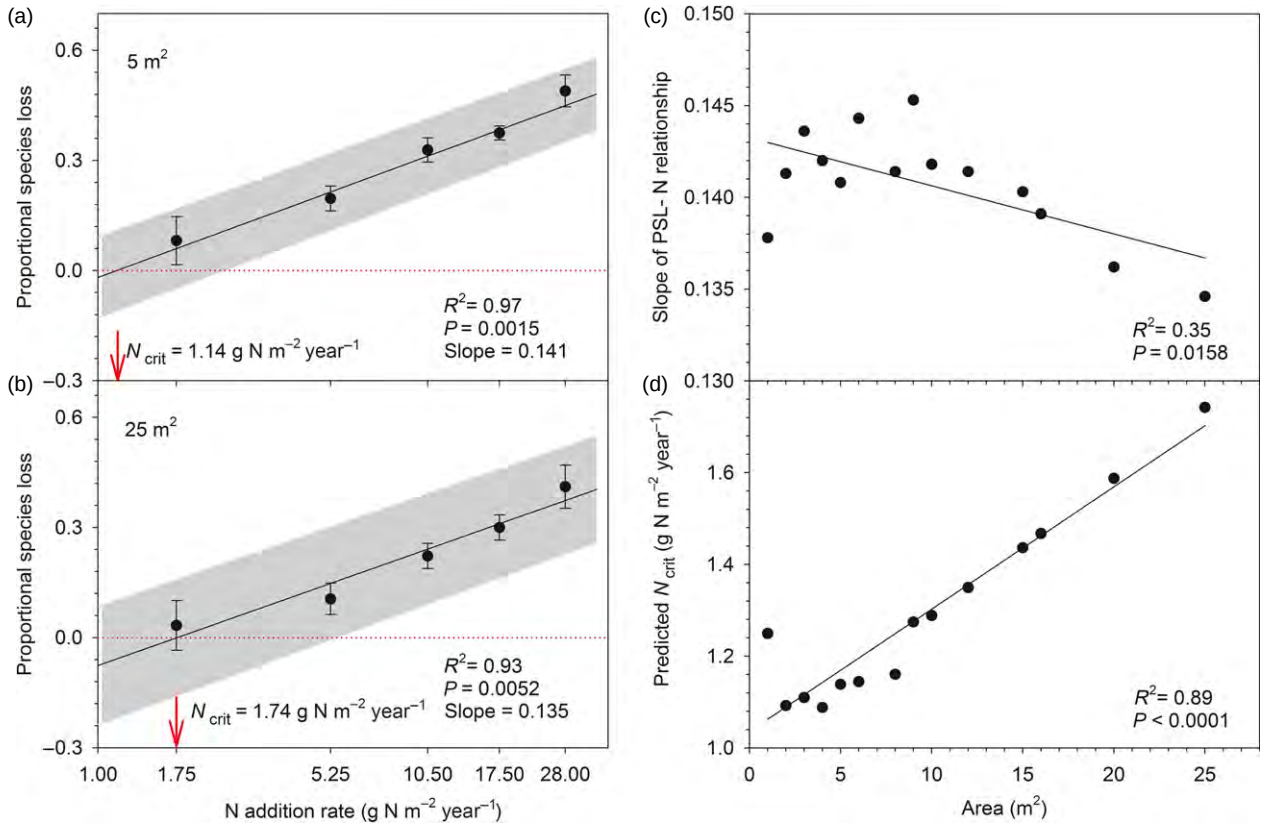


Fig. 3. Proportional species loss (PSL) across N treatments at sampling area (a) 5 m^2 and (b) 25 m^2. (c) Slope of the relationship between PSL and N addition rate and (d) predicted critical threshold across different sampling areas. Solid lines are plot averages for each treatment fitted to a logarithmic curve excluding the control (error bands correspond to 95% confidence interval). Arrow indicates the predicted critical threshold (N_{crit}) of N rate, below which there is no species loss at each sampling area. The *x*-axis is the logarithm of N addition rate for Fig. 3a and b.

Absolute species loss (i.e. Richness$_{control}$ − Richness$_{treat}$) responded nonlinearly to sampling area ($P < 0.05$; Fig. 2c). At sampling area < 8 m^2, the absolute species loss increased with sampling area; but when sampling area > 8 m^2, species loss was relatively constant or even decreased (Fig. 2c). For example, at the sampling area of 1 m^2, mean species richness of control and 5.25 g N m^{-2} year^{-1} treatment was 8.36 and 7.04, respectively, and absolute species loss was 1.32. At the sampling area of 8 m^2, mean species richness of these two treatments was 16.41 and 13.36, respectively, and absolute species loss increased to 3.05. At the sampling area of 25 m^2, mean species richness of these two treatments was 20.00 and 17.89, respectively, and absolute species loss decreased to 2.11 (Fig. 2c).

Proportional species loss (PSL, i.e. 1 − Richness$_{treat}$/Richness$_{control}$) significantly decreased with increasing sampling area for all N treatments (mean $R^2 = 0.82$, $P < 0.0001$; Fig. 2d). Relationships between PSL and N rate were well fitted by loglinear models at all sampling rates, that is PSL = Intercept + Slope × Log (N) ($R^2 > 0.90$, $P < 0.01$; Fig. 3a and b). Slope of PSL–N relationship significantly decreased with increasing sampling area ($R^2 = 0.54$, $P = 0.0017$; Fig. 3c). We extrapolated the fitted curve of PSL–N relationship and calculated the predicted critical threshold of N rate (N_{crit}) in which no species loss occurred at given sampling area. N_{crit} significantly increased with sampling area ($R^2 = 0.48$; $P = 0.0035$; Fig. 3d). The predicted N_{crit} was 1.14 (95% CI 0.52–2.45) and 1.74 (95% CI 0.52–5.44) g N m^{-2} year^{-1} at sampling areas of 5 and 25 m^2, respectively (Fig. 3d).

SPECIES–AREA RELATIONSHIPS (SARS)

N addition did not change the shape of SARs, and the SARs were best fitted by power-law model (mean $R^2 = 0.97$; Fig. 2a). Compared to control, SARs in N addition treatments saturated more slowly (Fig. 2b). For example, to encounter 90% of overall species richness in each plot, the minimum sampling area was about 13, 16 and 19 m^2 for treatment of control, 5.25 and 28.00 g N m^{-2} year^{-1}, respectively (Fig. 2b).

N addition significantly increased the slope (z-value) of SAR, which saturated at 10.50 g N m^{-2} year^{-1} ($R^2 = 0.92$, $P = 0.0236$; Fig. 4a). However, N addition decreased the intercept (c-value) of SARs with $c = 9.08$ in control and $c = 6.15$ in 10.50 g N m^{-2} year^{-1} (Fig. 4b). Relationships between c-value and N rate were best fitted by a loglinear model ($R^2 = 0.97$, $P = 0.0002$; Fig. 4b).

PLANT COMMUNITY COMPOSITION AND STRUCTURE

Compared to control plots, total number of individuals were slightly decreased at low N addition rates (1.75 and

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

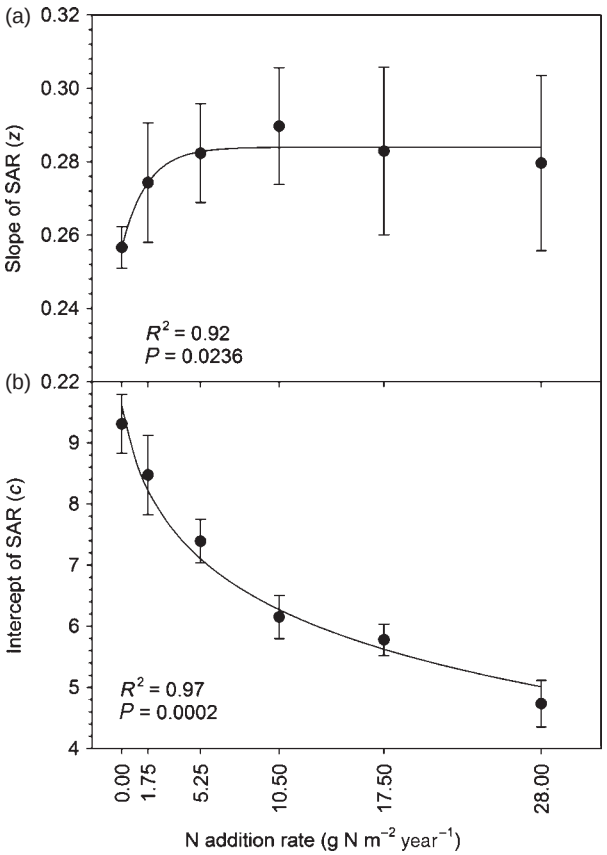


Fig. 4. Effects of N addition on (a) slope (*z*-value) and (b) intercept (*c*-value) of the species–area relationship (SAR). For each treatment, SAR was fitted by the power-law model ($S = cA^{z}$). The *z*- and *c*-values for each treatment were the average of nine replicates (error bars denote SEM).

5.25 g N m^{-2} year^{-1}), but increased at high N addition rates (10.50, 17.50 and 28.00 g N m^{-2} year^{-1}) by 36% (Fig. 5b). At the low N addition rates, decreases of individual numbers were mainly due to loss of small-sized species, *Carex korshinskyi* (perennial sedge). This species had the largest number of individuals among all species in control, but it was competitively excluded after N addition, leading to the decreased total individuals in the community. At the high N addition rates, the increase of individual numbers was due to the increase of a few N-favoured annual species (i.e. *C. glaucum and A. amaranthoides*).

N addition decreased the abundance of rare species and altered species abundance distribution (Fig. 5c). Shannon evenness firstly increased at lower N addition rates and then declined at higher N addition rates (R^2 = 0.79, P = 0.0442; Fig. 5c). To evaluate the effects of species aggregation on SAR, we calculated the rarefaction bias, with greater rarefaction bias indicating greater species aggregation. After N addition, rarefaction bias was significantly increased from 6.48% in control to 10.33% at the three highest N addition rates (R^2 = 0.91, P = 0.0021; Fig. 5d), indicating that plant species in N-fertilized communities were more aggregated.

PARTITIONING MECHANISMS CONTRIBUTING TO CHANGES IN SARS

Results from the simulations showed that, after N addition, changes in species abundance distribution linearly increased the slope (*z*-value) of SAR (R^2 = 0.89, P = 0.0106), but this positive effect was moderated by loss of overall species richness (R^2 = 0.99, P = 0.0002; Fig. 6a). However, the response of the intercept (*c*-value) of SAR to N were mainly due to changes in species abundance distribution (R^2 = 0.82, P = 0.0222), and loss of overall species richness had no significant effects on *c*-value (R^2 = 0.01, P = 0.7067; Fig. 6b). Compared to changes in species abundance distribution, changes in total number of individuals and species aggregation had much less effects on either *z*- or *c*-value (Fig. 6).

Discussion

Our study provides a critical test of the scale dependence of N effects on species richness with a gradient of N addition rates. Although N addition decreased species richness across all scales, the proportional loss of species richness decreased with increasing sampling area. Meanwhile, the predicted critical threshold (N_{crit}) of species loss increased with sampling area and ranged from 1.1 to 1.7 g N m^{-2} year^{-1}, which is greater than a previous study based on 0.5 m^2 quadrat (0.85 g N m^{-2} year^{-1}) (Lan & Bai 2012). Although the predicted N_{crit} is still within the range of N_{crit} (0.5–2.0 g N m^{-2} year^{-1}) reported from North American and European grasslands (Clark & Tilman 2008; Bobbink *et al.* 2010), our study clearly demonstrates that both the sensitivity (N_{crit}) and magnitude of species loss in response to N addition are scale dependent. The regional species pool is less sensitive to N addition, and the N_{crit} could be greater than this range at much larger scales. Our results are consistent with two other studies that N-induced species loss depends on scales (Crawley *et al.* 2005; Chalcraft *et al.* 2008). Our findings from long-term experimental studies in the Eurasian steppe, combined with those of related studies in European and North American terrestrial herbaceous plant communities (Crawley *et al.* 2005; Chalcraft *et al.* 2008), clearly suggest that N-induced species loss was generally mitigated at larger spatial scales. In addition, previous studies showed that N-induced species loss increased with experiment duration (Clark & Tilman 2008; Lan & Bai 2012). A recent study also found that the N effects on slope of SAR increased with experiment duration (Lepš 2014). Therefore, the effects of spatial scale on biodiversity loss may also depend on the duration of N enrichment.

Our results demonstrated that the scale dependence of N-induced biodiversity loss was characterized by changes in the slope and intercept of species–area relationship (SAR). Through SAR decomposition, we found that contributions to changes in SAR were highly uneven among four potential mechanisms, including overall species richness, number of individuals, species abundance distribution and species

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

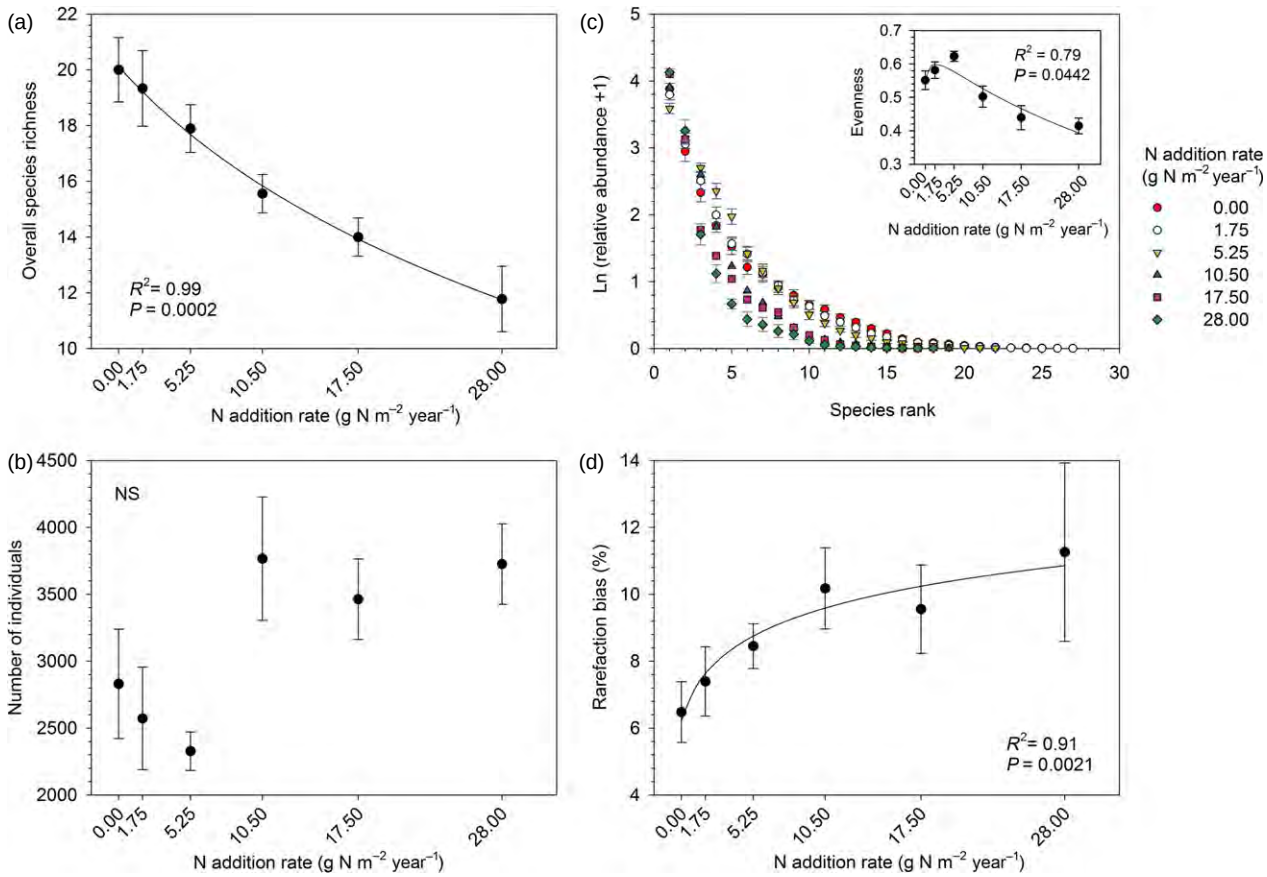


Fig. 5. Effects of N addition on (a) overall species richness, (b) number of individuals (or total abundance of all species), (c) species abundances distribution and (d) rarefaction bias for each plot (25 m^2). Evenness of species abundance distribution was calculated as Shannon evenness. A greater bias indicated that the community was more aggregated. For each treatment, the values were the average of nine replicates (error bars denote SEM).

aggregation. Changes in overall species richness and species abundance distribution significantly affected SAR after N addition, supporting the findings that these two factors were key to SAR (He & Legendre 2002; Tjørve *et al.* 2008; Chase & Knight 2013). The observed increases in the slope of SAR were mainly caused by the positive effect of changes in species abundance distribution over the negative effect of decline in overall species richness. Contrary to other studies (He & Legendre 2002; Tjørve *et al.* 2008; Chase & Knight 2013; Powell, Chase & Knight 2013), changes in total number of individuals had no significant effect on SAR in response to N addition. It seems likely that the total number of individuals in our study were so high (> 100 individual m^{-2}) that increasing individual numbers after N addition had a few effects on SAR. At low N addition rates (≤ 5.25 g N m^{-2} year^{-1}), the total number of individuals decreased because of the decline of *C. korshinskyi*, a small and short sedge species. However, at the high N addition rates (≥ 10.5 g N m^{-2} year^{-1}), the total number of individuals was increased. The increase in the total number of individuals at the high N addition rates was mainly caused by two reasons. First, in the highest N treatments, bunchgrasses (i.e. *S. grandis, A. cristatum*) were replaced by a large number of tall annual species (e.g. *A. amaranthoides, C. glaucum*); thus, the total individual number increases. Secondly, without N enrichment, plant above-ground cover was discontinuous in semi-arid grasslands because of strong below-ground competition (e.g. N and water) (Burke *et al.* 1998; Bai *et al.* 2008). The high levels of N inputs removed N limitation for plants, reduced below-ground competition and thereby increased the total number of individuals, which decreased community openness and increased above-ground vegetation cover (Bai *et al.* 2010; Lan & Bai 2012). Therefore, changes in species composition and decreased below-ground competition were attributable to the increased total number of individuals at the three highest N addition rates.

Moreover, the increases in species aggregation in response to N addition also had little effect on the slope SAR, which is consistent to previous findings (Tjørve *et al.* 2008). Effect size of species aggregation on SAR has been suggested to increase with spatial heterogeneity and the extent of study (Tjørve *et al.* 2008; Scheiner *et al.* 2011). The experimental area in our study is comparatively homogeneous, and the extent of study is relatively small (25 m^2) for each SAR. These factors could contribute to the limited effects of changes in species aggregation on SAR in our study. The N-induced decreases in the intercept (*c*-value) of SAR were mainly due to negative effects of changes in species abundance distribution and species aggregation. The decline in

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

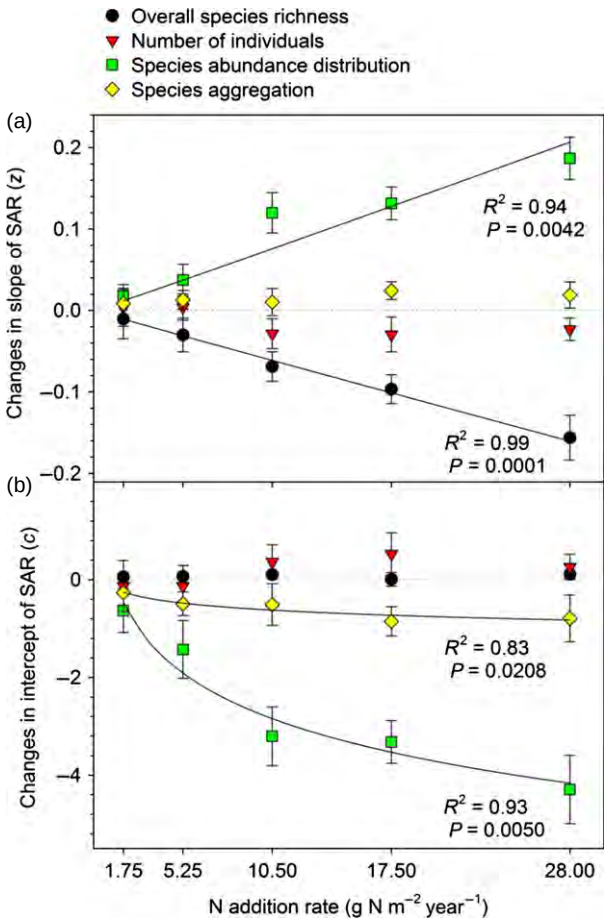


Fig. 6. Contribution of changes in overall species richness, number of individuals, species abundance distribution and species aggregation to the changes in (a) slope (*z*-value) and (b) intercept (*c*-value) of the species–area relationship (SAR) after N addition. For each treatment, the values were the average of nine replicates (error bars denote SEM).

overall species richness, in contrast, had no significant effects on the intercept of SAR. The result was inconsistent with the predictions of species pool hypothesis that species richness at small scales (associated with intercept of SAR) was determined by species pool size (Rosenzweig 1995; Pärtel *et al.* 1996; Zobel 1997). Following N addition, the decline of overall species richness was mainly caused by the loss of rare species, which had limited contribution to community species richness (or *c*-value) at small scales. Given that N addition intensified interspecific competition, the results support the hypothesis that strong species interactions would lead to curvilinear local–regional relationships, that is regional species richness changes had little effect on the local assemblage (Cornell & Lawton 1992).

Our results suggest that without identifying the scaling effects, we may substantially overestimate biodiversity losses associated with regional N deposition. For example, at addition rate of 5.25 g N m^{-2} year^{-1}, the proportional species loss was 16–20% at the sampling area of 1–4 m^2; however, it was only 11% at the sampling area of 25 m^2. Increase in the slope (*z*-value) of SAR was in response to the positive effect of changes in species abundance distribution over the negative effect of losses in overall species richness. The effects of N on overall species richness and species abundance distribution differ among ecosystems (Hillebrand *et al.* 2007; Chalcraft *et al.* 2008), and thus, slopes of SARs show context-dependent responses to N addition (Crawley *et al.* 2005; Lepš 2014). Meanwhile, as sampling increases to include more area and spatial heterogeneity, changes in SAR will be driven more by species aggregation at larger scales (Keil *et al.* 2011). Future efforts should include more ecosystem types and larger ranges of scales to identify how site-specific characteristics (i.e. moisture, temperature and spatial heterogeneity) influence N effects on slope of SAR, which is the key to understand the scale-dependent effects of N on biodiversity. Will regional species pool be maintained as *z*-value increases after N addition? Our findings showed that, at the treatments of 5.25 g N m^{-2} year^{-1}, species richness decreased at small scales, but it was not significantly different from control when sampling area ≥20 m^2. Above this rate of N addition, species richness declined at larger scales. Chalcraft *et al.* also found that, among 11 experiments which suffered N-induced plant diversity loss at small scales, only three of them maintained diversity at large scales after N addition (Chalcraft *et al.* 2008). In our study, the proportional species loss (i.e. $1 - \text{Richness}_{\text{treat}}/\text{Richness}_{\text{control}}$) and sampling area were significantly negatively correlated. By extrapolating the fitted curve of proportional species loss and sampling area, we predict that the smallest sampling area with no species loss compared to control is 41, 54, 85, 125 and 165 m^2 at the N addition rate of 1.75, 5.25, 10.50, 17.50 and 28.00 g N m^{-2} year^{-1}, respectively. Large-scale observational studies along N deposition gradients should be conducted as a first test of these predictions.

Our study has important implications for the biodiversity conservation and ecosystem management of the vast semi-arid grasslands in the Eurasian Steppe region. First, our results suggest that both the critical threshold and magnitude of N-induced biodiversity loss are scale dependant. These findings highlighted the urgency of reassessing the previously estimated values of critical loads, which have been widely used as the backbone of biodiversity conservation and environmental legislation on transboundary pollution in Europe and United States (Posch, Vries & Hettelingh 1995; Sala *et al.* 2000; Pardo *et al.* 2011). Secondly, our findings demonstrate that the scale dependence of N-induced biodiversity loss is mainly triggered by reductions in overall species richness and changes in species abundance distribution. It has also been predicted that N deposition will continue to increase in this century (Galloway *et al.* 2008). Therefore, future biodiversity conservation should put high priorities on the grassland management practices that could efficiently mitigate the negative consequences of N-induced decreases in species richness and shifts in species dominance, such as mowing or grazing (Collins *et al.* 1998).

Acknowledgements

We thank Dunmei Lin, Xihunghua Sui, Kristin Powell, Xiujuan Qiao, Zhiyao Tang, Lorraine Clarke and Liyin Liang for help with data analysis, and Xue

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Bai, Xiaoliang Wang and many others at the Inner Mongolia Grassland Ecosystem Research Station, Chinese Academy of Sciences for their help with fieldwork. This project was supported by the National Natural Science Foundation of China (31030013, 31320103916) and Strategic Priority Research Program of the Chinese Academy of Sciences (XDA05050400).

Data accessibility

Species richness and species abundance data are available from the Dryad Digital Repository (Lan *et al.* 2015).

References

Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

Bai, Y.F., Han, X.G., Wu, J.G., Chen, Z.Z. & Li, L.H. (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, **431**, 181–184.

Bai, Y.F., Wu, J.G., Xing, Q., Pan, Q.M., Huang, J.H., Yang, D.L. & Han, X.G. (2008) Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. *Ecology*, **89**, 2140–2153.

Bai, Y.F., Wu, J.G., Clark, C.M., Naeem, S., Pan, Q.M., Huang, J.H., Zhang, L.X. & Han, X.G. (2010) Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands. *Global Change Biology*, **16**, 358–372.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M. *et al.* (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications*, **20**, 30–59.

Burke, I.C., Lauenroth, W.K., Vinton, M.A., Hook, P.B., Kelly, R.H., Epstein, H.E., Aguiar, M.R., Robles, M.D., Aguilera, M.O., Murphy, K.L. & Gill, R.A. (1998) Plant-soil interactions in temperate grasslands. *Biogeochemistry*, **42**, 121–143.

Chalcraft, D.R., Cox, S.B., Clark, C., Cleland, E.E., Suding, K.N., Weiher, E. & Pennington, D. (2008) Scale-dependent responses of plant biodiversity to nitrogen enrichment. *Ecology*, **89**, 2165–2171.

Chase, J.M. & Knight, T.M. (2013) Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. *Ecology Letters*, **16**, 17–26.

Clark, C.M. & Tilman, D. (2008) Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, **451**, 712–715.

Clark, C.M., Bai, Y., Bowman, W.D., Cowles, J.M., Fenn, M.E., Gilliam, F.S., Phoenix, G.K., Siddique, I., Stevens, C.J., Sverdrup, H.U. & Throop, H.L. (2013) Nitrogen deposition and terrestrial biodiversity. *Encyclopedia of Biodiversity*, 2nd edn. (ed. S.A. Levin), pp. 519–536. Elsevier Publishing, Waltham, MA.

Cleland, E.E. & Harpole, W.S. (2010) Nitrogen enrichment and plant communities. *Year in Ecology and Conservation Biology 2010*, Vol. **1195** (eds R.S. Ostfeld & W.H. Schlesinger), pp. 46–61. Blackwell Publishing, Oxford.

Collins, M. & Simberloff, D. (2009) Rarefaction and nonrandom spatial dispersion patterns. *Environmental and Ecological Statistics*, **16**, 89–103.

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, **280**, 745–747.

Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, **61**, 1–12.

Crawley, M.J., Johnston, A.E., Silvertown, J., Dodd, M., de Mazancourt, C., Heard, M.S., Henman, D.F. & Edwards, G.R. (2005) Determinants of species richness in the Park Grass Experiment. *American Naturalist*, **165**, 179–192.

Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z.C., Freney, J.R., Martinelli, L.A., Seitzinger, S.P. & Sutton, M.A. (2008) Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science*, **320**, 889–892.

Gilliam, F.S. (2006) Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology*, **94**, 1176–1191.

Goldberg, D.E. & Miller, T.E. (1990) Effects of different resource additions on species-diversity in an annual plant community. *Ecology*, **71**, 213–225.

Guilhaumon, F., Mouillot, D. & Gimenez, O. (2010) mmSAR: an R-package for multimodel species-area relationship inference. *Ecography*, **33**, 420–424.

Hautier, Y., Niklaus, P.A. & Hector, A. (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science*, **324**, 636–638.

He, F. & Legendre, P. (2002) Species diversity patterns derived from species-area models. *Ecology*, **83**, 1185–1198.

Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E., Cleland, E.E., Elser, J.J., Harpole, W.S., Ngai, J.T., Seabloom, E.W. & Shurin, J.B. (2007) Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 10904–10909.

Jenerette, G.D. & Shen, W. (2012) Experimental landscape ecology. *Landscape Ecology*, **27**, 1237–1248.

Keil, P., Biesmeijer, J.C., Barendregt, A., Reemer, M. & Kunin, W.E. (2011) Biodiversity change is scale-dependent: an example from Dutch and UK hoverflies (Diptera, Syrphidae). *Ecography*, **34**, 392–401.

Lan, Z. & Bai, Y. (2012) Testing mechanisms of N-enrichment-induced species loss in a semiarid Inner Mongolia grassland: critical thresholds and implications for long-term ecosystem responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 3125–3134.

Lan, Z.C., Jennerette, G.D., Zhan, S.X., Li, W.H., Zheng, S.X. & Bai, Y.F. (2015) Data from: Testing the scaling effects and mechanisms of N-induced biodiversity loss: evidence from a decade-long grassland experiment. *Dryad Digital Repository*, doi: 10.5061/dryad.h7893.

Lepš, J. (2014) Scale- and time-dependent effects of fertilization, mowing and dominant removal on a grassland community during a 15-year experiment. *Journal of Applied Ecology*, **51**, 978–987.

Oksanen, J. (1996) Is the humped relationship between species richness and biomass an artefact due to plot size? *Journal of Ecology*, **84**, 293–295.

Oksanen, J. (1997) The no-interaction model does not mean that interactions should not be studied. *Journal of Ecology*, **85**, 101–102.

Pardo, L.H., Fenn, M.E., Goodale, C.L., Geiser, L.H., Driscoll, C.T., Allen, E.B. *et al.* (2011) Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecological Applications*, **21**, 3049–3082.

Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, **75**, 111–117.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. *et al.* (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167–234.

Phoenix, G.K., Hicks, W.K., Cinderby, S., Kuylenstierna, J.C.I., Stock, W.D., *et al.* (2006) Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. *Global Change Biology*, **12**, 470–476.

Posch, M., Vries, W.d. & Hettelingh, J.P. (1995) Critical loads of sulfur and nitrogen. *Calculation and Mapping of Critical Thresholds in Europe: Status Report 1995* (eds M. Posch, P.A.M. de Smet, J.P. Hettelingh & R.J. Downing), pp. 31–41. RIVM, Bilthoven. RIVM Rep. 259101004.

Powell, K.I., Chase, J.M. & Knight, T.M. (2013) Invasive plants have scale-dependent effects on diversity by altering species-area relationships. *Science*, **339**, 316–318.

Preston, F.W. (1960) Time and space and the variation of species. *Ecology*, **41**, 611–627.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Sandel, B. & Corbin, J.D. (2012) Scale-dependent responses of species richness to experimental manipulation of productivity and disturbance in Californian coastal grasslands. *Journal of Vegetation Science*, **23**, 906–918.

Scheiner, S.M. (2003) Six types of species-area curves. *Global Ecology and Biogeography*, **12**, 441–447.

Scheiner, S.M., Chiarucci, A., Fox, G.A., Helmus, M.R., McGlinn, D.J. & Willig, M.R. (2011) The underpinnings of the relationship of species richness with space and time. *Ecological Monographs*, **81**, 195–213.

Schellberg, J., Moseler, B.M., Kuhbauch, W. & Rademacher, I.F. (1999) Long-term effects of fertilizer on soil nutrient concentration, yield, forage quality and floristic composition of a hay meadow in the Eifel mountains, Germany. *Grass and Forage Science*, **54**, 195–207.

Socher, S.A., Prati, D., Boch, S., Müller, J., Klaus, V.H., Hölzel, N. & Fischer, M. (2012) Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *Journal of Ecology*, **100**, 1391–1399.

Stevens, C.J., Dise, N.B., Mountford, J.O. & Gowing, D.J. (2004a) Impact of nitrogen deposition on the species richness of grasslands. *Science*, **303**, 1876–1879.

Stevens, M.H., Bunker, D.E., Schnitzer, S.A. & Carson, W.P. (2004b) Establishment limitation reduces species recruitment and species richness as soil resources rise. *Journal of Ecology*, **92**, 339–347.

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas, D.G. & Pennings, S. (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 4387–4392.

Tilman, D. (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, **57**, 189–214.

Tjørve, E. (2003) Shapes and functions of species-area curves: a review of possible models. *Journal of Biogeography*, **30**, 827–835.

Tjørve, E., Kunin, W.E., Polce, C. & Tjørve, K.M.C. (2008) Species-area relationship: separating the effects of species abundance and spatial distribution. *Journal of Ecology*, **96**, 1141–1151.

Vitousek, P.M. & Howarth, R.W. (1991) Nitrogen limitation on land and in the sea – how can it occur. *Biogeochemistry*, **13**, 87–115.

Vitousek, P., Aber, J., Howarth, R., Likens, G., Matson, P., Schindler, D., Schlesinger, W. & Tilman, D. (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, **7**, 737–750.

Zobel, M. (1997) The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution*, **12**, 266–269.

Received 12 October 2014; accepted 9 March 2015
Handling Editor: Will Cornwell

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Comparisons of species area relationships (SARs) built from two different sampling schemes (Scheiner 2003).

Figure S2. Statistics of eight candidate models for the species area relationships (SARs).

Table S1. Hypotheses regarding the effects of N addition on the intercept (*c*- value) and slope (*z*-value) of species area relationship.

Table S2. Duncan's multiple range tests reported from one-way ANOVA among different N addition rates at each sampling area.

13652745, 2015, 3, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12395 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2012 doi: 10.1111/j.1365-2664.2012.02205.x

Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient

Yongfei Bai[1]*, Jianguo Wu[1,2], Chris M. Clark[2], Qingmin Pan[1], Lixia Zhang[1], Shiping Chen[1], Qibing Wang[1] and Xingguo Han[1]

[1]*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, 100093, China; and* [2]*School of Life Sciences and Global Institute of Sustainability, Arizona State University, Tempe, AZ, 85287-4501, USA*

Summary

1. The Eurasian steppe has long been subject to grazing by domestic ungulates at high levels, resulting in widespread deterioration of biodiversity and ecosystem services. While abundant evidence demonstrates that heavy grazing alters the ecosystem structure and function of grasslands, research on how grazing specifically affects ecosystem functioning and stoichiometry on broad scales is scarce because of a lack of adequate ungrazed reference sites.

2. We examined the effects of grazing on ecosystem functioning and C : N : P stoichiometry across a precipitation gradient along the 700 km China–Mongolia transect (CMT), covering three community types: meadow steppe, typical steppe and desert steppe.

3. Long-term grazing has dramatically altered the C, N and P pools and stoichiometry of steppe ecosystems along the CMT. Grazing reduced the C, N and P pools in above-ground biomass and litter, while the responses in below-ground biomass and soil C, N and P pools to grazing differed substantially among community types.

4. Grazing increased N content and decreased C : N ratios in all plant compartments, suggesting accelerated N cycling. The altered C : N : P stoichiometry may be explained by changes in the composition of species and functional groups as well as increased foliar N and P contents for the same species in grazed communities.

5. *Synthesis and applications*. Plant stoichiometric responses to grazing ranged from large in the meadow steppe to small in the typical steppe to generally insignificant in the desert steppe, implying that different underlying mechanisms operated along the regional precipitation gradient. Our findings suggest that reducing the stocking rate and restoring the vastly degraded steppes are essential to sustain native steppe biodiversity, ecosystem functioning and biological capacity for mitigating the impact of climate change in the Inner Mongolia grassland.

Key-words: China–Mongolia transect, N and P co-limitation, N cycling, plant and soil C, N and P pools, plant functional group composition, primary production, stoichiometry, the Eurasian steppe

Introduction

Grasslands have experienced dramatic shifts in structure and functioning driven primarily by human disturbances and global climate change (Milchunas & Lauenroth 1993; White, Murray & Rohweder 2000; Knapp *et al*. 2002; Wittmer *et al*. 2010). The Eurasian Steppe, which extends over 8000 km across northeastern China, Mongolia, Russia, Ukraine and Hungary (Coupland 1993), has been historically subjected to continuous grazing by domestic ungulates at increasingly high levels (White, Murray & Rohweder 2000). The long-term grazing has resulted in widespread declines in biodiversity and ecosystem functioning and services (White, Murray & Rohweder 2000; Bai *et al*. 2007). This is triggered by the direct and indirect effects of grazing and often mediated by the complex interactions between vegetation and environmental

*Corresponding author. E-mail: yfbai@ibcas.ac.cn

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society

drivers (Gillson & Hoffman 2007; Golluscio *et al.* 2009; Shan *et al.* 2011). Thus, it is critical to obtain a better understanding of how grazing, abiotic factors and biotic–abiotic interactions influence key properties of ecosystem functioning and sustainability and thereby provide guideline for improving grassland management practices in the Eurasian steppe.

Abundant evidence indicates that grazing affects plant diversity, species composition and primary production (Bai *et al.* 2007; Sasaki *et al.* 2008), as well as soil properties (e.g. soil C and N pools) in many arid, semi-arid and sub-humid grasslands (Frank *et al.* 1995; Reeder *et al.* 2004; Han *et al.* 2008). Few studies, however, have examined the mechanisms of ecosystem responses to grazing, and, in particular, the linkages between above-ground and below-ground components have received little attention (Bardgett & Wardle 2003). The grazing optimization hypothesis predicts that moderate grazing increases primary production through compensatory growth and recycling of limiting nutrients (McNaughton 1979), highlighting links and feedbacks between plant responses and nutrient cycling. Several previous studies propose that moderate grazing accelerated nutrient cycling by promoting the tissue loss of grazing-tolerant species with higher nutrient concentration, stimulating the compensatory growth and enhancing the dominance of these species, and by directly inputting urine and faeces into the system (McNaughton 1985; Frank & Evans 1997). Other studies, however, have shown that grazing decelerated nutrient cycling by inhibiting the growth of palatable and nutrient-rich species with high litter quality and promoting the dominance of those nutrient-poor or chemically defended species with low litter quality that slow rates of nutrient cycling (Ritchie, Tilman & Knops 1998). These seemingly contradictory hypotheses suggest that the effects of grazing on nutrient cycling and ecosystem functioning are contingent on a host of processes, including vegetation type (dry vs. mesic grasslands), evolutionary history of grazing (grazing tolerance of plants), species composition (e.g. plant tissue nutrient concentration, palatability), grazing intensity and N inputs and outputs of the system (Milchunas, Sala & Lauenroth 1988; Ritchie, Tilman & Knops 1998; Singer & Schoenecker 2003).

Ecological stoichiometry provides a powerful framework for studying how grazing affects the balance of essential nutrients (e.g. C, N and P) at different trophic levels and over a wide range of spatial and temporal scales (Sterner & Elser 2002). Two mechanisms of how grazing affects the C, N and P contents and stoichiometry at the community level have been proposed (Bardgett & Wardle 2003). First, grazing may change the contents and stoichiometry of the plant community through a cascade of plant–soil feedbacks (McNaughton 1985; Frank 2008). Grazing often increases C-rich root exudates that stimulate microbial activity and turnover, ultimately resulting in an increase in soil nutrients available to plants (Bardgett, Wardle & Yeates 1998; Hamilton & Frank 2001). However, these stimulatory feedbacks cannot be sustained at high grazing intensities and may be absent or weak in resource-poor conditions. Second, grazing may alter the species composition and thus stoichiometry of the community because species differ in their nutrient contents (Ritchie, Tilman & Knops 1998; Bardgett & Wardle 2003).

Spatial scale is an important dimension for understanding mechanisms underpinning the observed responses in ecosystem functioning (e.g. primary production, C, N and P pools and stoichiometry). This is because the direction and magnitude of these effects are system and/or scale dependent (Levin 1993; Milchunas & Lauenroth 1993), and they often interact with environmental conditions, such as water and N availability (Maschinski & Whitham 1989; Wise & Abrahamson 2005). Few studies have examined the effects of grazing on ecosystem functioning and C : N : P stoichiometry across broad geographic regions. Understanding these complex relationships requires large-scale reference sites that have not been grazed. The border between China and Mongolia, with a demilitarized fenced area preventing grazing, provides an ideal transect to address this deficiency because the buffer zone has not been grazed since the 1950s. The arid and semi-arid grasslands on the Mongolia plateau, representative of the Eurasian steppe region, are extremely water-limited, with a similar evolutionary history of grazing (Coupland 1993; Bai *et al.* 2008). However, it remains unclear to what extent the water availability affects functioning and stoichiometric responses of grasslands to long-term grazing across broad regions.

To test these hypotheses and predictions, we examined the effects of grazing on ecosystem functioning and C : N : P stoichiometry along the 700 km China–Mongolia transect (CMT) using consistent methods. The CMT, which covers a wide range of biotic and abiotic conditions, enables us to observe the total effects of multiple mechanisms that probably operate simultaneously but vary in their relative strengths across regions. Specifically, we address the following questions: (i) How has grazing affected ecosystem functioning (i.e. species richness, above- and below-ground biomass and litter biomass) and C : N : P stoichiometry of grasslands along the regional precipitation gradient during the last 50 years? (ii) How do the responses of plant and soil C, N and P pools and stoichiometry to grazing differ among community types? (iii) What is the relative importance of plant functional group (PFG) composition and species plasticity in influencing ecosystem functioning and stoichiometry?

Materials and methods

STUDY AREA AND EXPERIMENTAL DESIGN

This study was conducted in the Inner Mongolia grassland, a central part of the Eurasian steppe (Bai *et al.* 2007). The study area is located at 44·73º–46·74ºN in latitude and 111·96º–118·89ºE in longitude, and elevation is between 760 and 1450 m. The mean

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

annual temperature ranges from −1·8 to 1·6 °C, with the lowest mean monthly temperatures in January (−21·0 to −24·0 °C) and the highest in July (18·7–21·6 °C). The mean annual precipitation (MAP) is between 170 and 370 mm, about 80% of which falls in the growing season from May to August (Table S1, Supporting information). Soil types include dark chestnut, typical chestnut, calcic brown and light brown soils, corresponding to the different community types (Table S1, Supporting information).

We established a regional transect across a precipitation gradient along the China–Mongolia border, which runs 700 km and covers three major community types: meadow steppe, typical steppe and desert steppe (Table S1, Supporting information and Fig. 1). The meadow steppe, located at the eastern part of the transect, is dominated by *Stipa baicalensis* Roshev., *Leymus chinensis* (Trin.) Tzvel. and *Carex pediformis* C. A. Mey., with the highest species richness and above-ground productivity among the three community types. The typical steppe is dominated by *Stipa grandis* P. Smirn., *L. chinensis, Stipa krylovii* Roshev. and *Caragana microphylla* Lam., with intermediate levels of species richness and productivity. The desert steppe at the western part of the transect is dominated by *Stipa klemenzii* Roshev. and *Allium polyrhizum* Turcz. ex Regel, with low species richness and productivity. Within the transect, a total of nine pairs of grazed and ungrazed sites were selected, including two pairs for meadow steppe, five pairs for typical steppe and two pairs for desert steppe, with the number of sites being proportional to its area. The ungrazed (control) sites were located within the fenced buffer zone along the China–Mongolia border, which has not been grazed by large herbivores for more than 50 years. In contrast, the grazed sites were inside the Chinese border, which have been subjected to grazing of different intensities since the 1950s (Table S1, Supporting information).

FIELD SAMPLING AND MEASUREMENTS

Field sampling was carried out during 14–30 August 2003, corresponding to annual peak-standing biomass (Bai *et al.* 2008). At each site, above-ground standing biomass of herbaceous plants was sampled by ten 1 × 1 m quadrats located randomly within a 100 × 100 m area. For each quadrat, live and dead above-ground biomass was clipped at the ground level, and dead parts were removed and combined with litter. Vascular plants in five of the ten quadrats were sorted to species, with those other five kept as bulk samples. All plant materials in each quadrat were oven-dried at 65 °C for 48 h and weighed. Above-ground biomass for shrubs was measured by collecting leaves and current-year twigs of each species using five 5 × 5 m quadrats. The averaged total dry mass, number of species and biomass of each species were used to estimate above-ground biomass, species richness and functional composition for each site. Leaf samples of 15 dominant and subdominant species were collected in the same area for C, N and P analysis. At each site, according to leaf size, 50–200 fully expanded and mature leaves from 30 to 50 adult individuals of each of the dominant and subdominant species were picked and divided into five samples, each with 10–40 leaves. For all the grazed sites, no livestock grazing occurred during the growing season of our field sampling in 2003.

Four of the five bulk biomass quadrats at each site were selected randomly for below-ground plant biomass and soil sampling. Below-ground biomass was sampled by randomly taking a 30-cm-diameter soil core from 0 to 60 cm depth inside each quadrat, which samples 80–90% of total below-ground biomass in the top 100 cm of soil (Jiang *et al.* 1985). Soil was rinsed out from roots under running water over a 1-mm screen, and below-ground biomass was oven-dried at 65 °C and weighed. Soil samples were collected by taking three 5-cm-diameter soil cores from 0 to 20, 20 to 60 and 60 to 100 cm depths at each quadrat of below-ground biomass sampling. The three cores from each quadrat were mixed *in situ* as one composite sample and hand-sorted to remove rocks and visible plant materials. Masses and volumes of rocks were also measured for correcting soil C, N and P storage. Bulk density at each soil depth for each site was obtained by using a cylindrical sampler (50·46 mm in diameter and 50 mm in length). Soil cores were oven-dried at 105 °C to constant weight.

All samples were processed and analysed in the laboratories of the Inner Mongolia Grassland Ecosystem Research Station of Chinese Academy of Sciences (Bai *et al.* 2004). A subsample of

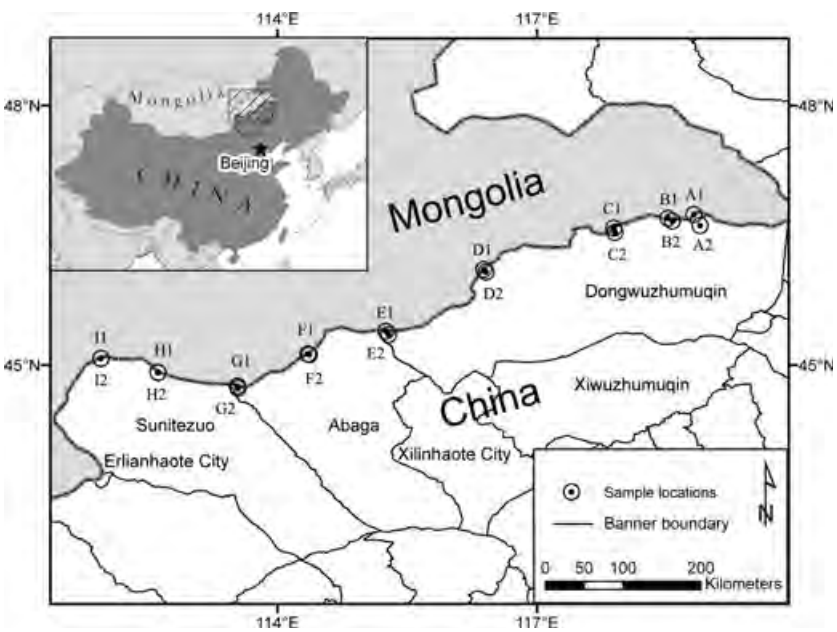


Fig. 1. Location map of the 18 paired study sites along the China–Mongolia transect.

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

10 g soil from each composite sample was dried at 105 °C for soil moisture measurement. The remaining soil was air-dried and ground to pass a 1-mm sieve for C, N and P analysis. Total organic C in soil and plant samples was analysed by the Walkley–Black modified acid-dichromate $FeSO_4$ titration method (Sparks *et al.* 1996). Total N in plant and soil samples was determined following Kjeldehl digestion by a Nitrogen Analyzer System (KJELTEC 2300 AUTO SYSTEM II, Foss Tecator AB, Höganäs, Sweden). Total P was determined by the H_2SO_4-$HClO_4$ fusion method (Sparks *et al.* 1996).

Stoichiometric ratios in plant, litter and soil samples, that is, C : N, C : P and N : P ratios, were calculated on mass basis. To examine the effects of grazing on C, N and P pools of plant and soil compartments, the total N, P and organic C contents (%) in soil and plant samples were converted from mass content basis (mg kg^{-1}) to land area basis (g m^{-2}). To present a quantitative measure independent of grazing-induced changes in soil bulk density, soil total N, P and organic C pools from each original depth interval were adjusted on an equivalent mass basis (Ellert & Bettany 1995). To assess the effects of shifts in functional group composition on ecosystem functioning, we classified all plants into five functional groups based on life forms, including perennial rhizome grasses (PR), perennial bunchgrasses (PB), perennial forbs (PF), shrubs and semi-shrubs (SS) and annuals (AS) as in Bai *et al.* (2004).

METEOROLOGICAL DATA

Meteorological data from 1961 to 2000 were obtained from 48 weather stations within and around the study area. Mean annual precipitation and mean annual temperature for each site were interpolated using a Geographic Information System (GIS)-based multiple regression method (Bai *et al.* 2007).

STATISTICAL ANALYSES

Statistical analyses were performed using SAS version 9·1 (SAS Institute, Cary, NC, USA, 2003). The effects of grazing on C, N and P contents and C : N : P stoichiometry in plant and soil pools, above-ground biomass, relative biomass of PFGs and below-ground biomass were tested with ANOVA, using Treatment (grazed or ungrazed), Community type, Site and all interactions as fixed-effects. These ANOVAS were followed by Duncan's multiple-range test to compare the grazing effects for each property and community type. To test the dependency of responses in stoichiometric ratios to grazing on precipitation, we further analysed the relationships between the responses of C : N, C : P and N : P ratios to grazing (i.e. $C : N_{grazed}/C : N_{ungrazed}$, $C : P_{grazed}/C : P_{ungrazed}$ and $N : P_{grazed}/N : P_{ungrazed}$) and MAP across the CMT. The responses of stoichiometric ratios to grazing were transformed with the natural logarithm before regression analysis to improve the normality.

Results

ABOVE- AND BELOW-GROUND BIOMASS, SPECIES RICHNESS AND PFG COMPOSITION

Plant species richness, above- and below-ground biomass and litter biomass at ungrazed sites all increased linearly with MAP across the CMT, and MAP alone explained 55–86% of the variance in these variables (Fig. 2). Species richness and standing above-ground biomass at the grazed sites showed a hump-shaped relationship with MAP, and both peaked at the intermediate level of MAP (Fig. 2). Below-ground biomass at the grazed sites followed the same pattern as that at the ungrazed sites, with litter biomass showing no significant relationship with MAP (Fig. 2).

When data were classified into community types, above-ground standing biomass and litter were significantly reduced by grazing in the three community types (data not shown). On average, the above-ground standing biomass decreased by 61% (1280 kg ha^{-1}) in the meadow steppe, by 27% (390 kg ha^{-1}) in the typical steppe and by 23% (170 kg ha^{-1}) in the desert steppe. Species richness

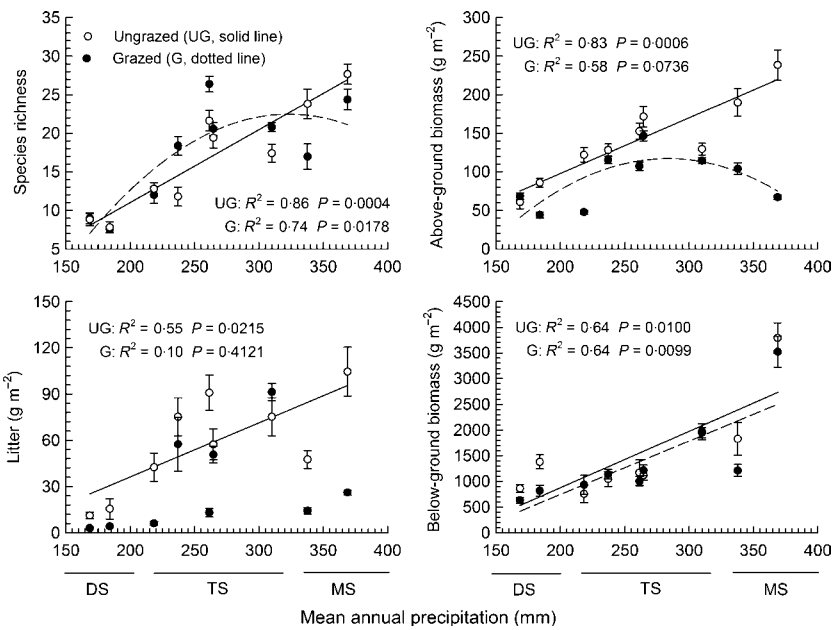


Fig. 2. Relationships of species richness, above- and below-ground biomass, and litter biomass with mean annual precipitation across the ungrazed (UG) and grazed (G) sites along the China–Mongolia transect. MS, meadow steppe; TS, typical steppe; and DS, desert steppe.

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

declined in the meadow steppe, increased in the typical steppe and remained relatively constant in the desert steppe. Below-ground biomass exhibited little change in the meadow and typical steppes, but decreased substantially in the desert steppe. At plant functional group level, responses of relative biomass to grazing were quite different among the three community types. In particular, relative above-ground biomass decreased for perennial forbs and increased for perennial bunchgrasses in the meadow steppe (both were dominant functional groups). The opposite trends were observed in the typical and desert steppe communities (Fig. 3). In general, perennial rhizomatous grasses decreased, annuals increased and shrubs and semi-shrubs either did not change or decreased in grazed sites from meadow, typical, to desert steppes across the regional precipitation gradient (Fig. 3).

C, N AND P POOLS AND STOICHIOMETRY IN PLANT MATERIALS

The C pools of all plant compartments, including above-ground standing biomass, litter and below-ground biomass, declined significantly in response to long-term grazing in the meadow steppe, typical steppe and desert steppe, except the below-ground biomass C for the typical steppe (Fig. 4). The N pools in above-ground biomass and litter were also reduced by grazing across the three community types. As compared with ungrazed sites, the above-ground biomass N decreased by 49% for the meadow steppe, 17% for the typical steppe and 41% for the desert steppe. Below-ground biomass N did not change in the meadow steppe, increased slightly in the typical steppe and decreased significantly in the desert steppe in response to grazing (Fig. 4). In the meadow and typical steppes, total P decreased in the above-ground biomass and litter but increased in below-ground biomass in response to grazing. In the desert steppe, grazing had no effect on above-ground biomass P, but significantly reduced litter and below-ground biomass P (Fig. 4).

The C : N ratios of all plant compartments were decreased by grazing in the meadow and typical steppes, but generally unaffected in the desert steppe (Fig. 5). The magnitude of the change was largest in the meadow steppe because of decrease in C and increase in N contents (%) in plant tissues (Fig. S1, Supporting information). In the typical steppe, reduced C : N was due primarily to increase in N content. In contrast to the relatively consistent responses of C : N in above- and below-ground, changes in the C : P ratio mainly occurred below-ground (Fig. 5). There was a sharp decrease in root C : P in the meadow and typical steppes, driven by changes in both C and P contents in the meadow steppe and by changes in P content in the typical steppe (Fig. S1, Supporting information).

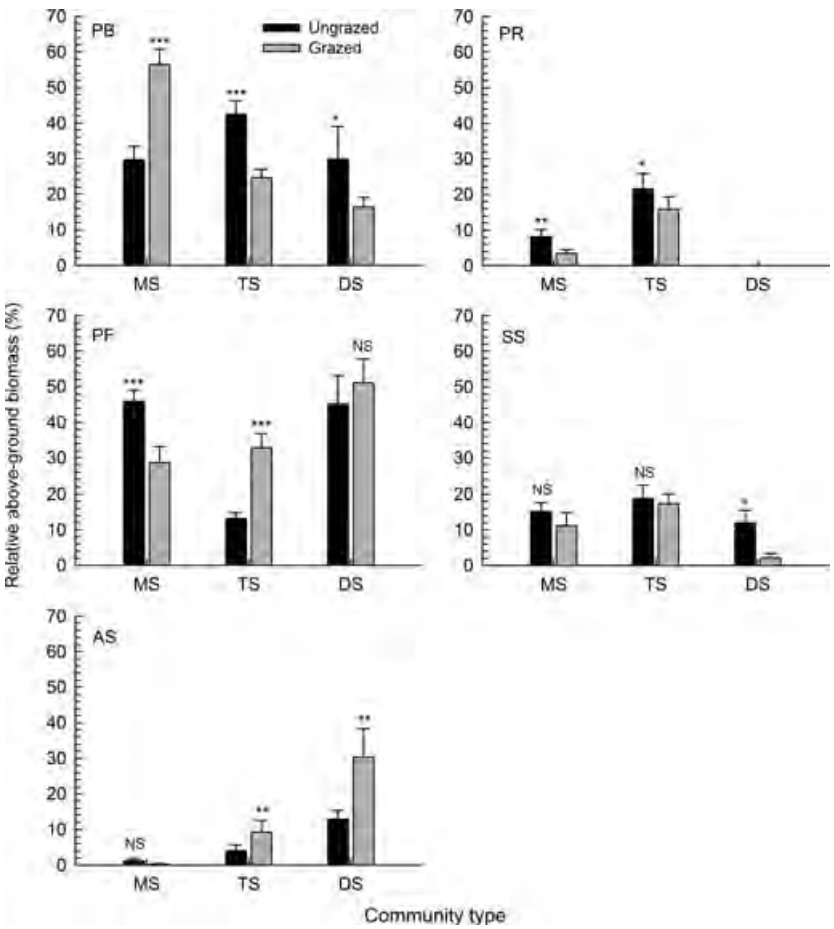


Fig. 3. Influence of grazing on plant functional group composition across different community types (error bars denote SE). MS, meadow steppe; TS, typical steppe; and DS, desert steppe. Abbreviations: PB, perennial bunchgrasses; PR, perennial rhizome grasses; PF, perennial forbs; SS, shrubs and semi-shrubs; and AS, annuals. Significant differences between the grazed and ungrazed sites are reported from ANOVA as NS, $P > 0{\cdot}1$; $+0{\cdot}05 < P < 0{\cdot}1$; $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}001$.

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

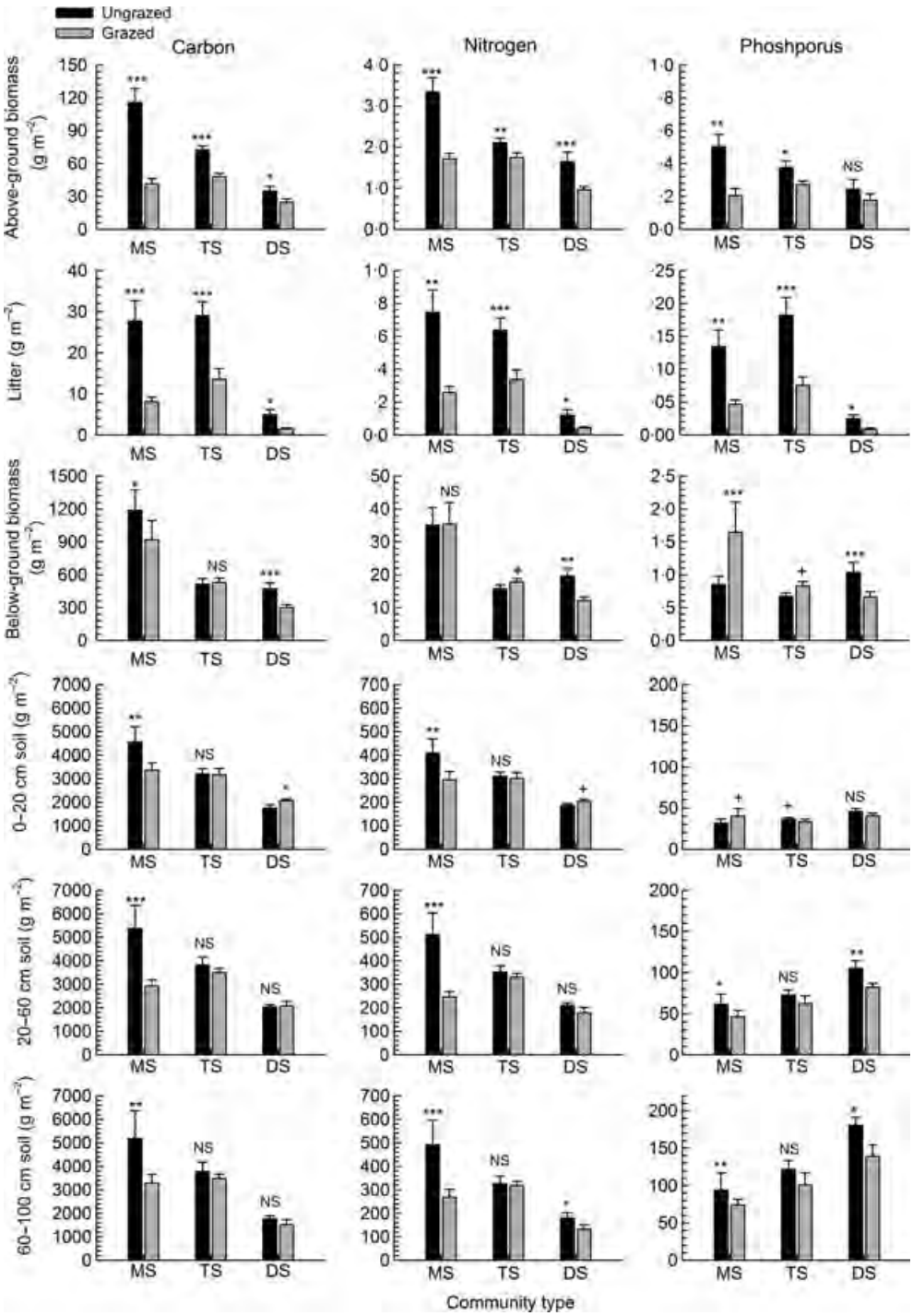


Fig. 4. Effects of grazing on C, N and P pools of plant, litter and soil across different community types on the China–Mongolia transect. Error bars represent SE. MS, meadow steppe; TS, typical steppe; and DS, desert steppe. Soil C, N and P pools at each depth were adjusted on an equivalent mass basis. Significant levels are as in Fig. 3.

At the plant species level, foliar C : N decreased in grazed sites for 11 of the 15 extant species examined (Fig. 6), because of increased N content and unchanged C content (Fig. S2, Supporting information). These changes were more consistent in the meadow steppe (seven of seven species) and typical steppe (eight of 10 species) than in the desert steppe (one of four species). Species in different communities responded similarly for all stoichiometric ratios (Fig. 6). There were no significant effects of community type and interaction of community type and species (data not shown). Responses of foliar P content to grazing varied considerably among species and showed no consistent trend (Fig. S2, Supporting information).

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

C, N AND P POOLS AND STOICHIOMETRY IN SOIL

Grazing decreased soil C and N pools in the meadow steppe, but had no effect in both the typical and desert steppes across all depths (Fig. 4). For the desert steppe, soil C and N increased at the depth of 0–20 cm and remained relatively unchanged at the depths of 20–60 and 60–100 cm (Fig. 4). At the depth of 0–20 cm, soil total P increased slightly in meadow steppe, decreased considerably in the typical steppe and did not change in the desert

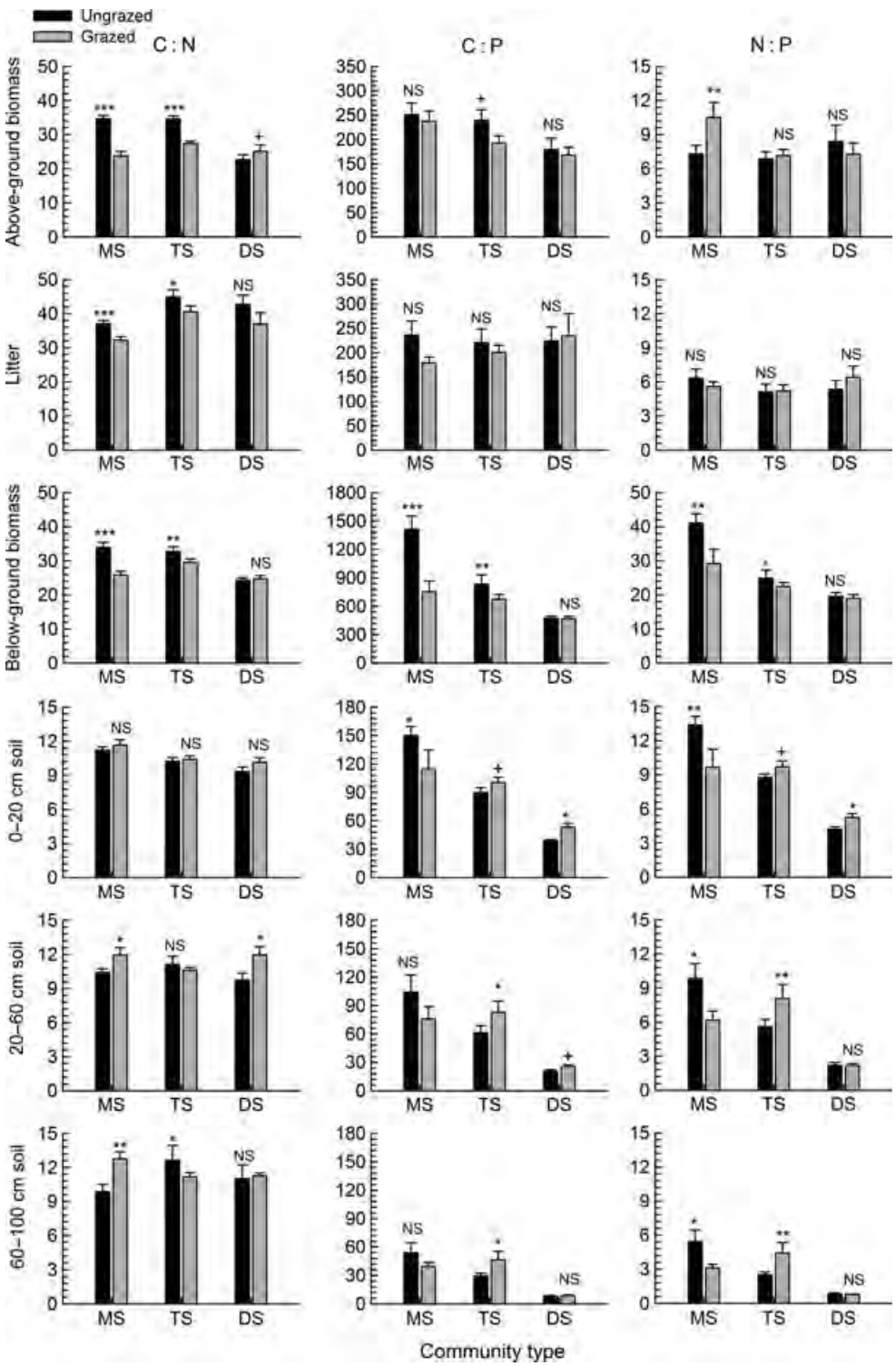


Fig. 5. Effects of grazing on the C : N : P stoichiometry of plant, litter and soil across different community types. All stoichiometric ratios are mass-based. Error bars represent SE. All symbols are derived as in Fig. 4.

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

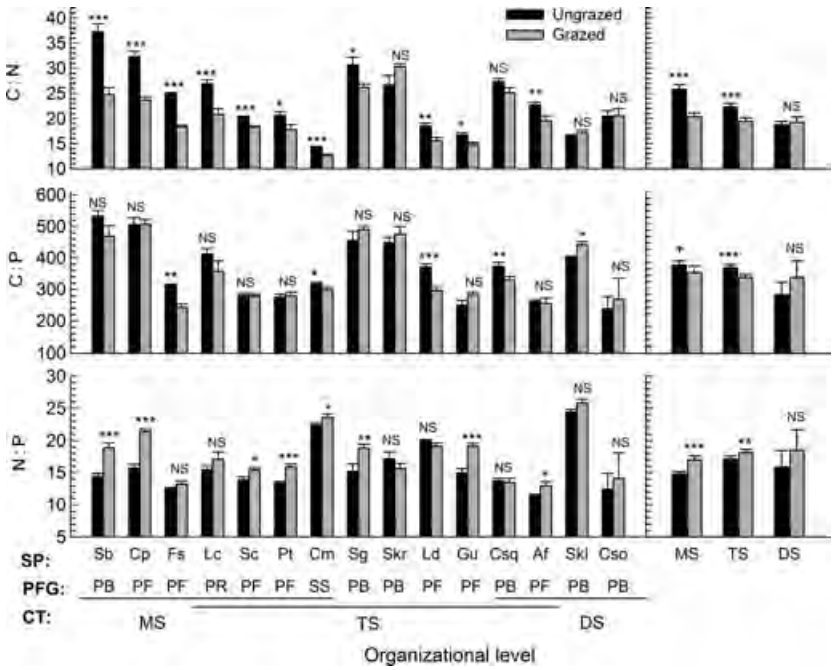


Fig. 6. Effects of grazing on the foliar C:N:P stoichiometry of dominant and subdominant species (error bars denote SE.). All stoichiometric ratios are mass-based. The C : N, C : P and N : P ratios for each species were the average of all samples from the grazed and ungrazed fields across the China–Mongolia transect. MS, meadow steppe; TS, typical steppe; and DS, desert steppe. Abbreviations: Lc, *Leymus chinensis*; Sb, *Stipa baicalensis*; Sg, *S. grandis*; Skr, *S. krylovii*; Skl, *S. klemenzii*; Csq, *Cleistogenes squarrosa*; Cso, *C. songorica*; Af, *Artemesia frigida*; Ld, *Lespedeza davurica*; Cm, *Canrogana microphylla*; Gu, *Glycyrrhiza uralensis*; Cp, *Carex pediformis*; Sc, *Serratula centauroides*; Pt, *Potentilla tanacetifolia*; Fs, *Filifolium sibiricum*; SP, species; PFG, plant functional group; and CT, community type. Significant levels are as in Fig. 3.

steppe. At the depths of 20–60 and 60–100 cm, total P decreased in the meadow and desert steppes and remained unchanged in the typical steppe (Fig. 4).

The responses of soil C : N ratio to grazing differed between soil depths for the three community types (Fig. 5). In both the meadow and desert steppes, C : N ratio increased in all three soil depths although grazing reduced C and N contents (%) in the meadow steppe but enhanced both in the desert steppe (Fig. S1, Supporting information). In the typical steppe, however, C : N ratio changed little in the top 20-cm soil layer and decreased in soil depths of 20–60 and 60–100 cm (Fig. 5). The responses of soil C : P to grazing differed among community types. In contrast to C : N ratio, C : P ratio decreased in all three soil depths in the meadow steppe. C : P ratio showed a clearly increasing trend in all soil depths in the typical and desert steppes. N : P ratio exhibited a similar response pattern to that of C : P ratio (Fig. 5).

RELATIONSHIPS BETWEEN STOICHIOMETRIC RESPONSES AND PRECIPITATION

In the ungrazed sites, the above-ground biomass C : N ratio and below-ground biomass and soil C : N, C : P and N : P ratios increased linearly with MAP across the CMT ($P < 0{\cdot}05$, data not shown). The above-ground biomass C : N response to grazing was negatively correlated with MAP (Fig. 7), but the responses of above-ground biomass C : P and N : P ratios had no significant relationships with MAP. The litter C : P response to grazing declined linearly with increasing MAP (Fig. 7). The responses of below-ground biomass C : N, C : P and N : P ratios to grazing all decreased with increasing MAP. The C : P and N : P responses to grazing also decreased with increasing MAP in the top 20-cm soil layer (Fig. 7). In the soil depths of 20–60 and 60–00 cm, the relationships between the responses of C : N, C : P and N : P ratios to grazing and MAP were not statistically significant (data not shown).

Discussion

DIFFERENTIAL EFFECTS OF GRAZING ON C, N AND P POOLS IN PLANT AND SOIL COMPARTMENTS

Our results indicate that the reduction in C, N, P pools in above-ground biomass and litter at the grazed sites were attributable mainly to the substantial decrease in standing biomass and litter, although grazing increased the N contents (%) of both above-ground biomass and litter in meadow and typical steppes. However, the responses of below-ground biomass and soil C, N and P pools differed among community types. Specifically, these changes in below-ground pool size were associated primarily with a decrease in C content and increases in N and P content in the meadow steppe, increases in N and P content in the typical steppe, and a reduction in below-ground biomass in the desert steppe.

Our results on the effects of grazing on soil C and N pools in the Inner Mongolia grassland were largely consistent with previous findings (Han *et al.* 2008; Li *et al.* 2008). The effects of grazing on soil C, N and P pools were mainly due to changes in C, N and P contents (Ellert & Bettany 1995). The differential responses of soil C, N and P pools among three community types may be related to the long-term nutrient export through livestock products (e.g. livestock biomass, faeces and urine), which increases with primary productivity (Oesterheld, Sala &

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

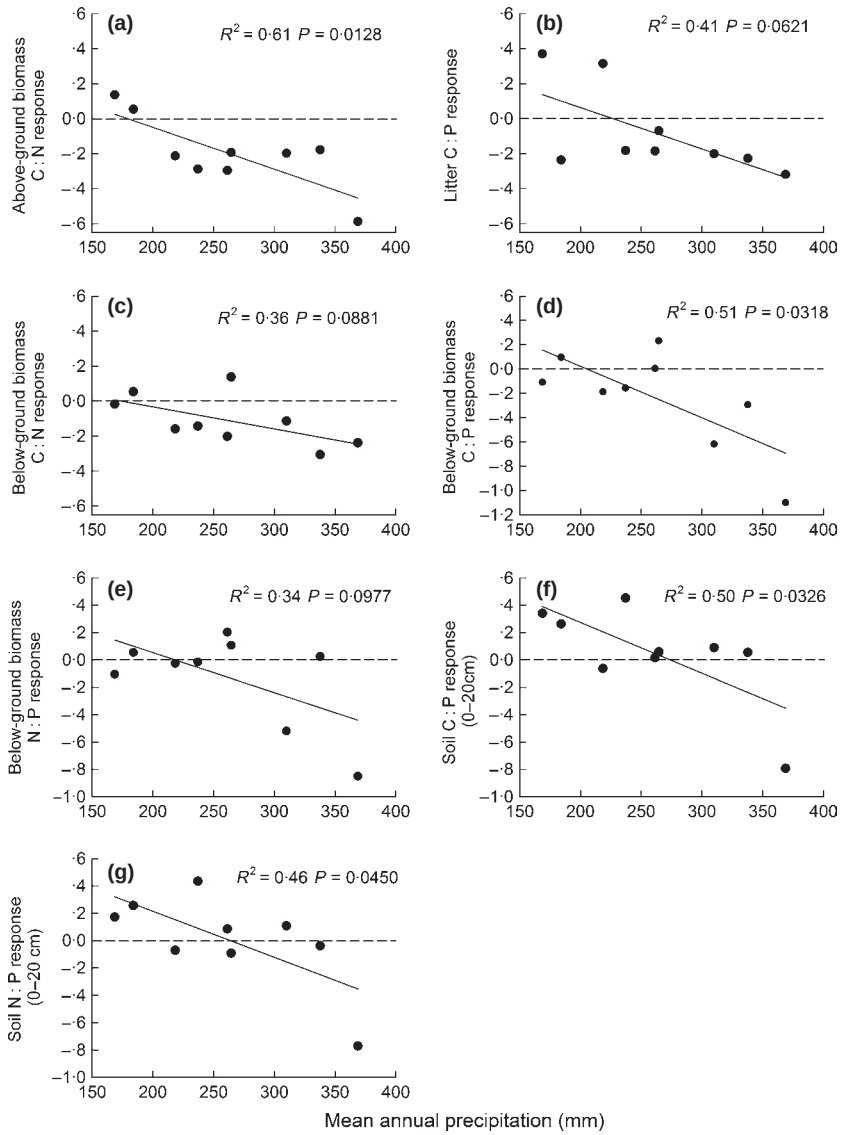


Fig. 7. Relationships between the responses of stoichiometric ratios in plant, litter and soil to grazing and mean annual precipitation across the China–Mongolia transect. The responses of C : N, C : P and N : P ratios to grazing were calculated as Ln ($C : N_{grazed}/C : N_{ungrazed}$), Ln ($C : P_{grazed}/C : P_{ungrazed}$), and Ln ($N : P_{grazed}/N : P_{ungrazed}$), respectively. The reference line (dashed line) in each panel indicates no change in stoichiometric ratio.

McNaughton 1992). Milchunas, Sala & Lauenroth (1988) hypothesized that differential responses of grasslands to grazing could result from differences in their evolutionary history of grazing and moisture. Given that the three grassland types have similar long-term grazing history, grazing intensity and precipitation may be the two important factors for the observed response patterns.

EFFECTS OF GRAZING ON PLANT AND SOIL C : N : P STOICHIOMETRY

Previous studies proposed that the stimulatory feedbacks between C-rich root exudates, microbial activity, and plant available soil nutrients (Bardgett, Wardle & Yeates 1998; Hamilton & Frank 2001), and shifts in plant species and functional group composition (Ritchie, Tilman & Knops 1998; Bardgett & Wardle 2003) were two major mechanisms underpinning the plant and soil stoichiometric responses to grazing. In our case, we hypothesize that both mechanisms may have operated to different degrees along the regional precipitation gradient, with the former predominating in the meadow steppe and the latter dominating in the desert steppe, because the proportional nutrient exports by livestock were much higher in the meadow steppe than in the desert steppe. In the meadow steppe, the predominant plant functional group, that is, perennial bunchgrasses, is well adapted to grazing. Grazing under fertile conditions could have stimulated root exudation of C-rich substances, elevated N mineralization, enhanced plant N content and thereby led to a reduction in C : N. This is evidenced by the elevated N contents in all plant apartments in the grazed meadow steppe. In the desert steppe, however, the species are not well adapted to grazing (Milchunas, Sala & Lauenroth 1988; Gillson & Hoffman 2007). Thus, there was a reduction in N pools, leading to an increase in C : N in the desert.

Our results suggest that the functional response mediated by changes in dominant species and plant functional group composition is a key mechanism underpinning the grazing-induced changes in ecological stoichiometry and

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

ecosystem functioning. For example, in the desert steppe, grazing increased the absolute and relative abundance of opportunistic and unpalatable annuals with shallow roots, for example, *Neopallasia pectinata* (Pall.) Poljak. and *Convolvulus ammannii* Desr. Annuals commonly have high tissue N levels, although they can still be unpalatable if the N is locked in compounds that dissuade herbivory (Throop & Lerdau 2004). These resource-acquiring annuals have a competitive advantage in depleting available N and water, resulting in increases in root litter input to the surface soil in the grazed sites because of a shift from a perennial-dominated to an annual-dominated community. Indeed, grazing increased the 0- to 20-cm soil carbon although it diminished the total below-ground biomass. These changes in plant species composition could lead to increases in soil C and N pools. In the typical steppe, on the other hand, the predominance of grazing-tolerant species with shallow roots led to a greater proportion of root biomass in the top 20-cm soil layer (Chen *et al.* 2001). As a consequence, soil C and N remained relatively unchanged.

Our findings demonstrate that the impacts of grazing on plant and soil C : N : P stoichiometry are strongly mediated by water availability across the regional transect. Responses of both above- and below-ground biomass C : N ratios to grazing were negatively correlated with MAP, indicating that these ratios were reduced in the meadow steppe but enhanced in the desert steppe. The negative relationship of MAP to both below-ground biomass and topsoil C : P responses suggest that grazing increased root and topsoil C : P ratios in the meadow steppe and reduced them in the desert steppe. Frank (2008) reported that grazing increased plant N contents and shifted the type of nutrient limitation towards N and P co-limitation. In our study, the below-ground biomass and soil N : P responses declined with increasing MAP, implying that long-term grazing is likely to increase the potential for N and P co-limitation in the desert steppe and N limitation in the meadow steppe.

ACCELERATED N CYCLING BY GRAZING

Our results show that grazing accelerated N cycling in the Inner Mongolian grasslands, especially in the meadow and typical steppes. Two contrasting mechanisms exist on the effects of grazing on N cycling. First, grazing may increase nutrient cycling through stimulation of microbial activity owing to input of defoliated fresh plant litter and animal excreta (Holland, Cheng & Crossley 1996; Hamilton & Frank 2001). Second, grazing may decrease nutrient cycling through increases in unpalatable plant species and production of higher concentrations of defensive compounds (Hobbie 1992; Ritchie, Tilman & Knops 1998). Our results suggest that grazing accelerated N cycling as evidenced by increased plant and litter N contents and decreased soil N content. This is particularly conspicuous in the meadow steppe. In the desert steppe, the increase in soil C and N contents suggests that the latter mechanism was in operation. These two opposing mechanisms may coexist in the typical steppe, resulting in only slightly accelerated N cycling.

Under nutrient-deficient conditions, defoliation often causes reductions in root nutrient content and biomass, as C-rich substrates are exuded into the rhizosphere to stimulate microbial activity and stored nutrients are reallocated to support regrowth above-ground (McNaughton 1985). When soil nutrients are abundant, plant nutrient content (especially P) may be unchanged or even increase following defoliation, as plants adapted to grazing are able to recoup losses to grazers (McNaughton & Chapin 1985). The lack of reduction in root or above-ground P content observed in the grazed sites suggests that P availability in the meadow and typical steppes may have been sufficient to support stoichiometrically balanced growth for plants following grazing. This is likely because most of the dominant and subdominant plant species in these steppe communities are colonized by arbuscular mycorrhizal fungi (Tian *et al.* 2009), which could have increased plant P uptake and thus lessened the defoliation-induced P limitation (van der Heijden *et al.* 1998). P availability may also have been sufficient to support balanced growth at higher tropic levels in these communities, as shoot C : P of all three community types across the CMT were below the hypothesized threshold of 250 : 1 required for efficient growth of P-rich herbivores feeding on comparably C-rich plants (Elser *et al.* 2000).

Large changes in N content following grazing in both the meadow and typical steppes, with minor changes in P content, may potentially increase N and P co-limitation in these communities. Grazing increased the N : P ratio of above-ground tissue in the meadow steppe and the soil N : P in the typical and desert steppes, suggesting that grazing accelerated N cycling more than P cycling. However, support for a shift towards P limitation was inconsistent across the different community types, as the N : P ratio of above-ground biomass was unaffected in typical and desert steppe communities, and soil N : P decreased in the meadow steppe, indicating that P cycling increased more than N cycling following grazing in this system. In addition, litter N : P was below all previously documented critical N : P ratios for N vs. P limitation (reported range of 9–25) (Güsewell & Verhoeven 2006), suggesting N-limited systems. Overall, although the increase in N cycling suggests a general shift towards P limitation for plant growth across the three community types, this potential may be buffered in the meadow steppe because of a large increase in P availability and is probably not a dominant process in the non-responsive (and water-limited) desert steppe. Thus, the potential for P limitation may be more likely to occur in the typical steppe. The changes in root P content observed across much of the CMT, however, suggest that the stoichiometric response to grazing may be more complex than previously understood, highlighting the need for more careful interpretation of foliar N : P ratio in determining nutrient limitation.

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

IMPLICATIONS FOR GRASSLAND MANAGEMENT AND CLIMATE CHANGE

Our study has important implications for the ecology and management of the vast grasslands in the Eurasian Steppe region. First, long-term grazing under high intensities not only alters ecosystem productivity and biodiversity (Bai *et al*. 2007), but also C, N and P pools and stoichiometry across the Inner Mongolian grassland. The results from the current study further demonstrated that both the species richness and above-ground standing biomass at the grazed sites were highest at the intermediate level of precipitation across the CMT, suggesting that the typical steppe seems to be more resilient to grazing than those meadow and desert steppes. Second, our results suggest that the effects of grazing on C : N : P stoichiometry and ecosystem functioning are strongly mediated by precipitation. Future climate change, particularly changes in precipitation amount and seasonality (Easterling *et al*. 2000), may have profound impacts on the ecosystem functioning of the Eurasian Steppe as a whole. Third, the accelerated N cycling reduces N limitation, but may potentially intensify N and P co-limitation. Given that applying fertilizers on large scales is not practical, reducing the currently high stocking rate and restoring the vast degraded steppes are essential to future ecosystem management in the Inner Mongolian grassland region.

Acknowledgements

We thank J. J. Elser, O. E. Sala and M. E. Ritchie for their insightful comments on an early version of this manuscript. We also gratefully acknowledge H. T. Zhao, Y. Yang, H. W. Wan and students from the Inner Mongolia Agriculture University for their help with fieldwork. This project was supported by the National Natural Science Foundation of China (30825008, 31030013, and 30770370), Strategic Priority Research Program of the Chinese Academy of Sciences (XDA05050400) and U.S. National Science Foundation (DEB-0618193).

References

Bai, Y.F., Han, X.G., Wu, J.G., Chen, Z.Z. & Li, L.H. (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, **431**, 181–184.

Bai, Y.F., Wu, J.G., Pan, Q.M., Huang, J.H., Wang, Q.B., Li, F.S., Buyantuyev, A. & Han, X.G. (2007) Positive linear relationship between productivity and diversity: evidence from the Eurasian steppe. *Journal of Applied Ecology*, **44**, 1023–1034.

Bai, Y.F., Wu, J.G., Xing, Q., Pan, Q.M., Huang, J.H., Yang, D.L. & Han, X.G. (2008) Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. *Ecology*, **89**, 2140–2153.

Bardgett, R.D. & Wardle, D.A. (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, **84**, 2258–2268.

Bardgett, R.D., Wardle, D.A. & Yeates, G.W. (1998) Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biology and Biochemistry*, **30**, 1867–1878.

Chen, S.H., Wang, L.Q., Zhanbula, & Zhao, M.L. (2001) *Root Systems of Grassland Plants in Northern China*. Jilin University Press, Chuangchun.

Coupland, R.T. (1993) *Ecosystems of the World. 8B Natural Grasslands: Eastern Hemisphere and Résumé*. Elsevier, Amsterdam.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.

Ellert, B.H. & Bettany, J.R. (1995) Calculation of organic matter and nutrients stored in soils under contrasting management regimes. *Canadian Journal of Soil Science*, **75**, 529–538.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H. & Sterner, R.W. (2000) Nutritional constraints in terrestrial and freshwater food webs. *Nature*, **408**, 578–580.

Frank, D.A. (2008) Ungulate and topographic control of nitrogen: phosphorus stoichiometry in a temperate grassland: soils, plants and mineralization rates. *Oikos*, **117**, 591–601.

Frank, D.A. & Evans, R.D. (1997) Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology*, **78**, 2238–2248.

Frank, A.B., Tanaka, D.L., Hofmann, L. & Follett, R.F. (1995) Soil carbon and nitrogen of northern great-plains grasslands as influenced by long-term grazing. *Journal of Range Management*, **48**, 470–474.

Gillson, L. & Hoffman, M.T. (2007) Rangeland ecology in a changing world. *Science*, **315**, 53–54.

Golluscio, R.A., Austin, A.T., Martínez, G.C.G., Gonzalez-Polo, M., Sala, O.E. & Jackson, R.B. (2009) Sheep grazing decreases organic carbon and nitrogen pools in the Patagonian steppe: combination of direct and indirect effects. *Ecosystems*, **12**, 686–697.

Güsewell, S. & Verhoeven, J.T.A. (2006) Litter N : P ratios indicate whether N or P limits the decomposability of graminoid leaf litter. *Plant and Soil*, **287**, 131–143.

Hamilton III, E.W. & Frank, D.A. (2001) Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass *Ecology*, **82**, 2397–2402.

Han, G., Hao, X., Zhao, M., Wang, M., Ellert, B.H., Willms, W. & Wang, M. (2008) Effect of grazing intensity on carbon and nitrogen in soil and vegetation in a meadow steppe in Inner Mongolia. *Agriculture Ecosystems & Environment*, **125**, 21–32.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A. & Sanders, I.R. (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, **396**, 69–72.

Hobbie, S.E. (1992) Effects of plant-species on nutrient cycling. *Trends in Ecology and Evolution*, **7**, 336–339.

Holland, J.N., Cheng, W.X. & Crossley, D.A. (1996) Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. *Oecologia*, **107**, 87–94.

Jiang, S., Qi, Q.H. & Kong, D.Z. (1985) A comparative study on production of *Aneurolepidium chinense* and *Stipa grandis steppe* communities at Baiinxile livestock farm in Inner Mongolia region. *Research on Grassland Ecosystem No.1* (ed. Inner Mongolia Grassland Ecosystem Research Station), pp. 12–23. Science Press, Beijing.

Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S. & McCarron, J.K. (2002) Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. *Science*, **298**, 2202–2205.

Levin, S.A. (1993) Grazing theory and rangeland management. *Ecological Applications*, **3**, 1.

Li, C., Hao, X., Zhao, M., Han, G. & Willms, W.D. (2008) Influence of historic sheep grazing on vegetation and soil properties of a desert steppe in Inner Mongolia. *Agriculture, Ecosystems & Environment*, **128**, 109–116.

Maschinski, J. & Whitham, T.G. (1989) The continuum of plant responses to herbivory: the influence of plant-association, nutrient availability, and timing. *American Naturalist*, **134**, 1–19.

McNaughton, S.J. (1979) Grazing as an optimization process: grass ungulate relationships in the serengeti. *American Naturalist*, **113**, 691–703.

McNaughton, S.J. (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, **55**, 259–294.

McNaughton, S.J. & Chapin III, F.S. (1985) Effects of phosphorus nutrition and defoliation on C_4 graminoids from the serengeti plains. *Ecology*, **66**, 1617–1629.

Milchunas, D.G. & Lauenroth, W.K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327–366.

Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, **132**, 87–106.

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

Oesterheld, M., Sala, O.E. & McNaughton, S.J. (1992) Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature*, **356**, 234–236.

Reeder, J.D., Schuman, G.E., Morgan, J.A. & Lecain, D.R. (2004) Response of organic and inorganic carbon and nitrogen to long-term grazing of the shortgrass steppe. *Environmental Management*, **33**, 485–495.

Ritchie, M.E., Tilman, D. & Knops, J.M.H. (1998) Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology*, **79**, 165–177.

Sasaki, T., Okayasu, T., Jamsran, U. & Takeuchi, K. (2008) Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. *Journal of Ecology*, **96**, 145–154.

Shan, Y.M., Chen, D.M., Guan, X.X., Zheng, S.X., Chen, H.J., Wang, M.J. & Bai, Y.F. (2011) Seasonally dependent impacts of grazing on soil nitrogen mineralization and linkages to ecosystem functioning in Inner Mongolia grassland. *Soil Biology & Biochemistry*, **43**, 1943–1954.

Singer, F.J. & Schoenecker, K.A. (2003) Do ungulates accelerate or decelerate nitrogen cycling? *Forest Ecology and Management*, **181**, 189–204.

Sparks, D.L., Page, A.L., Loeppert, P.A., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T. & Sumner, M.E. (1996) *Methods of Soil Analysis Part 3: Chemical methods*. Soil Science Society of America and American Society of Agronomy, Madison, WI.

Sterner, R.W. & Elser, J.J. (2002) *Ecological Stoichiometry: The Biology of Elements from Molecular to the Biosphere*. Princeton University Press, Princeton, NJ.

Throop, H.L. & Lerdau, M.T. (2004) Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. *Ecosystems*, **7**, 109–133.

Tian, H., Gai, J.P., Zhang, J.L., Christie, P. & Li, X.L. (2009) Arbuscular mycorrhizal fungi associated with wild forage plants in typical steppe of eastern Inner Mongolia. *European Journal of Soil Biology*, **45**, 321–327.

White, R., Murray, S. & Rohweder, M. (2000) *Pilot Analysis of Global Ecosystems: Grassland Ecosystems*. World Resources Institute, Washington, DC.

Wise, M.J. & Abrahamson, W.G. (2005) Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. *Oikos*, **109**, 417–428.

Wittmer, M.H.O.M., Auerswald, K., Bai, Y.F., Schäufele, R. & Schnyder, H. (2010) Changes in the abundance of C3/C4 species of Inner Mongolia grassland: evidence from isotopic composition of soil and vegetation. *Global Change Biology*, **16**, 605–616.

Received 10 April 2012; accepted 20 August 2012
Handling Editor: Brian Wisley

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Effects of grazing on C, N, and P contents (%) in above- and below-ground biomass, litter, and soil across different community types of the China–Mongolia transect (Error bars represent SE).

Fig. S2. Effects of grazing on foliar C, N, and P contents of dominant and subdominant species (error bars denote SE).

Table S1. Abiotic and biotic characteristics of the 18 paired study sites along the China–Mongolia transect.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

© 2012 The Authors. Journal of Applied Ecology © 2012 British Ecological Society, *Journal of Applied Ecology*

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Testing mechanisms of N-enrichment-induced species loss in a semiarid Inner Mongolia grassland: critical thresholds and implications for long-term ecosystem responses

Zhichun Lan and Yongfei Bai

Phil. Trans. R. Soc. B 2012 **367**, 3125-3134
doi: 10.1098/rstb.2011.0352

Supplementary data

"Data Supplement"
http://rstb.royalsocietypublishing.org/content/suppl/2012/10/03/rstb.2011.0352.DC1.html

References

This article cites 43 articles, 6 of which can be accessed free
http://rstb.royalsocietypublishing.org/content/367/1606/3125.full.html#ref-list-1

Article cited in:
http://rstb.royalsocietypublishing.org/content/367/1606/3125.full.html#related-urls

Subject collections

Articles on similar topics can be found in the following collections

ecology (399 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Phil. Trans. R. Soc. B* go to: **http://rstb.royalsocietypublishing.org/subscriptions**

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

CrossMark click for updates

Phil. Trans. R. Soc. B (2012) **367**, 3125–3134
doi:10.1098/rstb.2011.0352

Research

Testing mechanisms of N-enrichment-induced species loss in a semiarid Inner Mongolia grassland: critical thresholds and implications for long-term ecosystem responses

Zhichun Lan[1,2] and Yongfei Bai[1,*]

[1]*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, People's Republic of China*
[2]*Graduate University of Chinese Academy of Sciences, Beijing 100049, People's Republic of China*

The increase in nutrient availability as a consequence of elevated nitrogen (N) deposition is an important component of global environmental change. This is likely to substantially affect the functioning and provisioning of ecosystem services by drylands, where water and N are often limited. We tested mechanisms of chronic N-enrichment-induced plant species loss in a 10-year field experiment with six levels of N addition rate. Our findings on a semi-arid grassland in Inner Mongolia demonstrated that: (i) species richness (SR) declined by 16 per cent even at low levels of additional N (1.75 $g\,N\,m^{-2}\,yr^{-1}$), and 50–70% species were excluded from plots which received high N input (10.5–28 $g\,N\,m^{-2}\,yr^{-1}$); (ii) the responses of SR and above-ground biomass (AGB) to N were greater in wet years than dry years; (iii) N addition increased the inter-annual variations in AGB, reduced the drought resistance of production and hence diminished ecosystem stability; (iv) the critical threshold for chronic N-enrichment-induced reduction in SR differed between common and rare species, and increased over the time of the experiment owing to the loss of the more sensitive species. These results clearly indicate that both abundance and functional trait-based mechanisms operate simultaneously on N-induced species loss. The low initial abundance and low above-ground competitive ability may be attributable to the loss of rare species. However, shift from below-ground competition to above-ground competition and recruitment limitation are likely to be the key mechanisms for the loss of abundant species, with soil acidification being less important. Our results have important implications for understanding the impacts of N deposition and global climatic change (e.g. change in precipitation regimes) on biodiversity and ecosystem services of the Inner Mongolian grassland and beyond.

Keywords: chronic nitrogen enrichment; above-ground competition; recruitment limitation; soil acidification; stability; drought resistance

1. INTRODUCTION

Nitrogen (N) is one of the most limiting nutrient elements controlling plant growth, reproduction, species composition and primary production in many terrestrial ecosystems [1–3]. Global nitrogen availability, which has doubled globally over the last 50 years through industrial and agricultural processes, is one of the major drivers of widespread biodiversity loss and degradation of ecosystem services worldwide [4–6]. Experimental studies in grasslands have demonstrated N addition consistently decreases species richness (SR) and promotes a few species with particular traits that enable them to exploit the additional N [7–10]. Such reductions in SR and shifts in functional groups composition can have profound impacts on multiple ecosystem functions, such as N retention, carbon sequestration, above- and below-ground biomass, and stability [11–14]. Thus, a better understanding of how changes in biodiversity and ecosystem services following N enrichment are affected by key abiotic and biotic factors is fundamental to management and preservation of biodiversity in the light of global change [4,15,16].

Several hypotheses regarding N-enrichment-induced species loss are focused mainly on the direct effects of N accumulation and indirect effects of soil mediated acidification on plant growth [10,17]. N addition increases primary production and hence causes cascading effects on competitive exclusion including

* Author for correspondence (yfbai@ibcas.ac.cn).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rstb.2011.0352 or via http://rstb.royalsocietypublishing.org.

One contribution of 10 to a Theme Issue 'Impacts of global environmental change on drylands: from ecosystem structure and functioning to poverty alleviation'.

This journal is © 2012 The Royal Society

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

assemblage thinning [7,18], the relative importance of above-ground or light competition over below-ground competition [19,20] and reduction of species recruitment [21,22]. For some systems, N addition increases soil acidity and results in toxicity through mobilization of metals, leaching of base cations and changing the balance between nitrogenous compounds [23–25]. After decades of efforts, however, there are few agreements but, rather, results are case-dependent [4,10,17] or even opposite of expectations [26]. This is probably because plant community-level responses to N addition depend on environmental conditions, production response, community composition, species' relative abundance (RA) and traits of individual species, indicating the importance of species-level responses [9,27]. Compared with the relatively extensive research at the plant community level, only a few studies have evaluated the species-level responses using functional trait-based approach [7,28].

Temporal scale is an important dimension for understanding plant community response to N addition because of the cumulative and lagged effects of N inputs [17,29]. This suggests that there exist ecosystem-specific critical thresholds for N enrichment, below which N might be unavailable to plants as microbial and abiotic processes outcompete plants for excess N [8,30,31]. For example, Bai *et al.* [8] found that the reduction in SR occurred after three years of N addition at both mature and degraded communities in the semiarid Inner Mongolia steppe, with the critical threshold for N-induced species loss being around 1.75 $g\,N\,m^{-2}\,yr^{-1}$. After 20 years of N enrichment in the North American grasslands, SR decreased even at the rate of 1 $g\,N\,m^{-2}\,yr^{-1}$, which was previously suggested to be safe to community diversity [32]. Another long-term study in the semi-natural central European grassland found that SR initially declined but began to recover after 25 years of continued N enrichment [33].

In arid and semiarid ecosystems, plant diversity and primary production are co-limited by water and N [34–36], and thus the responses of plant community to N addition are probably mediated by water availability [37]. Plant responses to N addition were greater in more mesic than drier ecosystems [38], and for a given grassland above-ground biomass (AGB) increase was much larger in wet than dry years [34,35]. According to hypotheses concerning N-induced species loss, high water availability could elevate the rate of species loss because of greater production increase and thus more light limitation. A recent study, however, showed that fertilization diminished plant diversity even when light is not limiting [26]. Harpole *et al.* [39] proposed that water addition promoted the production in response to N addition, but had no effect on SR response. Thus, it remains unclear to what extent water and light availability affect SR response to N addition.

In this study, we present results from a 10-year field experiment with six levels of N addition rate at a semiarid Inner Mongolia grassland [8], which is part of widely distributed grassland across the Eurasian Steppe region [35]. Our study addresses the following three questions: first, how do the patterns and critical thresholds for N-induced plant species loss vary across different levels of organization (i.e. plant species, functional group and community) and with experimental duration? Second, how does water availability (i.e. wet versus dry years) affect the responses of SR and primary production to N addition? Third, what are major mechanisms controlling chronic N enrichment-induced losses of plant species and changes in ecosystem functioning in terms of biomass production, stability and drought resistance? To address the first and second questions, we used several statistical approaches for assessing long-term changes in species diversity and ecosystem functioning at the levels of plant species, functional group and the whole community resulting from N enrichment. To address the third question, using functional trait-based approach, we tested six interrelated hypotheses which have been proposed to be the major mechanisms driving the N^{-} enrichment-induced changes in plant species diversity and ecosystem functioning [7,19,22,23,29,35]. These hypotheses include the random loss, shift from below-ground competition to above-ground or light competition, recruitment limitation, N addition duration, water and N co-limitation, and soil acidification.

2. MATERIAL AND METHODS

(a) *Study site*

The study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS; 116°42′ E, 43°38′ N and 1250 m a.s.l.), which is located in the Xilin River Basin, Inner Mongolia Autonomous Region of China [8]. The mean annual temperature in the study area is 0.3°C, with mean monthly temperature ranging from −21.6°C in January to 19.0°C in July. The mean annual precipitation is 346.1 mm, with about 80 per cent occurring in the growing season from May to September. The field experiment was carried out on a natural steppe community, which has been fenced against grazing by large animals since 1979. The soil is a dark chestnut (Calcic Chernozem according to ISSS Working Group RB, 1998) or loamy sand in terms of texture [8]. Soil pH value is 7.5 and cation exchange capacity (CEC) is 15.7 $cmol\,kg^{-1}$. Soil organic carbon, total nitrogen and total phosphorous contents at the top 20 cm layer are 15.0, 1.7 and 0.3 $g\,kg^{-1}$, respectively. No fertilizer had been used before this experiment. Before beginning the experiment, the plant community was dominated by *Leymus chinensis* (Trin.) Tzvel., a widely distributed perennial C_3 rhizomatous grass in the Eurasia steppe region [8,35].

(b) *N addition experiment*

To explore the effects of N on plant species diversity and ecosystem functioning (i.e. biomass production, stability and drought resistance), we established an N addition experiment in the autumn of 1999. The N addition experiment has been maintained since 2000. There were seven treatments and nine replicates for each treatment, a total number of 63 plots. The plots, each 5 × 5 m in size, were arranged in a randomized block design and separated by 1 m buffers. Each block included a control (no nutrient

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

addition) and six levels of N addition rate, i.e. 0, 1.75, 5.25, 10.50, 17.5, and 28.0 g N m^{-2} yr^{-1}. Nitrogen was added as commercial pelletized NH_4NO_3 fertilizer. To ensure that N was the only limiting nutrient [8,40], for all treatments except the control, we also added the same amount of P (10 g P_2O_5 m^{-2} yr^{-1}), S (0.2 mg m^{-2} yr^{-1}) and trace elements (Zn, 190 mg m^{-2} yr^{-1}, Mn, 160 mg m^{-2} yr^{-1} and B, 31 mg m^{-2} yr^{-1}) based on the soil census data [41]. Each year, nutrients were uniformly applied to each N-treatment plot with manual broadcasting in the mid-growing season (1–5 July), coinciding with high temperature and precipitation.

(c) *Soil acidification experiment*

To assess the relative importance of N input versus soil acidification in influencing SR, we established an additional soil acidification experiment near the N addition experimental site within the same plant community in 2009. There were eight treatments and five replicates for each treatment. A total of 40 plots, each of 2 × 2 m, were laid out in a randomized block design and separated by 1 m walkways. Each plot was fenced with a 25 cm height iron sheet, of which 20 cm was driven into soil. The treatments include a control (nothing added) and seven levels of acid addition rate (i.e. 0, 2.76, 5.52, 8.28, 11.04, 13.80 and 16.56 mol H^+m^{-2}) in the form of sulphuric acid solution. Acid addition was carried out in September 2009, June 2010 and September 2010, respectively. For each time, one dose of 98 per cent of sulphuric acid was diluted into 80 l solution with well water. To diminish the direct damage of acid to plants and soil organisms, each plot received an additional 30 and 50 l well water, respectively, before and after the acid solution was sprayed.

(d) *Filed sampling and measurements*

For the N addition experiment, above-ground vegetation was sampled each year between 25 August and 2 September by clipping all plants at the soil surface using a 0.5 × 1 m quadrat, which was randomly placed in each plot without spatial overlap of quadrats among all years [8]. To avoid edge effects, the quadrat was placed at least 50 cm inside each plot. For each species, the plant height and number of individuals were measured before clipping. Living vascular plants were sorted into species, and all plant materials, including litter and standing dead, were oven-dried at 65°C for 48 h and weighed. For each treatment, the dry mass of all living plants and number of species per quadrat were averaged over the nine replicates to estimate the total AGB and SR [8]. For the soil acidification experiment, plant height, density and number of species were measured during 28–30 August in 2010 and 2011 using a 0.5 × 0.5 m quadrat, which was located in the northeast part of each 2 × 2 m plot.

For the N addition experiment, soil samples were taken from the surface to a depth of 20 cm in 7–18 July, 2009. Within each plot, one soil core was randomly collected using a 3-cm diameter soil auger. Soil cores were sieved through a 2-mm mesh and air-dried. The soil pH values were measured in water suspension (water : soil = 2.5 : 1) by a pH metre (FE20—FiveEasy). For the soil acidification experiment, soil samples were collected on 25 August in 2010 and 2011, and soil pH values were determined using the same method.

(e) *Plant functional traits*

To test the relative importance of abundance versus functional trait-based mechanisms underlying the chronic N enrichment-induced species loss, we quantified 17 plant functional traits for all species in the experiment (see the electronic supplementary material, table S1). These traits, including mass- and area-based leaf N contents, leaf C : N, specific leaf area, plant height, stem : leaf biomass ratio, root : shoot biomass ratio, net photosynthetic rate, instantaneous water use efficiency, specific root length of the first-, second- and third-order roots, reproductive allocation (fruit to total plant biomass ratio), and seed size and grain mass, were measured using standard methods [42]. Foliar $\delta^{13}C$ values, leaf nitrogen resorption efficiency, and leaf nitrogen use efficiency were obtained from published data (see electronic supplementary material, table S1). Data of plant life history, clonality and life form for different species were obtained from the Flora of Inner Mongolia. Trait plasticity index was calculated as in Godoy *et al.* [43].

(f) *Species abundance class and response variables*

To facilitate our analysis and interpretations, based on average RA of each species in control plots during 2005–2009, plant species were classified into two abundance classes, i.e. common species (RA > 1%) and rare species (RA < 1%) [32]. To allow direct comparison across time and between N addition and soil acidification experiments, the SR response ratio was calculated as the ratio of the mean SR in each N treatment to the mean SR in control (i.e. $SR_{treat}/SR_{control}$). Similarly, the AGB response ratio was calculated as the ratio of the mean AGB in each N treatment to the mean AGB in control (i.e. $AGB_{treat}/AGB_{control}$).

To evaluate the effect of chronic N enrichment on stability of production, we used the coefficient of variation of AGB and drought resistance as indices of stability. The coefficient of variation of AGB over nine replicates of each treatment was used as the measure of intra-annual variance of AGB (intra-annual CV_{AGB}). The inter-annual variance of AGB (inter-annual CV_{AGB}) was calculated as the coefficient of variation of AGB of each plot over five years (2005–2009). For each treatment, the drought resistance was expressed as the ratio of the AGB in dry year to the AGB in normal year [44], i.e. AGB_{2009}/AGB_{2006} in this study.

(g) *Statistical analyses*

Statistical analyses were performed using SAS v. 8.0 (SAS Institute, Cary, NC, USA, 2001). Repeated measures analyses for SR and AGB were performed with mixed linear model (Proc Mixed) using N treatment, year and their interactions as fixed effects. ANOVAs followed by a Duncan's multiple-range test

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

Table 1. Repeated measures analyses with mixed linear model (PROC MIXED) for species richness and above-ground biomass using N treatment (N), year (Y) and their interactions as fixed effects.

response	term	F	p-value
all species	N	41.79	<0.0001
	Y	41.31	<0.0001
	N × Y	1.13	0.3129
common species	N	26.65	<0.0001
	Y	58.27	<0.0001
	N × Y	2.34	0.0008
rare species	N	28.65	<0.0001
	Y	19.77	<0.0001
	N × Y	2.53	0.0003
above-ground biomass	N	25.50	<0.0001
	Y	43.32	<0.0001
	N × Y	2.92	<0.0001

were performed to test for differences between controls and each N-treatment level each year. Regression models were used to determine the relationship between N addition rate and various responses (adjustments for non-linearity were made as needed). We used linear regressions to examine relationships between responses of SR and biomass and experimental duration and June–July precipitation. The critical threshold (N_{crit}) was estimated by extrapolating the fitted curve and its 95% confidence interval (CI) [32].

3. RESULTS

(a) *Response of species richness*

Repeated measures analysis with PROC MIXED for SR, using N treatment (N), year (Y) and their interactions as fixed effects, showed that the effects of N and experimental duration were highly significant for total SR and two abundance classes, i.e. common species and rare species (table 1). The interactions of N × Y were significant for both the common and rare species (table 1). Our analysis further revealed that the effects of N treatment, year and N × Y on SR response ratio were all significant for both the common and rare species (see electronic supplementary material table S2). Total SR declined with increasing N addition rate throughout the 5-year period (figure 1*a*). The slope of the SR–N relationship decreased linearly with increasing N addition duration ($R^2 = 0.70$, $p < 0.05$; data not shown). By 2009 (the 10th year), nine species (approx. 75%), on average, were excluded from plots at the two highest N addition rates (17.5 and 28 g N m^{-2} yr^{-1}), compared with those of control plots in 2005 and 2006 (figure 1*a*). Patterns of SR response to N were comparable between the common and rare species (figure 1*b*,*c*). No significant difference in SR was found between the control (no nutrients added) and the zero-N treatment (added P, S and trace elements but not N) (For Treatment, $F = 0.14$, $p = 0.7054$; for time × treatment, $F = 1.36$, $p = 0.2557$).

SR response ratio showed a log-linear function of N addition rate; and SR started to decline at the addition rate of 1.75 g N m^{-2} yr^{-1} throughout four of the five years, saturating at 17.5 g N m^{-2} yr^{-1} (figure 2*a*). Total SR decreased by 15 per cent relative to control even at the lowest addition rate of 1.75 g N m^{-2} yr^{-1}. The predicted critical threshold (N_{crit}) was 0.85 g N m^{-2} yr^{-1} with a 95% CI of 0.44–1.51 g N m^{-2} yr^{-1}.

For rare species, a similar negative relationship between SR response and N addition rate was observed, with richness reduction occurring at the addition rate of 1.75 g N m^{-2} yr^{-1} (figure 2*c*). The slope of the fitted curve for rare species was significantly steeper (slope = −0.26) than that for total species (slope = −0.15, $p < 0.01$), and it was greater at lower N addition rates. The N_{crit} for rare species was 0.22 g N m^{-2} yr^{-1}, with a 95% CI of 0.09–0.50 g N m^{-2} yr^{-1}. For common species, in contrast, the reduction in SR increased linearly with N addition rate, and SR began to decline mostly at the 10.5 g N m^{-2} yr^{-1} rate, saturating at 17.5 g N m^{-2} yr^{-1} (figure 2*b*). The N_{crit} for common

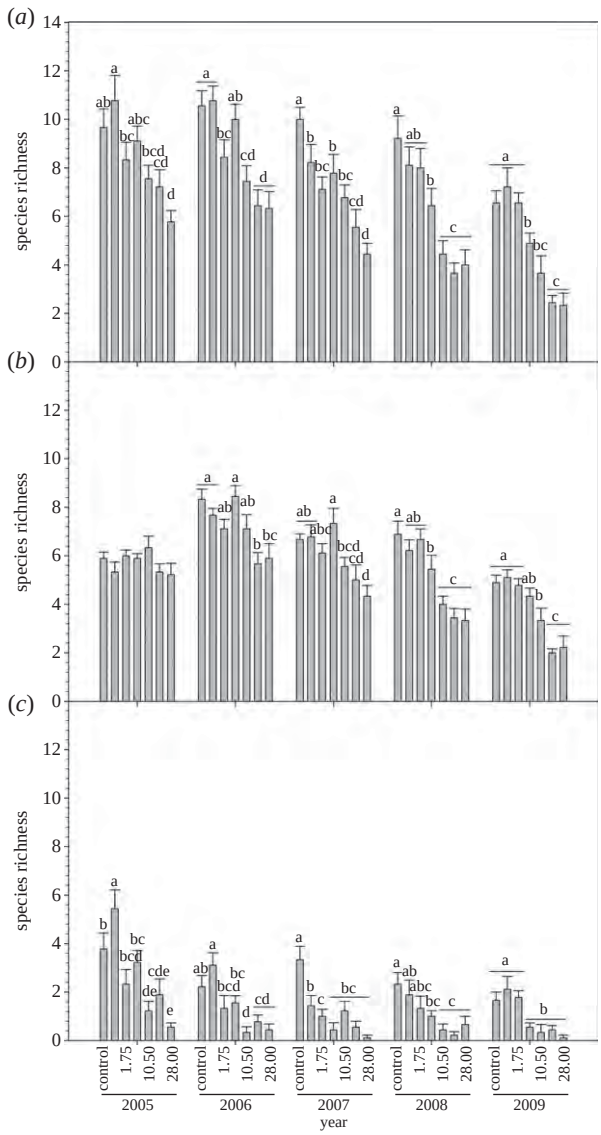


Figure 1. Effects of N addition on species richness of (*a*) all species, (*b*) common species and (*c*) rare species during 2005–2009 (error bars denote s.e.m.). Bars with the same letter were not significantly different in Duncan's multiple range tests reported from one-way ANOVA.

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

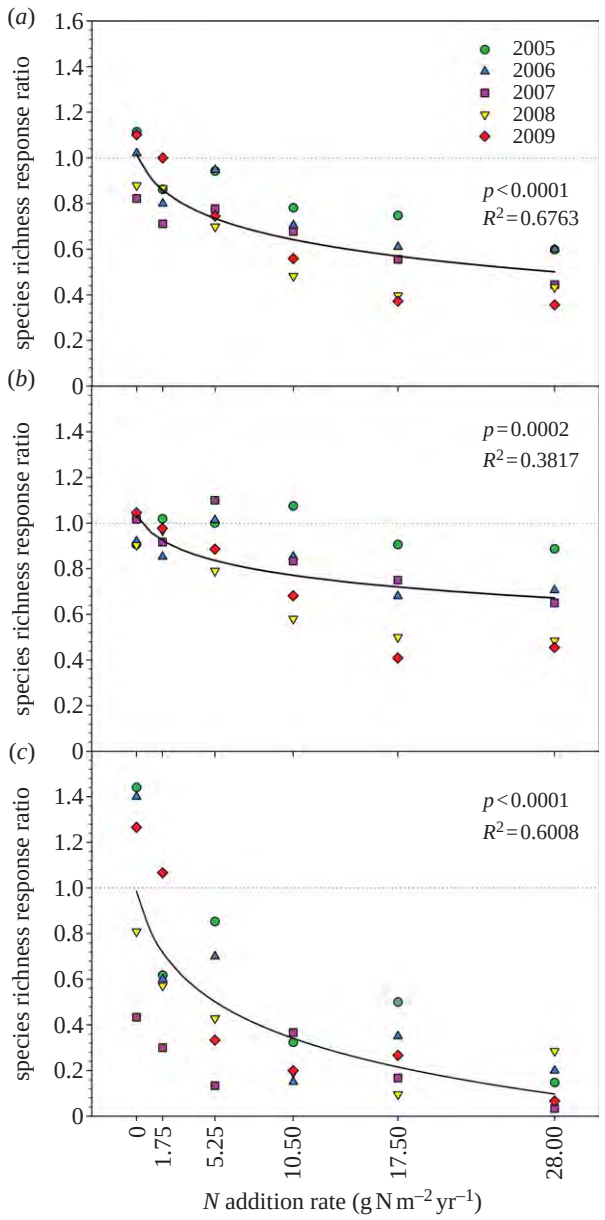


Figure 2. Relationships between species richness response ratio and N addition rate for (*a*) all species, (*b*) common species and (*c*) rare species over five years. Species richness response ratio was the average of nine replicates of each treatment. Regression parameters were estimated using log-linear model with N treatment as a continuous predictor, i.e. Species richness response = Intercept + Slope × Ln ($N + 1$).

species was 1.84 g N m^{-2} yr^{-1}, with a 95% CI of 0.59–3.92 g N m^{-2} yr^{-1}. The negative effect of N addition on SR was greater in the wet year (2008) than dry year (2009), particularly at moderate and high addition rates (5.25 and 10.5 g N m^{-2} yr^{-1}). For both common and rare species, the reduction in SR tended to increase with experimental duration across different N addition rates from 5.25 to 28.0 g N m^{-2} yr^{-1}.

(b) *Above-ground biomass, intra- and inter-annual variability and drought resistance*

AGB was significantly affected by N treatment, experimental duration and their interactions (table 1). Although the critical N addition rate for AGB varied substantially over time (year), it was generally lower than 5.25 g N m^{-2} yr^{-1} (see electronic supplementary material, figure S1). Throughout the five years, the AGB response showed a log-linear function of N addition rate (see the electronic supplementary material, figure S1). The slope of the biomass–N relationship tended to increase with June–July precipitation ($R^2 = 0.63$, $p = 0.0687$, $N = 5$; data not shown). It was significantly greater in normal and wet years (e.g. 2006 and 2008) than in dry years (e.g. 2005, 2007 and 2009; $p < 0.01$; see electronic supplementary material, figure S1). For example, AGB increased by 87 per cent in 2008 (a wet year; June–July precipitation = 170.7 mm) and only by 32 per cent in 2009 (an extremely dry year, June–July precipitation = 93.7 mm) at the additional rate of 10.5 g N m^{-2} yr^{-1}, compared with control plots (see the electronic supplementary material, figure S1).

The coefficients of intra-annual variation in AGB did not show significant response to N treatment (figure 3*a*). The coefficients of inter-annual variation in AGB at first increased with N addition rate, peaked approximately at the addition rate of 17.5 g N m^{-2} yr^{-1}, and then declined at the highest N addition rate (figure 3*b*). For a given treatment, the magnitude of inter-annual variation in AGB was generally greater than the intra-annual variation (variation among replicates). The drought resistance declined with increasing N addition rate (figure 3*c*).

(c) *Plant species responses*

At the beginning of the experiment, there were 48 vascular plant species and 80 per cent of them were rare species (RA < 1%). The loss of rare species continued throughout five years of the experiment (the 6–10th year; figure 1*c*). At species level, AGB of rare species varied among N treatments and over time, owing mainly to their low initial abundance (data not shown).

For common species, both the patterns and magnitude of AGB response to N addition differed substantially among species (see electronic supplementary material, figure S2). The critical thresholds for N addition ranged from 1.75 (*Carex korshinskyi*) to 10.5 g N m^{-2} yr^{-1} (i.e. *Leymus chinensis*, *Achnatherum sibiricum* and *Agropyron cristatum*; electronic supplementary material, figure S2). For *Stipa grandis*, *Chenopodium glaucum* and *Axyris amaranthoides*, AGB tended to either increase or decline at the addition rate of 5.25 g N m^{-2} yr^{-1} (see electronic supplementary material, figure S2).

(d) *Relationships of species richness with soil pH and above-ground biomass*

For both N addition and soil acidification experiments, plant SR declined with reduction in soil pH, which is expressed as $pH_{control} - pH_{treat}$ of the top 20 cm of soil (Δ soil pH, figure 4*a*). For a given reduction in soil pH, however, greater reduction in SR was found in the N-treatment plots than in the acid-treatment plots. In the N addition experiment, SR tended to decline even with relatively small reduction in soil pH (e.g. Δ soil pH = 0.4). In the

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

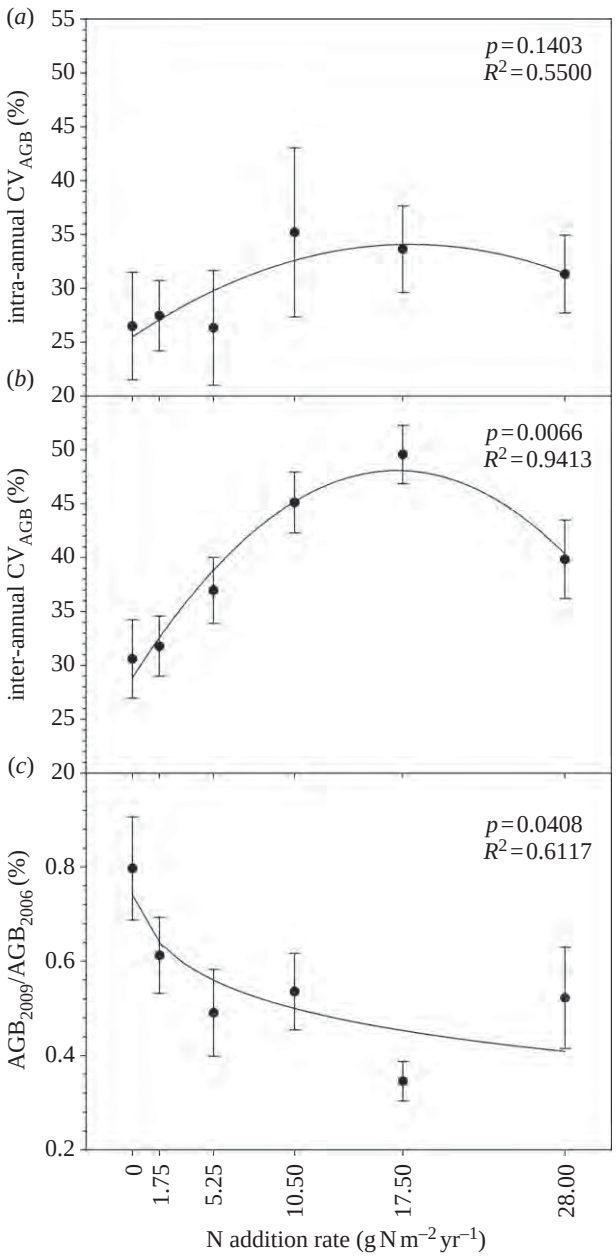


Figure 3. Effects of N addition on intra- and inter-annual variation in above-ground biomass (AGB) and drought resistance (error bars denote s.e.m.). (*a*) Intra-annual CV_{AGB}; (*b*) Inter-annual CV_{AGB}; (*c*) AGB_{2009}/AGB_{2006}. Intra-annual CV_{AGB} for each treatment was the average of five years (2005–2009). Inter-annual CV_{AGB} and AGB_{2009}/AGB_{2006} for each treatment were the average of nine replicates.

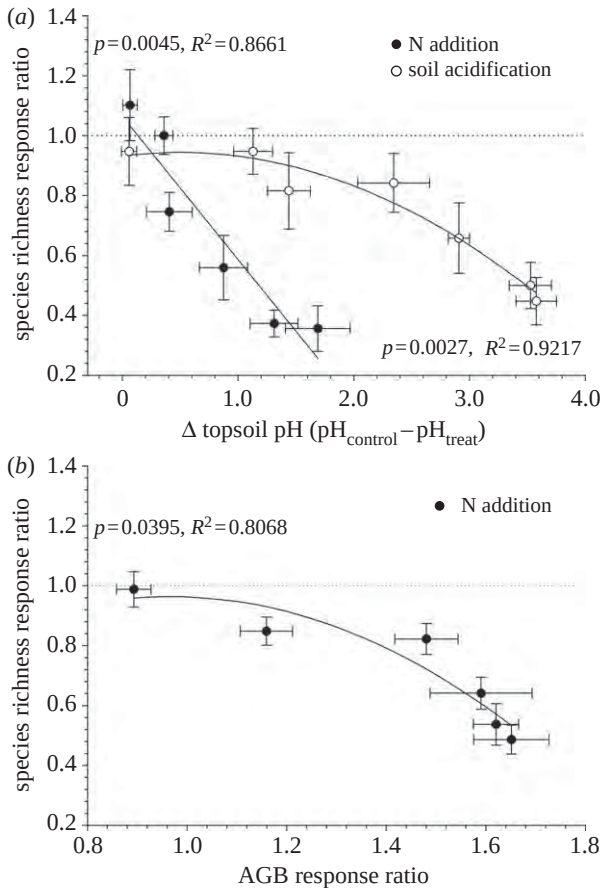


Figure 4. Relationships of species richness response with changes in (*a*) soil pH and (*b*) above-ground biomass (AGB) (error bars denote s.e.m.). In the N addition experiment, species richness and AGB response ratios were the average of nine replicates of each treatment. In the soil acidification experiment, species richness response ratio was the average of five replicates of each treatment in 2011.

soil acidification experiment, in contrast, no significant reduction in SR was observed until the Δ soil pH exceeded 1.2 by the third year (2011) (figure 4*a*).

In the N addition experiment, SR response was negatively correlated with AGB response, which explained 81 per cent of the variance in richness (figure 4*b*). Greater reduction in SR occurred with larger biomass increment, corresponding to high levels of N addition rates (i.e. 10.5 to 28.0 g N m^{-2} yr^{-1}). Stepwise multiple linear regressions, using the Δ soil pH and biomass increase as independent variables, further revealed that biomass increase had much greater partial R^2 (partial $R^2 = 0.39$, $p < 0.0001$) than that of the Δ soil pH (partial $R^2 = 0.08$, $p = 0.0082$).

(e) *Plant functional traits and trait plasticity*

Among seven common species, which together accounted for 86 per cent of the total community AGB in control plots, the relative AGB of three species significantly increased with N while that of the other four species declined (see electronic supplementary material table, S3). Multi-trait comparison showed that positive and negative response species differed substantially in nine out of 19 plant functional traits, including whole plant, leaf, root, reproductive and life-history traits (see electronic supplementary material, table S3). Species showing positive response to N exhibited greater mass-based leaf N content, stem : leaf biomass ratio, net photosynthetic rate, reproductive allocation and specific root length of the second- and third-order roots but lower leaf C : N and root : shoot ratio than those showing negative response to N (see electronic supplementary material, table S3). For the positive response species, plasticity of both mass- and area-based leaf N contents to medium rate of N addition (5.25 g N m^{-2} yr^{-1}) were significantly lower than those of negative response species, with other traits showing little plasticity (see electronic supplementary material, table S3). In addition, our results illustrated that rare species, in general, showed lower photosynthetic rate and stem : leaf ratio but higher

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

root : shoot ratio, compared with common species (data not shown).

4. DISCUSSION

(a) *Patterns of species richness response to chronic N enrichment and critical threshold*

Our results have shown that patterns of SR response differed substantially among N treatments, between the common and rare species, and through time. These patterns suggest the following four conclusions.

First, plant diversity was highly sensitive to chronic N enrichment in the semiarid steppe, and species loss occurred even at very low rates of N input. Although we did observe a critical threshold for N-induced species loss within the range of N addition rates tested in this study, the predicted N_{crit} was 0.85 g N m^{-2} yr^{-1}. This is only partially showed by our results that SR decreased by 15 per cent relative to control even at the addition rate of 1.75 g N m^{-2} yr^{-1}, below which we lack data to estimate the actual N_{crit} for our system. However, the predicted N_{crit} is within the range of N_{crit} (0.5–2.0 g N m^{-2} yr^{-1}) reported from the North American and European grasslands [4,32].

Second, the rare species, which accounted for up to 80 per cent of the total plant species numbers, were more sensitive to chronic N enrichment than common species. The average numbers of rare species reduced by 47 per cent relative to control at the rate of 1.75 g N m^{-2} yr^{-1}, implying that the actual N_{crit} for rare must be lower than our lowest addition rate. This is most probable because of the unique geographical and climatic conditions of the Inner Mongolian steppe, where species have evolved strategies of conservative resource use in water limited and infertile conditions [35,45]. The Inner Mongolia steppe historically received little N deposition (less than 0.05 g N m^{-2} yr^{-1}), and the current level of N deposition is still very low (less than 0.3 g N m^{-2} yr^{-1}); although it is projected to have N deposition 0.5–1.0 g N m^{-2} yr^{-1} in 2030 [4]. Hence, it has not yet experienced a rapid loss of plant species induced by chronic N input. The North American and European grasslands, in contrast, have received high levels of anthropogenic N deposition for several decades, and the loss of highly sensitive rare species has already occurred [4,32,46]. Our findings highlight the impacts of chronic low-level N enrichment on highly sensitive rare species and ecosystem functioning.

Third, the responses of SR and AGB to N enrichment tended to saturate at addition rates more than or equal to 10.5 g N m^{-2} yr^{-1}, beyond which little additional increase in biomass and/or reduction in plant diversity were observed. This is consistent with our previous findings from the first 4-year results of the same experiment [8], and it is also supported by long-term data of extractable soil NH_4^+-N and NO_3^--N concentrations (Y. F. B. Bai 2010, unpublished data).

Fourth, the negative impacts of N enrichment on SR seemed to increase with N addition duration. Our results showed that SR response ratio declined with increasing experimental duration, particularly at moderate (5.25 g N m^{-2} yr^{-1}) and high addition rates (10–28 g N m^{-2} yr^{-1}). This finding is further corroborated by our previous study using the first 4-year data from the same experiment [8].

(b) *Water-mediated N effects*

Our results demonstrate that the June–July precipitation was an important predictor of AGB and SR responses to N. Greater responses of AGB to N addition were found in wet years, with high June–July precipitation (e.g. 2008). The reduction in SR relative to control also tended to be greater in wet years than dry years at addition rates of 1.75–10.5 g N m^{-2} yr^{-1}. These results suggest two conclusions: first, above-ground net primary production is co-limited by water and N availability. Although we did not find strong evidence for a critical precipitation level, below which water availability was seriously limiting and AGB exhibited little response to N, our results showed that AGB response saturated at addition rates more than or equal to 5.25 g N m^{-2} yr^{-1} in 2009 (an extremely dry year), indicating that primary production was more limited by water than N. Second, the seasonal distribution of precipitation, such as June–July precipitation, is more important than total annual precipitation in controlling community and species responses to N. This may be because N was added in early July each year, and temperature usually reached its annual peak in July. If the precipitation was also high in June and July, all of these key factors could be synchronized in a manner stimulating plant growth [34,37]. Therefore, our results are consistent with the pulse-reserve/threshold hypothesis that plant growth and primary production in drylands are driven by the complex interactions among key abiotic and biotic factors [36].

(c) *Mechanisms underlying N-induced species loss*

Our results demonstrated that rare species were highly sensitive to N enrichment, with low initial abundance (less than 1%) and low critical threshold but high risk of species loss. The loss of rare species occurred continuously throughout the experimental period from 2000 to 2009 (also see Bai *et al.* [8]) and across all N addition rates. Our findings support the general projections of the random loss hypothesis which posits loss of rare species with N enrichment is mostly owing to their low initial abundance. However, our results showed that rare species generally exhibited the lower photosynthetic rate and stem : leaf ratio but higher root : shoot ratio, compared with common species. This indicates that both the low initial abundance and low above-ground competitive ability may be attributable to the loss of rare species in our system.

For common species, shifts in species dominance and composition were mainly caused by functionally based mechanisms. The experimental evidence supports our original hypotheses that chronic N enrichment increased the relative importance of above-ground competition over below-ground competition. We found that shifts in species dominance favoured acquisitive versus conservative resource-use strategies. Species with acquisitive resource-use strategies showed high leaf N content, net photosynthetic rate and stem : leaf ratio

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

but low root : shoot ratio, corresponding to high above-ground/light competitive ability. These species, such as *A. amaranthoides*, *C. glaucum* and *L. chinensis*, exhibited competitive advantage over others when N limitation was released following N enrichment. In contrast, species with conservative resource-use strategies were characterized by high leaf C : N, specific leaf area and root : shoot ratio but low leaf N content and net photosynthetic rate, corresponding to high below-ground competitive ability. Hence, species that dominated at original community, such as *S. grandis*, *A. cristatum* and *A. sibiricum*, were potentially outcompeted by those with high above-ground competitive ability following N enrichment. The trait trade-offs of plants observed in our experiment reflect the nature of fundamental trade-offs between productivity and persistence among coexisting species [47].

It has been proposed that recruitment limitation is predominant in underpinning the chronic N enrichment-induced loss of plant species [4,22]. Our findings illustrated that species with acquisitive resource-use strategies exhibited substantially higher reproductive output than those with conservative resource-use strategies. This indicates that, for resource conservative species, recruitment limitation was intensified owing to low reproductive output and competitive disadvantage in above-ground competition. Our field observations further revealed that the seedling density of these resource conservative species was very low following 10 years of N enrichment. For species with acquisitive resource-use strategies, however, greater seedling density was observed (Z. Lan, X. Bai and Y. Bai 2011, unpublished data). Thus, we conclude that chronic N enrichment increased recruitment limitation of the resource conservative species.

Our results, in general, support the projections of the soil acidification hypothesis, but we further found that the effect of soil pH reduction on species loss was relatively minor in magnitude compared with the direct effect of chronic N input. Multiple linear regressions revealed that the proportion of variance in SR explained by biomass increment was much greater (partial $R^2 = 0.39$) than the soil pH reduction (partial $R^2 = 0.08$) in the N addition experiment. Thus, the chronic N enrichment-induced biomass increment is likely to be a major driver of N-induced plant species loss. Our findings were different from those of previous studies in the European grasslands regarding the relative importance of N availability versus soil acidification [4,24,25]. This may be attributed to high initial soil pH, high CEC and low mean annual precipitation in the semiarid Inner Mongolia grassland, which together suggest that the soils of our system are less sensitive to acidification and nutrient cation loss than those of acidic soils in the European grasslands following N addition [4,9].

(d) *Implications of ecosystem functioning and services under global change*

Our findings have shown that chronic N enrichment substantially reduced plant species diversity, led to the loss of species with resource conserving strategies and shifted species dominance. These changes in plant diversity and species composition affected ecosystem functioning and provisioning of services in different ways. First, stability of primary production was reduced considerably. The decreased stability is mainly attributed to the increased inter-annual variations in AGB with N addition. Second, ecosystem drought resistance declined with increasing N addition rate. This is probably caused by the reduction in RA of perennial bunchgrasses (e.g. *S. grandis*, *A. cristatum* and *A. sibiricum*) and increased dominance of N demanding annuals (i.e. *C. glaucum* and *A. amaranthoides*). Third, the replacement of perennial bunchgrasses by annuals may also decrease below-ground biomass allocation and reduce non-growing vegetation cover. This could diminish snow-holding capacity, increase soil erosion owing to the strong fall and winter winds and reduce soil carbon sequestration potential [48].

Our findings have important implications for better understanding the effects of global change on ecosystem services of the Inner Mongolia grassland. It has been projected that future climatic change will increase the extreme droughts and intense rainfall events [16,49]. The projected increase in N deposition and change in precipitation regimes may act together to accelerate the loss of rare species, shift species dominance and composition, elevate water limitation, and consequently diminish ecosystem stability and services [4,14,16,37].

We are grateful to Qingmin Pan, Darrel Jenerette, Victor Squires and Rob Salguero-Gómez for comments on an early version of this manuscript. We thank Hong Wang for help with statistical analysis and Shuxia Zheng, Hongtao Zhao, Chunmei Pan and many others at the Inner Mongolia Grassland Ecosystem Research Station, Chinese Academy of Sciences for their help with fieldwork. This project was supported by the State Key Basic Research Development Program of China (2009CB421102) and the National Natural Science Foundation of China (30825008, 31030013).

REFERENCES

1 Vitousek, P. M. & Howarth, R. W. 1991 Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* **13**, 87–115. (doi:10.1007/BF00002772)
2 Elser, J. J. *et al.* 2007 Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* **10**, 1135–1142. (doi:10.1111/j.1461-0248.2007.01113.x)
3 Aerts, R. & Chapin III, F. S. 2000 The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* **30**, 1–67. (doi:10.1016/s0065-2504(08)60016-1)
4 Bobbink, R. *et al.* 2010 Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* **20**, 30–59. (doi:10.1890/08-1140.1)
5 Sala, O. E. 2000 Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774. (doi:10.1126/science.287.5459.1770)
6 Vitousek, P. M., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H. & Tilman, D. G. 1997 Human alteration of the global nitrogen cycle: sources and consequences. *Ecol. Appl.* **7**, 737–750. (doi:10.2307/2269431)
7 Suding, K. N. 2005 Functional- and abundance-based mechanisms explain diversity loss due to N fertilization.

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

Proc. Natl Acad. Sci. USA **102**, 4387–4392. (doi:10.1073/pnas.0408648102)

8 Bai, Y., Wu, J., Clark, C. M., Naeem, S., Pan, Q., Huang, J., Zhang, L. & Han, X. 2010 Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands. *Glob. Change Biol.* **16**, 358–372. (doi:10.1111/j.1365-2486.2009.01950.x)

9 Clark, C. M. *et al.* 2007 Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecol. Lett.* **10**, 596–607. (doi:10.1111/j.1461-0248.2007.01053.x)

10 Bobbink, R., Hornung, M. & Roelofs, J. G. M. 1998 The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J. Ecol.* **86**, 717–738. (doi:10.1046/j.1365-2745.1998.8650717.x)

11 Wedin, D. A. & Tilman, D. 1996 Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* **274**, 1720–1723. (doi:10.1126/science.274.5293.1720)

12 Hector, A. & Bagchi, R. 2007 Biodiversity and ecosystem multifunctionality. *Nature* **448**, 188–190. (doi:10.1038/nature05947)

13 Tilman, D., Reich, P. B. & Knops, J. M. H. 2006 Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* **441**, 629–632. (doi:10.1038/nature04742)

14 Maestre, F. T. *et al.* 2012 Plant species richness and ecosystem multifunctionality in global drylands. *Science* **335**, 214–218. (10.1126/science.1215442)

15 Millennium Ecosystem Assessment. 2005 *Ecosystems and human well-being: synthesis*. Washington, DC: Island Press.

16 Maestre, F. T., Salguero-Gómez, R. & Quero, J. L. 2012 It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. *Phil. Trans. R. Soc. B* **367**, 3062–3075. (doi:10.1098/rstb.2011.0323)

17 Cleland, E. E. & Harpole, W. S. 2010 *Nitrogen enrichment and plant communities. Year in ecology and conservation biology 2010*, pp. 46–61. Oxford, UK: Blackwell Publishing.

18 Oksanen, J. 1996 Is the humped relationship between species richness and biomass an artefact due to plot size? *J. Ecol.* **84**, 293–295. (doi:10.2307/2261364)

19 Hautier, Y., Niklaus, P. A. & Hector, A. 2009 Competition for light causes plant biodiversity loss after eutrophication. *Science* **324**, 636–638. (doi:10.1126/science.1169640)

20 Pan, Q. M., Bai, Y. F., Wu, J. G. & Han, X. G. 2011 Hierarchical plant responses and diversity loss after nitrogen addition: testing three functionally-based hypotheses in the Inner Mongolia grassland. *PLoS ONE* **6**, e20078. (doi:10.1371/journal.pone.0020078)

21 Tilman, D. 1993 Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* **74**, 2179–2191. (doi:10.2307/1939572)

22 Stevens, M. H. H., Bunker, D. E., Schnitzer, S. A. & Carson, W. P. 2004 Establishment limitation reduces species recruitment and species richness as soil resources rise. *J. Ecol.* **92**, 339–347. (doi:10.1111/j.0022-0477.2004.00866.x)

23 Crawley, M. J., Johnston, A. E., Silvertown, J., Dodd, M., de Mazancourt, C., Heard, M. S., Henman, D. F. & Edwards, G. R. 2005 Determinants of species richness in the park grass experiment. *Am. Nat.* **165**, 179–192. (doi:10.1086/427270)

24 Stevens, C. J., Thompson, K., Grime, J. P., Long, C. J. & Gowing, D. J. G. 2010 Contribution of acidification and eutrophication to declines in species richness of calcifuge grasslands along a gradient of atmospheric nitrogen deposition. *Funct. Ecol.* **24**, 478–484. (doi:10.1111/j.1365-2435.2009.01663.x)

25 Roem, W. J., Klees, H. & Berendse, F. 2002 Effects of nutrient addition and acidification on plant species diversity and seed germination in heathland. *J. Appl. Ecol.* **39**, 937–948. (doi:10.1046/j.1365-2664.2002.00768.x)

26 Dickson, T. L. & Foster, B. L. 2011 Fertilization decreases plant biodiversity even when light is not limiting. *Ecol. Lett.* **14**, 380–388. (doi:10.1111/j.1461-0248.2011.01599.x)

27 Pennings, S. C., Clark, C. M., Cleland, E. E., Collins, S. L., Gough, L., Gross, K. L., Milchunas,, D. G. & Suding, K. N. 2005 Do individual plant species show predictable responses to nitrogen addition across multiple experiments? *Oikos* **110**, 547–555. (doi:10.1111/j.0030-1299.2005.13792.x)

28 McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. 2006 Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **21**, 178–185. (doi:10.1016/j.tree.2006.02.002)

29 De Schrijver, A., De Frenne, P., Ampoorter, E., Van Nevel, L., Demey, A., Wuyts, K. & Verheyen, K. 2011 Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Global Ecol. Biogeogr.* **20**, 803–816. (doi:10.1111/j.1466-8238.2011.00652.x)

30 Bobbink, R., Ashmore, M., Braun, S., Flückiger, W. & Van den Wyngaert, I. J. J. 2002 Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update. In *Empirical critical loads for nitrogen* (eds B. Achermann & R. Bobbink), pp. 40–170. Berne: Swiss Agency for the Environment, Forests and Landscape (SAEFL).

31 Nilsson, J. & Grennfelt, P. (eds) 1988 *Critical loads for sulphur and nitrogen*. Environmental Report 1988:15. Copenhagen, Denmark: Nordic Council of Ministers.

32 Clark, C. M. & Tilman, D. 2008 Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature* **451**, 712–715. (doi:10.1038/nature06503)

33 Pierik, M., van Ruijven, J., Bezemer, T. M., Geerts, R. H. E. M. & Berendse, F. 2011 Recovery of plant species richness during long-term fertilization of a species-rich grassland. *Ecology* **92**, 1393–1398. (doi:10.1890/10-0210.1)

34 Hooper, D. U. & Johnson, L. 1999 Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry* **46**, 247–293. (doi:10.1023/A:1006145306009)

35 Bai, Y. F., Wu, J. G., Xing, Q., Pan, Q. M., Huang, J. H., Yang, D. L. & Han, X. G. 2008 Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. *Ecology* **89**, 2140–2153. (doi:10.1890/07-0992.1)

36 Reynolds, J. F., Kemp, P. R., Ogle, K. & Fernandez, R. J. 2004 Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* **141**, 194–210. (doi:10.1007/s00442-004-1524-4)

37 Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbágy, E. & Peters, D. 2012 Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Phil. Trans. R. Soc. B* **367**, 3135–3144. (doi:10.1098/rstb.2011.0347)

38 Xia, J. Y. & Wan, S. Q. 2008 Global response patterns of terrestrial plant species to nitrogen addition. *New Phytol.* **179**, 428–439. (doi:10.1111/j.1469-8137.2008.02488.x)

39 Harpole, W. S., Potts, D. L. & Suding, K. N. 2007 Ecosystem responses to water and nitrogen amendment in a California grassland. *Glob. Change Biol.* **13**, 2341–2348. (doi:10.1111/j.1365-2486.2007.01447.x)

40 Tilman, D. 1987 Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.* **57**, 189–214. (doi:10.2307/2937080)

Downloaded from rstb.royalsocietypublishing.org on October 11, 2012

41 Inner Mongolia Soil Census Office & Inner Mongolia Soil and Fertilizer Service. (eds) 1994 *The soils of Inner Mongolia*. Beijing, People's Republic of China: Science Press.

42 Cornelissen, J. H. C. *et al.* 2003 A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Austral. J. Bot.* **51**, 335–380. (doi:10.1071/BT02124)

43 Godoy, O., Valladares, F. & Castro-Díez, P. 2011 Multispecies comparison reveals that invasive and native plants differ in their traits but not in their plasticity. *Funct. Ecol.* **25**, 1248–1259. (doi:10.1111/j.1365-2435.2011.01886.x)

44 Tilman, D. & Downing, J. A. 1994 Biodiversity and stability in grasslands. *Nature* **367**, 363–365. (doi:10.1038/367363a0)

45 Coupland, R. T. (ed.) 1993 *Ecosystems of the world 8B. Natural grasslands: Eastern hemisphere and résumé*. Amsterdam, The Netherlands: Elsevier.

46 Stevens, C. J., Dise, N. B., Mountford, J. O. & Gowing, D. J. 2004 Impact of nitrogen deposition on the species richness of grasslands. *Science* **303**, 1876–1879. (doi:10.1126/science.1094678)

47 He, J.-S., Wang, X., Flynn, D. F. B., Wang, L., Schmid, B. & Fang, J. 2009 Taxonomic, phylogenetic, and environmental trade-offs between leaf productivity and persistence. *Ecology* **90**, 2779–2791. (doi:10.1890/08-1126.1)

48 Shan, Y. M., Chen, D. M., Guan, X. X., Zheng, S. X., Chen, H. J., Wang, M. J. & Bai, Y. F. 2011 Seasonally dependent impacts of grazing on soil nitrogen mineralization and linkages to ecosystem functioning in Inner Mongolia grassland. *Soil Biol. Biochem.* **43**, 1943–1954. (doi:10.1016/j.soilbio.2011.06.002)

49 Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R. & Mearns, L. O. 2000 Climate extremes: observations, modeling, and impacts. *Science* **289**, 2068–2074. (doi:10.1126/science.289.5487.2068)

Global Change Biology

Global Change Biology (2010) **16**, 358–372, doi: 10.1111/j.1365-2486.2009.01950.x

Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands

YONGFEI BAI*, JIANGUO WU*†, CHRISTOPHER M. CLARK†, SHAHID NAEEM‡, QINGMIN PAN*, JIANHUI HUANG*, LIXIA ZHANG* and XINGGUO HAN*

*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China, †School of Life Sciences and Global Institute of Sustainability, Arizona State University, Tempe, Arizona 85287-4501, USA, ‡Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA

Abstract

Nitrogen (N) deposition is widely considered an environmental problem that leads to biodiversity loss and reduced ecosystem resilience; but, N fertilization has also been used as a management tool for enhancing primary production and ground cover, thereby promoting the restoration of degraded lands. However, empirical evaluation of these contrasting impacts is lacking. We tested the dual effects of N enrichment on biodiversity and ecosystem functioning at different organizational levels (i.e., plant species, functional groups, and community) by adding N at 0, 1.75, 5.25, 10.5, 17.5, and 28.0 g N m^{-2} yr^{-1} for four years in two contrasting field sites in Inner Mongolia: an undisturbed mature grassland and a nearby degraded grassland of the same type. N addition had both quantitatively and qualitatively different effects on the two communities. In the mature community, N addition led to a large reduction in species richness, accompanied by increased dominance of early successional annuals and loss of perennial grasses and forbs at all N input rates. In the degraded community, however, N addition increased the productivity and dominance of perennial rhizomatous grasses, with only a slight reduction in species richness and no significant change in annual abundance. The mature grassland was much more sensitive to N-induced changes in community structure, likely as a result of higher soil moisture accentuating limitation by N alone. Our findings suggest that the critical threshold for N-induced species loss to mature Eurasian grasslands is below 1.75 g N m^{-2} yr^{-1}, and that changes in aboveground biomass, species richness, and plant functional group composition to both mature and degraded ecosystems saturate at N addition rates of approximately 10.5 g N m^{-2} yr^{-1}. This work highlights the tradeoffs that exist in assessing the total impact of N deposition on ecosystem function.

Keywords: aboveground biomass, ecological restoration, ecosystem management, Eurasia steppe, nitrogen enrichment, plant functional group composition, species richness

Received 21 January 2009 and accepted 22 March 2009

Introduction

Although nitrogen (N) is the dominant elemental constituent of Earth's atmosphere, stoichiometric and energetic constraints on its biological fixation to soluble, inorganic forms amenable for plant uptake frequently make it one of the most limiting resources in terrestrial ecosystems (Vitousek & Howarth, 1991). Widespread nitrogen enrichment through industrial and agricultural processes, however, lessens N limitation and, in so doing, dramatically impacts ecosystem functioning (Galloway *et al.*, 1995; Jordan & Weller, 1996; Vitousek *et al.*, 1997; Phoenix *et al.*, 2003). While its impacts vary considerably among ecosystems (DiTommaso & Aarssen, 1989; Matson *et al.*, 1999; Suding *et al.*, 2005; Clark *et al.*, 2007; LeBauer & Treseder, 2008), N enrichment generally increases aboveground net primary production and reduces plant species richness by favoring a

Correspondence: Yongfei Bai, tel. +86 10 6283 6272, fax +86 10 8259 5771, e-mail: yfbai@ibcas.ac.cn

© 2009 Blackwell Publishing Ltd

small number of opportunistic species, as indicated by grassland studies in Europe (Bobbink *et al*., 1998; Stevens *et al*., 2004) and North America (Wedin & Tilman, 1996; Collins *et al*., 1998; Gough *et al*., 2000). Such losses in plant richness, in turn, can have marked impacts on ecosystem productivity (Tilman *et al*., 1996; Hector *et al*., 1999) and stability (Tilman & Downing, 1994; Pfisterer & Schmid, 2002; Bai *et al*., 2004; Tilman *et al*., 2006).

It is unclear, however, to what extent the observed shifts in community composition and functioning are dependent on either the rate of N addition or on properties of the extant community. Ecological theory predicts that N addition to degraded, resource poor communities may alleviate ecosystem N limitation and lead to an increase in diversity. In contrast, N addition to a mature community within the same ecosystem may disrupt mechanisms of community coexistence, leading to a decrease in diversity as a small number of opportunistic species are favored. These changes in community structure are likely influenced by the functional traits that species possess, and recent work suggests that both functional- and neutral- based processes operate simultaneously (Suding *et al*., 2005). Theory does not predict that these broad processes are rate-specific; however, it has been generally assumed that there exist ecosystem-specific rates of N input for which no deleterious effects occur, an assumption that forms the backbone of a substantial body of environmental legislation (NEGTAP, 2001); However, explicit tests are lacking. Studies that add N at a range of rates generally report qualitative agreement in system responses at low vs. high rates of treatment (Tilman, 1987; Morecroft *et al*., 1994; Bowman *et al*., 2006; Britton & Fisher, 2007), suggesting that thresholds, if present, may be lower than previously thought (Stevens *et al*., 2004; Clark & Tilman, 2008).

From a management perspective, N fertilization has been used to restore the productivity and improve the forage quality of grasslands degraded by overgrazing (Schellberg *et al*., 1999; Conant *et al*., 2001). Of the 40% of the Earth's land surface that is grassland, over half has been converted to managed grazing ecosystems with a substantial area already degraded (White *et al*., 2000). This situation is likely to worsen if grazing pressure continues to increase as projected (Reynolds & Smith, 2002; Asner *et al*., 2004; Millennium Ecosystem Assessment, 2005). Systems degraded by grazing are often species poor, dominated by less palatable species, and have lowered productivity and vegetation cover, with corresponding increases in wind erosion, nutrient loss, and water runoff (Asner *et al*., 2004). In such systems N enrichment can increase primary production and ground cover and subsequently reduce wind erosion and soil nutrient loss, slowing the process of anthropogenic desertification – a threat confronted by an estimated 41% of the grasslands of the world (Lal, 2001; Malhi *et al*., 2003; Li *et al*., 2007).

Reconciliation of these two contrasting perceptions of N enrichment, that it is detrimental for some systems (e.g. unperturbed or natural) but beneficial for others (e.g. degraded), is a result of divergent research goals and insufficient cross-comparisons among fields. Studies in natural ecosystems often focus on biodiversity and ecosystem properties (e.g., production and soil C and/or N pools), while responses in managed ecosystems often focus on ecosystem properties as they refer to ecosystem goods (e.g., forage and livestock production). Clearly these are interrelated topics. However, few studies to date have explicitly compared on a common set of standards both natural and degraded sites within an ecosystem, for which differences in regional species pools, climate, and geomorphology are likely to be minor. The few that have often find that natural systems are less sensitive to N enrichment than currently or recently managed systems (Tilman, 1987, 1993), though this response is far from general (Grime *et al*., 2000).

Here we report the impacts of a range of N addition rates to two contrasting sites in the Inner Mongolian grassland, which is part of the largest contiguous grassland of the world – the Eurasian steppe. We selected an undisturbed mature grassland and a degraded grassland of the same type to address two primary questions. First, how do several key biotic (i.e. biomass production, species richness, and plant functional group composition) and abiotic (inorganic soil N and soil moisture) ecosystem characteristics respond to various rates of N addition in the Inner Mongolia grassland? And second, do these patterns vary between the degraded and mature sites within this ecosystem?

Materials and methods

Experimental sites

The field experiment was carried out at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), which is located in the Xilin River Basin, Inner Mongolia Autonomous Region of China (116°42′E, 43°38′N). IMGERS is one of the key members of the Chinese Ecological Research Network (CERN), and is administrated by the Institute of Botany, Chinese Academy of Sciences. Topographic relief exhibits little variation, with elevation ranging from 1250 to 1260 m at our experimental sites. The mean annual temperature in the study area is 0.3 °C with mean monthly temperatures ranging from −21.6 °C in January to 19.0 °C in July. The mean annual precipitation is 346.1 mm with 60–80%

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

falling during the growing season from May to August. The soil in both sites is classified as dark chestnut (Calcic Chernozem according to ISSS Working Group RB, 1998) or loamy sand in terms of texture with similar physiochemical properties (Table 1).

In 1999, two 120 × 70 m locations with fairly uniform vegetation were established within the permanent research plots of IMGERS as contrasting experimental sites. No fertilizer had been applied in either site before this study. The first site was an undisturbed mature grassland community that had been fenced to exclude large animals since 1979 (Bai *et al*., 2004). Before beginning the experiment, the mature site was dominated by *Leymus chinensis*, a widely distributed perennial C_3 rhizome grass in the Eurasia steppe region. About 100 meters west of the mature site, the degraded site was an overgrazed area with its dominant species having shifted from the rhizomatous C_3 *L. chinensis* to the non-rhizomatous C_3 bunchgrasses *Stipa grandis* and *Cleistogenes squarrosa* (a C_4 short bunchgrass) due to uncontrolled grazing since the early 1980s (Li, 1988). The degraded site, which had the same plant species composition to the mature site before 1979, was fenced in 1999 six months before the beginning of the experiment. Thus, upon initiation of the experiment, the two sites differed dramatically in structure and function, with the degraded site having fewer species, lower production, and which had experienced a shift in community composition from dominance by perennial rhizomatous grasses to perennial bunchgrasses, with little change in other functional groups (Table 1).

Table 1 Soil and plant community properties (means ± SE) of the mature and degraded sites before treatment

	Term	Mature	Degraded
Soil Property (0–20 cm)	SOM (%)	2.76 ± 0.06^{NS}	2.87 ± 0.09
	TN (%)	1.73 ± 0.02^{NS}	1.77 ± 0.04
	pH	7.52 ± 0.04^{NS}	7.54 ± 0.13
	Sand (%)	80.18 ± 0.38^{NS}	78.41 ± 1.17
	Silt (%)	17.60 ± 0.50^{NS}	19.11 ± 1.04
	Clay (%)	2.22 ± 0.23^{NS}	2.48 ± 0.22
Community Property	Richness	51	36
	Biomass ($g\,m^{-2}$)	150.32 ± 7.82**	116.08 ± 5.52
	PR (%)	41.07 ± 5.52**	19.99 ± 2.42
	PB (%)	31.99 ± 4.25**	50.65 ± 4.79
	PF (%)	23.42 ± 3.24^{NS}	27.80 ± 4.23
	SS (%)	3.17 ± 1.46^{NS}	1.44 ± 0.49
	AB (%)	0.35 ± 0.29^{NS}	0.12 ± 0.08

Note: Significant differences between sites are reported from one-way ANOVA as NS, $P > 0.05$;
**, $P < 0.01$. The particle size is 0.02–2.0 mm for sand, 0.002–0.02 mm for silt, and <0.002 mm for clay. PR = perennial rhizome grasses, PB = perennial bunchgrasses, PF = perennial forbs, SS = shrubs and semi-shrubs, and AS = annuals.

Experimental design

Identical treatments were applied to both mature and degraded sites. At each site, 162 5 m × 5 m plots were laid out in a randomized block design. Plots were separated by 1-meter walkways. There were 9 replicates for each of the 19 treatments which included a control treatment (i.e. no nutrient addition), and 6 levels of N enrichment at 3 application times. N was added at 0, 1.75, 5.25, 10.5, 17.5, and 28.0 $g\,N\,m^{-2}\,yr^{-1}$ as commercial NH_4NO_3. The three different application times were: (1) the early growing season (May 1–3), (2) the middle of the growing season (July 1–5), and (3) 50% of N applied at each time period (except for the level of 1.75 $g\,N\,m^{-2}\,yr^{-1}$ which was too low to split). To assure that N was the only limiting nutrient (Tilman, 1987), we also added the same amount of P (10 $g\,P_2O_5\,m^{-2}\,yr^{-1}$), S (0.2 $mg\,m^{-2}\,yr^{-1}$), and trace elements (Zn: 190 $\mu g\,m^{-2}\,yr^{-1}$, Mn: 160 $\mu g\,m^{-2}\,yr^{-1}$, B: 31 $\mu g\,m^{-2}\,yr^{-1}$) for all treatments with the exception of control based on the soil census data (Inner Mongolia Soil Census Office & Inner Mongolia Soil and Fertilizer Service, 1994). We did not add K, Mg, Ca and Fe in our experiment because dark chestnut soils were rich in K, Mg, Ca and Fe (Inner Mongolia Soil Census Office & Inner Mongolia Soil and Fertilizer Service, 1994). Since our preliminary analysis found no significant effects of the timing of N addition on the response patterns of biomass, species richness, and functional group composition, we only report the results based on the July data (126 plots in total) in this paper.

Field sampling and measurements

We classified all plants into five functional groups based on life forms, including perennial rhizome grasses (PR), perennial bunchgrasses (PB), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals (AS) as in Bai *et al*. (2004). Aboveground vegetation was sampled each year between 25 August and 2 September by clipping all plants at the soil surface using a 0.5 × 1 m quadrat randomly placed in the plot with the restriction of no spatial overlap of quadrats among all years. To avoid edge effects, the quadrat was placed at least 50 cm inside each plot. All living vascular plants were sorted to species, and all plant materials, including litter and standing dead, were oven-dried at 65 °C for 48 h and weighed. The dry mass of all living plants per quadrat averaged over the nine replicates for each treatment

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

was used to estimate the aboveground community biomass.

Soil samples were taken from the surface to a depth of 20 cm in early July and early September of 2003. For each plot, three soil cores were collected using a 3-cm diameter soil auger and mixed *in situ* into one composite sample. All soil samples were stored in a refrigerator at 4 °C until being processed and analyzed. Within 10 days of the collection, all soil samples were extracted with 50 mL of 2 M KCl (soil to extractant ratio = 1 : 10) (Mulvaney, 1996), and ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were analyzed with a FIASTAR 5000 (Dual Channel Soil Nitrogen Analyzer System, FOSS, Höganäs, Sweden). Concentrations of extractable soil NH_4^+-N and NO_3^--N were expressed as milligrams per kilogram on the basis of dry soil mass. The concentrations of soil NH_4^+-N and NO_3^--N reported here were the averages of the samples from early July and early September for each treatment.

Soil moisture was determined using the gravimetric method. For both sites, three soil cores (3.5 cm in diameter) at each depth of 0–20, 20–40, and 40–110 cm were taken weekly from control plots from May to early September during 2000–2002, and bi-weekly in 2003. The soil samples were weighed before and after being oven-dried at 105 °C for 48 h. We also measured soil moisture in the treatment plots at 0–20 and 20–40 cm at the end of August in 2003. For each treatment, five of the nine replications were selected randomly, and soil moisture was measured using the same method.

Statistical analyses

Statistical analyses were performed using SAS Version 8.0 (SAS Institute, Cary, North Carolina, USA, 2001). Analyses across time were performed using repeated measures ANOVA for both sites, Geisser-Greenhouse adjusted F-statistic to test for multivariate significance, using Year, Site (mature or degraded), N addition rate (categorical), and all interactions as fixed-effects. As anticipated, many high order interactions were significant (i.e. treatment responses differed through time); thus, we ran additional analyses for each field and for each year to determine the pattern and magnitude of response. Regression models with N as a continuous variable were used to determine the general relationship between N addition and various responses (adjustments for non-linearity were made as needed). Regression models with N as an ordinal variable were used to determine the relationship between each rate of N addition and various responses (i.e. to estimate threshold levels). These ANOVAS were followed by a Duncan's multiple-range test to compare the N-addition effects for each rate. To test the dependency of biomass and species richness (SR) responses to N on soil moisture (SM), we further analyzed the relationships between biomass response ($Biomass_{treatment}/Biomass_{control}$) and corresponding soil moisture response ($SM_{treatment}/SM_{control}$) and between species richness response ($SR_{treatment}/SR_{control}$) and soil moisture response.

Results

Aboveground biomass

Repeated measure ANOVA of aboveground biomass, using site, N-treatment, year, and all interactions as fixed-factors, showed that the effects of site, treatment, and year on aboveground biomass were highly significant, and that all interactions were also highly significant (Table 2). Although neither site responded strongly to treatment in the first year of study (2000), by the fourth year (2003), aboveground biomass increased across the N addition gradient by 98–271% in the mature site, and by 13–62% in the degraded site (Fig. 1). Aboveground biomass tended to increase at all treatment rates in both sites, significantly increasing in the mature site even at the 1.75 g N m^{-2} yr^{-1} rate. Little additional response in either site was found for N addition rates $\geq$ 10.5 g N m^{-2} yr^{-1}. Patterns in the degraded site were less dramatic overall and individual differences between controls and treated plots were only found at higher treatment rates (Fig. 1). Thus, throughout the study period, the undisturbed mature

Table 2 Repeated measures analysis of variance for aboveground biomass and species richness using Site, N-Treatment, Year, and all interactions as fixed-effects

Response	Term	Df	*F*	*P*
Aboveground biomass	Site (S)	1	103.74	<0.0001
	N-Treatment (N)	6	36.4	<0.0001
	Year (Y)	3	323.83	<0.0001
	S × N	6	10.3	<0.0001
	S × Y	3	14.99	<0.0001
	N × Y	18	9.49	<0.0001
	S × N × Y	18	4.53	<0.0001
Species richness	Site (S)	1	530.86	<0.0001
	N-Treatment (N)	6	7.35	<0.0001
	Year (Y)	3	106.38	<0.0001
	S × N	6	1.62	0.1590
	S × Y	3	17.5	<0.0001
	N × Y	18	5.32	<0.0001
	S × N × Y	18	2.02	0.0110

Note: There are 168 degrees of freedom for error.

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

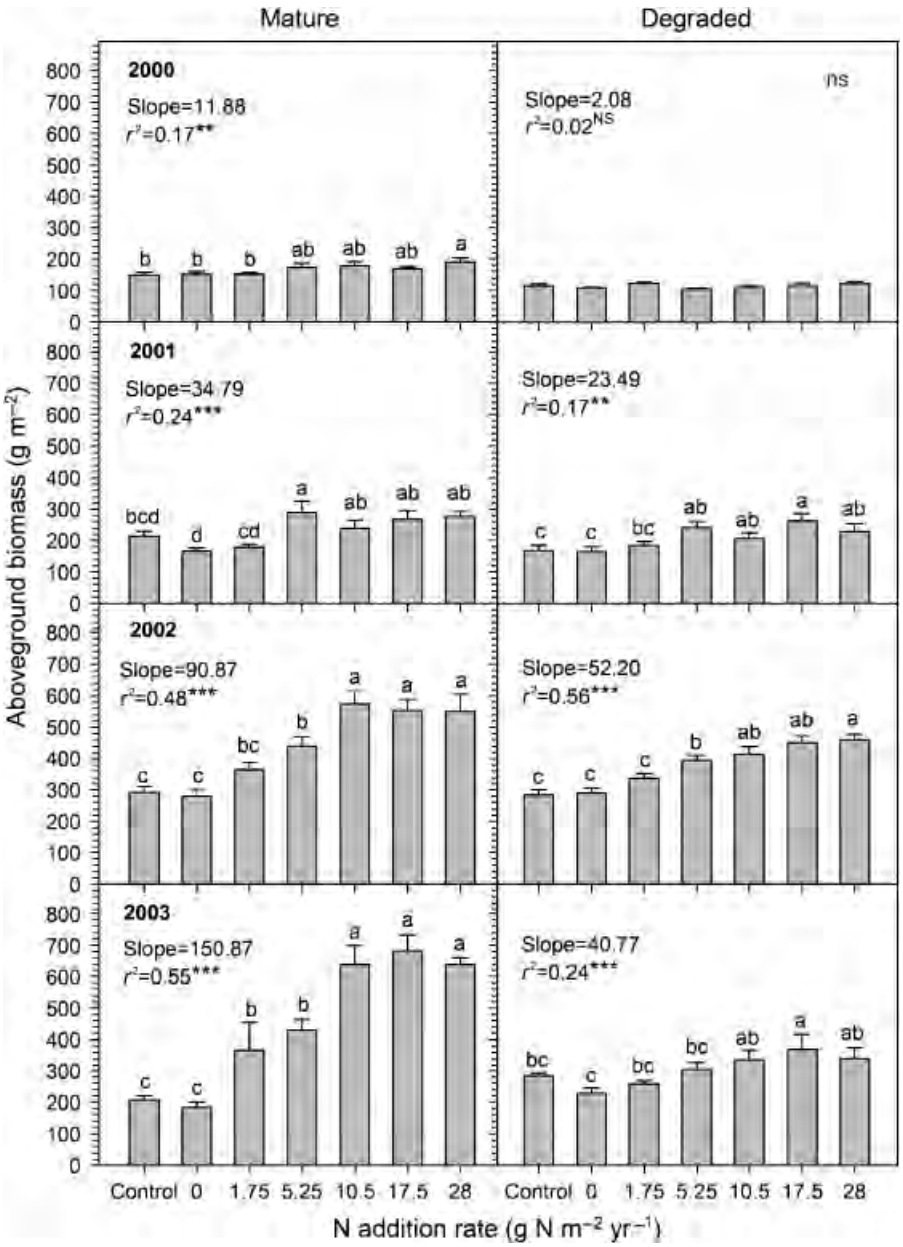


Fig. 1 Effects of N addition on aboveground biomass of the mature and degraded communities. Aboveground biomass for each treatment was the average of nine replicates (error bars denote SEM). Bars with the same letter were not significantly different in Duncan's multiple range tests reported from one-way ANOVA, and NS indicates non-significant ($P > 0.05$). For both sites, regression parameters were estimated each year using log-linear model with N treatment as a continuous predictor, i.e., *Aboveground biomass* = Intercept + *Slope* × Ln (*N*). Significant differences are reported as NS, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

community showed a stronger overall response to N addition at all treatment rates than the degraded site.

In both the mature and degraded sites, no significant difference in aboveground biomass was found between the control (no nutrients added) and the zero-N treatment (added other nutrients but not N) from year to year or through time (Repeated-measures ANOVA: for the mature site, Time × Treatment, $F_{3,48} = 1.15$, $P = 0.326$; for the degraded site, Time × Treatment, $F_{3,48} = 1.78$, $P = 0.180$; Fig. 1).

Plant species richness

In general, plant species responded substantially between sites, among treatments, and through time, and there were significant site × year, treatment × year, and

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

site × treatment × year interactions (Table 2). At the mature site, species richness increased with N addition in 2000, demonstrated no response in 2001, and significantly declined in 2002 and 2003 (Fig. 2). By the fourth year of the study, species richness in the mature site had declined by 20–36% across the N addition gradient; and, there was a significant reduction at the lowest treatment rate when compared with controls in 2002 and with the zero-N added treatment in 2003. Species richness in the degraded site responded more weakly in general, with no change in the first two years and significantly declining with N addition in 2002 and 2003 (Fig. 2). Individual differences with controls, however, were only significant at higher treatment rates. There were

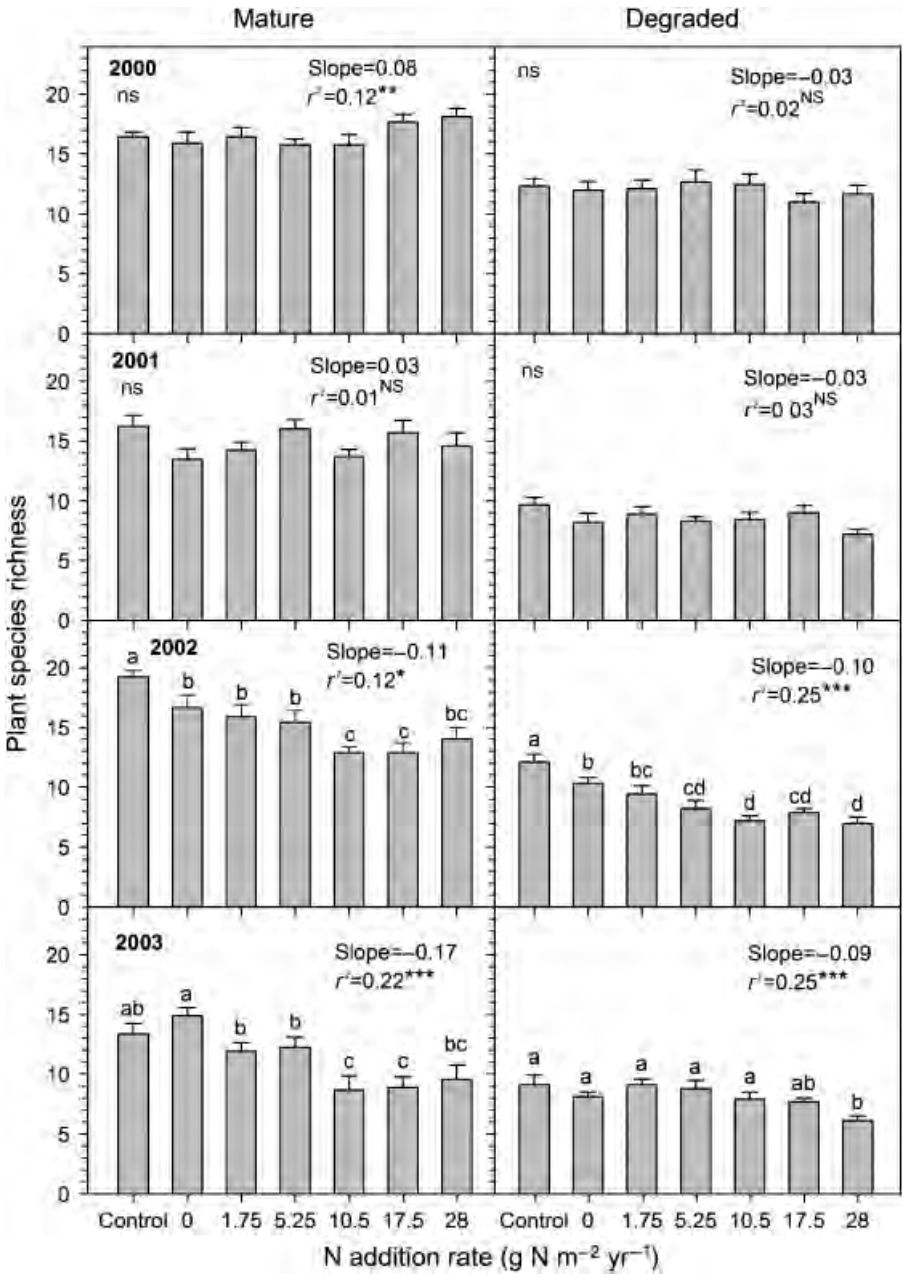


Fig. 2 Effects of nitrogen addition on plant species richness of the mature and degraded communities. Species richness is the average number of plant species in the 9 replicates of each treatment using a $0.5 \times 1.0\,m^2$ quadrat (error bars denote SEM). For both sites, regression parameters were estimated each year using log-linear model with N treatment as a continuous predictor, i.e., *Species richness* = Intercept + *Slope* × Ln (*N*). All symbols are derived as from Fig. 1.

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

no consistent differences between the control and zero-N treatment in either site (Fig. 2) or through time (analyses not shown). Our results further showed that species richness response was negatively correlated with aboveground biomass response at the mature site ($R^2 = 0.21$, $P = 0.0005$), while no significant relationship between species richness response and aboveground biomass response was found at the degraded site ($P > 0.05$).

Plant functional group composition

Patterns of functional group responses to treatment in the two sites were strikingly different both quantitatively and qualitatively (Table 3). For each of five plant functional groups, however, the effects of site, year, and site × year were highly significant (Table 3). At the mature site, there were no significant treatment effects for any functional group in the first two years of the study (Fig. 3). However, beginning in 2002, annuals (AS), which had been nearly absent in 2000, increased strongly across the N addition gradient, dominating by 2003 and leading to a sharp decline in perennial rhizome grasses (PR), perennial bunchgrasses (PB), and perennial forbs (PF) functional groups (Fig. 3). No significant response was found for shrubs and subshrubs (SS) over the four years (Fig. 3). Compared to zero-N treatment, the average aboveground biomass of the AS functional group in 2003 increased by approximately 20-fold at the two lowest N addition rates and 50-fold at the three highest, comprising 62% and 91% of the aboveground production respectively in these treatment groups. In contrast, by 2003 the average aboveground biomass of the PR, PB, and PF functional groups declined respectively by 53%, 44%, and 54% at the two lowest treatment rates and by 95%, 94%, and 92% at the three highest.

There was a markedly different functional response in the degraded site (Fig. 4). Although there were no treatment effects in 2000, beginning in 2001 and continuing to 2002, the aboveground biomass of both PR and PB functional groups increased, with a corresponding decline in PF species (Fig. 4). Between 2002 and 2003, there was a continued increase in PR species and a dramatic decline in PB species. No significant response was found in the aboveground biomass of AS or SS functional groups over the four years (Fig. 4).

These observed shifts in functional composition were consistent at low and high N addition rates in the mature site, but were only significant in the degraded site at higher N addition rates. At both sites, no significant difference in the aboveground biomass of PFGs was found between the control and the zero-N treatment for all functional groups and all years, except perennial forbs at the degraded site in 2002 and 2003 (Figs 3 and 4).

Table 3 *P* values of repeated measures analysis of variance for each plant functional group using Site, N-Treatment, Year, and all interactions as fixed-effects

Term	PR	PB	PF	SS	AS
Site (S)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
N-Treatment (N)	<0.0001	0.106	0.0065	0.3408	<0.0001
Year (Y)	<0.0001	<0.0001	<0.0001	0.0003	<0.0001
S × N	<0.0001	0.1577	0.3523	0.3839	<0.0001
S × Y	<0.0001	<0.0001	0.0005	0.0008	<0.0001
N × Y	0.0013	<0.0001	0.0053	0.5864	<0.0001
S × N × Y	<0.0001	0.2059	0.1694	0.8696	<0.0001

Note: There are 168 degrees of freedom for error. PR = perennial rhizome grasses, PB = perennial bunchgrasses, PF = perennial forbs, SS = shrubs and semi-shrubs, and AS = annuals.

Soil inorganic N

Our results showed that there was a significant treatment effect on soil inorganic N concentrations (NO_3^--N plus NH_4^+-N), whereas no significant site and site × treatment effects were found (ANOVA: Treatment, $F_{6,56} = 13.35$, $P < 0.0001$; Site, $F_{1,56} = 2.36$, $P = 0.1298$; Treatment × Site, $F_{6,56} = 1.05$, $P = 0.4058$). For both the mature and degraded sites, soil N availability (growing season NO_3^--N and NH_4^+-N concentrations) remained relatively unchanged at N addition rates $\leq 10.5\,g\,N\,m^{-2}\,yr^{-1}$ (Fig. 5). At N addition rates $> 10.5\,g\,N\,m^{-2}\,yr^{-1}$, soil NO_3^--N and NH_4^+-N increased dramatically (Fig. 5).

Soil moisture

The soil moisture at 0–20 cm depth differed substantially between sites and among treatments at the time of peak aboveground biomass in 2003 (ANOVA: Site, $F_{1,56} = 11.92$, $P = 0.0011$; Treatment, $F_{6,56} = 4.04$, $P = 0.0020$; Site × Treatment, $F_{6,56} = 0.66$, $P = 0.6831$); it was higher in the mature than the degraded site, and declined with increasing N addition rate at both sites (Fig. 6). For the mature site, a similar pattern of declining soil moisture was found at 20–40 cm depth across the N addition gradient, with no significant differences between the two sites and among treatments for the degraded site (ANOVA: Site, $F_{1,56} = 3.01$, $P = 0.0881$; Treatment, $F_{6,56} = 2.79$, $P = 0.0192$; Site × Treatment, $F_{6,56} = 0.49$, $P = 0.8100$).

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

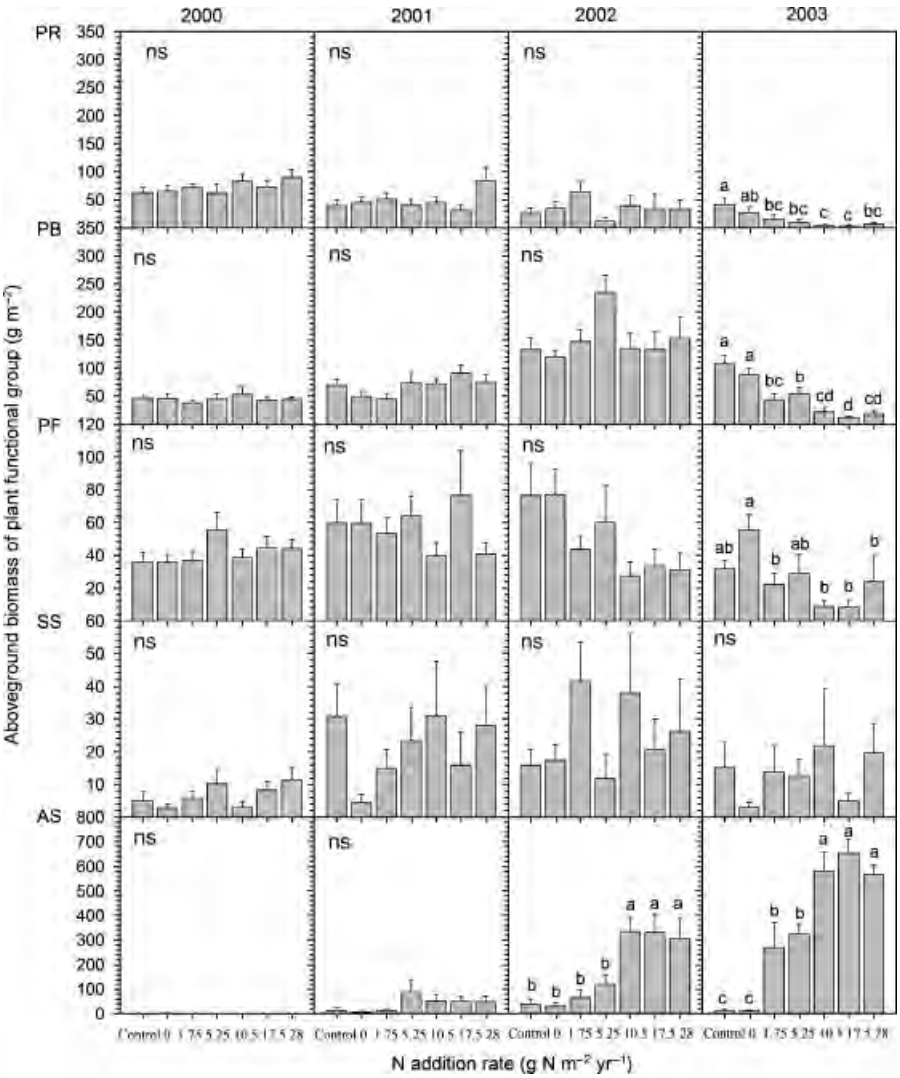


Fig. 3 Responses of the aboveground biomass of PFGs to N addition rates at the mature site (error bars denote SEM). The above ground biomass of each PFG was the average of the nine replicates of a treatment (note difference in scales). Bars with the same letter were not significantly different in Duncan's multiple range tests reported from one-way ANOVA, and NS indicates non-significant ($P > 0.05$). PR = perennial rhizome grasses, PB = perennial bunchgrasses, PF = perennial forbs, SS = shrubs and semi-shrubs, and AS = annuals.

Although the average soil moisture contents in control plots varied between the two sites, among the different years, and with time within a growing season, it was consistently higher in the mature than the degraded site at three different soil depths (Fig. S1). All interactions between site, year, and sampling date were significant using repeated measures ($P < 0.01$). From May to early August when plants grew most vigorously, soil moisture for the mature site was, on average, about 30% higher than that of the degraded site throughout the soil profile (Fig. S1).

Our further analysis showed that aboveground biomass response was negatively correlated with soil moisture response at 0–20 cm for both the mature ($R^2 = 0.25$, $P = 0.0054$) and degraded sites ($R^2 = 0.39$, $P = 0.0002$; Fig. 7). On average, soil moisture decreased by 24% for the mature site and by 17% for the degraded site at the two highest N addition rates when compared to the control treatment (Fig. 7). No significant relationship, however, was found between species richness response and soil moisture response for both the mature and degraded site ($P > 0.05$).

Discussion

We found that the aboveground biomass and species richness responses were qualitatively similar between

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

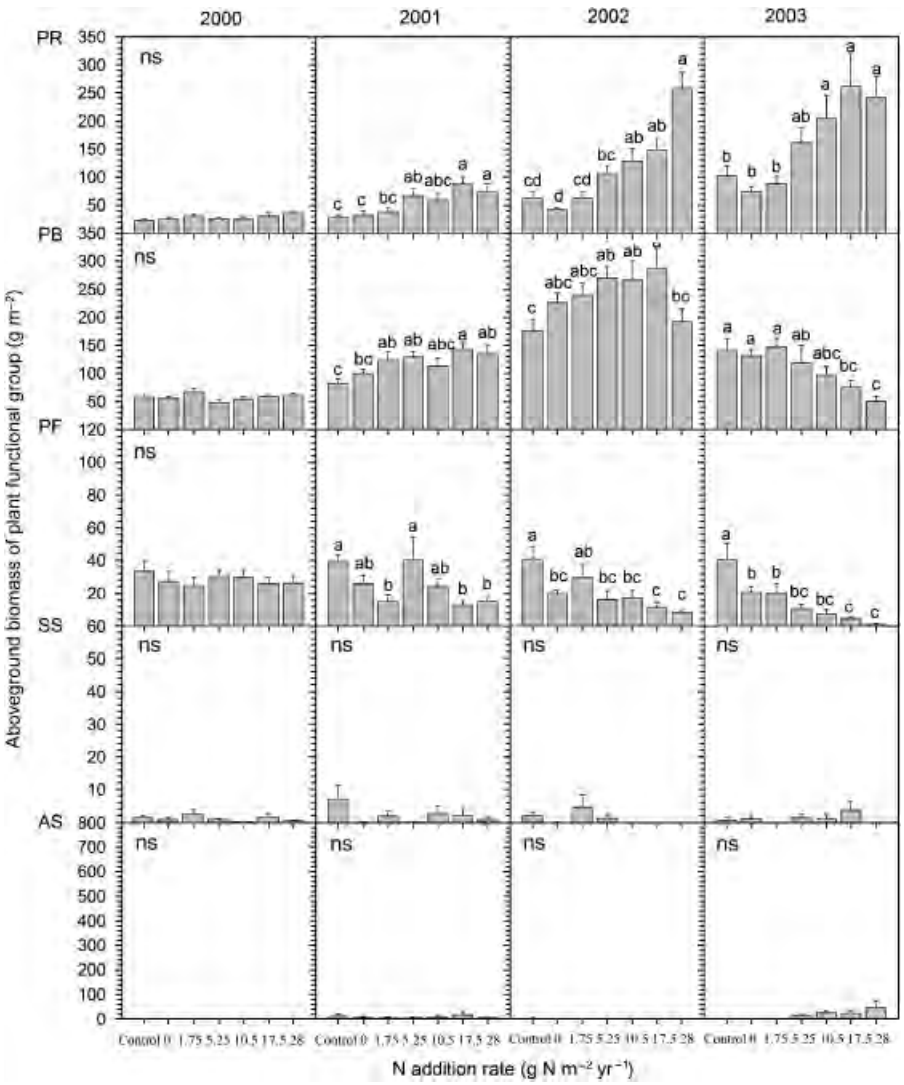


Fig. 4 Responses of the aboveground biomass of PFGs to N addition rates at the degraded site (error bars denote SEM). The aboveground biomass of each PFG was the average of the nine replicates of a treatment. All symbols are derived as from Fig. 3.

the two sites and across the N addition gradient, although large quantitative differences emerged. These quantitative differences appeared to be driven by divergent functional responses in the two sites.

Patterns of aboveground biomass

Our experiment in the Inner Mongolian grassland demonstrated that although the qualitative effects of N addition were similar between sites, their quantitative effects varied substantially. Aboveground biomass in both communities tended to increase relative to controls at all rates of N addition, saturating at rates $\geq 10.5\,\mathrm{g\,N\,m^{-2}\,yr^{-1}}$. By 2003, increased aboveground biomass was detected for every treatment rate in the mature community; and, although individual differences were only significant for higher treatment rates in the degraded community, trends were qualitatively similar. The magnitude of these increases, however, was markedly different, with average aboveground biomass increased by 199% at the mature site and 41% at the degraded site after 4 years. These patterns suggest three conclusions. First, N was limiting at both mature and degraded sites, addition of which at any rate increased aboveground biomass. As such, we did not find strong evidence for a critical threshold within the range tested here, where N addition at rates below this threshold might be unavailable to plants as microbial and abiotic processes likely outcompeted plants for excess N (Johnson *et al*., 2000; Barrett *et al*., 2002; Davidson *et al*., 2003). Second, there appeared to be a saturation rate of N addition above which the production potential of the

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

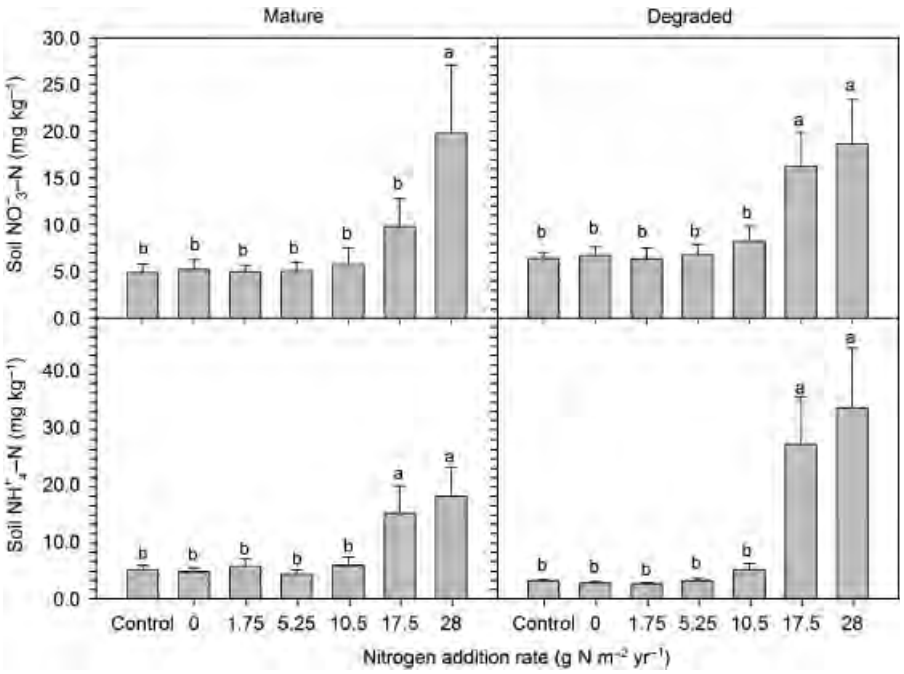


Fig. 5 Seasonal average extractable soil NO_3^--N and NH_4^+-N concentration in the fourth year (error bars denote SEM). Bars with the same letter were not significantly different in Duncan's multiple range tests reported from one-way ANOVA.

existing community was saturated with N. At input rates above this, there was little additional increase in aboveground biomass and N began showing up in the extractable soil pools, as other resources likely became limiting (e.g. light, water, phosphorous). Third, the difference observed in the magnitude of aboveground biomass increase between the two sites suggest that site-specific dynamics such as differences in plant communities, soil properties, or both, modulate the impact of a given input rate of N.

We hypothesize that the differential responses in aboveground biomass at the two sites stem from differences in plant-soil feedbacks influencing water availability. The soils in the degraded and mature sites were initially similar in many physiochemical properties; however, the mature site had consistently higher soil moisture in control plots during the 4 years of study, particularly from May to early August when plants grew most vigorously. High vegetation cover and abundant litter in the mature site likely increased the water-conserving capacity for both rain and snow (Bai *et al* unpublished data), as compared with the degraded site. This relationship with water was supported by our observations that the greatest absolute responses in aboveground biomass were found in wet years (2002 and 2003, Bai *et al*., 2008). A negative correlation between aboveground biomass response and soil moisture response in both the mature and degraded sites indicates that the productivity response to N addition is dependent on soil moisture. Thus, these findings highlight the importance of coupled N and water biogeochemical cycles in grassland and dryland ecosystems (Lauenroth *et al*., 1978; Hooper & Johnson, 1999; Knapp & Smith, 2001; Liu *et al*., 2009).

Patterns of species richness

Similar to aboveground biomass, we found qualitative agreement between the two sites in the impacts of N addition on species richness, though quantitative differences were large. Specifically, we found a greater magnitude of species loss in the mature site compared with the degraded site. This was likely a result of differential responses of plant functional groups in the two sites mediated by N and water availability. These findings differ from Tilman (1987, 1993) which found a weaker overall response to N enrichment in a native savannah grassland compared to three abandoned agricultural fields. These varied responses are probably not due to any fundamental difference between legacies left by heavy grazing vs. agriculture, as both often deplete soil nutrients (Ritchie *et al*., 1998; Brathen *et al*., 2007). Rather, we suggest that the dynamics in both studies result from interactions with the availability of other resources. The weak response in native savannah of Minnesota as compared with nearby abandoned agricultural fields was explained primarily by less litter buildup in the native savannah

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

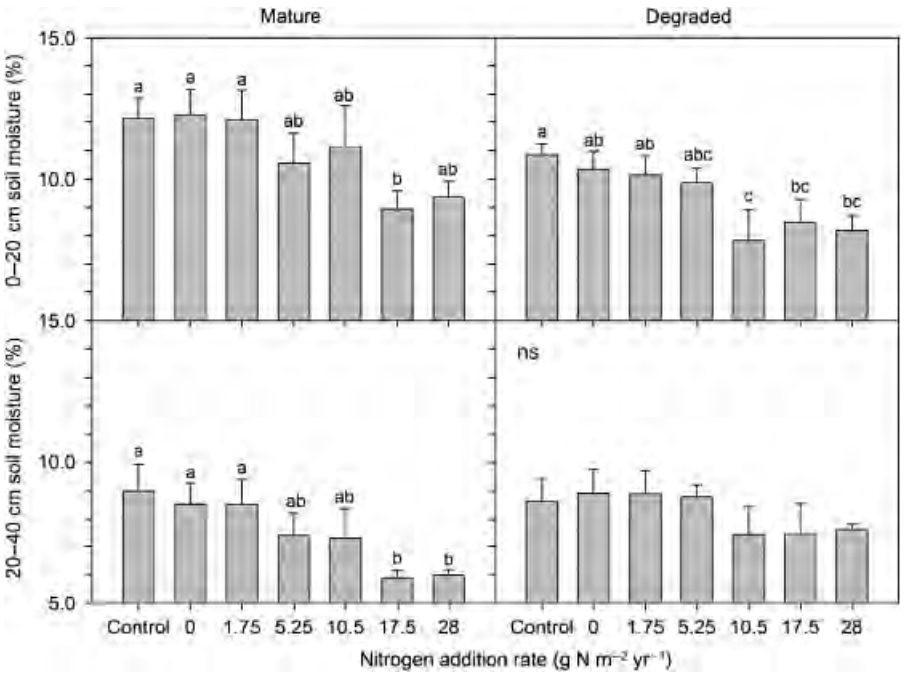


Fig. 6 Responses of soil moisture to N addition rates at the mature and degraded site (error bars denote SEM). The soil moisture was the average of the five replicates of a treatment. Bars with the same letter were not significantly different in Duncan's multiple range tests reported from one-way ANOVA.

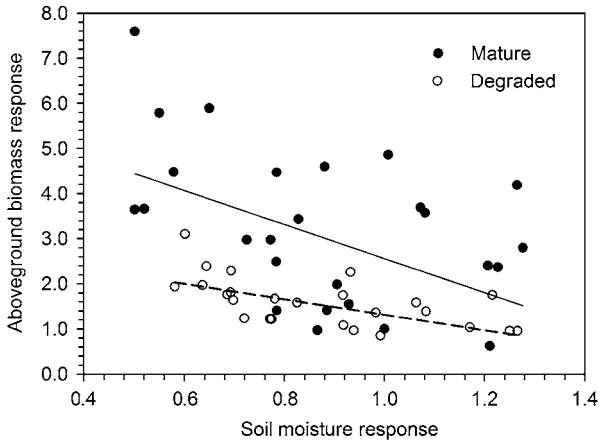


Fig. 7 The relationship between aboveground biomass response and soil moisture response in the mature and degraded sites.

due to periodic burning, resulting in more colonization sites and less potential for light limitation following N addition (Tilman, 1993). Light may have already been limiting in the mature site due to the accumulation of a thick litter layer; and, in the degraded site, heavy grazing likely prevented the accumulation of litter as forage was removed. The strong response in the mature site may have also been influenced by its higher soil moisture, resulting in more severe limitation by N availability alone. We found that species loss increased linearly with production response, which explained 21% of the variation in richness response in the mature site. Regardless of the exact mechanism, our results demonstrate that natural sites are not generally less sensitive to N-induced reductions in diversity, and instead suggest that the relative responses between ecosystems and between communities within an ecosystem likely depend on interactions with other potentially limiting factors.

Shift in plant functional group composition

The most conspicuous effects of N addition were the shifts in aboveground biomass of different PFGs at the two sites. Surprisingly, fast-growing annuals that are usually abundant only in the early stages of grassland succession (Inouye *et al.*, 1987; Li & Xu, 2002), almost completely replaced the perennials in the mature site. The rapid growth of annuals (e.g. *Axyris amaranthoides*, *Chenopodium glaucum*, *and Cannabis sativa L. f. ruderalis*) was facilitated by their species traits, including abundant seed production, rapid growth, and tall stature. In contrast, the decline in abundance of perennials (e.g., *L. chinensis*, *S. grandis*, *Achnatherum sibiricum*, *Agropyron cristatum* and *Carex korshinskyi*) was attributable to their conservative resource-use strategies, with great leaf C:N and root:shoot ratios, high water use efficiency, and high nonstructural carbohydrates reserve in the below-

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

ground organs (Xu *et al*., 1994; Chen *et al*., 2001). These results support the functional-based hypothesis that N enrichment allows species with acquisitive resource-use strategies to exclude those with conservative resource-use strategies (Diaz *et al*., 2004; Suding *et al*., 2005). However, these dynamics clearly interacted with site characteristics, as no similar functional pattern was observed in the degraded site. At the degraded site, we found that the perennial rhizome grass (*L. chinensis*) became increasingly dominant as the experiment progressed. Annuals were unable to take advantage of the added N possibly due to insufficient soil moisture affecting germination, whereas drought-tolerant and rhizomatous perennials with high recruitment rates, including *L. chinensis and A. cristatum* (a C_3 bunchgrass with short rhizomes), benefited most from N enrichment (Chen *et al*., 2001). The rapid dominance of annuals following N addition in other previously degraded sites was short-lived (<2 years, Tilman, 1987) likely because the perennial grasses were more dominant in the long run on these dry-sandy soils as opposed to the more moist soils of the mature grassland of Inner Mongolia. However, only long-term sampling of these plots will resolve whether dominance by annuals is transient in this ecosystem, or sustained as a result of less limitation by non-N resources. We suggest that it is the interplay between nitrogen and water that drives the differential responses of PFGs between the two sites, consequently governing the trajectory of ecosystem dynamics.

Implications for biodiversity conservation and ecosystem management

Our results clearly demonstrate that ecosystem sensitivity to low N input rates are likely to vary among ecosystems. In the mature site, production increased and species richness decreased significantly even at the $1.75\,g\,N\,m^{-2}\,yr^{-1}$ treatment rate, an input rate comparable to estimated critical thresholds for several herbaceous communities of Europe (Bobbink *et al*., 2002). Patterns in the degraded site were much less distinct, possibly resulting from several mechanisms, including a lower number of species initially present, different functional responses, or interactions with other resources.

It seems logical that at sufficiently low rates of N enrichment there is likely to be a net benefit to ecosystems. This apparently inflammatory statement is founded on two generally accepted propositions. First, it is likely that there exist ecosystem-specific thresholds for N enrichment, below which there are no negative ecological impacts as the extant community is capable of sequestering the additional N (Nilsson & Grennfelt, 1988; Bobbink *et al*., 2002). Although the currently estimated values of these thresholds have been called into question (Stevens *et al*., 2004; Clark & Tilman, 2008), their hypothesized existence forms the backbone of a substantial body of environmental legislation on transboundary pollution (NEGTAP, 2001). Second, Liebig's Law of the Minimum predicts that in N limited ecosystems, common throughout the temperate world, N addition is likely to stimulate plant production. Acceptance of these two propositions leads to the conclusion that there exist rates of N addition for which there are increases in production with no reductions in diversity. We found no strong evidence for this conclusion over the range tested, and indeed many studies find qualitatively similar responses at low vs. high N input rates (Morecroft *et al*., 1994; Bowman *et al*., 2006; Clark & Tilman, 2008). These findings suggest that critical thresholds may be lower than previously supposed, and highlight the urgency in assessing the impacts of the low N input rates experienced over much of the globe.

Similar to other studies, we detected evidence for the N addition treatment in the plant community (i.e. changes in production, richness, function) at lower rates than we detected changes in soil (i.e. changes in extractable inorganic N) (Wedin & Tilman, 1996; Bowman *et al*., 2006). Specifically, we found increases in soil N at rates $\geq 10.5\,g\,N\,m^{-2}\,yr^{-1}$ in both sites, but increases in biomass and decreases in richness at rates as low as $1.75\,g\,N\,m^{-2}\,yr^{-1}$ in the mature site and at rates as low as $5.25\,g\,N\,m^{-2}\,yr^{-1}$ in the degraded site. These findings support the suggestions of Bowman *et al*. (2006) that plant responses rather than soil responses may provide more sensitive measures of the impacts of human-caused N deposition.

Previous work in this system has demonstrated that *L. chinensis*, which had the highest relative biomass and lowest interannual variability of biomass production among all species at the undisturbed mature community, plays a key role in dampening ecosystem variability (Bai *et al*., 2004). Thus, despite decreased richness reducing some the redundancy aspect of ecosystem resilience (Naeem, 1998), the increased dominance of *L. chinensis* may facilitate restoring the ecosystem resilience of degraded communities to precipitation fluctuations. Our findings were also corroborated by a recent study indicating that the increased production of dominant species compensated the negative effect of nonrandom species loss (Smith & Knapp, 2003). In the mature site, however, the decreased abundance of *L. chinensis* coupled with reductions in richness predicts a decrease in both aspects of ecosystem resilience.

Our results have important implications for restoring and managing the biodiversity and ecosystem functioning of the vast semiarid grasslands in the Eurasian Steppe region which stretches from eastern China in

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Asia to Hungary in Europe. In mature and moderately grazed grasslands, N enrichment will generally increase aboveground biomass and decrease plant species richness. These changes will likely reduce ecosystem resilience to variation in precipitation because of declined species diversity and altered PFG compositions (Bai *et al*., 2004). Though qualitatively similar, N enrichment to degraded or heavily grazed grasslands leads to small increases in aboveground biomass and decreases in richness. However, increased aboveground biomass, especially of rhizomatous perennial grasses, may reduce the nutrient and water losses through wind erosion and runoff (Li *et al*., 2007), improve forage quality (Schellberg *et al*., 1999), and increase grassland resilience to precipitation variability (Bai *et al*., 2004). Clearly, there are a set of contrasting goals for restoration of ecosystem services (Suding *et al*., 2004), among which the trade-offs may exist between the increases in productivity and forage quality vs. losses of biodiversity.

Acknowledgements

We thank O. E. Sala and O. J. Sun for their helpful comments on an earlier version of this manuscript. We thank L. Li, Q. Wang, H. Zhao, Y. Yang, H. Wan, and many others at the Inner Mongolia Grassland Ecosystem Research Station, Chinese Academy of Sciences for their help with fieldwork. We are grateful to Y. Chen at Inner Mongolia Agriculture University for his help with soil moisture measurements. This project was supported by the State Key Basic Research Development Program of China (2009CB421102), the Natural Science Foundation of China (90711002, 30825008), and US National Science Foundation (DEB-0618193).

References

Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT (2004) Grazing systems, ecosystem response, and global change. *Annual Review of Environment and Resources*, **29**, 261–299.

Bai YF, Han XG, Wu JG, Chen ZZ, Li LH (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, **431**, 181–184.

Bai YF, Wu JG, Xing Q, Pan QM, Huang JH, Yang DL, Han XG (2008) Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. *Ecology*, **89**, 2140–2153.

Barrett JE, Johnson DW, Burke IC (2002) Abiotic nitrogen uptake in semiarid grassland soils of the U.S. Great Plains. *Soil Science Society of America Journal*, **66**, 979–987.

Bobbink R, Ashmore M, Braun S, Flückiger W, Van den Wyngaert IJJ (2002) Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update. In: *Empirical Critical Loads for Nitrogen* (eds Achermann B, Bobbink R), pp. 40–170. Swiss Agency for the Environment, Forests and Landscape (SAEFL), Berne.

Bobbink R, Hornung M, Roelofs JGM (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology*, **86**, 717–738.

Bowman WD, Gartner JR, Holland K, Wiedermann M (2006) Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: are we there yet? *Ecological Applications*, **16**, 1183–1193.

Brathen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH (2007) Induced shift in ecosystem productivity ? Extensive scale effects of abundant large herbivores. *Ecosystems*, **10**, 773–789.

Britton AJ, Fisher JM (2007) Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate *Calluna vulgaris* heathland. *Journal of Applied Ecology*, **44**, 125–135.

Chen SH, Zhang H, Wang LQ, Zhanbula, Zhao ML (2001) *Root Systems of Grassland Plants in Northern China*. Jilin University Press, Chuangchun.

Clark CM, Cleland EE, Collins SL *et al*. (2007) Environmental and plant community determinants of species loss following nitrogen enrichment. *Ecology Letters*, **10**, 596–607.

Clark CM, Tilman D (2008) Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, **451**, 712–715.

Collins SL, Knapp AK, Briggs JM, Blair JM, Steinauer EM (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, **280**, 745–747.

Conant RT, Paustian K, Elliott ET (2001) Grassland management and conversion into grassland: effects on soil carbon. *Ecological Applications*, **11**, 343–355.

Davidson EA, Chorover J, Dail DB (2003) A mechanism of abiotic immobilization of nitrate in forest ecosystems: the ferrous wheel hypothesis. *Global Change Biology*, **9**, 228–236.

Diaz S, Hodgson JG, Thompson K *et al*. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.

DiTommaso A, Aarssen LW (1989) Resource manipulations in natural vegetation: a review. *Vegetatio*, **84**, 9–29.

Galloway JN, Schlesinger WH, Levy HI, Michaels A, Schoor JL (1995) Nitrogen fixation: anthropogenic enhancement-environmental response. *Global Biogeochemical Cycles*, **9**, 235–252.

Gough L, Osenberg CW, Gross KL, Collins SL (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos*, **89**, 428–439.

Grime JP, Brown VK, Thompson K *et al*. (2000) The response of two contrasting limestone grasslands to simulated climate change. *Science*, **289**, 762–765.

Hector A, Schmid B, Beierkuhnlein C *et al*. (1999) Plant diversity and productivity experiments in European grasslands. *Science*, **286**, 1123–1127.

Hooper DU, Johnson L (1999) Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry*, **46**, 247–293.

Inner Mongolia Soil Census Office, Inner Mongolia Soil and Fertilizer Service (1994) *The Soils of Inner Mongolia*. Science Press, Beijing.

Inouye RS, Huntly NJ, Tilman D, Tester JR, Stillwell M, Zinnel KC (1987) Old-field succession on a Minnesota sand plain. *Ecology*, **68**, 12–26.

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Johnson DW, Cheng W, Burke IC (2000) Biotic and abiotic nitrogen retention in a variety of forest soils. *Soil Science Society of America Journal*, **64**, 1503–1514.

Jordan TE, Weller DE (1996) Human contributions to terrestrial nitrogen flux. *BioScience*, **46**, 655–664.

Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science*, **291**, 481–484.

Lal R (2001) Potential of desertification control to sequester carbon and mitigate the greenhouse effect. *Climatic Change*, **51**, 35–72.

Lauenroth WK, Dodd JL, Sims PL (1978) The effects of water-induced and nitrogen-induced stresses on plant community structure in a semi-arid grassland. *Oecologia*, **36**, 211–222.

LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, **89**, 371–379.

Li J, Okin GS, Alvarez L, Epstein H (2007) Quantitative effects of vegetation cover on wind erosion and soil nutrient loss in a desert grassland of southern New Mexico, USA. *Biogeochemistry*, **85**, 317–332.

Li YH (1988) The divergence and convergence of *Aneurolepidium chinense* steppe and *Stipa grandis* steppe under the grazing influence in Xilin river valley, Inner Mongolia. *Acta Phytoecologica et Geobotanica Sinica*, **12**, 189–196.

Li YQ, Xu ZX (2002) Changes of species diversity in succession of plant community of abandoned land in typical steppe. *Journal of Inner Mongolia Agricultural University (Natural Science Edition)*, **23**, 26–31.

Liu WX, Zhang Z, Wan SQ (2009) Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. *Global Change Biology*, **15**, 184–195.

Malhi SS, Harapiak JT, Nyborg M, Gill KS, Monreal CM, Gregorich EG (2003) Total and light fraction organic C in a thin Black Chernozemic grassland soil as affected by 27 annual applications of six rates of fertilizer N. *Nutrient Cycling in Agroecosystems*, **66**, 33–41.

Matson PA, McDowell WH, Townsend AR, Vitousek PM (1999) The globalization of N deposition: ecosystem consequences in tropical environments. *Biogeochemistry*, **46**, 67–83.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, DC.

Morecroft MD, Sellers EK, Lee JA (1994) An experimental investigation into the effects of atmospheric nitrogen deposition on two semi-natural grasslands. *Journal of Ecology*, **82**, 475–483.

Mulvaney RL (1996) Nitrogen: inorganic forms. In: *Methods of Soil Analysis. Part 3. Chemical Methods* (eds Sparks DL, Page AL, Helmke PA *et al*.), pp. 1123–1184. Soil Science Society of American and American Society of Agronomy, Madison, WI, USA.

Naeem S (1998) Species redundancy and ecosystem reliability. *Conservation Biology*, **12**, 39–45.

NEGTAP (2001) Transboundary Air Pollution: Acidification, Eutrophication and Ground Level Ozone in the UK. In. Department Environment, Food and Rural Affairs, London

Nilsson J, Grennfelt P (1988) *Critical loads for sulphur and nitrogen (Report 1988:15)*. Nordic Council of Ministers, Copenhagen, Denmark.

Pfisterer AB, Schmid B (2002) Diversity-dependent productivity can decrease the stability of ecosystem functioning. *Nature*, **416**, 85–86.

Phoenix GK, Booth RE, Leake JR, Read DJ, Grime JP, Lee JA (2003) Effects of enhanced nitrogen deposition and phosphorus limitation on nitrogen budgets of semi-natural grasslands. *Global Change Biology*, **9**, 1309–1321.

Reynolds JF, Smith DMS (2002) *Global Desertification: Do Humans Cause Deserts?* Dahlem University Press, Berlin.

Ritchie ME, Tilman D, Knops JMH (1998) Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology*, **79**, 165–177.

Schellberg J, Moseler BM, Kuhbauch W, Rademacher IF (1999) Long-term effects of fertilizer on soil nutrient concentration, yield, forage quality and floristic composition of a hay meadow in the Eifel mountains, Germany. *Grass and Forage Science*, **54**, 195–207.

Smith MD, Knapp AK (2003) Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters*, **6**, 509–517.

Stevens CJ, Dise NB, Mountford JO, Gowing DJ (2004) Impact of nitrogen deposition on the species richness of grasslands. *Science*, **303**, 1876–1879.

Suding KN, Collins SL, Gough L *et al*. (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences (USA)*, **102**, 4387–4392.

Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, **19**, 46–53.

Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, **57**, 189–214.

Tilman D (1993) Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology*, **74**, 2179–2191.

Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature*, **367**, 363–365.

Tilman D, Reich PB, Knops JMH (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, **441**, 629–632.

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718–720.

Vitousek PM, Aber JD, Howarth RW *et al*. (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, **7**, 737–750.

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur. *Biogeochemistry*, **13**, 87–115.

Wedin D, Tilman D (1996) Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science*, **274**, 1720–1723.

White R, Murray S, Rohweder M (2000) *Pilot Analysis of Global Ecosystems: Grassland Ecosystems*. In. World Resources Institute, Washington, D.C.

Xu ZX, Bai YF, Duan CQ (1994) Study on patterns of carbohydrate reserves in Inner Mongolia steppe. *Acta Prataculturae Sinica*, **3**, 27–31.

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Soil moisture in control plots with depth for the mature and degraded sites averaged over all four years (error bars indicate SEM). Significant differences between sites are reported from one-way ANOVA as NS, $P>0.05$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

13652486, 2010, 1, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2009.01950.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Ecology, 89(8), 2008, pp. 2140–2153
© 2008 by the Ecological Society of America

PRIMARY PRODUCTION AND RAIN USE EFFICIENCY ACROSS A PRECIPITATION GRADIENT ON THE MONGOLIA PLATEAU

Yongfei Bai,[1,5] Jianguo Wu,[1,2] Qi Xing,[3] Qingmin Pan,[1] Jianhui Huang,[1] Dianling Yang,[4] and Xingguo Han[1]

[1]*State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093 China*
[2]*School of Life Sciences and Global Institute of Sustainability, Arizona State University, Tempe, Arizona 85287-4501 USA*
[3]*Inner Mongolia Rangeland Survey and Planning Institute, Hohhot 010051 China*
[4]*Agro-Environmental Protection Institute of the Ministry of Agriculture, Tianjin 300191 China*

Abstract. Understanding how the aboveground net primary production (ANPP) of arid and semiarid ecosystems of the world responds to variations in precipitation is crucial for assessing the impacts of climate change on terrestrial ecosystems. Rain-use efficiency (RUE) is an important measure for acquiring this understanding. However, little is known about the response pattern of RUE for the largest contiguous natural grassland region of the world, the Eurasian Steppe. Here we investigated the spatial and temporal patterns of ANPP and RUE and their key driving factors based on a long-term data set from 21 natural arid and semiarid ecosystem sites across the Inner Mongolia steppe region in northern China. Our results showed that, with increasing mean annual precipitation (MAP), (1) ANPP increased while the interannual variability of ANPP declined, (2) plant species richness increased and the relative abundance of key functional groups shifted predictably, and (3) RUE increased in space across different ecosystems but decreased with increasing annual precipitation within a given ecosystem. These results clearly indicate that the patterns of both ANPP and RUE are scale dependent, and the seemingly conflicting patterns of RUE in space vs. time suggest distinctive underlying mechanisms, involving interactions among precipitation, soil N, and biotic factors. Also, while our results supported the existence of a common maximum RUE, they also indicated that its value could be substantially increased by altering resource availability, such as adding nitrogen. Our findings have important implications for understanding and predicting ecological impacts of global climate change and for management practices in arid and semiarid ecosystems in the Inner Mongolia steppe region and beyond.

Key words: ANPP; arid and semiarid land; ecosystem management; Eurasian Steppe; Inner Mongolia grassland; mean annual precipitation; nitrogen addition; plant functional group composition; rain-use efficiency.

Introduction

Precipitation is an essential factor in controlling biodiversity and ecosystem functioning of terrestrial biomes, especially arid and semiarid ecosystems which account for ~45% of the earth's land surface and accommodate about 20% of the world's human population (Reynolds and Stafford Smith 2002). Global climate change is likely to produce more frequent extreme precipitation and drought events (Easterling et al. 2000), which may have greater impacts on ecosystem processes than effects of elevated CO_2 and temperature alone or in combination (Melillo et al. 1993, Weltzin et al. 2003). It has been well documented that aboveground net primary production (ANPP), a key integrative measure of ecosystem functioning, increases across ecosystem types with increasing mean annual precipitation (MAP) in space (Rosenzweig 1968, Leith and Whittaker 1975, Le Houérou et al. 1988, Sala et al. 1988, McNaughton et al. 1989, Paruelo et al. 1999, Knapp and Smith 2001, Huxman et al. 2004). The response of ANPP to precipitation variation in time, however, varies among different ecosystems (Le Houérou 1984, Lauenroth and Sala 1992, Epstein et al. 1999, Paruelo et al. 1999, Knapp and Smith 2001, Austin 2002, Bai et al. 2004, Huxman et al. 2004). Most of the existing studies have focused mainly on North and South America, and a comprehensive understanding of the spatiotemporal pattern of ANPP in relation to precipitation in world's arid and semiarid lands is yet to be achieved.

Rain-use efficiency (RUE), the ratio of ANPP to precipitation, has been suggested as an effective integral measure for evaluating the response of primary productivity to spatial and temporal changes in precipitation in arid and semi-arid ecosystems (Le Houérou 1984, Le Houérou et al. 1988, Sala et al. 1988). In general, RUE tends to decrease spatially with increasing aridity and potential evapotranspiration, both of which are closely related to ecosystem-level water balance (Le Houérou 1984). However, this widely accepted view recently has

Manuscript received 20 June 2007; revised 20 November 2007; accepted 3 January 2008. Corresponding Editor: R. D. Evans.
[5] E-mail: yfbai@ibcas.ac.cn

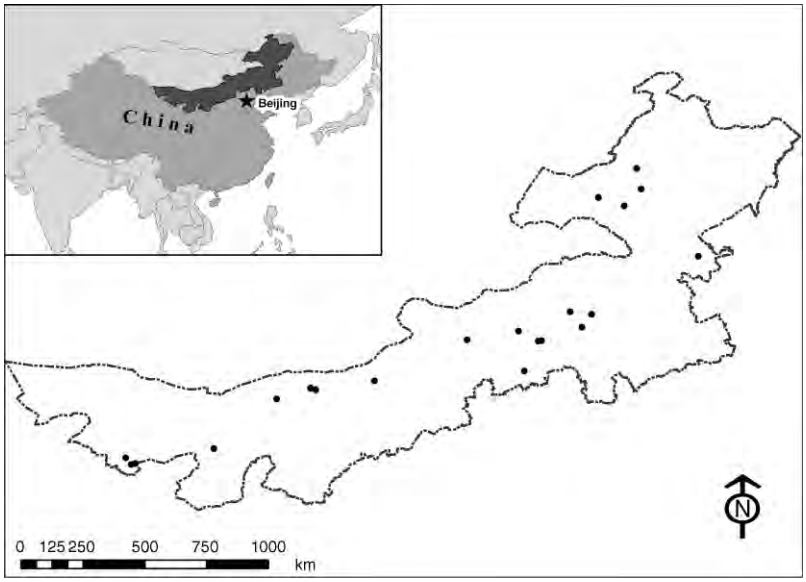


FIG. 1. Location map of the 21 study sites across the Inner Mongolia steppe region of northern China.

been challenged on several grounds (Paruelo et al. 1999, Huxman et al. 2004). For example, considering nine different terrestrial biomes in North and South America, Huxman et al. (2004) found that mean RUE declined from deserts, grasslands, to forests with increasing MAP, and that during the driest years all biomes converged to a common maximum RUE (RUE_{max} = ANPP/minimum precipitation) that was typical of deserts. In contrast, focusing on 11 temperate grassland sites worldwide, Paruelo et al. (1999) showed that RUE increased first, peaked at ~475 mm/yr, and then declined along a precipitation gradient (200–1200 mm/yr). For a given ecosystem, a number of studies have shown that RUE decreases over time with increasing annual precipitation (Lauenroth and Sala 1992, Briggs and Knapp 1995, Paruelo et al. 1999, Lauenroth et al. 2000). These seemingly conflicting patterns of RUE at different organizational levels and in space vs. time may be attributable to the controlling processes of RUE that vary with the scale of analysis: a general phenomenon commonly encountered with a variety of ecological patterns and processes (Wu and Loucks 1995, Wu et al. 2006).

Previous studies have suggested that RUE may be affected by several factors, including vegetation composition, edaphic condition, and biogeochemical constraints (Le Houérou 1984, Lauenroth and Sala 1992, Paruelo et al. 1999, Huxman et al. 2004). First, communities with higher diversity of plant species and functional groups may have greater RUE through increased ANPP (Hooper and Vitousek 1997, Tilman et al. 1997, Hector et al. 1999) and lower temporal variability through a combination of selection effects (more diverse communities tend to have a higher probability of including highly productive species), complementarity effects (more diverse communities tend to be more productive because of fuller resource utilization and synergistic interactions among species), and statistical averaging effects (variability tends to be dampened at higher organizational levels; Loreau and Hector 2001, Loreau et al. 2001, Tilman et al. 2006). Second, traits of dominant plant species and functional groups may affect both ANPP and RUE significantly (Hooper and Vitousek 1997, Paruelo et al. 1999, Eviner and Chapin 2003). For example, grasslands dominated by mesophytic grasses are more productive and less variable than those dominated by xerophytic grasses or shrubs (Bai et al. 2000, 2002, Chen et al. 2003, 2007). Third, ANPP in arid and semiarid ecosystems is usually limited or co-limited by N availability, which is tightly coupled with water availability through biogeochemical feedbacks (Lauenroth et al. 1978, Chapin et al. 1986, Vitousek and Howarth 1991, Schimel et al. 1997, Burke et al. 1998, Hooper and Johnson 1999, Xiao et al. 2007). Furthermore, soil characteristics, such as water-holding capacity, texture, permeability, and depth are major determinants of soil water availability and have important effects on the site-level RUE (Noy-Meir 1973, Le Houérou 1984, Sala et al. 1988).

However, the relative importance of these abiotic and biotic factors and their interactions in relation to the spatiotemporal patterns of ANPP and RUE are yet to be fully understood. Therefore, this study was designed to investigate the spatial and temporal patterns of ecosystem responses to variations in precipitation and their underlying mechanisms based on a long-term data set composed of 21 natural arid and semiarid ecosystem sites across the Inner Mongolia region of China (Fig. 1). These ecosystems are representative of the Eurasian steppe region that stretches over 8000 kilometers from

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1. Abiotic and biotic characteristics of the 21 study sites in the Inner Mongolia steppe region.

Site ID no.	Site	Community type	Vegetation type	Longitude
1	Xieertala	*Filifolium sibiricum* + *Stipa baicalensis*	meadow steppe	120°7′29″ E
2	Ewenke Qi	*Leymus chinensis* + *Carex pediformis*	meadow steppe	120°18′7″ E
3	Modamuji	*L. chinensis* + *Stipa grandis*	typical steppe	118°45′0″ E
4	Ewenke Qi	*S. baicalensis* + *L. chinensis*	meadow steppe	119°41′17″ E
5	Zalaite Qi	*F. sibiricum* + *S. baicalensis*	meadow steppe	122°22′59″ E
6	Xiwu Qi	*S. grandis* + *L. chinensis*	typical steppe	117°43′19″ E
7	Xiwu Qi	*S. baicalensis* + *L. chinensis*	meadow steppe	118°30′0″ E
8	Balinzuo Qi	*S. grandis* + *Artemisia sacrorum*	typical steppe	118°9′0″ E
9	Xilinhaote	*S. grandis* + *L. chinensis*	typical steppe	115°50′20″ E
10	Sunitezuo Qi	*S. krylovii* + *Cleistogenes squarrosa*	typical steppe	113°58′1″ E
11	IMGERS†	*L. chinensis* + *S. grandis*	typical steppe	116°40′30″ E
12	IMGERS	*S. grandis* + *L. chinensis*	typical steppe	116°33′32″ E
13	Zhenglan Qi	*L. chinensis* + *S. grandis*	typical steppe	116°2′53″ E
14	Damao Qi	*S. klemenzii* + *Cleistogenes songorica*	desert steppe	110°36′32″ E
15	Wulatezhong Qi	*Caragana tibetica* + *S. gobica*	desert steppe	108°16′59″ E
16	Wulatezhong Qi	*S. klemenzii* + *Agropyron desertorum*	desert steppe	108°28′12″ E
17	Wulatehou Qi	*Reaumuria soongorica* + *Salsola passerina* + *S. gobica*	desert	107°3′0″ E
18	Alashanzuo Qi	*Potaninia mongolica* + *R. soongorica* + *S. passerina*	desert	104°46′1″ E
19	Alashanyou Qi	*Sympegma regelii* + *Nitraria sphaerocarpa*	desert	101°33′25″ E
20	Alashanyou Qi	*Brachanthemum gobicum* + *Ceratoides latens* + *N. sphaerocarpa*	desert	101°54′29″ E
21	Alashanyou Qi	*C. latens* + *N. sphaerocarpa* + *Zygophyllum xanthoxylon*	desert	101°45′0″ E

Notes: Mean annual precipitation (MAP), mean annual temperature (MAT), and mean annual net primary production ($ANPP_{mean}$) are shown with standard error in parentheses. For each site, MAP and MAT were calculated for the same time period when ANPP measurements were made.

† IMGERS is the abbreviation for the Inner Mongolia Grassland Ecosystem Research Station, Chinese Academy of Sciences.

northern China and Mongolia in the east to Hungary in the west (Chinese Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia 1985, Coupland 1993). This region is quite different from North American prairies and African savannas in terms of climate, soils, and dominant plant functional types, despite of some taxonomical similarities at the levels of genera and families (Coupland 1992, 1993, Sankaran et al. 2005, Bai et al. 2007, Qian et al. 2007). Specifically, we address the following four research questions: First, how does ANPP and its variability change along a precipitation gradient across the arid and semiarid region of the Eurasian Continent? Second, how do plant species richness and functional group composition change along the precipitation gradient? Third, what is the spatial and temporal pattern of RUE along the precipitation gradient? Fourth, how does N availability affect the observed pattern of RUE?

MATERIALS AND METHODS

Study area

This study was conducted in the Inner Mongolia Autonomous Region (IMAR) in northern China (Fig. 1), covering an area of 1.18 million km^2. IMAR has 78.8 million hectares of natural grasslands which account for 66% of the region's total land area. The Inner Mongolia Grassland biogeographically belongs to the Eurasia Steppe region (Chinese Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia 1985). In this study, 21 natural arid and semiarid ecosystem sites on the Inner Mongolia Plateau were selected along an east–west transect, which runs from 39°6′–49°48′ N latitude and 101°36′–122°24′ E longitude. This transect includes several vegetation types: meadow steppe, typical steppe, desert steppe, and desert from east to west with decreasing annual precipitation. The topography of the study area consists of gently rolling hills and tablelands, with elevation ranging from 700 m in the east to 1500 m in the west. Based on long-term meteorological data (1961–2000), the mean annual temperature (MAT) ranges from −1.7° to 8.6°C, with minimum mean monthly temperatures in January (−26.5° to −8.5°C) and maximum temperatures in July (19.9° to 24.0°C). The mean annual precipitation ranges from 113.9 to 425.5 mm, 70–80% of which occurs during the growing season (May–August) in synchrony with the peak temperature. The soils of the study sites are Mollisols, including chernozems, chestnut, calcic brown, and desert soils.

Several plant community types are found corresponding to zonal changes in climate and soils. At the eastern end of the gradient, the meadow steppe, dominated by *Stipa baicalensis*, *Filifolium sibiricum*, *Leymus chinensis*, and *Carex pediformis,* is the highest in both ANPP and species richness among grassland types. The typical steppe, dominated by *S. grandis*, *L. chinensis*, *S. krylovii*, *Cleistogenes squarrosa*, and *Artemisia sacrorum,* is found in the vast chestnut-soil zone of the plateau and has an intermediate level of productivity and plant richness. The desert steppe on calcic brown soils is low in ANPP and species richness, and is dominated by *S. klemenzii*, *C. songorica*, *Agropyron desertorum*, *Caragana tibetica*,

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

TABLE 1. Extended.

Latitude	Soil type	MAP (mm)	MAT (°C)	Number of species	Record length (yr)	$ANPP_{mean}$ (g/m^2)
49°49′1″ N	chernozem soil	365.4 (28.6)	−0.7 (0.3)	74	15	266.92 (16.15)
49°3′50″ N	chernozem soil	353.4 (35.6)	−1.5 (0.3)	70	8	261.00 (16.84)
48°46′1″ N	chernozem soil	288.6 (28.3)	0.2 (0.3)	42	11	161.93 (15.32)
48°27′40″ N	dark chestnut soil	348.5 (18.2)	−1.1 (0.2)	58	16	229.61 (12.59)
46°37′59″ N	dark chestnut soil	526.7 (71.7)	4.7 (0.3)	53	6	242.80 (11.63)
44°36′47″ N	dark chestnut soil	303.0 (27.4)	1.6 (0.2)	43	13	194.30 (11.47)
44°30′47″ N	dark chestnut soil	308.9 (26.9)	1.5 (0.3)	46	9	216.38 (9.62)
44°3′0″ N	dark chestnut soil	410.4 (39.3)	5.2 (0.3)	26	7	218.50 (22.74)
43°54′11″ N	typical chestnut soil	303.4 (27.2)	3.0 (0.2)	40	8	119.29 (17.10)
43°34′59″ N	light chestnut soil	189.9 (20.9)	3.4 (0.2)	38	7	68.19 (11.65)
43°33′11″ N	dark chestnut soil	340.9 (15.1)	0.6 (0.2)	86	24	192.51 (8.87)
43°32′31″ N	typical chestnut soil	340.9 (15.1)	0.6 (0.2)	61	24	127.04 (7.08)
42°27′4″ N	dark chestnut soil	374.8 (20.6)	2.1 (0.2)	42	14	215.67 (18.94)
42°5′38″ N	dark brown soil	244.5 (10.8)	4.0 (0.2)	28	20	32.87 (2.15)
41°49′44″ N	typical brown soil	173.5 (12.3)	5.1 (0.2)	28	8	59.68 (7.82)
41°46′26″ N	typical brown soil	181.5 (15.0)	5.2 (0.2)	26	8	41.34 (5.76)
41°27′0″ N	light brown soil	98.9 (6.3)	4.7 (0.2)	19	5	40.11 (5.83)
39°37′59″ N	grey desert soil	197.7 (11.8)	8.6 (0.2)	12	8	36.29 (4.56)
39°18′0″ N	light brown soil	111.5 (11.6)	8.7 (0.2)	11	7	44.36 (5.89)
39°5′31″ N	light brown soil	111.5 (11.6)	8.7 (0.2)	8	7	42.16 (6.45)
39°3′22″ N	light brown soil	111.5 (11.6)	8.7 (0.2)	7	7	37.96 (5.00)

and *S. gobica*. At the western edge of the gradient is desert, which is dominated by xerophytic shrubs, including *Reaumuria soongorica*, *Salsola passerine*, *Potaninia mongolica*, *Sympegma regelii*, *Nitraria sphaerocarpa*, *Brachanthemum gobicum*, *Ceratoides latens*, and *Zygophyllum xanthoxylon* (Chinese Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia 1985, U.S. National Research Council 1992, Coupland 1993, Inner Mongolia Soil Census Office and Inner Mongolia Soil and Fertilizer Service 1994).

Data collection and sampling methods

Most of our data was acquired from the Long-Term Monitoring of Primary Productivity of Inner Mongolia Grassland Ecosystems Project under the auspices of the government of the Inner Mongolia Autonomous Region (Li 1993, CAAS Grassland Research Institute 1996). This data set contains information on the geographic coordinates, elevation, soil type, concentrations of soil organic carbon and total nitrogen, vegetation type, plant species composition, and aboveground biomass production of 21 ecosystem sites across the Inner Mongolia Autonomous Region (Table 1). Long-term meteorological data were obtained from the nearest weather station to each site.

For 19 of the 21 sites, permanent study plots of 250 × 40 m were fenced from grazing from large animals one year before the beginning of the field sampling. At the time of enclosure, all the sites were considered in excellent conditions, representative of undisturbed, mature communities of the four vegetation types on the Mongolia plateau (i.e., meadow steppe, typical steppe, desert steppe, and desert). Five equal-sized blocks (50 × 40 m) for meadow steppe and typical steppe and 10 equal-sized blocks (40 × 25 m) for desert steppe and desert were established. ANPP for herbaceous plants was sampled on 15 August each year with a 1 × 1 m quadrat randomly located within each block. The only exception was the Damao Qi site where ANPP was measured on 1 September each year using the same method. All living vascular plants in each quadrat were clipped at the ground level and sorted to species. ANPP for shrubs was sampled with a 10 × 10 m quadrat at the same time. The leaves and current-year twigs of shrubs in each quadrat were collected and separated to species. Aboveground biomass was dried at 65°C for 48 h and weighed. Because the standing crop of these steppe and desert communities reached the annual peak at the middle to end of August, the estimated community biomass approximated ANPP of these ecosystems (Li 1993, Bai et al. 2004).

For the remaining two sites, data were obtained from 500 × 500 m enclosures from the Inner Mongolia Grassland Ecosystem Research Station (IMGERS) of Chinese Academy of Sciences, which is located in the Xilin River Basin, Inner Mongolia Autonomous Region (Bai et al. 2004). For the two sites, i.e., *L. chinensis* and *S. grandis* communities, ANPP of 24 continuous years was used for analysis (Table 1). Sampling methods and time were comparable with those for the 19 sites (Bai et al. 2004).

N-addition experiment

To help elucidate possible mechanisms of RUE patterns involving N availability, we also conducted an N-addition experiment in an *L. chinensis* typical steppe community located in IMGERS, a widely distributed ecosystem type in the Eurasia steppe region (Chinese

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia 1985, Wu and Loucks 1992, Bai et al. 2004). Mean annual temperature (years 1980–2003) in the study area is 0.6°C, and mean annual precipitation is 340.9 mm (Table 1). The experiment site was established in 2000 and had never received any fertilizers before this study. Fifty-four 5×5 m plots were laid out following a randomized block design. Plots were separated by 1-m walkways. We had six treatments that included five levels of N enrichment (0, 5.25, 10.5, 17.5, and 28.0 g $N \cdot m^{-2} \cdot yr^{-1}$ of commercial NH_4NO_3) and control (i.e., no nutrient addition). Except for the control, all treatments also received the same amount of P (10 $g \cdot m^{-2} \cdot yr^{-1}$ P_2O_5), S (0.2 $mg \cdot m^{-2} \cdot yr^{-1}$), and trace elements (190 $\mu g \cdot m^{-2} \cdot yr^{-1}$ Zn, 160 $\mu g \cdot m^{-2} \cdot yr^{-1}$ Mn, 31 $\mu g \cdot m^{-2} \cdot yr^{-1}$ B). This was done to make sure that N was the only limiting nutrient (Tilman 1987). We did not add K, Mg, Ca, or Fe in our experiment because dark chestnut soil is rich in these elements, based on the soil census data (Inner Mongolia Soil Census Office and Inner Mongolia Soil and Fertilizer Service 1994). Nutrients were added twice a year in the growing season, half in the early growing period (1–3 May) and the other half in the start of the fastest growing period (1–5 July), when high temperature and precipitation coincide. Aboveground vegetation within each of the 54 plots was sampled each year by clipping all plants at the soil surface within a strip of 0.5×1 m. Samples were taken at least 50 cm apart from the edge of the plots to avoid potential edge effects. All living vascular plants were sorted to species, dried, and weighed. Sampling occurred during 25 August to 2 September each year, which corresponded to the peak biomass (Bai et al. 2004).

Data analysis

Statistical analyses were performed using SAS Version 9.1 (SAS Institute, Cary, North Carolina, USA). We used simple linear regressions to evaluate effects of MAP on mean ANPP ($ANPP_{mean}$), interannual variation of ANPP (measured as the coefficient of variation; CV_{ANPP}), and RUE across 21 sites. RUE has been computed in two ways in the literature. First, according to its definition, RUE can be calculated directly as the ratio of ANPP to the corresponding precipitation (PPT), i.e.,

$$\mathrm{RUE} = \frac{\mathrm{ANPP}}{\mathrm{PPT}}.$$

We used this formula to obtain all site-level mean RUEs in our study. The second common way of estimating RUE is to equate it to the slope of the ANPP–precipitation relationship ($\mathrm{ANPP} = a + b(\mathrm{PPT})$, e.g., Paruelo et al. [1999], Lauenroth et al. [2000], Huxman et al. [2004]). We obtained the regional-scale overall RUEs (overall mean RUE, RUE_{max}, and RUE_{min}) using this linear regression method. However, Veron et al. (2005) pointed out that the slope of the ANPP–precipitation relationship is not equal to RUE unless the intercept in the regression equation is 0 (i.e., $\mathrm{RUE} = b$ only if $a = 0$). In most practical cases, the intercept is not zero, thus the values of RUE obtained from this regression method should be adjusted using the formula $RUE_{adj} = \mathrm{ANPP/PPT} = (b + a)/\mathrm{PPT}$ (Veron et al. 2005). To facilitate the comparison between our results with others in the literature, we provide both the unadjusted and adjusted values of RUE when obtained from the regression method.

We also analyzed the effects of MAP on the sensitivity of ANPP (slope of ANPP to interannual variation in precipitation at each site) as proposed by Huxman et al. (2004). Based on the long temporal records of ANPP and corresponding precipitation in each site, we also examined how ANPP was related to annual precipitation, January–July precipitation, and ANPP of the previous year across all sites. To assess how ecosystems respond to wet vs. dry years, we further analyzed the relationships between relative precipitation maxima [$RP_{maxa} = (\mathrm{maximum} - \mathrm{mean})/\mathrm{mean}$] and relative ANPP pulses [$ANPP_{pul} = (\mathrm{maximum} - \mathrm{mean})/\mathrm{mean}$] for the wettest year and between relative precipitation minima [$RP_{mina} = (\mathrm{mean} - \mathrm{minimum})/\mathrm{mean}$] and relative ANPP decline [$ANPP_{dec} = (\mathrm{mean} - \mathrm{minimum})/\mathrm{mean}$] for the driest year, as per Knapp and Smith (2001).

To identify possible factors responsible for both the $ANPP_{mean}$ and CV_{ANPP} along the environmental gradients, we regressed the $ANPP_{mean}$ and CV_{ANPP} by multiple regressions with stepwise backward elimination against several abiotic and biotic variables: topsoil total N concentration (TN), species richness (SR), MAP, mean annual temperature (MAT), variability of annual precipitation (CV_{MAP}), RP_{maxa}, RP_{mina}, and mean January–July precipitation (MJJ). To explore how differences in local plant functional group (PFG) composition would affect the regional patterns of variation in ANPP (CV_{ANPP}), we classified all plant species into four functional groups based on life forms: perennial grasses (PG), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals (AS). Then, we used the ordinary least squares (OLS) regression to examine the relationships between the mean relative aboveground biomass of PFGs and MAP across the 21 ecosystem sites.

For temporal patterns of RUE, we focused on two of the most widely distributed steppe communities, the *L. chinensis* community and *S. grandis* community, for which a 24-year data set from IMGERS was available. For the N-addition experiment, one-way ANOVA, followed by Duncan's multiple-range test, was performed to compare the N-addition effects on RUE for each year.

Results

In this section, we present our results in the order of the four research questions outlined in the *Introduction* section: aboveground net primary productivity (ANPP)

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

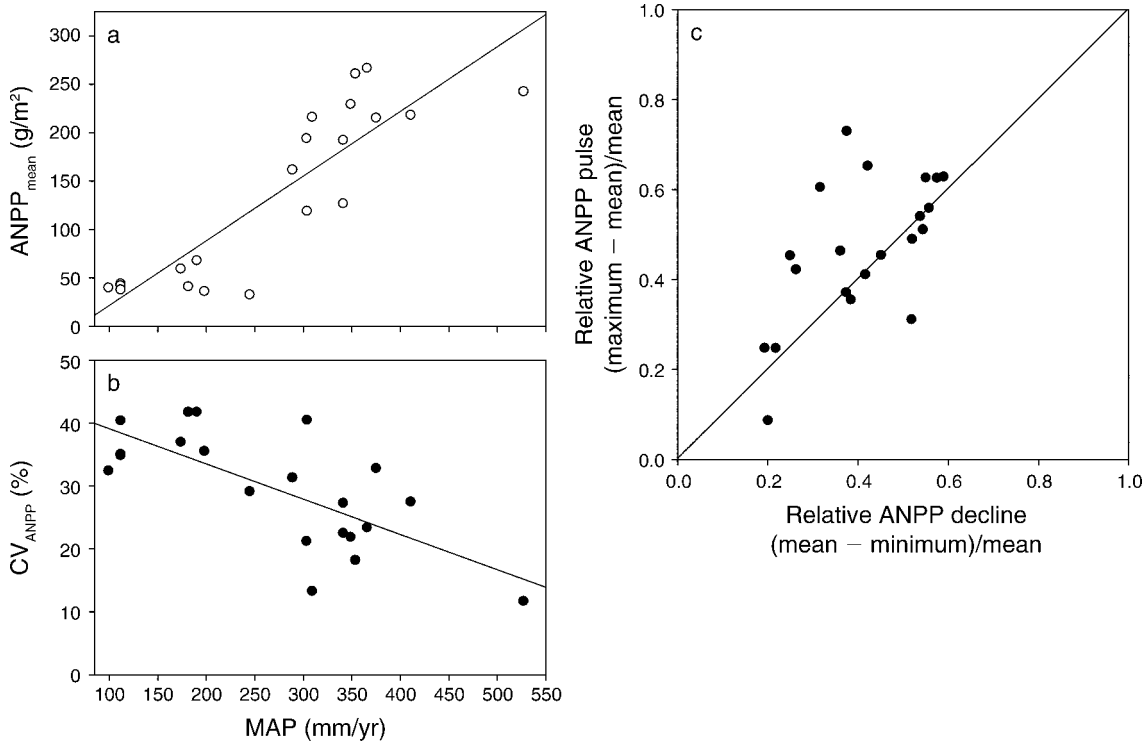


FIG. 2. Annual net primary production (ANPP) and its variability along a precipitation gradient for 21 arid and semiarid ecosystems in the Inner Mongolia steppe region. (a) $ANPP_{mean}$ is positively related to mean annual precipitation (MAP; $r^2 = 0.76$, $P < 0.0001$). The slope of the regression line represents the overall rain-use efficiency (RUE) at the regional scale. (b) The interannual variation of ANPP (measured as the coefficient of variation; CV_{ANPP}) is negatively correlated with MAP ($r^2 = 0.51$, $P = 0.0003$). (c) Relative ANPP pulses ($ANPP_{pul}$) and declines ($ANPP_{dec}$) are positively correlated ($r^2 = 0.37$, $P < 0.01$). The 1:1 line was used to denote the asymmetric relationship between $ANPP_{pul}$ and $ANPP_{dec}$.

and its variability, plant species richness and plant functional group composition, the spatial and temporal patterns of rain use efficiency (RUE), and the effects of N addition.

ANPP and its variability along a precipitation gradient

Our analysis of the 21 sites showed that the $ANPP_{mean}$ of ecosystems increased significantly with increasing mean annual precipitation (mean annual precipitation [MAP]; $ANPP_{mean} = -45.13 + 0.67(MAP)$; $r^2 = 0.76$, $P < 0.0001$; Fig. 2a). Precipitation accounted for 76% of the variation in ANPP across the region. The linear relationship between $ANPP_{mean}$ and MAP can be rewritten in the form of Noy-Meir's (1973) model: $ANPP_{mean} = 0.67(MAP - 67.3)$. This indicates that the overall mean RUE of our study region is 0.67 $g \cdot m^{-2} \cdot mm^{-1}$ ($RUE_{adj} = 0.50$ $g \cdot m^{-2} \cdot mm^{-1}$). Our results also showed that ANPP was significantly correlated with January–July precipitation, but not with May–August precipitation. When the time-series data were combined into the analysis, ANPP was still positively correlated with annual precipitation ($r^2 = 0.43$, $P < 0.0001$) as well as with January–July precipitation ($r^2 = 0.40$, $P < 0.0001$) across all sites. A further analysis with multiple regressions showed that, among all the abiotic and biotic variables examined, only topsoil nitrogen concentration (TN), mean January–July precipitation (MJJ), variability of MAP (measured as the coefficient of variation; CV_{MAP}), and species richness (SR) were significant factors, together explaining 96% of the variation in ANPP ($ANPP_{mean} = 717.6TN + 0.38SR + 0.17MJJ + 1.38CV_{MAP} - 39.96$; $r^2 = 0.96$, $F_{4,20} = 104.49$, $P < 0.0001$). Also, ANPP for all sites were temporally autocorrelated, i.e., ANPP of a given year was significantly correlated with ANPP of the previous year across the regional gradient.

In contrast with ANPP itself, the variability of ANPP, CV_{ANPP}, decreased from desert, desert steppe, typical steppe, to meadow steppe ($r^2 = 0.51$, $P = 0.0003$; Fig. 2b). Following the method by Knapp and Smith (2001), we further explored the relationship between precipitation maxima (RP_{maxa}) and ANPP pulses ($ANPP_{pul}$) for the wettest year and the relationship between precipitation minima (RP_{mina}) and ANPP declines ($ANPP_{dec}$) for the driest year for all sites. Although neither of the above two relationships was found to be significant ($P > 0.05$), ANPP pulses were positively correlated with ANPP declines ($r^2 = 0.37$, $P < 0.01$; Fig. 2c). In general, ANPP pulses in wet years were much stronger than the declines in dry years (Fig. 2c). For example, $ANPP_{pul}$ for typical

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

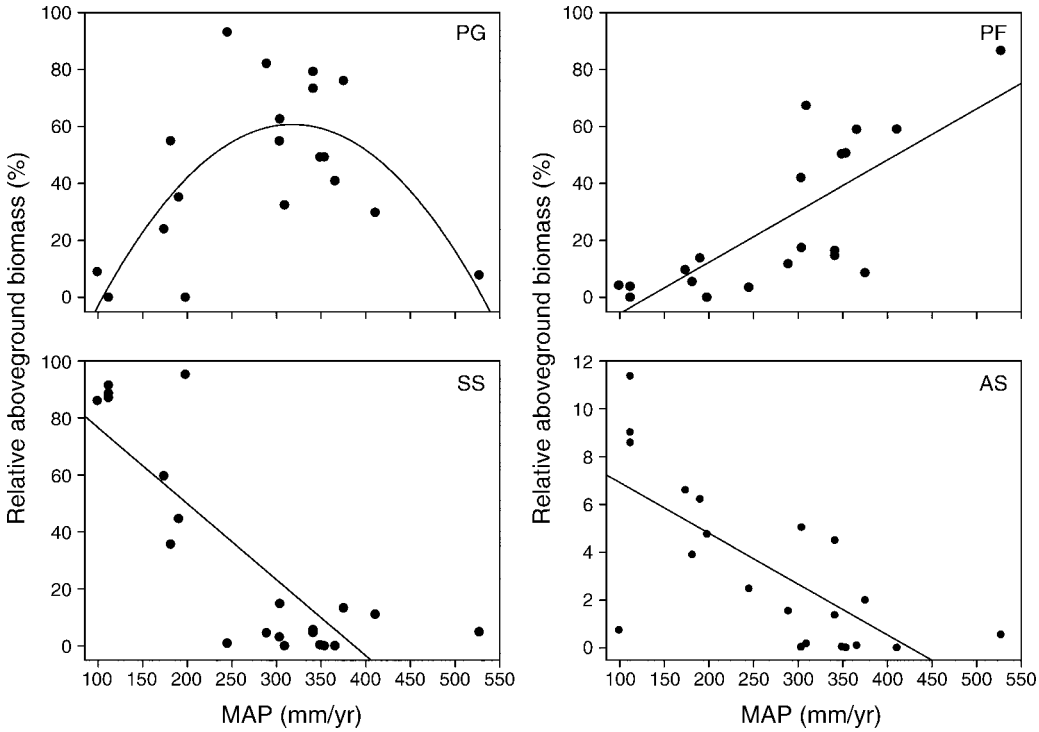


FIG. 3. Changes in plant functional group composition along a precipitation gradient in the Inner Mongolia steppe region. A unimodal relationship was found between the mean relative biomass (MRB) of perennial grasses (PG) and MAP across all sites ($MRB_{PG} = -0.001(MAP)^2 + 0.852(MAP) - 74.76$; $r^2 = 0.62$, $P = 0.0002$). The MRB of perennial forbs (PF) was positively correlated with MAP ($MRB_{PF} = 0.179(MAP) - 23.58$; $r^2 = 0.61$, $P < 0.0001$), but both MRB of shrubs and semi-shrubs (SS) and MRB of annuals (AS) were negatively correlated with MAP ($MRB_{SS} = -0.267(MAP) - 103.28$; $r^2 = 0.69$, $P < 0.0001$; $MRB_{AS} = -0.021(MAP) - 9.04$; $r^2 = 0.50$, $P = 0.0003$).

steppe dominated by *L. chinensis* and *S. grandis* was 0.61, whereas $ANPP_{dec}$ for the same community was 0.32. Our multiple regression analysis with stepwise backward elimination showed that SR, RP_{maxa}, RP_{mina}, and MJJ were significant factors affecting the interannual variation of ANPP ($CV_{ANPP} = -0.18SR + 58.41RP_{maxa} - 28.84RP_{mina} - 0.06MJJ + 35.07$; $r^2 = 0.80$, $F_{4,20} = 16.25$, $P < 0.0001$). This means that ANPP becomes less variable with increasing species richness, January–July precipitation, and relative precipitation minima, but with decreasing relative precipitation maxima.

Species richness and plant functional group (PFG) composition along the precipitation gradient

Plant species richness also increased linearly with MAP ($r^2 = 0.52$, $P = 0.0002$) and $ANPP_{mean}$ ($r^2 = 0.60$, $P < 0.0001$). The composition of PFGs in terms of relative aboveground biomass differed among ecosystems with increasing MAP. The mean relative biomass of perennial grass (PG), the most dominant functional group in both typical and desert steppe, increased at low levels of MAP and decreased at high levels of MAP, producing a unimodal relationship ($r^2 = 0.62$, $P = 0.0002$; Fig. 3a). On average, the relative biomass of PG was 36% for meadow steppe, 62% for typical steppe, 57% for desert steppe, and 2% for desert. The mean relative aboveground biomass of PF increased monotonically with MAP ($r^2 = 0.61$, $P < 0.0001$; Fig. 3b). That is, perennial forbs (PF) were more abundant in the wetter sites. For example, the mean relative biomass of PF was 63% for meadow steppe, 23% for typical steppe, 6% for desert steppe, and <2% for desert. On the other hand, the relative biomass of shrubs and semi-shrubs (SS) declined linearly with increasing MAP ($r^2 = 0.69$, $P < 0.0001$; Fig. 3c). In desert communities, SS was the most predominant among the four PFGs in terms of relative biomass, whereas PG and PF were least abundant. The mean relative biomass of SS was 90% for desert, 32% for desert steppe, 13% for typical steppe, and only 1% for meadow steppe. Moreover, the relative biomass of annuals (AS) also decreased linearly with increasing MAP ($r^2 = 0.50$, $P = 0.0003$; Fig. 3d).

Spatial and temporal patterns of RUE

Along the regional-scale precipitation gradient, RUE_{mean}, RUE_{max}, and RUE_{min} all tended to increase with MAP from desert in the west to the meadow steppe in the east (Fig. 4a). Regressing ANPP for all 21 sites against historic minimum annual precipitation resulted in an overall RUE_{max} of 1.08 $g \cdot m^{-2} \cdot mm^{-1}$ ($r^2 = 0.43$, $P = 0.0012$; adjusted $RUE_{max} = 0.78$ $g \cdot m^{-2} \cdot mm^{-1}$;

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

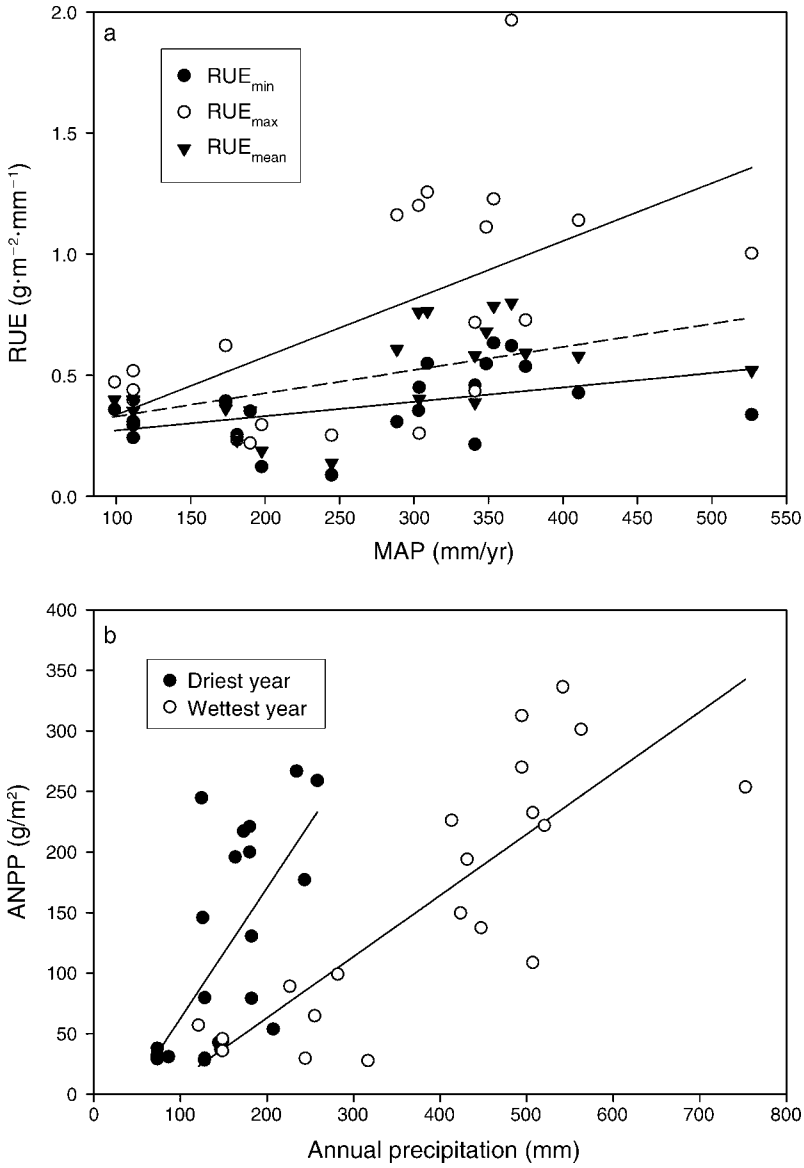


FIG. 4. Variation in mean, maximum, and minimum RUE of the 21 ecosystems along a precipitation gradient in the Inner Mongolia steppe region. (a) RUE_{mean}, RUE_{max}, and RUE_{min} are all positively correlated to MAP (for RUE_{mean}, $r^2 = 0.35$, $P = 0.005$; for RUE_{max}, $r^2 = 0.33$, $P = 0.0069$; for RUE_{min}, $r^2 = 0.21$, $P = 0.0349$). All data points but one (RUE_{max}) fall within the 95% confidence intervals for each regression line. (b) The relationship between ANPP and annual precipitation (AP) in driest years (solid circles, ANPP = −1.08(AP) + 44.95; $r^2 = 0.43$, $P = 0.0012$) and wettest years (open circles, ANPP = 0.51(AP) − 38.15; $r^2 = 0.69$, $P < 0.0001$). The slopes of the two regression lines represent the overall RUE_{max} (driest years) and RUE_{min} (wettest years) for the 21 ecosystems.

Fig. 4b). This indicates that, during the driest years, all ecosystems in the Inner Mongolia steppe region converged to a common maximum RUE ($cRUE_{max}$). Similarly, we obtained an overall minimum RUE_{min} of 0.51 g·m^{-2}·mm^{-1} as the slope of the regression line between ANPP and maximum annual precipitation ($r^2 = 0.69$, $P < 0.0001$; adjusted $RUE_{min} = 0.29$ g·m^{-2}·mm^{-1}; Fig. 4b), suggesting that during the wettest years all ecosystems converged to a common minimum RUE ($cRUE_{min}$).

The general increasing trend for the three RUE measures still held true when site-level data were aggregated by vegetation types (figure not shown). The mean value of RUE_{mean} was 0.71 g·m^{-2}·mm^{-1} for meadow steppe, 0.53 g·m^{-2}·mm^{-1} for typical steppe, 0.24 g·m^{-2}·mm^{-1} for desert steppe, and 0.35 g·m^{-2}·mm^{-1} for desert. The mean value of RUE_{max} was 1.31 g·m^{-2}·mm^{-1} for meadow steppe, 0.73 g·m^{-2}·mm^{-1} for typical steppe, 0.37 g·m^{-2}·mm^{-1} for desert steppe, and 0.42 g·m^{-2}·mm^{-1} for desert. The mean value of RUE_{min}

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

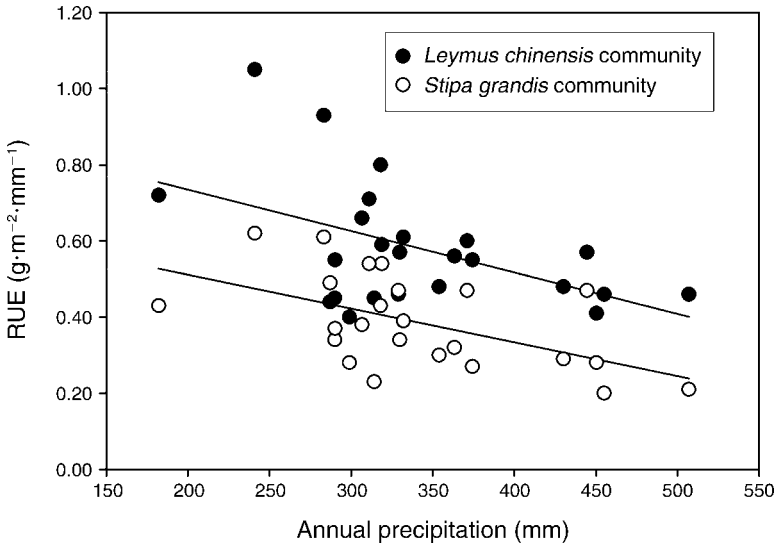


FIG. 5. Responses of RUE to variation in annual precipitation in two Inner Mongolia steppe communities. RUE of the two steppe communities decreased with increasing annual precipitation over a 24-yr period (for the *L. chinensis* community, RUE = −0.001(AP) + 0.95; $r^2 = 0.24$, $P = 0.0144$; for the *S. grandis* community, RUE = −0.001(AP) + 0.69; $r^2 = 0.29$, $P = 0.0062$). The values of RUE for each community were means of five replicates.

for meadow steppe, typical steppe, desert steppe, and desert, were 0.54, 0.39, 0.24, and 0.26 $g \cdot m^{-2} \cdot mm^{-1}$, respectively. For all the RUE measures, values between desert and desert steppe were not statistically significant.

We also examined the temporal pattern of RUE on the site level based on a 24-year data set for two typical steppe communities, one dominated by a rhizomatous grass (*L. chinensis*) and the other by a bunchgrass (*S. grandis*). The results showed that RUE for both sites decreased with increasing annual precipitation with a similar slope, while the *L. chinensis* community had consistently higher RUE for all years than the *S. grandis* community (Fig. 5). Due to the short and uneven time series for the other 19 sites, the temporal pattern of RUE was only analyzed for the two sites at IMGERS.

Effects of N addition on ANPP and RUE

Nitrogen addition significantly increased the ANPP of the *L. chinensis* community over three consecutive years (Fig. 6a). No significant difference was found between the control and zero-N treatment ($P > 0.05$). Plots receiving 5.25–28.00 g $N \cdot m^{-2} \cdot yr^{-1}$ had significantly higher ANPP than those without N addition, except for the treatment with 5.25 g $N \cdot m^{-2} \cdot yr^{-1}$ in the first year (Fig. 6a). For example, at high N-addition rates (17.5 and 28.0 g $N \cdot m^{-2} \cdot yr^{-1}$), ANPP increased by 55% in 2001, 107% in 2002, and 212% in 2003, as compared to the zero-N treatment.

Similarly, RUE was enhanced by N addition in all three years (Fig. 6b), with a 55% increase in the first year at high N-addition rates of 17.5 and 28.0 g $N \cdot m^{-2} \cdot yr^{-1}$. A greater increase of RUE following N addition, however, was found in the dry year (2002, with growing season precipitation of 183 mm) than the wet year (2003, with growing season precipitation of 273 mm; Fig. 6b). For example, the mean value of RUE at the high N-addition rates was 2.4 $g \cdot m^{-2} \cdot mm^{-1}$ in 2002, but only 1.6 $g \cdot m^{-2} \cdot mm^{-1}$ in 2003. Compared to $cRUE_{max}$, the mean RUE was 110% higher in 2002 and 40% higher in 2003, but 28% lower in 2001. Without N addition, the RUE was comparable with the $cRUE_{min}$ in both 2001 and 2003 (Fig. 6b).

We further examined whether changes in plant species composition were responsible for the observed patterns of ANPP and RUE. Results showed that the relative biomass of perennial grasses remained constant in the first two years, but declined with increasing N-addition rate in the third year ($P < 0.0001$). The relative biomass of perennial forbs decreased significantly with increasing N-addition rates in the second and third year ($P < 0.01$). In contrast, the nitrophilous annuals that are rare in undisturbed mature steppe communities increased dramatically with N-addition rate in the second and third year ($P < 0.0001$). However, we found little response of shrubs and semi-shrubs to N-addition rates over the three years ($P > 0.05$).

DISCUSSION

Patterns of ANPP and their controlling factors

This study represents the first comprehensive examination of the spatial and temporal variation in ANPP among ecosystems based on long-term data from the Inner Mongolia steppe region, part of the largest contiguous grassland in the world. Our results have shown that, at the regional scale, ANPP increased significantly across ecosystems with increasing MAP, which accounted for 76% of the variation in ANPP. The

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

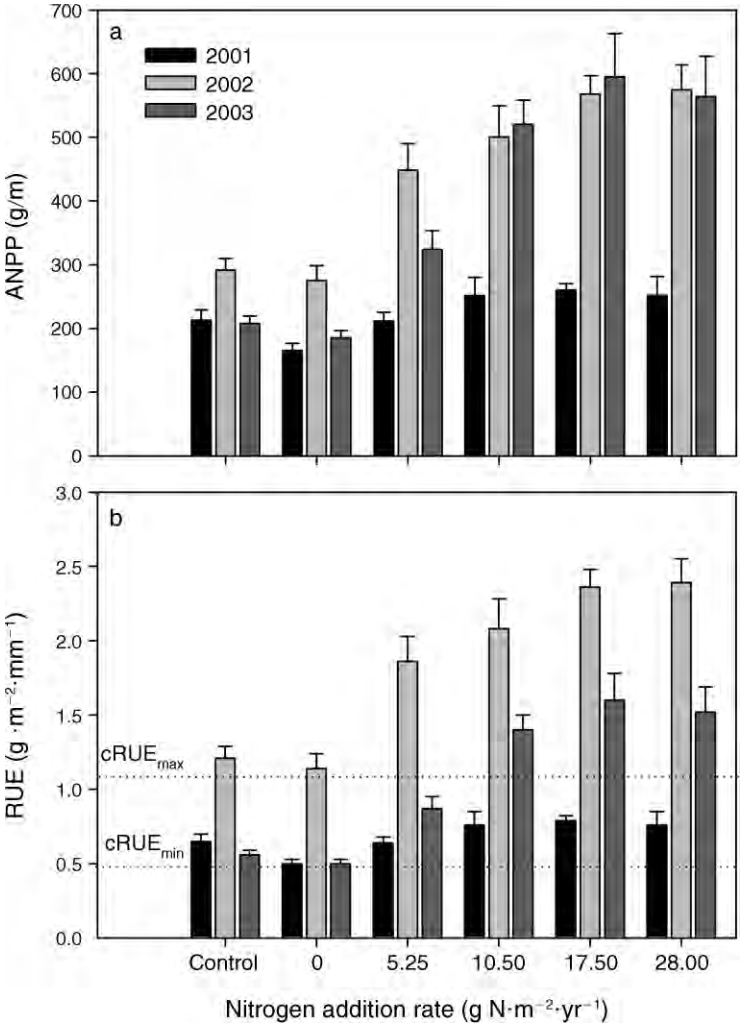


FIG. 6. Effects of N addition on ANPP and RUE of the *L. chinensis* community in the Inner Mongolia steppe region. The precipitation was 329.8 mm in 2001, 240.9 mm in 2002, and 371.0 mm in 2003. (a) ANPP increased significantly with N-addition levels in three consecutive years (ANOVA for 2001, $F_{5,53} = 3.32$, $P = 0.0118$; for 2002, $F_{5,53} = 14.22$, $P < 0.0001$; for 2003, $F_{5,53} = 17.91$, $P < 0.0001$). (b) RUE increased significantly with N-addition rates. Results from the ANOVA analysis were qualitatively similar to those for ANPP over the three years. The values of ANPP and RUE were the means of nine replicates, and error bars indicate the standard error. The horizontal dotted lines denote the common RUE maximum and minimum ($cRUE_{max}$ and $cRUE_{min}$) computed for all 21 sites.

controlling effect of precipitation on grassland productivity was corroborated by previous studies (Bai 1999, Bai et al. 2000, 2001, Guo et al. 2006). The overall mean RUE (0.67 $g \cdot m^{-2} \cdot mm^{-1}$ or $RUE_{adj} = 0.50$ $g \cdot m^{-2} \cdot mm^{-1}$) for the Inner Mongolia steppe region is within the broad range of RUE (0.05–1.81 $g \cdot m^{-2} \cdot mm^{-1}$) reported for the rest of the world's arid and semiarid ecosystems (Le Houérou et al. 1988), and comparable with the mean RUE (0.73–0.82 $g \cdot m^{-2} \cdot mm^{-1}$ or $RUE_{adj} = 0.49$–0.54 $g \cdot m^{-2} \cdot mm^{-1}$) for the North America grassland (Epstein et al. 1996, Burke et al. 1997, Lauenroth et al. 2000). The response pattern of ANPP to precipitation in the Inner Mongolia steppe was generally congruent with previous studies in grasslands elsewhere (Le Houérou et al. 1988, Sala et al. 1988, Burke et al. 1997, Hooper and Johnson 1999, Lauenroth et al. 2000). However, the "ineffective precipitation," i.e., water loss through evaporation and runoff (Noy-Meir 1973), in Inner Mongolia was ~65% lower than that of the North America grassland (Epstein et al. 1996, Burke et al. 1997, Lauenroth et al. 2000). This may be explained in part by the lower MAT and lower MAP in Inner Mongolia. The relatively low ineffective precipitation may also be attributable to the sandy loam and sandy soils with 80–98% sand (0.02–2.0 mm) found at most sites along the precipitation gradient in Inner Mongolia (Inner Mongolia Soil Census Office and Inner Mongolia Soil and Fertilizer Service 1994).

ANPP is affected by an array of biotic and abiotic factors, including precipitation, nutrient availability, physical properties of soil, and intertwining biotic

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

interactions (Lauenroth et al. 1978, Sala et al. 1988, Lauenroth and Sala 1992, Paruelo et al. 1999, Knapp and Smith 2001, Bai et al. 2004). In arid and semiarid ecosystems, water is often considered the most important factor (Noy-Meir 1973), and the effect of N on ANPP has been overlooked (Vitousek and Howarth 1991). Our results indicate that both factors significantly affect ANPP because N and water availability are tightly coupled in these arid and semiarid ecosystems. This was corroborated by our result that ANPP responded to N addition more strongly in wet than dry years, although it is almost impossible to separate the relative importance of water and N availability on ANPP as stated by Burke et al. (1997). Available soil N (rather than total N) directly affects the ANPP in most terrestrial as well as aquatic ecosystems (Vitousek and Howarth 1991). Nevertheless, both total N and soil organic matter (SOM) are closely related to N availability in grassland ecosystems, so they can serve as proxies for N availability. For example, in North American grasslands net N mineralization rates are positively related to SOM (Burke et al. 1997). In several sites of the Inner Mongolia grassland, net N mineralization rates are positively correlated with total soil N and MAP (H. Zhao, Y. Bai, Q. Wang, and X. Han, *unpublished data*). In our study of the *L. chinensis* typical steppe, when N was added ANPP increased in all three years, implying an apparent N limitation. Therefore, our results support the hypothesis of co-limitation by water and nitrogen (Hooper and Johnson 1999, Chapin et al. 2002).

Ecosystem stability and its controlling factors

The interannual variability of ANPP (CV_{ANPP}), which is conversely related to ecosystem stability (Bai et al. 2004, Tilman et al. 2006), decreased progressively across sites with increasing MAP. Our analyses suggest that increased stability is associated with increased species richness, January–July precipitation, and relative precipitation minima, but with decreased relative precipitation maxima. This indicates that greater ecosystem stability was associated simultaneously with the high species richness and January–July precipitation. For meadow steppe and typical steppe ecosystems, the complementary interactions between PG and PF may have contributed to the high ANPP and low CV_{ANPP} in the face of environmental fluctuations. In contrast, the low species diversity, low growth potential and increased dominance of SS may have been responsible for the low ANPP and high CV_{ANPP} in desert steppe and desert ecosystems. These results lend further support to the findings on ecosystem stability in our previous study (Bai et al. 2004).

Across sites, the relative precipitation minima (RP_{mina}) and relative precipitation maxima (RP_{maxa}) also contributed to the interannual variability of ANPP. However, RP_{mina} and RP_{maxa} showed clearly opposite effects on CV_{ANPP}. RP_{maxa} had a positive effect on CV_{ANPP}, reflecting a sharply pulsed increase of ANPP in extremely wet years, whereas RP_{mina} was negatively correlated with CV_{ANPP}. This suggests that extremely high precipitation events had greater impacts on drier sites, whereas extreme droughts had greater impacts on wetter sites. As a result, the correlation coefficients for RP_{mina} and RP_{maxa} had the opposite signs. For a given site, total soil N exhibited the least variation and was eliminated from the multiple-regression model, suggesting that N may not be an important factor determining ecosystem stability. Moreover, we found an asymmetric relationship between ANPP pulse and decline: greater ANPP pulses were found in wet years than ANPP declines in dry years, a result also found in the North American grassland (Knapp and Smith 2001). This was likely caused in part by increased water-use efficiency through stomatal control mechanisms in dry years (Chen et al. 2005). In addition, a positive linear relationship between the current-year ANPP and previous-year ANPP across the 21 sites indicates a carry-over effect (O'Connor et al. 2001), which is caused primarily by the lagged effects of previous-year precipitation induced transfer of soil water, nonstructural carbohydrate reserves in plant belowground tissues, and bud density on current-year plants (Cable 1975, Hanson et al. 1982, O'Connor et al. 2001).

Spatial vs. temporal patterns of RUE

The increasing trend of RUE_{mean}, RUE_{max}, and RUE_{min} with MAP in the Inner Mongolia steppe region is in contrast with the continental-scale pattern found in the Americas that the mean RUE declines from deserts, grasslands, to forests with increasing MAP (Huxman et al. 2004). This difference may be due, at least in part, to the scale of analysis. However, whether the spatial pattern of RUE differs on the regional vs. continental scale in such a diametrical way still needs further confirmation. Alternatively, these different patterns may reflect the different relationships between ANPP and MAP on the two continents. One useful study would be to analyze the RUE pattern for all major biomes on the Eurasian Continent, including deserts, grasslands, and forests, and then compare the results with those of Huxman et al. (2004).

However, previous studies also showed that drier sites tend to have lower and less variable RUE because of low plant density, low production potential, high evaporation potential, and high tolerance to water stress (Noy-Meir 1973, Grime 1977, Paruelo et al. 1999). In the Serengeti grassland of East Africa, McNaughton (1985) found that RUE increased from 0.17 to 0.94 $g \cdot m^{-2} \cdot mm^{-1}$ along a precipitation gradient (480–1150 mm/yr). Based on 11 temperate grassland sites (seven from the USA and four from Eurasia) with annual precipitation ranging from 200 to 1200 mm, Paruelo et al. (1999) found that RUE_{mean} first increased and then decreased with increasing MAP, peaking around 475 mm. Our results are congruent with this pattern up to 500 mm in MAP, close to the upper limit of annual

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

precipitation for the Eurasian steppe region. All these studies together seem to suggest that regional and continental patterns of RUE are significantly different. Because RUE is simply the ratio of ANPP to precipitation, the increase in RUE along the precipitation gradient in the Inner Mongolia steppe region may be attributable to several factors that affect ANPP, as discussed earlier.

Huxman et al. (2004) showed that during the driest years, all biomes in North and South America converge to a common RUE_{max} that is typical of deserts. Our results support the existence of a common RUE, but the value of RUE_{max} we obtained for the Inner Mongolia steppe region (1.08 $g \cdot m^{-2} \cdot mm^{-1}$ or adjusted $RUE_{max} = 0.78$ $g \cdot m^{-2} \cdot mm^{-1}$) is much higher than that for North and South America (0.42 $g \cdot m^{-2} \cdot mm^{-1}$) reported in Huxman et al. (2004). The difference may be attributed to several factors. First, the scale of analysis may directly affect the absolute value of RUE. For example, at the continental scale, the mean RUE for different biomes of North and South America is 0.51 $g \cdot m^{-2} \cdot mm^{-1}$ (Huxman et al. 2004). Within North America, the mean RUE is 0.65 $g \cdot m^{-2} \cdot mm^{-1}$ for semiarid ecosystems and drops to 0.44 $g \cdot m^{-2} \cdot mm^{-1}$ for subhumid and humid ecosystems (Knapp and Smith 2001). At a finer scale, the mean RUE for the Great Plains grassland of the United States is 0.73–0.82 $g \cdot m^{-2} \cdot mm^{-1}$ or $RUE_{adj} = 0.49$–0.54 $g \cdot m^{-2} \cdot mm^{-1}$ (Epstein et al. 1996, Burke et al. 1997, Lauenroth et al. 2000). Second, the higher RUE in the Inner Mongolia steppe region may result partly from the synchronized rainfall and temperature, both peaking in July. Third, the regression method for estimating RUE without adjustments used in Huxman et al. (2004) may have introduced errors into their analysis (Veron et al. 2005).

In addition, our result of RUE for the two widely distributed steppe communities, based on a 24-year data set, suggests that RUE of different ecosystems within the same biome may respond similarly to temporal variation in precipitation even though the absolute value of RUE varies. Also, the ecosystem-level temporal pattern of RUE which decreases with increasing annual precipitation is the opposite of the regional-scale cross-ecosystem spatial pattern. We hypothesize that the differences between spatial and temporal patterns of RUE in the Inner Mongolia steppe region reflect different underlying mechanisms on regional and local ecosystem scales. That is, the regional pattern of RUE is determined primarily by precipitation and N gradients as well as the greater range of biological responses provided by distinctive plant communities, whereas the temporal pattern of RUE for a given ecosystem is influenced mainly by the interaction between water and N availability as well as the limited response capacity of the single ecosystem. Our analysis indicated that the overall mean RUE declined by 25% when the long-term temporal data were incorporated into the regression analysis across arid and semiarid ecosystems in the Inner Mongolia steppe region. This hypothesis is also consistent with the previous finding from the North American shortgrass steppe that the ANPP–annual-precipitation relationship at the regional scale had a much steeper slope than that at the ecosystem scale, meaning that the regional model will generally overestimate ecosystem productivity in wet years and underestimate it in dry years (Lauenroth and Sala 1992).

Effects of N addition

Our field manipulative experiment with the *L. chinensis* community showed that N addition significantly increased both ANPP and RUE. The claim by Huxman et al. (2004) that $cRUE_{max}$ could not be increased by altering resource availability was only supported by our first year finding. The dramatic increase in RUE in the second and third years was caused by N addition and concurrent changes in species composition and precipitation. In particular, the explosive increase in annuals, with higher relative growth rate and greater growth response to added N, was a main cause for the increase in ANPP and RUE. This indicates that the $cRUE_{max}$ could be substantially increased by chronically altering resource availability, such as N addition.

Implications for global change and ecosystem management

Our findings have several implications for understanding ecological impacts of global climate change and better managing arid and semiarid ecosystems in the Inner Mongolia region and beyond. Global climate change is projected to increase MAP by 30–100 mm and MAT by ~3°C in the next 100 years in the Inner Mongolia steppe, with slightly less precipitation during growing season because almost all the increase in MAP occurs in winter (Ni and Zhang 2000). We expect that ANPP will consequently increase on a regional scale and that the magnitude of change will increase from desert to meadow steppe because of increased RUE, resource availability, and biodiversity along this gradient. However, the regional-scale increase in ANPP will be limited by several ecosystem-level factors, including elevated N limitation and enhanced evapotranspiration associated with increased MAT.

Our results also suggest that the spatial relationship between ANPP and MAP is not appropriate for predicting the response of ANPP to temporal variation in precipitation for a given ecosystem because the specific patterns of both ANPP and RUE differ with scale. Finally, a key to increasing the primary production of arid and semiarid ecosystems is to improve RUE, and our study indicates that this can be achieved by improving N availability as well as other measures of conserving biodiversity and ecosystem functioning through management practices that control overgrazing and soil erosion.

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

ACKNOWLEDGMENTS

We are grateful to Chris M. Clark, Travis E. Huxman, and Alan K. Knapp for their constructive comments on an earlier version of this paper. Our sincere thanks also go to D. S. Liu, Y. P. Dong, X. L. Lü, W. J. Wang, S. Q. Bai, L. Z. Xin, D. H. Huang, S. Jiang, Z. Z. Chen, Y. H. Li, Q. H. Qi, S. P. Wang, Yanfen Wang, Yifeng Wang, Z. G. Yang, and others for their contributions to the long-term data collection. This research was supported by National Natural Science Foundation of China (30521002 and 30670346), the State Key Basic Research Development Program of China (2007CB106801), the Ministry of Science and Technology (2006BAD26B05), and U.S. National Science Foundation (DEB-0618193).

LITERATURE CITED

Austin, A. T. 2002. Differential effects of precipitation on production and decomposition along a rainfall gradient in Hawaii. Ecology 83:328–338.

Bai, Y. F. 1999. Influence of seasonal distribution of precipitation on primary productivity of *Stipa krylovii* community. Acta Phytoecologica Sinica 23:155–160.

Bai, Y. F., X. G. Han, J. G. Wu, Z. Z. Chen, and L. H. Li. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431:181–184.

Bai, Y. F., L. H. Li, J. H. Huang, and Z. Z. Chen. 2001. The influence of plant diversity and functional composition on ecosystem stability of four *Stipa* communities in the Inner Mongolia Plateau. Acta Botanica Sinica 43:280–287.

Bai, Y. F., L. H. Li, Q. B. Wang, L. X. Zhang, Y. Zhang, and Z. Z. Chen. 2000. Changes in plant species diversity and productivity along gradients of precipitation and elevation in the Xilin River Basin, Inner Mongolia. Acta Phytoecologica Sinica 24:667–673.

Bai, Y. F., J. G. Wu, Q. M. Pan, J. H. Huang, Q. B. Wang, F. S. Li, A. Buyantuyev, and X. G. Han. 2007. Positive linear relationship between productivity and diversity: evidence from the Eurasian steppe. Journal of Applied Ecology 44: 1023–1034.

Bai, Y. F., L. X. Zhang, Y. Zhang, and Z. Z. Chen. 2002. Changes in plant functional composition along gradients of precipitation and temperature in the Xilin river basin, Inner Mongolia. Acta Phytoecologica Sinica 26:308–316.

Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil-moisture, topographic position, and fire as determinants of aboveground biomass. American Journal of Botany 82: 1024–1030.

Burke, I. C., W. K. Lauenroth, and W. J. Parton. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecology 78:1330–1340.

Burke, I. C., W. K. Lauenroth, M. A. Vinton, P. B. Hook, R. H. Kelly, H. E. Epstein, M. R. Aguiar, M. D. Robles, M. O. Aguilera, K. L. Murphy, and R. A. Gill. 1998. Plant–soil interactions in temperate grasslands. Biogeochemistry 42: 121–143.

CAAS Grassland Research Institute. 1996. Dynamic monitoring of grassland ecosystems in northern China: the dataset. Inner Mongolia University Press, Hohhot, China.

Cable, D. R. 1975. Influence of precipitation on perennial grass production in the semidesert southwest. Ecology 56:981–986.

Chapin, F. S., III, P. A. Matson, and H. A. Mooney. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag, New York, New York, USA.

Chapin, F. S., III, P. M. Vitousek, and K. Vancleve. 1986. The nature of nutrient limitation in plant communities. American Naturalist 127:48–58.

Chen, S. P., Y. F. Bai, and X. G. Han. 2003. Variations in composition and water use efficiency of plant functional groups based on their water ecological groups in the Xilin River Basin. Acta Botanica Sinica 45:1251–1260.

Chen, S. P., Y. F. Bai, G. H. Lin, J. H. Huang, and X. G. Han. 2007. Variations in $\delta^{13}C$ values among major plant community types in the Xilin River Basin, Inner Mongolia, China. Australian Journal of Botany 55:48–54.

Chen, S. P., Y. F. Bai, L. X. Zhang, and X. G. Han. 2005. Comparing physiological responses of two dominant grass species to nitrogen addition in Xilin River Basin of China. Environmental and Experimental Botany 53:65–75.

Chinese Academy of Sciences: Integrative Expedition Team to Inner Mongolia and Ningxia. 1985. The vegetation of Inner Mongolia. Science Press, Beijing, China.

Coupland, R. T. 1992. Ecosystems of the world 8A. Natural grasslands: introduction and Western Hemisphere. Elsevier, Amsterdam, The Netherlands.

Coupland, R. T. 1993. Ecosystems of the world 8B. Natural grasslands: Eastern Hemisphere and résumé. Elsevier, Amsterdam, The Netherlands.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science 289:2068–2074.

Epstein, H. E., I. C. Burke, and W. K. Lauenroth. 1999. Response of the shortgrass steppe to changes in rainfall seasonality. Ecosystems 2:139–150.

Epstein, H. E., W. K. Lauenroth, I. C. Burke, and D. P. Coffin. 1996. Ecological responses of dominant grasses along two climatic gradients in the Great Plains of the United States. Journal of Vegetation Science 7:777–788.

Eviner, V. T., and F. S. Chapin, III. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology, Evolution, and Systematics 34:455–485.

Grime, J. P. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169–1194.

Guo, R., X. K. Wang, Z. Y. Ouyang, and Y. N. Li. 2006. Spatial and temporal relationships between precipitation and ANPP of four types of grasslands in northern China. Journal of Environmental Sciences 18:1024–1030.

Hanson, C. L., J. R. Wight, J. P. Smith, and S. Smoliak. 1982. Use of historical yield data to forecast range herbage production. Journal of Range Management 35:614–616.

Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127.

Hooper, D. U., and L. Johnson. 1999. Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. Biogeochemistry 46:247–293.

Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305.

Huxman, T. E., et al. 2004. Convergence across biomes to a common rain-use efficiency. Nature 429:651–654.

Inner Mongolia Soil Census Office and Inner Mongolia Soil and Fertilizer Service. 1994. The soils of Inner Mongolia. Science Press, Beijing, China.

Knapp, A. K., and M. D. Smith. 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291:481–484.

Lauenroth, W. K., I. C. Burke, and J. M. Paruelo. 2000. Patterns of production and precipitation-use efficiency of winter wheat and native grasslands in the Central Great Plains of the United States. Ecosystems 3:344–351.

Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water-induced and nitrogen-induced stresses on plant community structure in a semi-arid grassland. Oecologia 36: 211–222.

Lauenroth, W. K., and O. E. Sala. 1992. Long-term forage production of North American shortgrass steppe. Ecological Applications 2:397–403.

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Le Houérou, H. N. 1984. Rain use efficiency: a unifying concept in arid-land ecology. Journal of Arid Environments 7:213–247.

Le Houérou, H. N., R. L. Bingham, and W. Skerbek. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. Journal of Arid Environments 15:1–18.

Leith, H., and R. H. Whittaker. 1975. Primary productivity of the biosphere. Springer, New York, New York, USA.

Li, B. 1993. Dynamic monitoring of grassland ecosystems in northern China: the design on technical implementation. Agricultural Science and Technology Press of China, Beijing, China.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808.

McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. Ecological Monographs 55:259–294.

McNaughton, S. J., M. Oesterheld, D. A. Frank, and K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341:142–144.

Melillo, J. M., A. D. McGuire, D. W. Kicklighter, B. Moore III, C. J. Vorosmarty, and A. L. Schloss. 1993. Global climate change and terrestrial net primary production. Nature 363:234–240.

Ni, J., and X. S. Zhang. 2000. Climate variability, ecological gradient and the Northeast China Transect (NECT). Journal of Arid Environments 46:313–325.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4: 25–51.

O'Connor, T. G., L. M. Haines, and H. A. Snyman. 2001. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. Journal of Ecology 89:850–860.

Paruelo, J. M., W. K. Lauenroth, I. C. Burke, and O. E. Sala. 1999. Grassland precipitation-use efficiency varies across a resource gradient. Ecosystems 2:64–68.

Qian, H., P. S. White, and J.-S. Song. 2007. Effects of regional vs. ecological factors on plant species richness: an intercontinental analysis. Ecology 88:1440–1453.

Reynolds, J. F., and D. M. Stafford Smith. 2002. Do humans cause deserts? Pages 1–21 *in* J. F. Reynolds and D. M. Stafford Smith, editors. Global desertification: do humans cause deserts? Dahlem University Press, Berlin, Germany.

Rosenzweig, M. L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. American Naturalist 102:67–74.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40–45.

Sankaran, M., et al. 2005. Determinants of woody cover in African savannas. Nature 438:846–849.

Schimel, D. S., et al. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecological Monographs 67:251–271.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs 57:189–214.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302.

Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632.

U.S. National Research Council. 1992. Grasslands and grassland sciences in northern China. National Academy Press, Washington, D.C., USA.

Veron, S. R., M. Oesterheld, and J. M. Paruelo. 2005. Production as a function of resource availability: slopes and efficiencies are different. Journal of Vegetation Science 16:351–354.

Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13: 87–115.

Weltzin, J. F., et al. 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. BioScience 53:941–952.

Wu, J., and O. L. Loucks. 1992. Xilingele. Pages 67–84 *in* The U.S. National Research Council, editor. Grasslands and grassland sciences in northern China. National Academy Press, Washington, D.C., USA.

Wu, J., and O. L. Loucks. 1995. From balance-of-nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology 70:439–466.

Wu, J. G., K. B. Jones, H. B. Li, and O. L. Loucks. 2006. Scaling and uncertainty analysis in ecology: methods and applications. Springer, Dordrecht, The Netherlands.

Xiao, C., I. A. Janssens, P. Liu, Z. Zhou, and O. J. Sun. 2007. Irrigation and enhanced soil carbon input effects on belowground carbon cycling in semiarid temperate grasslands. New Phytologist 174:835–846.

19399170, 2008, 8, Downloaded from https://esajournals.onlinelibrary.wiley.com/doi/10.1890/07-0992.1 by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Journal of Applied Ecology 2007
44, 1023–1034

Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe

YONGFEI BAI*, JIANGUO WU*†, QINGMIN PAN*, JIANHUI HUANG*, QIBING WANG*, FUSHENG LI‡, ALEXANDER BUYANTUYEV† and XINGGUO HAN*

**State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China; †School of Life Sciences and Global Institute of Sustainability, Arizona State University, Tempe, Arizona 85287, USA; and ‡Xilingol Grassland Management Station, Xilinhot 02600, China*

Summary

1. Understanding the productivity–diversity relationship (PDR) is a key issue in biodiversity–ecosystem functioning research, and has important implications for ecosystem management. Most studies have supported the predominance of a hump-shaped form of PDR in which species richness peaks at an intermediate level of productivity. However, this view has been challenged recently on several grounds.
2. Based on data from 854 field sites across the Inner Mongolia region of the Eurasian Steppe, we tested the form of PDR at different organizational levels (association type, vegetation type and biome) and multiple spatial scales (local, landscape and regional).
3. Our results showed that a positive linear, rather than hump-shaped, form was ubiquitous across all organizational levels and spatial scales examined. On the regional scale, this monotonic PDR pattern corresponded closely with the gradient in mean annual precipitation (MAP) and soil nitrogen. Increasing species dissimilarity with productivity could also contribute to the positive linear form of PDR.
4. Our results also indicated that grazing decreased both primary productivity and species richness but, intriguingly, not the form of PDR.
5. *Synthesis and applications.* This study provides the first direct test of the productivity–diversity relationship for the world's largest contiguous terrestrial biome – the Eurasian Steppe. The predominance of a positive linear relationship in this region defies the commonly held view that a unimodal form of PDR dominates terrestrial ecosystems, supported mainly by studies in Africa, Europe and North America. It suggests that precipitation has a greater control on the productivity–diversity relationship in the Eurasian Steppe than grasslands elsewhere. Also, the positive linear relationship is surprisingly robust to grazing. Our results provide new insight into the productivity–diversity relationship and have several implications for restoring degraded lands and understanding ecological consequences of climate change in the Eurasian Steppe.

Key-words: ecosystem management, Eurasian steppe, grazing land, Inner Mongolia grassland, precipitation gradient, productivity–diversity relationship, spatial scale, species dissimilarity

Journal of Applied Ecology (2007) **44**, 1023–1034
doi: 10.1111/j.1365-2664.2007.01351.x

Introduction

The relationship between species diversity and ecosystem productivity has been a central issue in ecology for decades (Rosenzweig 1992; Tilman 1999; Waide *et al.* 1999; Chapin *et al.* 2000; Sala *et al.* 2000; Mittelbach *et al.* 2001; Loreau, Naeem & Inchausti 2002; Hooper

© 2007 The Authors.
Journal compilation
© 2007 British
Ecological Society

Correspondence: Xingguo Han, State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, the Chinese Academy of Sciences, 20 Nanxincun, Xiangshan 100093, Beijing, China. Tel: (86) 10 6283 6636; Fax: (86) 10 8259 5771: E-mail: xghan@ibcas.ac.cn

et al. 2005). However, several key questions are yet to be answered fully regarding both the form and underlying mechanisms of the productivity–diversity relationship (PDR). For example, does productivity control, or is it controlled by, species diversity? Is there really a general pattern of PDR that exists in different biomes across the world? In particular, is the form of PDR predominantly monotonic or unimodal across different ecosystems and on spatial scales? These are not only fundamental research questions, but also have important implications for biodiversity conservation and ecosystem management.

The dominant view has been that PDR most frequently assumes a hump-shaped or unimodal form in terrestrial ecosystems (Grime 1973; Al-Mufti *et al*. 1977; Huston 1979; Tilman 1982; Rosenzweig 1992; Waide *et al*. 1999; Mittelbach *et al*. 2001). A hump-shaped form means that species diversity increases at low levels of productivity and decreases at high levels of productivity. In the lower range of productivity levels, species diversity increases with productivity because higher resource availability associated with increasing productivity leads to larger populations and lower extinction rates. In the higher range of productivity levels, spatial heterogeneity of limiting resources is reduced, interspecific competition is intensified and as a result species diversity tends to decrease (Grime 1973; Huston 1979; Rosenzweig 1992; Rosenzweig & Abramsky 1993; Tilman & Pacala 1993). However, this widely accepted view has been challenged recently on several grounds (Abrams 1995; Oksanen 1996; Whittaker & Heegaard 2003; Gillman & Wright 2006). Disagreements hinge on both the predominant form of PDR and its underlying causes.

For example, a meta-analysis of 171 published studies by Mittelbach *et al*. (2001) showed that the hump-shaped curve was the dominant form of PDR for plants at local and regional scales. However, Whittaker & Heegaard (2003) pointed out that Mittelbach *et al*.'s (2001) study had several problems associated with spatial scale, surrogates for productivity and statistical methods. To alleviate these problems, Gillman & Wright (2006) reanalysed the pattern of PDR using data in Mittelbach *et al*. (2001) and other studies with a rigorous experimental design. These authors found that the form of PDR was almost always monotonic from regional to global scales, whereas a hump-shaped relationship occurred only rarely on local and landscape scales (Gillman & Wright 2006). Thus, it remains debatable whether a monotonic or hump-shaped form of PDR is dominant in ecosystems.

Accordingly, multiple explanations exist for the various forms of PDR. For example, Grace (1999) suggested that productivity was just one of several factors influencing plant species diversity. Other processes, such as disturbance, spatial heterogeneity and gradients in the species pool, may also be important in controlling species diversity (Grace 1999). Based on theoretical and empirical evidence, Abrams (1995) argued that processes of competition and coexistence could produce a monotonic form of PDR, but that empirical support is lacking for the hypothesis that high productivity decreases heterogeneity. The unimodal relationship could also be an artefact of sampling schemes as using small plots of fixed size can give rise to the maximum species diversity at intermediate levels of productivity if plants are of varying sizes (Oksanen 1996; Weiher 1999). In a nutshell, studies have shown that PDR may be determined by the interplay of multiple abiotic and biotic factors, including the availability of energy and resources (Currie 1991; Gaston 2000; Fridley 2002; Baer *et al*. 2003; Cornwell & Grubb 2003; Hawkins *et al*. 2003; Evans, Warren & Gaston 2005), species pool (Taylor, Aarssen & Loehle 1990), disturbance (O'Connor 2005), herbivory (Olff & Ritchie 1998; Worm *et al*. 2002), the history of community assembly (Fukami & Morin 2003), spatial heterogeneity (Ritchie & Olff 1999; Mouquet, Moore & Loreau 2002; Anderson, McNaughton & Ritchie 2004) and the scale of analysis (Weiher 1999; Gross *et al*. 2000; Chase & Leibold 2002; Weiher & Howe 2003; Steiner & Leibold 2004; Harrison *et al*. 2006). The relative importance of these factors in determining the form of PDR, however, needs further clarification.

Most of the recent challenges to the prevailing view of PDR were based on either theoretical arguments or meta-analysis of already published studies. While these studies are useful direct tests of the productivity–diversity relationship, using data from a broad spectrum of ecosystems and across a range of scales are much needed. Also, existing studies of PDR for grasslands have been conducted primarily in North America, Europe and Africa (Grace 1999; Gross *et al*. 2000; Mittelbach *et al*. 2001; Anderson, McNaughton & Ritchie 2004; Jennings, Williams & Stromberg 2005; Gillman & Wright 2006), and many have potential problems associated with data acquisition, sample size and surrogates for productivity (i.e. productivity estimated from precipitation, soil nitrogen and potential evapotranspiration rather than field measurements) (Whittaker & Heegaard 2003; Gillman & Wright 2006). Surprisingly, few studies of PDR have ever been reported from the largest grassland region, the Eurasian Steppe.

Here, we examine the form and underlying causes of PDR using multiscaled data collected systematically from 854 field sites in the Inner Mongolia grassland region of China (Fig. 1), which is part of the Eurasian Steppe that extends over 8000 km from north-eastern China, Mongolia, Russia and Ukraine to Hungary (Coupland 1993). The Eurasian steppe is quite different from the prairie of North America in terms of climate, soils and dominant plant functional types, despite taxonomical similarities at the levels of genera and families (Coupland 1992, 1993; US National Research Council 1992). For example, the mean annual precipitation (MAP) of Eurasian grasslands ranges from 150 to 500 mm, whereas MAP of the North American grasslands varies from 300 to about 1000 mm (Coupland

© 2007 The Authors. Journal compilation © 2007 British Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

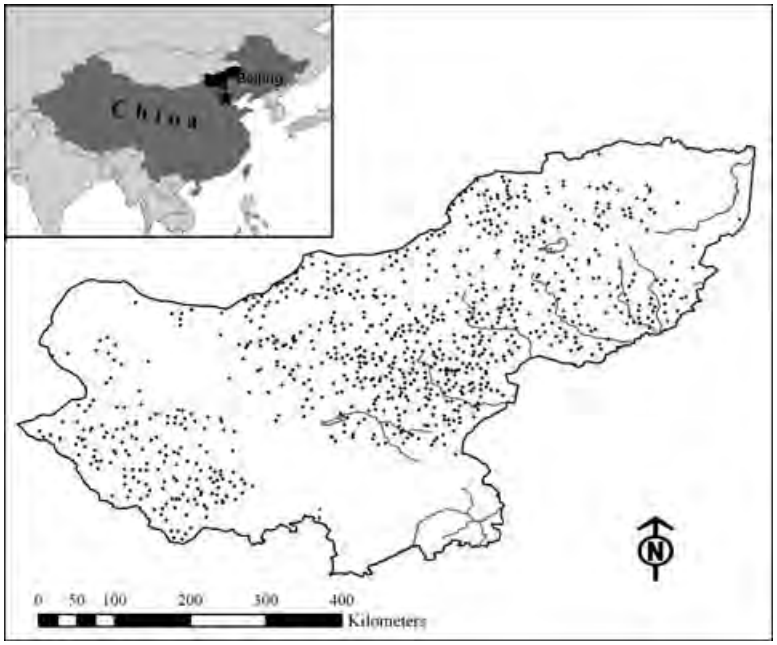


Fig. 1. Location map of the study region, the Xilingol Grassland of Inner Mongolia in northern China, and spatial distribution of sampling sites.

1992, 1993). In Eurasian grasslands, the dominant plant functional type (PFT) is perennial C_3 grasses. In North America, however, perennial C_4 grasses predominate in short and tall prairies, and C_3 and C_4 grasses codominate in mixed prairies (Coupland 1992, 1993).

Recognizing the multitude of factors and the effect of spatial scale on PDR, we followed a hierarchical approach to facilitate our analysis and interpretation (O'Neill *et al*. 1986; Wu & Levin 1994; Wu & Loucks 1995). We organized data into a nested hierarchy of three levels: association type, vegetation type and biome. In terms of spatial extent, these three organizational levels correspond to the local, landscape and regional scales, respectively. We intended to address three specific questions: first, how does plant species richness respond to variations in productivity at different organizational levels and across spatial scales in the Eurasian Steppe region? Secondly, how does grazing affect the form of PDR? Thirdly, what are the possible underlying processes responsible for the observed form of PDR, particularly in terms of abiotic factors and changes in species composition along the environmental gradient?

Materials and methods

STUDY AREA

Our study was conducted in the Xilingol grassland, located in the middle part of the Inner Mongolia Autonomous Region, China (Fig. 1). The study area runs from 41·4° N to 46·6° N latitude and 111·1° E to 119·7° E longitude, covering an area of 203 000 km^2. The Xilingol grassland, where agricultural, residential and forested areas account for less than 10% of the total land area, is representative of the Eurasian steppe in terms of topography, climate, soils, vegetation composition and land use history (Wu & Loucks 1992; Coupland 1993). The topography of the study area consists of gently rolling hills, tablelands and sand dunes, with elevation between about 1000 and 1300 m. The mean annual temperature ranges from –2·3 to 5·6 °C with the lowest mean monthly temperatures in January (–15·4 to –22·4 °C) and the highest in July (18·2–23·4 °C). The mean annual precipitation ranges from 104 to 411 mm, with 60–80% occurring in the growing season (May–August) which coincides with the peak temperature. Several soil types are found in this region, including chernozem, chestnut, calcic brown and aeolian soils. Along an East–West precipitation gradient, the study area includes five vegetation types: meadow steppe, typical steppe, sandy land, desert steppe and desert. The Xilingol grassland is composed primarily of C_3 perennial bunchgrasses and perennial rhizome grasses, two dominant functional groups in most plant communities. Perennial forbs are found commonly in meadow steppe and typical steppe communities, while shrubs and semishrubs dominate in sandy land, degraded typical steppe and desert communities (Chinese Academy of Sciences Integrative Expedition Team to Inner Mongolia and Ningxia 1985).

DATA COLLECTION AND SAMPLING METHODS

Data used in this study were acquired primarily from the Xilingol Grassland Management Station. Our data set is composed of 854 field sites, representing 13 association types that belong to five vegetation types in the study area (Table 1). The sampling sites were distributed fairly evenly across the Xilingol grassland with a 10–15 km spatial interval between sites, and the number of sites for each association was proportional to its area (Fig. 1). Data for each site include geographical coordinates, elevation, soil type, land use type, association type, vegetation type, plant species richness and above-ground biomass production at both species and community levels.

Above-ground biomass was sampled at its peak time in late July and August from 1981 to 1985, which approximated the above-ground net primary productivity (ANPP) in temperate grasslands (Sala & Austin 2000; Bai *et al*. 2004). At each site, ANPP of herbaceous plants was sampled in three 1 × 1 m quadrats, located randomly within a 100 × 100 m area. Above-ground biomass of all vascular plants in each quadrat was harvested at ground level and sorted to species. ANPP for shrubs was sampled using three 5 × 5 m quadrats at the same time. The leaves and current-year twigs of shrubs in each quadrat were collected and separated to species. The average dry mass and the total number of plant species of three quadrats were used to estimate ANPP and species richness for each of the 854 sites.

© 2007 The Authors. Journal compilation © 2007 British Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 1. Abiotic and biotic characteristics of the 13 association types in the Xilingol grassland

No.	Association type (named after dominant species)	Vegetation type	MAP (mm)	MAT (°C)	Soil type	Species richness		ANPP (g m^{-2})		Dominant plant functional group
						Mean	Range	Mean	Range	
1	*Filifolium sibiricum-Carex pediformis*	Meadow steppe	350·2	0·0	Typical chernozem soil Light chernozem soil	22·25	10–36	184·85	36·81–334·35	Perennial forbs
2	*Leymus chinensis-Stipa baicalensis*	Meadow steppe	332·7	0·5	Light chernozem soil	21·58	8–32	128·25	27·02–299·27	Perennial rhizome and bunch grasses
3	*Stipa baicalensis*	Meadow steppe	328·3	0·3	Typical chernozem soil Light chernozem soil	18·97	12–33	117·29	42·49–259·08	Perennial bunch grasses
4	*Leymus chinensis*	Typical steppe	283·5	1·0	Dark chestnut soil	14·04	4–29	88·61	11·99–324·67	Perennial rhizome grass
5	*Stipa grandis*	Typical steppe	277·6	1·2	Typical chestnut soil	15·98	7–25	91·09	16·73–270·18	Perennial bunch grasses
6	*Cleistogenes squarrosa*	Typical steppe	267·8	1·4	Typical chestnut soil Light chestnut soil	13·53	6–27	56·86	17·18–134·33	Perennial bunch grasses
7	*Artemisia frigida*	Typical steppe	267·2	1·8	Typical chestnut soil Light chestnut soil	13·23	7–25	60·05	9·40–164·58	Semi-shrubs and perennial bunch grasses
8	*Caragana microphylla*	Typical steppe	249·1	2·5	Typical chestnut soil Light chestnut soil	14·38	5–20	48·33	11·59–152·71	Shrubs and perennial bunch grasses
9	*Artemisia intramongolica-Psammochloa villosa*	Sandy land	274·2	2·3	Aeolian soil	12·45	7–23	62·82	10·84–201·76	Semi-shrubs and perennial bunch grasses
10	*Stipa krylovii*	Typical steppe	242·0	2·3	Typical chestnut soil Light chestnut soil	12·81	5–22	49·57	6·12–130·27	Perennial bunch grasses
11	*Allium polyrhizum-Cleistogenes songorica*	Desert steppe	180·8	4·6	Typical calcic brown soil	12·22	5–17	39·89	2·91–85·79	Perennial forbs and perennial bunch grasses
12	*Stipa klemenzii*	Desert steppe	169·1	3·9	Typical calcic brown soil	11·00	5–19	22·06	1·57–64·23	Perennial bunch grasses and annuals
13	*Reamuria soongorica-Salsola passerina*	Desert	168·5	3·9	Light calcic brown soil	8·80	2–20	18·56	5·55–41·88	Shrub and semishrubs

© 2007 The Authors.
Journal compilation
© 2007 British
Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Long-term meteorological data from 1961 to 2000 were obtained from 48 weather stations within and adjacent to the study area.

SCHEME FOR DATA ANALYSIS

In general, levels of nested hierarchies can be related to spatial scales (Wu 1999). In our case, the three organizational levels – association type, vegetation type and biome – correspond to the local, landscape and regional scales (in terms of spatial extent). Relating organizational units to spatial scales helps to reduce the potential confusion caused by using terms such as local or regional scales with arbitrary spatial extents, and facilitates the analysis and interpretation of results by providing a unifying structure (Collins & Glenn 1990; Wu & Levin 1994; Wu & Loucks 1995; Pickett, Wu & Cadenasso 1999).

To address our first question of the form of PDR at different organizational level and corresponding scales, prior to statistical analyses data from different sites were aggregated into three organizational levels: association type (local scale), vegetation type (landscape scale) and biome (regional scale). Specifically, the 854 field sites from the Inner Mongolia grassland biome were classified into 13 association types that belonged to five vegetation types. At the landscape scale, we considered only data from meadow steppe, typical steppe and desert steppe. Data from sandy land and desert, both of which had only one single association type in the region, were excluded from the analysis because they were already used in the analysis at the association level (to avoid repeating the analysis at two levels using the same data set). At the regional scale, the form of PDR is represented in terms of local sites, association types and the vegetation types within the entire biome.

To examine the effects of grazing on PDR, we focused our analysis on the regional scale only, because further grouping data into vegetation and association types for this analysis would result in an insufficient sample size. Our data fell into four land use types representing a gradient of increasing grazing intensity: hayfields (HF), winter-grazing grasslands (WG), year-round-grazing grasslands (YG) and summer-grazing grasslands (SG). Summer grazing is the most intensified land use practice in the Inner Mongolia Grassland because of the highest stocking rate due to the excessively large number of animals in a limited area. We assessed the effects of grazing intensity on ANPP, species richness and forms of PDR. To make the analysis more robust, we used only data from 688 sites of meadow steppe and typical steppe that had all the four land use types and similar land use history.

To explore possible environmental factors responsible for the observed forms of PDR, we examined how ANPP and species richness were related to MAP and MAT (mean annual temperature), respectively, across the region using simple regressions. At the regional scale, we also assessed how the slope (a) and intercept (b) in the linear regression model (species richness = a × productivity + b) were related to MAP across different association types. To investigate how the form of PDR may be influenced by differences in species composition (β-diversity) along the environmental gradient, we calculated the dissimilarity index (1 – Jaccard's similarity) for all possible pairs among sites within each association type (Chase & Leibold 2002). To examine further if high average productivity was related to high degree of environmental heterogeneity at the regional scale, we analysed the relationship between the variance in ANPP among sites within each association type and the average ANPP of association types (Chase & Leibold 2002). Similarly, we also analysed the relationship between the variance in MAP within each association type and the average MAP across association types within the region.

STATISTICAL ANALYSIS

Statistical analysis was performed using SAS version 9·1 (SAS Institute Inc. 2004). We used both ordinary least squares (OLS) regression and Poisson regression using generalized linear models (GLM) to examine whether PDR was positive linear or quadratic at each organizational level and corresponding scale as per Mittelbach *et al.* 2001) and Gillman & Wright 2006). For the Poisson GLM, Pearson's χ^2 was used to correct for over-dispersion and output statistics in cases where species richness data violated the assumption of Poisson errors. In addition, the Mitchell-Olds and Shaw (MOS) test (Mitchell-Olds & Shaw 1987) was used to examine whether a significant quadratic relationship reached the predicted peak within the observed range of ANPP. A given PDR was considered significantly 'positive linear' or 'unimodal' only if the results of both OLS and Poisson GLM regressions were congruent (significant at $P < 0{\cdot}05$). MAP and MAT for each site were interpolated using a Geographical Information System (GIS)-based multiple regression method developed by Ninyerola *et al.* (Ninyerola, Pons & Roure 2000).

Results

FORM OF PDR AT DIFFERENT ORGANIZATIONAL LEVELS AND SPATIAL SCALES

At the association type level or local spatial scale, 11 of the 13 association types exhibited a statistically significant, positive linear form of PDR (Fig. 2a–c and Table 2), with two of the 11 also showing a significant unimodal relationship (Table 2). The other two association types, i.e. *Filifolium sibiricum* + *Carex pediformis* association and *Caragana microphylla* association, showed no significant relationship (Table 2). At the vegetation type level or landscape scale, we found a

© 2007 The Authors. Journal compilation © 2007 British Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

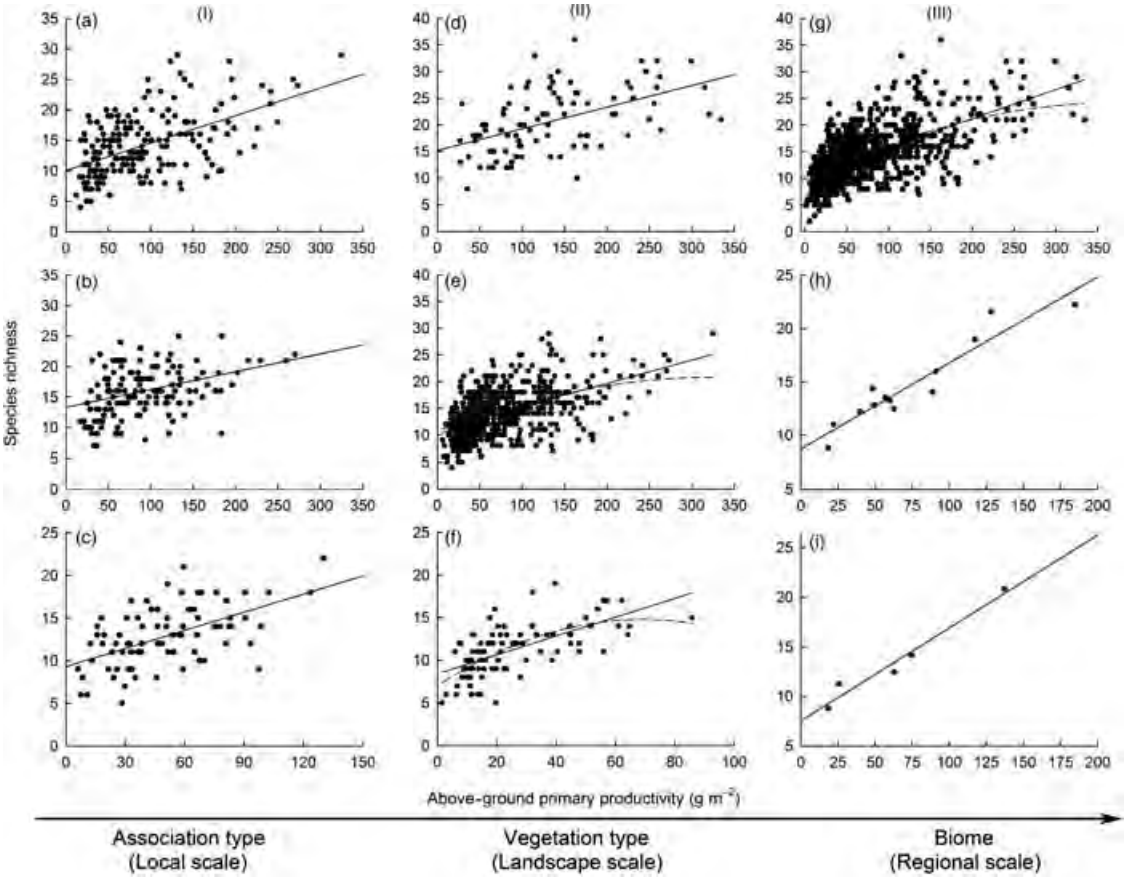


Fig. 2. Relationships between productivity and species richness at different organizational levels and spatial scales. (1) At the level of association type or the local scale, three association types are shown as examples: a, *Leymus chinensis* association; b, *Stipa grandis* association; c, *S. krylovii* association. (2) At the level of vegetation type or the landscape scale: d, meadow steppe; e, typical steppe; f, desert steppe. (3) At the level of biome or the regional scale: g, by individual site; h, by association type; i, by vegetation type. The fitted lines represent statistically significant linear (solid line) and quadratic (dashed line) relationships between productivity and species richness.

Table 2. Summary of regression analyses of the forms of PDR at different organizational levels and corresponding spatial scales

Organizational level and scale	No. of sites	OLS† regression				MOS*	Poisson GLM‡		MOS	Pattern summary§
		P_{linear}	R^2	$P_{quadratic}$	R^2		P_{linear}	$P_{quadratic}$		
Association type (local scale)										
Filifolium sibiricum–Carex pediformis	20	0·1599	0·11	0·1586	0·21		0·1522	0·1153		NS
Leymus chinensis–Stipa baicalensis	38	0·0002	0·33	0·8498	0·33		< 0·0001	0·6180		PL
Stipa baicalensis	31	0·0008	0·33	0·6484	0·33		0·0002	0·8676		PL
Leymus chinensis	202	< 0·0001	0·29	0·8713	0·29		< 0·0001	0·2662		PL
Stipa grandis	138	< 0·0001	0·13	0·2420	0·14		< 0·0001	0·1729		PL
Cleistogenes squarrosa	62	< 0·0001	0·33	0·0018	0·44	UN	< 0·0001	0·0002	UN	PL, UN
Artemisia frigida	92	< 0·0001	0·21	0·2202	0·23		< 0·0001	0·1289		PL
Caragana microphylla	24	0·4605	0·03	0·4371	0·05		0·4565	0·4284		NS
Artemisia intramongolica–Psammochloa villosa	58	< 0·0001	0·31	0·8118	0·31		< 0·0001	0·4747		PL
Stipa krylovii	81	< 0·0001	0·30	0·6587	0·30		< 0·0001	0·3562		PL
Allium polyrhizum–Cleistogenes songorica	18	0·0005	0·55	0. 1717	0·60		< 0·0001	0·0866		PL
Stipa klemenzii	75	< 0·0001	0·33	0·0289	0·38	UN	< 0·0001	0·0113	UN	PL, UN
Reamuria soongorica–Salsola passerina	15	0·0368	0·29	0·6707	0·31		0·0222	0·8908		PL
Vegetation type (landscape scale)										
Meadow steppe	89	< 0·0001	0·25	0·0882	0·28		< 0·0001	0·0378		PL
Typical steppe	599	< 0·0001	0·25	0·0102	0·26	UN	< 0·0001	0·0003	UN	PL, UN
Desert steppe	93	< 0·0001	0·40	0·0112	0·44	UN	< 0·0001	0·0032	UN	PL, UN
Biome (regional scale)										
By individual site	854	< 0·0001	0·37	0·0001	0·38	UN	< 0·0001	< 0·0001	UN	PL, UN
By association type	13	< 0·0001	0·90	0·4218	0·90		< 0·0001	0·0400		PL
By vegetation type	5	0·0033	0·96	0·4642	0·97		< 0·0001	0·9525		PL

†OLS = ordinary least squares; ‡GLM = general linear model; §PL = positive linear relationship; UN = unimodal relationship; NS = non-significant relationship. *MOS = the Mitchell-Olds and Shaw test.

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 3. Effects of grazing on the relationship between productivity and species richness. The abbreviations are the same as in Table 1

Land use type (grazing intensity)	No. of sites	OLS† regression				MOS*	Poisson GLM‡		MOS	Pattern summary§
		P_{linear}	R^2	$P_{quadratic}$	R^2		P_{linear}	$P_{quadratic}$		
Hay fields	52	< 0·0001	0·41	0·7952	0·41		< 0·0001	0·6701		PL
Winter-grazed	168	< 0·0001	0·37	0·6687	0·37		< 0·0001	0·1761		PL
Year-round-grazed	140	< 0·0001	0·30	0·0049	0·33	UN	< 0·0001	0·0006	UN	PL, UN
Summer-grazed	328	< 0·0001	0·24	0·0235	0·25	UN	< 0·0001	0·0031	UN	PL, UN

†OLS = ordinary least squares. ‡GLM = general linear model; §PL = positive linear relationship; UN = unimodal relationship; NS = non-significant relationship. *MOS = the Mitchell-Olds and Shaw test.

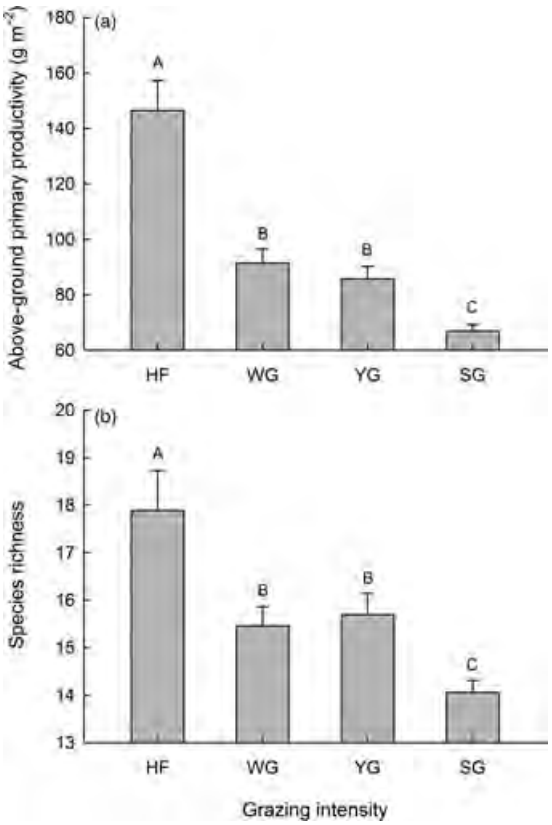


Fig. 3. The effects of the grazing intensity on productivity and species richness (error bars denote standard errors). a, Productivity; b, species richness. Bars with the same letter were not significantly different in Duncan's multiple range tests. HF, hayfields; WG, winter-grazing grasslands; YG, year-round-grazing grasslands; SG, summer-grazing grasslands.

significant positive linear form of PDR in all three major vegetation types (meadow steppe, typical steppe and desert steppe; Fig. 2d–f and Table 2). For the typical steppe and the desert steppe, a unimodal form of PDR was also statistically significant, but the MOS test indicated that there was only one data point beyond the predicted peak value of the quadratic model (Fig. 2e,f), suggesting that the relationship was weak. At the biome level or regional scale a positive linear form of PDR was found across local sites, association types and vegetation types (Fig. 2g–i and Table 2). The regional-scale PDR for local sites also showed a significant quadratic relationship (Fig. 2g), but again only a few data points fell beyond the predicted peak value in the MOS test.

EFFECTS OF GRAZING ON THE FORM OF PDR

At the regional scale, both ANPP and species richness decreased significantly with increasing grazing intensity (GLM; for ANPP, $F = 10{\cdot}88$, $P < 0{\cdot}0001$; for species richness, $F = 35{\cdot}25$, $P < 0{\cdot}0001$; Fig. 3). Among the four land use types, hayfields, which had no grazing, showed the highest average ANPP and species richness. In contrast, summer-grazing grasslands, with the highest grazing intensity, exhibited the lowest average ANPP and species richness (Fig. 3). A positive linear PDR form was found for all four land use types (Fig. 4 and Table 3). Although a unimodal relationship was also statistically significant for both the year-round-grazing and summer-grazing grasslands, only few data points existed beyond the peak value in the MOS test (Fig. 4).

In the linear regression model (species richness = a × productivity + b), the slopes for HF, WG, YG and SG were 0·050, 0·049, 0·055 and 0·053, respectively. The intercepts for HF, WG, YG and SG were 10·59, 10·98, 11·02 and 10·50, respectively. We further examined if there were quantitative differences among the four land use types in terms of the slope and intercept. Results showed that neither the slope ($F = 0{\cdot}19$, $P > 0{\cdot}05$) nor the intercept ($F = 1{\cdot}52$, $P > 0{\cdot}05$) differed significantly along the gradient of grazing intensity.

EFFECTS OF PRECIPITATION ON ANPP, SPECIES RICHNESS AND PDR

At the regional scale, both ANPP and species richness were correlated linearly with MAP (Fig. 5) as well as with MAT. Results from simple regressions showed that MAP alone explained 41% of the variation in ANPP (ANPP = $0{\cdot}654MAP - 99{\cdot}486$; $n = 854$, $F = 592{\cdot}03$, $R^2 = 0{\cdot}41$, $P < 0{\cdot}0001$) and 25% of the variation in species richness (species richness = $0{\cdot}046MAP + 2{\cdot}241$; $n = 854$, $F = 280{\cdot}62$, $R^2 = 0{\cdot}25$, $P < 0{\cdot}0001$), while MAT explained only 4% of the variation in

© 2007 The Authors. Journal compilation © 2007 British Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

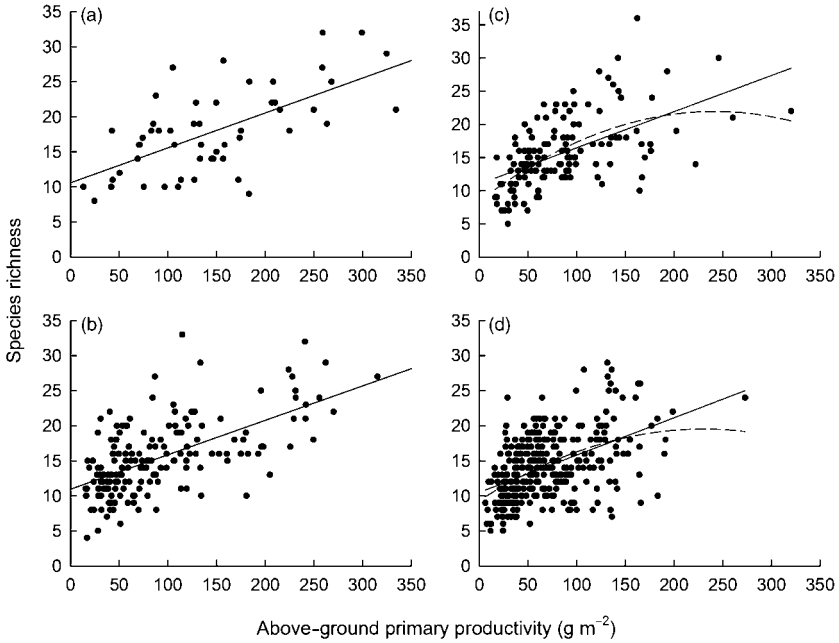


Fig. 4. Effects of grazing on the relationship between productivity and species diversity. a, Hayfields; b, winter-grazing grasslands; c, year-round-grazing grasslands; d, summer-grazing grasslands.

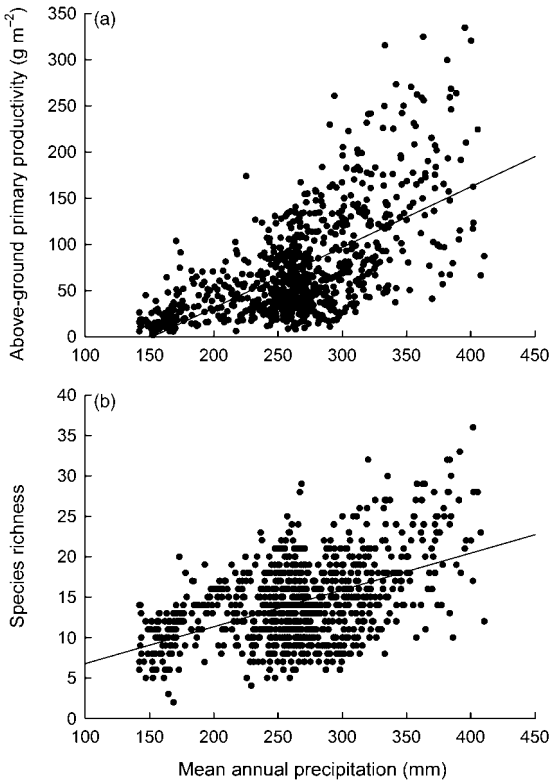


Fig. 5. Relationship of mean annual precipitation to productivity and species richness. a, Productivity was positively correlated with MAP across all sites; b, species richness was positively correlated with MAP.

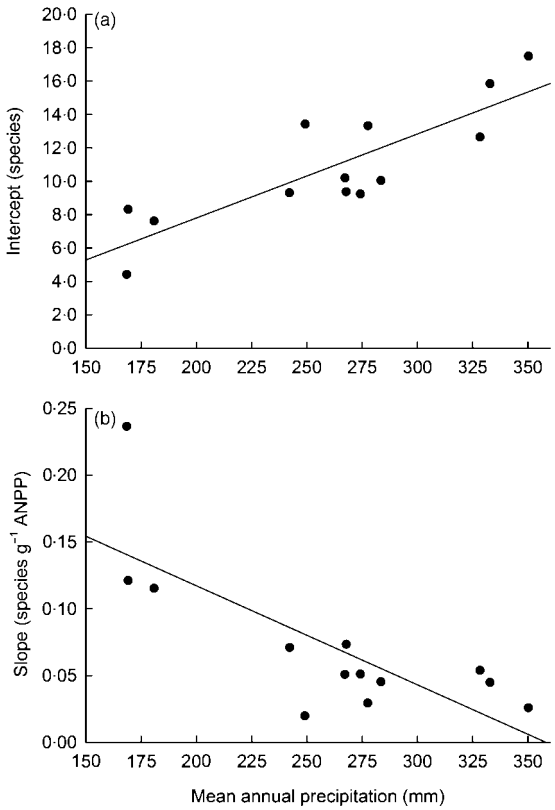


Fig. 6. Effects of precipitation on the relationship between productivity and species diversity at regional scale. a, The intercept of the linear regression model (species richness = a × productivity + b) was positively correlated with MAP across different association types. b, The slope was negatively correlated with MAP.

species richness ($F = 39{\cdot}47$, $R^2 = 0{\cdot}04$, $P < 0{\cdot}0001$) and 6% of variation in ANPP ($F = 53{\cdot}84$, $R^2 = 0{\cdot}06$, $P < 0{\cdot}0001$). For the linear regression model of PDR, the intercept increased linearly with MAP ($n = 13$, $F = 27{\cdot}28$, $R^2 = 0{\cdot}31$, $P = 0{\cdot}0003$; Fig. 6a), whereas the slope declined linearly with MAP ($n = 13$, $F = 14{\cdot}84$, $R^2 = 0{\cdot}57$, $P = 0{\cdot}0027$; Fig. 6b) across different association types along the precipitation gradient.

© 2007 The Authors. Journal compilation © 2007 British Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

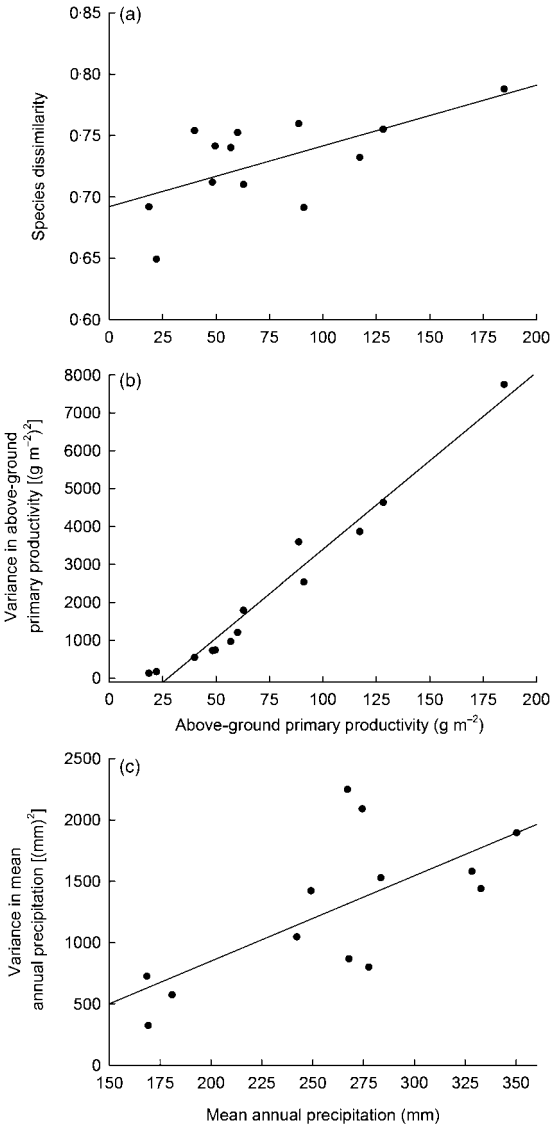


Fig. 7. Change in species dissimilarity and variability in precipitation and productivity at the regional scale. a, Species dissimilarity–productivity relationship, each point being the average of the dissimilarity estimates among all sites of the same association type; b, productivity variance–productivity relationship; c, precipitation variance–precipitation relationship.

EFFECTS OF ENVIRONMENTAL HETEROGENEITY ON SPECIES DISSIMILARITY

Our analysis showed that the dissimilarity in species composition, a measure of β-diversity, increased significantly with productivity across association types in the region (n = 13, R^2 = 0·43, F = 8·25, P = 0·0152; Fig. 7a). Species dissimilarity was highest in meadow steppe and lowest in desert. The variance in ANPP among sites within each association type increased with the mean ANPP for each association type (n = 13, R^2 = 0·97, F = 333·03, P < 0·0001; Fig. 7b). Similarly, the variance in MAP within each association type was correlated positive with the mean MAP for each association type (n = 13, R^2 = 0·47, F = 9·94, P = 0·0092; Fig. 7c).

Discussion

This study represents the first comprehensive test of the relationship between productivity and species richness from the Eurasian steppe. Our results have shown that the form of PDR in the Inner Mongolia grassland is predominantly positive linear at multiple organizational levels across local, landscape and regional scales. Although a statistically significant unimodal form was also found in a few cases, this relationship was apparently weak because only a few data points existed beyond the predicted peak value in the MOS test. This means that, within the range of the observed productivity in the Inner Mongolia grassland, a unimodal form of PDR is either a rare situation or an artefact of the statistical analysis. Our general conclusion on the dominance of a positive linear PDR was also corroborated by two recent studies using different and smaller data sets at local to regional scales (Bai *et al.* 2000; Ma & Fang 2006). Lavrenko *et al.* (1993) showed that, along a gradient from the meadow steppe of the Black Sea region to the extremely dry desert steppe of Mongolia, species richness decreased from 33–36 to 7–10 species per m^2, and ANPP declined from 320–420 to 6–30 g m^{-2}. Our re-analysis, after incorporating the most and least productive areas from Lavrenko *et al.* (1993) into our data set, again showed a positive linear PDR across different vegetation types (results not shown here), suggesting that the positive linear relationship may be dominant over the entire Eurasian steppe region.

This finding is in sharp contrast with the commonly held view that a hump-shaped form of PDR is predominant in terrestrial ecosystems of Europe, Africa and North America from local to continental scales (Waide *et al.* 1999; Mittelbach *et al.* 2001; Chalcraft *et al.* 2004; Jennings, Williams & Stromberg 2005). However, our results are congruent with the general conclusion of Gillman & Wright (2006), that a positive, rather than humped-shaped, relationship of PDR predominates terrestrial ecosystems. One may argue that the lack of a unimodal relationship in our analysis may be due to the limited range of productivity. However, our data set covered almost the full range of ANPP in the Eurasian steppe region, which is supported by much less precipitation (< 500 mm year^{-1}) than that in North American prairies (up to about 1000 mm year^{-1}).

Although our study has demonstrated the unequivocal dominance of a positive linear form of PDR in the Inner Mongolia Grassland, it does not exclude the existence of other forms in this region. Indeed, our results showed that the degree of predominance or exclusiveness of the positive linear form depended on organizational levels and spatial scales. For example, at higher levels of organization (vegetation type and biome) and broader scales (landscape and region), a positive linear form was observed consistently. At the level of association type or local spatial scale, cases in which productivity and diversity showed either no

© 2007 The Authors. Journal compilation © 2007 British Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

relationship or a unimodal relationship also existed. At an even finer scale of local plots, no consistent form of PDR was detected (Bai *et al.* unpublished results). Therefore, our results are not inconsistent with the hypothesis that the form of PDR varies with spatial scale and ecological hierarchy (Chase & Leibold 2002).

Ellis & Swift (1988) suggested that many semiarid and arid grassland ecosystems are non-equilibrium grazing systems, which is characterized by stochastic abiotic conditions (e.g. fluctuations in precipitation and perturbations of extended droughts), variable plant growing conditions and density-independent herbivore population patterns. Under these conditions, both above-ground net primary productivity and species richness are controlled primarily by abiotic factors, while interspecific competition and competitive exclusion should not be important regulatory processes of plant communities (Ellis & Swift 1988). This hypothesis seems to be corroborated by our results, that MAP alone explained 41% of the variation in ANPP and 25% of the variation in species richness across the region. At regional scale, we further evaluated how the slope and intercept in the linear regression model of PDR (species richness = a × productivity + b) were affected by precipitation across different association types. Our study indicated that the intercept increased linearly with MAP, suggesting that, for a given association, the higher local species richness is related to higher MAP. The slope, however, decreased linearly with MAP, which means that the relative importance of precipitation as a controlling variable on PDR also varies between associations. In general, plant associations in the driest sites showed the greatest slopes of PDR, and those in the wettest sites showed the lowest slopes. In the Inner Mongolia grassland region, MAP and total soil N exhibit a linearly increasing trend from desert to meadow steppe (Chinese Academy of Sciences Integrative Expedition Team to Inner Mongolia & Ningxia 1985; Inner Mongolia Soil Census Office & Inner Mongolia Soil and Fertilizer Service 1994). Our previous study also showed that both productivity and species richness were positively correlated to total soil N, which accounted for 44–57% of the variations at regional scale (Bai *et al.* 2000). This is because, in addition to water, both productivity and species richness in arid and semiarid grasslands are limited substantially by nitrogen (Vitousek & Howarth 1991). Thus, MAP and soil N might be the two most important environmental factors controlling productivity, species richness and consequently the regional-scale pattern of PDR in the Inner Mongolia grassland.

Spatial heterogeneity, the manifestation of intertwined patchiness and gradients, underlies many observed ecological patterns at different levels of organization and across a wide range of scales (Levin 1992; Wu & Levin 1994; Wu & Loucks 1995). While the theory of hump-shaped PDR focuses on the patchiness aspect of heterogeneity that tends to increase species diversity, our study suggests that the spatial gradient of environmental conditions (mainly precipitation) can dictate the pattern of PDR on the Eurasian continent. This does not mean that patchiness is not relevant to our observed pattern of PDR. In fact, our study indicated that species dissimilarity also increased with productivity across the region. Associations with low productivity shared more common species, whereas associations with high productivity shared only a small number of species. Chase & Leibold (2002) proposed that environmental heterogeneity is one of the three possible mechanisms leading to increased species dissimilarity with increasing productivity. Chalcraft *et al.* (2004) also showed that, in the arid and subhumid North American grasslands, increased species dissimilarity among local communities with greater productivity was the key mechanism determining the form of PDR at the regional scale. Our study showed that the variance in ANPP within each association type increased linearly with the average ANPP of association types at the regional scale. We also found a significantly positive relationship between the variance in MAP within each association type and the average MAP of association types across the region. Thus, local community-level patchiness, including both composition and configuration of microhabitats, may increase with productivity along the precipitation gradient.

Much of the Inner Mongolia grassland has been degraded due, primarily, to overgrazing (Jiang, Han & Wu 2006), and we hypothesized originally that the form of PDR might be affected by different land use practices. However, the results of our study showed otherwise, although grazing did decrease both ANPP and species richness. Reduced above-ground biomass and species richness by overgrazing in the Inner Mongolia Grassland had been documented in previous studies (e.g. Li 1988, 1993). Elsewhere, Milchunas *et al.* (1988) indicated that, in North American grasslands with a long history of grazing, plant diversity decreased linearly with increasing grazing intensity as grazing-intolerant rare species were eliminated. Milchunas & Lauenroth (1993) further examined 236 field sites world-wide and found that in most cases grazing negatively affected grassland ANPP.

Drylands occupy more than 50% of the Earth's land surface, and 54% of grasslands have been converted to managed grazing lands (Asner *et al.* 2004). Thus, our results have important implications for understanding the potential effects of climate change and improving the current practices of grassland management in a global context. First, alterations in regional precipitation pattern due to global climate change are likely to affect grassland productivity, species richness and their relationship. These changes may further influence ecosystem resilience in this region (Bai *et al.* 2004). Secondly, as the form of PDR does not seem sensitive to grazing, PDR is apparently a poor indicator of the overgrazing-induced ecosystem degradation that has occurred over vast areas across the Eurasian Steppe region. Instead, a measure of the reduction in species richness or productivity is related more directly to the

© 2007 The Authors. Journal compilation © 2007 British Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

actual ecosystem condition. Finally, because species diversity plays an important role in maintaining ecosystem resilience through compensatory interactions (Bai *et al*. 2004), grassland communities in dryer sites are not only species poor and less productive, but also more vulnerable to disturbances and slow to recover. To restore and maintain a high level of biodiversity and ecosystem functioning in this region, it is necessary to reduce the excessively high stocking rate at present to a moderate level in future. We have suggested elsewhere that, to achieve this goal, a landscape-level framework based on sustainability science must be developed to integrate ecological, economic and social dimensions in both research and management policies (Jiang, Han & Wu 2006; Wu 2006).

Acknowledgements

We thank S. L. Collins, S. Naeem and the anonymous referees for their helpful comments on our manuscript. We are also grateful to X. Bao, Y. S. Shi, Y. H. Xu, J. P. Luo, Z. H. Yan, X. Q. Duan and L. T. Song for their assistance in data collection. This research was supported by National Natural Science Foundation of China (30521002, 30330150 and 30670346), the State Key Basic Research Development Program of China (2007CB106800) and the US National Science Foundation (DEB-0618193).

References

Abrams, P.A. (1995) Monotonic or unimodal diversity productivity gradients: what does competition theory predict? *Ecology*, **76**, 2019–2027.

Al-Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. (1977) Quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology*, **65**, 759–791.

Anderson, T.M., McNaughton, S.J. & Ritchie, M.E. (2004) Scale-dependent relationships between the spatial distribution of a limiting resource and plant species diversity in an African grassland ecosystem. *Oecologia*, **139**, 277–287.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E. & Harris, A.T. (2004) Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources*, **29**, 261–299.

Baer, S.G., Blair, J.M., Collins, S.L. & Knapp, A.K. (2003) Soil resources regulate productivity and diversity in newly established tallgrass prairie. *Ecology*, **84**, 724–735.

Bai, Y.F., Han, X.G., Wu, J.G., Chen, Z.Z. & Li, L.H. (2004) Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, **431**, 181–184.

Bai, Y.F., Li, L.H., Wang, Q.B., Zhang, L.X., Zhang, Y. & Chen, Z.Z. (2000) Changes in plant species diversity and productivity along gradients of precipitation and elevation in the Xilin River Basin, Inner Mongolia. *Acta Phytoecologica Sinica*, **24**, 667–673.

Chalcraft, D.R., Williams, J.W., Smith, M.D. & Willig, M.R. (2004) Scale dependence in the species-richness–productivity relationship: the role of species turnover. *Ecology*, **85**, 2701–2708.

Chapin,F.S. III, Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. (2000) Consequences of changing biodiversity. *Nature*, **405**, 234–242.

Chase, J.M. & Leibold, M.A. (2002) Spatial scale dictates the productivity–biodiversity relationship. *Nature*, **416**, 427–430.

Chinese Academy of Sciences Integrative Expedition Team to Inner Mongolia and Ningxia (1985) *The Vegetation of Inner Mongolia*. Science Press, Beijing.

Collins, S.L. & Glenn, S.M. (1990) A hierarchical analysis of species abundance patterns in grassland vegetation. *American Naturalist*, **135**, 633–648.

Cornwell, W.K. & Grubb, P.J. (2003) Regional and local patterns in plant species richness with respect to resource availability. *Oikos*, **100**, 417–428.

Coupland, R.T. (ed.) (1992) *Ecosystems of the World 8A. Natural Grasslands: Introduction and Western Hemisphere*. Elsevier, Amsterdam.

Coupland, R.T. (ed.) (1993) *Ecosystems of the World 8B. Natural Grasslands: Eastern Hemisphere and Résumé*. Elsevier, Amsterdam.

Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist*, **137**, 27–49.

Ellis, J.E. & Swift, D.M. (1988) Stability of African pastoral ecosystems: alternate paradigms and implications for development. *Journal of Range Management*, **41**, 450–459.

Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1–25.

Fridley, J.D. (2002) Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia*, **132**, 271–277.

Fukami, T. & Morin, P.J. (2003) Productivity–biodiversity relationships depend on the history of community assembly. *Nature*, **424**, 423–426.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.

Gillman, L.N. & Wright, S.D. (2006) The influence of productivity on the species richness of plants: a critical assessment. *Ecology*, **87**, 1234–1243.

Grace, J.B. (1999) The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution and Systematics*, **2**, 1–28.

Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.

Gross, K.L., Willig, M.R., Gough, L., Inouye, R. & Cox, S.B. (2000) Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos*, **89**, 417–427.

Harrison, S., Davies, K.F., Safford, H.D. & Viers, J.H. (2006) Beta diversity and the scale-dependence of the productivity–diversity relationship: a test in the Californian serpentine flora. *Journal of Ecology*, **94**, 110–117.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hooper, D.U., Chapin, F.S. III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Huston, M.A. (1979) A general hypothesis of species diversity. *American Naturalist*, **113**, 81–101.

Inner Mongolia Soil Census Office & Inner Mongolia Soil and Fertilizer Service (1994) *The Soils of Inner Mongolia*. Science Press, Beijing.

Jennings, M.D., Williams, J.W. & Stromberg, M.R. (2005) Diversity and productivity of plant communities across the Inland Northwest, USA. *Oecologia*, **143**, 607–618.

© 2007 The Authors. Journal compilation © 2007 British Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Jiang, G.M., Han, X.G. & Wu, J.G. (2006) Restoration and management of the Inner Mongolia Grassland require a sustainable strategy. *AMBIO*, **35**, 269–270.

Lavrenko, E.M., Karamysheva, Z.V., Borisova, I.V., Popova, T.A., Guricheva, N.P. & Nikulina, R.I. (1993) Steppes of the former Soviet Union and Mongolia. *Ecosystems of the World 8B. Natural Grasslands: Eastern Hemisphere and Résumé* (ed. R.T. Coupland), pp. 3–55. Elsevier, Amsterdam.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.

Li, Y.H. (1988) The divergence and convergence of *Aneurolepidium chinense* steppe and *Stipa grandis* steppe under the grazing influence in Xilin river valley, Inner Mongolia. *Acta Phytoecologica et Geobotanica Sinica*, **12**, 189–196.

Li, Y.H. (1993) Grazing dynamics of the species diversity in *Aneurolepidium chinense* steppe and *Stipa grandis* steppe. *Acta Botanica Sinica*, **35**, 877–884.

Loreau, M., Naeem, S. & Inchausti, P. (eds) (2002) *Biodiversity and Ecosystem Functioning Synthesis and Perspectives*. Oxford University Press, Oxford.

Ma, W.H. & Fang, J.Y. (2006) The relationship between species richness and productivity in four typical grasslands of northern China. *Biodiversity Science*, **14**, 21–28.

Milchunas, D.G. & Lauenroth, W.K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327–366.

Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist*, **132**, 87–106.

Mitchell-Olds, T. & Shaw, R.G. (1987) Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution*, **41**, 1149–1161.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Goughh, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.

Mouquet, N., Moore, J.L. & Loreau, M. (2002) Plant species richness and community productivity: why the mechanism that promotes coexistence matters. *Ecology Letters*, **5**, 56–65.

Ninyerola, M., Pons, X. & Roure, J.M. (2000) A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. *International Journal of Climatology*, **20**, 1823–1841.

O'Connor, T.G. (2005) Influence of land use on plant community composition and diversity in Highland Sourveld grassland in the southern Drakensberg, South Africa. *Journal of Applied Ecology*, **42**, 975–988.

O'Neill, R.V., DeAngelis, D.L., Waide, J.B. & Allen, T.F.H. (1986) *A Hierarchical Concept of Ecosystems*. Princeton University Press, Princeton.

Oksanen, J. (1996) Is the humped relationship between species richness and biomass an artefact due to plot size? *Journal of Ecology*, **84**, 293–295.

Olff, H. & Ritchie, M.E. (1998) Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, **13**, 261–265.

Pickett, S.T.A., Wu, J. & Cadenasso, M.L. (1999) Patch dynamics and the ecology of disturbed ground. *Ecosystems of the World 16: Ecosystems of Disturbed Ground* (ed. L.R. Walker), pp. 707–722. Elsevier, Amsterdam.

Ritchie, M.E. & Olff, H. (1999) Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*, **400**, 557–560.

Rosenzweig, M.L. (1992) Species diversity gradients: we know more and less than we thought. *Journal of Mammalogy*, **73**, 715–730.

Rosenzweig, M.L. & Abramsky, Z. (1993) How are diversity and productivity related? *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds R.E. Ricklefs & D. Schluter), pp. 52–65. University of Chicago Press, Chicago.

Sala, O.E. & Austin, A.T. (2000) Methods of estimating aboveground net primary productivity. *Methods in Ecosystem Science* (eds O.E. Sala, R.B. Jackson, H.A. Mooney & R.W. Howarth), pp. 31–43. Springer, New York, USA.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Steiner, C.F. & Leibold, M.A. (2004) Cyclic assembly trajectories and scale-dependent productivity–diversity relationships. *Ecology*, **85**, 107–113.

Taylor, D.R., Aarssen, L.W. & Loehle, C. (1990) On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos*, **58**, 239–250.

Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455–1474.

Tilman, D. & Pacala, S. (1993) The maintenance of species richness in plant communities. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds R.E. Ricklefs & D. Schluter), pp. 13–25. University of Chicago Press, Chicago.

US National Research Council (1992) *Grasslands and Grassland Sciences in Northern China*. National Academy Press, Washington, DC.

Vitousek, P.M. & Howarth, R.W. (1991) Nitrogen limitation on land and in the sea: how can it occur. *Biogeochemistry*, **13**, 87–115.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257–300.

Weiher, E. (1999) The combined effects of scale and productivity on species richness. *Journal of Ecology*, **87**, 1005–1011.

Weiher, E. & Howe, A. (2003) Scale-dependence of environmental effects on species richness in oak savannas. *Journal of Vegetation Science*, **14**, 917–920.

Whittaker, R.J. & Heegaard, E. (2003) What is the observed relationship between species richness and productivity? [Comment]. *Ecology*, **84**, 3384–3390.

Worm, B., Lotze, H.K., Hillebrand, H. & Sommer, U. (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature*, **417**, 848–851.

Wu, J. (1999) Hierarchy and scaling: extrapolating information along a scaling ladder. *Canadian Journal of Remote Sensing*, **25**, 367–380.

Wu, J. (2006) Landscape ecology, cross-disciplinarity, and sustainability science. *Landscape Ecology*, **21**, 1–4.

Wu, J.G. & Levin, S.A. (1994) A spatial patch dynamic modeling approach to pattern and process in an annual grassland. *Ecological Monographs*, **64**, 447–464.

Wu, J. & Loucks, O.L. (1992) Xilingole grassland. *Grasslands and Grassland Sciences in Northern China* (ed. US National Research Council), pp. 67–84. National Academy Press, Washington, DC.

Wu, J. & Loucks, O.L. (1995) From balance-of-nature to hierarchical patch dynamics: a paradigm shift in ecology. *Quarterly Review of Biology*, **70**, 439–466.

Received 20 February 2007; final copy received 3 May 2007
Editor: Ron Freckleton

© 2007 The Authors. Journal compilation © 2007 British Ecological Society,

13652664, 2007, 5, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2664.2007.01351.x by Institute Of Botany, Wiley Online Library on [06/05/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

27. Roderick, G. K. & Navajas, M. Genes in new environments: genetics and evolution in biological control. *Nature Rev. Genet.* **4,** 889–899 (2003).
28. Macey, J. R., Larson, A., Ananjeva, N. B. & Papenfuss, T. J. Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. *J. Mol. Evol.* **44,** 660–674 (1997).
29. Huelsenbeck, J. P. & Ronquist, F. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17,** 754–755 (2001).
30. Nylander, J.A.A. MrModeltest v1.0b (Department of Systematic Zoology, Uppsala University, 2002).

Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank T. Campbell, D. Cardace, P. Colbert, K. de Queiroz, A. Echternacht, J. Gaskin, L. Harmon, J. Knouft, K. Kozak, R. Muller, G. Norval, S. Poe, R. Powell, V. Rivalta Gonzalez, A. Torres Barboza and A. Wright for advice and assistance, and the National Science Foundation and the Environmental Protection Agency Science to Achieve Results (STAR) program for funding.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to J.J.K. (kolbe@biology.wustl.edu).

Ecosystem stability and compensatory effects in the Inner Mongolia grassland

Yongfei Bai[1], Xingguo Han[1], Jianguo Wu[1,2], Zuozhong Chen[1] & Linghao Li[1]

[1]*Laboratory of Quantitative Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China*
[2]*Faculty of Ecology, Evolution and Environmental Science, School of Life Sciences, Arizona State University, Tempe, Arizona 85287-4501, USA*

Numerous studies have suggested that biodiversity reduces variability in ecosystem productivity through compensatory effects[1–6]; that is, a species increases in its abundance in response to the reduction of another in a fluctuating environment[1,7]. But this view has been challenged on several grounds[8–10]. Because most studies have been based on artificially constructed grasslands with short duration, long-term studies of natural ecosystems are needed. On the basis of a 24-year study of the Inner Mongolia grassland, here we present three key findings. First, that January–July precipitation is the primary climatic factor causing fluctuations in community biomass production; second, that ecosystem stability (conversely related to variability in community biomass production) increases progressively along the hierarchy of organizational levels (that is, from species to functional group to whole community); and finally, that the community-level stability seems to arise from compensatory interactions among major components at both species and functional group levels. From a hierarchical perspective, our results corroborate some previous findings of compensatory effects[1,4,7,11]. Undisturbed mature steppe ecosystems seem to culminate with high biodiversity, productivity and ecosystem stability concurrently. Because these relationships are correlational, further studies are necessary to verify the causation among these factors. Our study provides new insights for better management and restoration of the rapidly degrading Inner Mongolia grassland.

The role of compensatory interactions between species[6,7] has been a key issue in the debate concerning the diversity–stability relationship of an ecosystem. In particular, because different species respond to environmental fluctuations differently, the reduction in biomass of a certain species is more likely to be recompensed by the increased biomass of other species in a species-rich rather than species-poor community[1,4,6]. Such compensatory effects have been reported for both plant and animal communities[1,7,11–14]. However, others have argued that plant diversity has no consistent effect, or even a negative effect, on biomass production and ecosystem stability[10,15,16]. Undoubtedly, ecosystem stability depends not only on community composition but also on disturbance, nutrient supply and climatic conditions[3,4,9,13,15,17], and long-term studies of natural ecosystems are needed for better understanding of compensatory effects and thus the diversity–stability relationship.

Here we present the results of a long-term (1980–2003) study of two natural steppe communities in the Inner Mongolia grassland. The first (site A) is a rhizome-grass-dominated community, and the second (site B) is a bunchgrass-dominated community (see Methods). We classified species into the following five plant functional groups (PFGs) primarily on the basis of life forms: perennial rhizome grass (PR), perennial bunchgrasses (PB), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals and biennials (AB). PFGs also differ in plant stature, rooting depth, root-to-shoot ratio, water use efficiency, nutrient use efficiency and C:N:P stoichiometry[18–21] (Supplementary Information). Our study addresses the following three questions: first, what are the most important climatic drivers for the aboveground biomass production of steppe communities? Second, how does biomass production respond to precipitation fluctuations at different levels of organization (that is, at the species, plant functional group and community level)? And third, are there detectable compensatory effects reducing the variability in biomass production and thus increasing ecosystem stability?

To address the first question, we used multiple regressions to examine how the aboveground community biomass (B_{comm}) was related to several climatic variables: precipitation (annual, January–July, January–August and May–August); cumulative temperature (°C), that is, the accumulated excess when temperature exceeded 0 °C (January–July and January–August), 5 °C (annual) and 10 °C

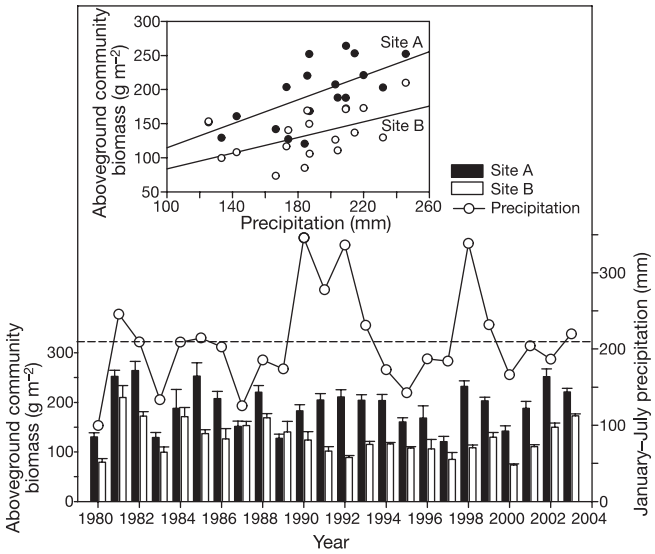


Figure 1 The relationship between January–July precipitation and total community aboveground biomass (B_{comm}) for the *Leymus chinensis* (site A) and *Stipa grandis* (site B) steppe ecosystems of the Inner Mongolia grassland, using data from 1980 to 2003. Bottom panel: B_{comm} was positively correlated to January–July precipitation in site A ($r^2 = 0.25$, $P = 0.01$), but not in site B ($r^2 = 0.003$, $P = 0.81$; $n = 24$). Error bars represent s.e.m., and the horizontal dashed line is the mean January–July precipitation from 1980 to 2003. Top panel: a significant positive correlation was found between B_{comm} and January–July precipitation in both sites after removing the four extraordinarily wet years (1990, 1991, 1992 and1998). For site A (black dots) $r^2 = 0.49$, $P < 0.001$, $n = 19$; for site B (open circles) $r^2 = 0.35$, $P < 0.01$, $n = 19$.

©2004 Nature Publishing Group

(annual); and the number of days on which temperature-dependent plant growth occurred (≥5 °C growing degree days and ≥10 °C growing degree days). For site A, only January–July precipitation remained as a significant variable in simplified multiple regressions obtained by backward elimination ($r^2 = 0.25$, $P < 0.01$), whereas no significant variable was found for site B. This lack of statistical significance was due mainly to the influence of four extraordinarily wet years (1990, 1991, 1992 and 1998) to which community biomass did not respond proportionately (Fig. 1). When these four years were excluded, January–July precipitation became a highly significant variable for both site A ($r^2 = 0.49$, $P < 0.001$) and site B ($r^2 = 0.35$, $P < 0.01$), and was highly correlated with B_{comm} (Fig. 1). January–July precipitation alone explained 35–49% of the variation in biomass for the two sites.

To address the second question, we compared the coefficient of variation in biomass at the levels of individual species ($CV_{sp.}$), plant functional group (CV_{PFG}) and the whole community (CV_{comm}) (Fig. 2). We calculated $CV_{sp.}$ for 22 commonly found species in site A and 16 in site B, and the values ranged from 53.56% to 259.06% for site A and from 55.12% to 260.17% for site B. In both sites, species with higher relative biomass tended to have lower $CV_{sp.}$ (Fig. 2a). The coefficient of variation in aboveground biomass varied significantly among certain PFGs in both sites ($F = 38.51$, $P < 0.0001$ for site A; $F = 23.28$, $P < 0.0001$ for site B). Specifically, the values of CV_{PFG} were significantly different among PR, SS and AB ($P < 0.01$) in site A and among PB, PR and AB in site B (Fig. 2b). CV_{PFG} was negatively related to the relative biomass of PFGs (B_{rel}) in both site A ($CV_{PFG} = -2.77B_{rel} + 159.34$; $r^2 = 0.44$, $P < 0.001$) and site B ($CV_{PFG} = -2.03B_{rel} + 157.7$; $r^2 = 0.45$, $P < 0.001$).

At the community level, the aboveground biomass (B_{comm}) was significantly different between the two sites over the 24-yr period ($F = 112.99$, $P < 0.0001$, $n = 120$). The average B_{comm} was 192.51 g m^{-2} (s.e.m. = 13.92, $n = 5$) for site A and 127.04 g m^{-2} (s.e.m. = 10.14, $n = 5$) for site B. However, the coefficient of variation in B_{comm} was not significantly different between the two sites ($CV_{comm} = 27.06\%$ for site A and 31.92% for site B; $P > 0.05$). The values of CV_{comm} for these Inner Mongolia steppes are comparable to those for the North America grasslands (25–35%)[22,23], but much lower than those for semi-arid African grasslands (60–70%)[24]. Ecosystem stability, measured as the coefficient of variation in aboveground biomass[4,10], increased systematically from the species to the PFG to the community level (that is, $CV_{sp.} > CV_{PFG} > CV_{comm}$) for both site A ($F = 16.09$, $P < 0.0001$) and site B ($F = 13.71$, $P < 0.001$) (Fig. 2c). Such 'metastability' has been widely observed in complex hierarchical systems whose apparent stability hinges on the more transient dynamics of their components[25,26].

Were compensatory effects responsible for the increased stability at the community level? To address this question, we assumed that if an ecosystem in a changing environment had compensatory mechanisms, at least some of its major components (species or PFGs) would show negative correlations in terms of biomass production over time. At the species level, correlation analyses for 231 species pairs in site A and 120 pairs in site B showed that a negative correlation existed for 10 pairs in site A and 15 pairs in site B, whereas a positive correlation was found for 19 pairs in site A and 24 pairs in site B (Supplementary Information). Importantly, the negative correlation existed between dominant and sub-dominant species as well as between dominant and non-dominant species at both sites. In contrast, the positive correlation was found mainly between sub-dominant and non-dominant species or between non-

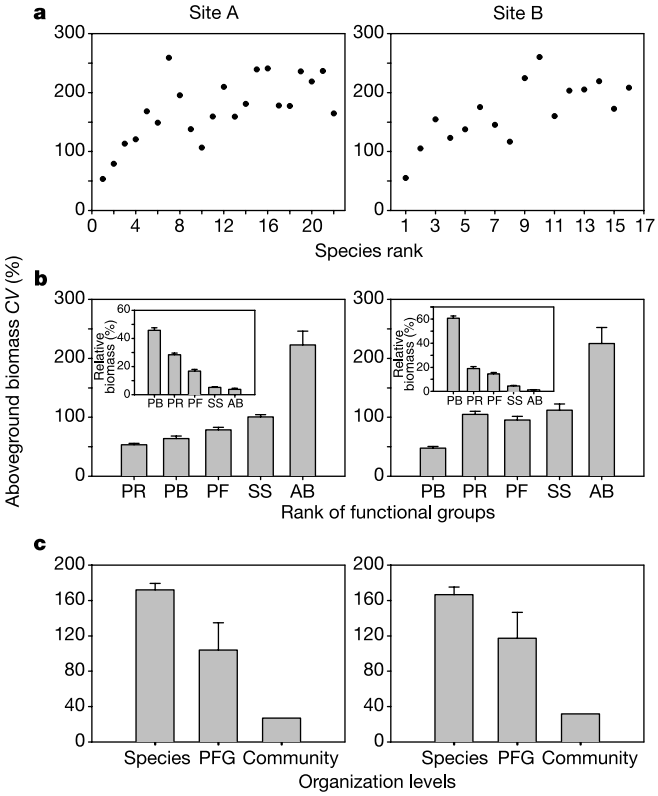


Figure 2 Coefficients of variation (*CV*s) in aboveground biomass at different organizational levels in the two study sites. **a**, Scatter-plots of species-level *CV*s against relative biomass-based species rank in which only common species were included. **b**, Relationship between *CV*s of plant functional groups (PFGs) and relative biomass-based ranks of PFGs, with insets showing the average relative biomass values of PFGs in descending order. PR, perennial rhizome grass; PB, perennial bunchgrasses; PF, perennial forbs; SS, shrubs and semi-shrubs; and AB, annuals and biennials. **c**, Comparison of average *CV*s at the species, PFG and community levels (means differ significantly at $P < 0.0001$ in both sites). Error bars in **b** and **c** represent s.e.m.

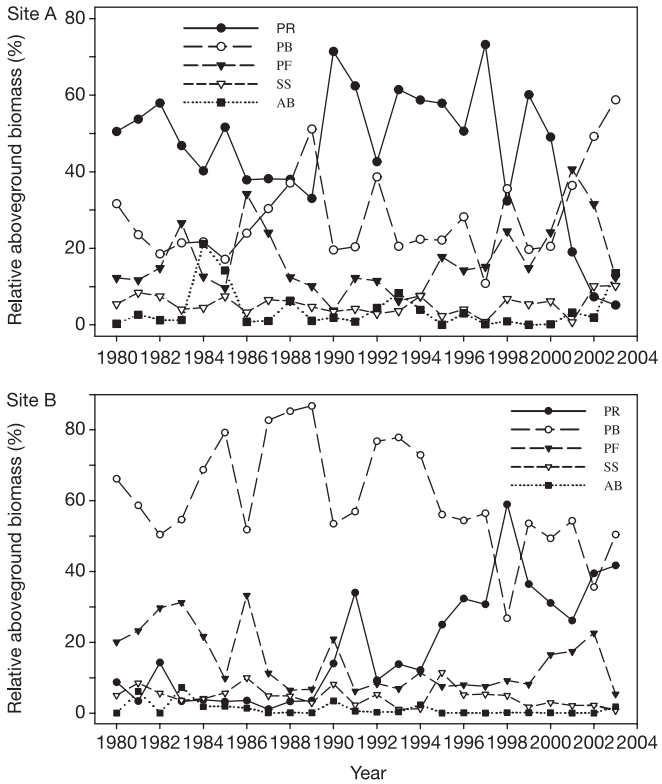


Figure 3 Time series of the relative aboveground biomass of plant functional groups from 1980 to 2003. Abbreviations are as in Fig. 2.

©2004 Nature Publishing Group

Table 1 **Correlation coefficients* between plant functional groups in terms of aboveground biomass**

Plant functional groups†	Site A		Site B	
	Correlation coefficient (*r*)	*P*	Correlation coefficient (*r*)	*P*
PR vs PB	−0.2673	0.0032	−0.4843	<0.0001
PR vs PF	−0.3019	0.0008	−0.3312	0.0002
PR vs SS	0.1648	0.0721	−0.2989	0.0010
PR vs AB	0.1616	0.0778	−0.3189	0.0004
PB vs PF	0.1297	0.1580	0.0747	0.4197
PB vs SS	0.2302	0.0114	0.2516	0.0058
PB vs AB	0.2668	0.0032	0.3001	0.0009
PF vs SS	0.0690	0.4537	0.0770	0.4050
PF vs AB	−0.2452	0.0069	0.2812	0.0020
SS vs AB	0.2233	0.0142	0.1587	0.0848

*Spearman's rank correlation coefficients.
†PR, perennial rhizome grass; PB, perennial bunchgrasses; PF, perennial forbs; SS, shrubs and semi-shrubs; and AB, annuals and biennials.

dominant species themselves. A similar trend was found at the PFG level. In site A, a negative correlation existed between PR and PB, between PR and PF, and between PF and AB, whereas a significant positive correlation was found between PB and SS, between PB and AB, and between SS and AB (Table 1). In site B, there was a significant negative correlation between PR and PB, PR and PF, PR and SS, and PR and AB, and a significant positive correlation between PB and SS, PB and AB, and PF and AB (Table 1 and Supplementary Information).

The observation that certain PFGs and species were negatively correlated suggests that compensatory effects may take place at both levels, but primarily among dominant components (that is, species and PFGs with high relative biomass). For example, the perennial rhizome grass, *Leymus chinensis*, alone made up 44.85% of B_{comm} in site A, and perennial bunchgrasses made up 61.6% of B_{comm} in site B (Fig. 3). Positive correlations at the species and PFG levels, a possible indication of the existence of complementary effects[4,6], could increase temporal ecosystem variation. Most species pairs (87.4% in site A and 67.5% in site B) did not show any statistically significant correlations in terms of biomass production. This may imply that at the species level a statistical averaging effect might have been operating. But because of the small relative biomass of the species or the PFGs involved (Fig. 3), these effects did not seem significant. The stabilizing effects of the compensatory interactions were also corroborated by the relatively high drought resistance and resilience of these steppe communities. The average value of drought resistance ($(B_{\mathrm{drought}} - B_{\mathrm{pre\text{-}drought}})/B_{\mathrm{pre\text{-}drought}}$) for five significantly drier years (1980, 1983, 1987, 1995 and 2000 when January–July precipitation was 50–80% of the mean) was −0.27 for site A and −0.22 for site B. These values were higher than those for species-rich (≥11 species) experimental grassland plots in North America (about −0.35)[11]. The average values of ecosystem resilience ($B_{\mathrm{post\text{-}drought}}/B_{\mathrm{pre\text{-}drought}}$) for the five dry years were 1.19 for site A and 1.22 for site B, slightly higher than those for species-rich experimental grassland plots in North America (about 1.1)[11].

On the basis of a short-term (3 yr) field manipulative drought experiment with artificial grassland plots, it has been suggested that there is a potential trade-off between ecosystem production and stability with increasing species richness[10]. Our results indicate that plant communities in the Inner Mongolia grassland achieve high species richness, productivity and ecosystem stability simultaneously at the late successional stage[18,27,28] (Supplementary Information). These findings shed new light on the effects of precipitation fluctuations on the structure and functioning of the steppe ecosystems, and have important implications for understanding future impacts of climate change, and improving current grassland management practices. For example, as the precipitation regime and dry period pattern are altered, a shift in dominance of species and functional groups may occur. For restoring the vast areas of degraded grasslands in Inner Mongolia[29], it is important to establish and maintain grassland communities with a high diversity of dominant species and functional groups, such that compensatory mechanisms can enhance long-term ecosystem productivity and stability in the face of eternal climatic fluctuations (Supplementary Information). □

Methods

Study sites and field sampling

The two study sites, each 500 m by 500 m, are the permanent field sites of the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), located in the Xilin River Basin, Inner Mongolia Autonomous Region, China (116°42′ E, 43°38′ N) and administered by the Institute of Botany, the Chinese Academy of Sciences, Beijing. The growing season in the Inner Mongolia grassland runs from early April to late September for perennial plant species, whereas annual plants usually germinate in early July following the rains. Site A was dominated by a perennial rhizome grass, *Leymus chinensis*, whereas site B was dominated by a perennial bunchgrass, *Stipa grandis*. These two community types represent the most widely distributed grassland communities in the Eurasia steppe region[18,27,28,30], which is the largest contiguous grassland area in the world. Both sites have been fenced-off since 1979, preventing grazing by large animals. At the time of enclosure, both sites were considered to be in excellent condition, representative of undisturbed, climax steppe communities[28,30]. In 1980, site A and site B had 86 and 61 vascular plant species, respectively, and neither of them changed in species richness over the 24-yr period.

At each site, an east–west transect of 200 × 100 m was established with five equal-sized replicate blocks (40 × 100 m each). Aboveground biomass was sampled during 28–30 August each year by clipping all plants within a 1 × 1 m^2 quadrat that was randomly located within each block. All living vascular plants were sorted into species, dried and weighed. The dry mass of all plant species per quadrat averaged over the five blocks was used to estimate the aboveground community biomass. Because the standing crop of these steppe communities reached the annual peak at the end of August, our estimated community biomass approximated the aboveground net primary productivity of these ecosystems. All meteorological data were obtained from the weather stations of IMGERS.

Data analysis

Statistical analyses were performed using SAS version 8.0. Analysis of variance (ANOVA) and general linear models were used for analysis of variance. The coefficient of variation was calculated as: $CV =$ (standard deviation/mean) × 100. Spearman's rank correlation was used to analyse possible correlations among species and PFGs in terms of their aboveground biomass. Multiple regressions and backwards elimination were used to determine the effects of climatic variables on the total community biomass. At the species level, only commonly found species (that is, those present in at least 17 out of the 24 years) were considered. The biomass of the rare species excluded from the analysis was deemed trivial in relation to the total community biomass.

Received 16 May; accepted 13 July 2004; doi:10.1038/nature02850.

1. Naeem, S. & Li, S. Biodiversity enhances ecosystem reliability. *Nature* **390,** 507–509 (1997).
2. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. USA* **96,** 1463–1468 (1999).
3. Tilman, D. *et al.* The influence of functional diversity and composition on ecosystem processes. *Science* **277,** 1300–1302 (1997).
4. Tilman, D. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80,** 1455–1474 (1999).
5. Loreau, M. Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Natl Acad. Sci. USA* **95,** 5632–5636 (1998).
6. Loreau, M. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91,** 3–17 (2000).
7. McNaughton, S. J. Diversity and stability of ecological communities: A comment on the role of empiricism in ecology. *Am. Nat.* **111,** 515–525 (1977).
8. Givnish, T. J. Does diversity beget stability? *Nature* **371,** 113–114 (1994).
9. Huston, M. A. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110,** 449–460 (1997).
10. Pfisterer, A. B. & Schmid, B. Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature* **416,** 84–86 (2002).
11. Tilman, D. & Downing, J. A. Biodiversity and stability in grasslands. *Nature* **367,** 363–365 (1994).

©2004 Nature Publishing Group

12. Brown, J. H., Whitham, T. G., Ernest, S. K. M. & Gehring, C. A. Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science* **293,** 643–650 (2001).
13. Wardle, D. A., Bonner, K. I. & Barker, G. M. Stability of ecosystem properties in response to aboveground functional group richness and composition. *Oikos* **89,** 11–23 (2000).
14. McNaughton, S. J. Ecology of a grazing ecosystem: The Serengeti. *Ecol. Monogr.* **55,** 259–294 (1985).
15. McCann, K. S. The diversity–stability debate. *Nature* **405,** 228–233 (2000).
16. Huston, M. A. *et al.* No consistent effect of plant diversity on productivity. *Science* **289,** 1255 (2000).
17. Hooper, D. U. & Vitousek, P. M. The effects of plant composition and diversity on ecosystem processes. *Science* **277,** 1302–1305 (1997).
18. Chen, Z. Z. & Wang, S. P. *Typical Steppe Ecosystems of China* (Science, Beijing, 2000).
19. Chen, S. H., Zhang, H., Wang, L. Q., Zhanbula & Zhao, M. L. *Root Systems of Grassland Plants in Northern China* (Jilin Univ. Press, Chuangchun, 2001).
20. Inner Mongolia Grassland Ecosystem Research Station, Chen, Z. Z., Huang, D. H. & Zhang, H. F. *Research on Grassland Ecosystems* No. 1 112–131 (Science, Beijing, 1985).
21. Bai, Y. F. Influence of seasonal distribution of precipitation on primary productivity of *Stipa krylovii* community. *Acta Phytoecol. Sin.* **23,** 155–160 (1999).
22. Knapp, A. K. & Smith, M. D. Variation among biomes in temporal dynamics of aboveground primary production. *Science* **291,** 481–484 (2001).
23. Knapp, A. K. *et al.* Rainfall variability, carbon cycling and plant species diversity in a mesic grassland. *Science* **298,** 2202–2205 (2002).
24. O'Connor, T. G., Haines, L. M. & Snyman, H. A. Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *J. Ecol.* **89,** 850–860 (2001).
25. Wu, J. & Levin, S. A. A spatial patch dynamic modeling approach to pattern and process in an annual grassland. *Ecol. Monogr.* **64,** 447–464 (1994).
26. Wu, J. & Loucks, O. L. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q. Rev. Biol.* **70,** 439–466 (1995).
27. Inner Mongolia Grassland Ecosystem Research Station, Li, B., Yong, S. P. & Li, Z. H. *Research on Grassland Ecosystem* No. 3 84–183 (Science, Beijing, 1988).
28. US National Research Council, Wu, J. & Loucks, O. L. *Grasslands and Grassland Sciences in Northern China* 67–84 (National Academy Press, Washington DC, 1992).
29. Tong, C., Wu, J., Yong, S. P., Yang, J. R. & Yong, W. Y. A landscape-scale assessment of steppe degradation in the Xilin River Basin, Inner Mongolia, China. *J. Arid Environ.* **59,** 133–149 (2004).
30. Inner Mongolia Grassland Ecosystem Research Station & Jiang, S. *Research on Grassland Ecosystem* No. 1 1–11 (Science, Beijing, 1985).

Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank D. Huang, Y. Li, Q. Pan, Q. Qi, S. Wang, Yanfen Wang, Yifeng Wang, Z. Yang and others for their contributions to the long-term data collection at IMGERS. This project was supported by the State Key Basic Research and Development Plan of China, the Natural Science Foundation of China and the Knowledge Innovation Program of the Chinese Academy of Sciences.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to J.W. (Jingle.Wu@asu.edu).

Epigenetic regulation of translation reveals hidden genetic variation to produce complex traits

Heather L. True*, Ilana Berlin & Susan L. Lindquist

Whitehead Institute for Biomedical Research, Cambridge, Massachusetts 02142, USA

* Present address: Washington University Medical School, Department of Cell Biology and Physiology, St Louis, Missouri 63130, USA

Phenotypic plasticity and the exposure of hidden genetic variation both affect the survival and evolution of new traits[1–3], but their contributing molecular mechanisms are largely unknown. A single factor, the yeast prion [*PSI*$^+$], may exert a profound effect on both[4]. [*PSI*$^+$] is a conserved, protein-based genetic element that is formed by a change in the conformation and function of the translation termination factor Sup35p[5], and is transmitted from mother to progeny. Curing cells of [*PSI*$^+$] alters their survival in different growth conditions and produces a spectrum of phenotypes in different genetic backgrounds[4]. Here we show, by examining three plausible explanations for this phenotypic diversity, that all traits tested involved [*PSI*$^+$]-mediated read-through of nonsense codons. Notably, the phenotypes analysed were genetically complex, and genetic re-assortment frequently converted [*PSI*$^+$]-dependent phenotypes to stable traits that persisted in the absence of [*PSI*$^+$]. Thus, [*PSI*$^+$] provides a temporary survival advantage under diverse conditions, increasing the likelihood that new traits will become fixed by subsequent genetic change. As an epigenetic mechanism that globally affects the relationship between genotype and phenotype, [*PSI*$^+$] expands the conceptual framework for phenotypic plasticity, provides a one-step mechanism for the acquisition of complex traits and affords a route to the genetic assimilation of initially transient epigenetic traits.

There are three possible explanations for the diversity of phenotypes that are produced when different [*PSI*$^+$] strains are cured of the prion by growth on guanidine hydrochloride (GdHCl)[4]. Firstly, several yeast prions have now been identified[5] (and others probably exist)[6,7], each with different potential biological consequences. As growth on GdHCl cures all known naturally occurring prions in *Saccharomyces cerevisiae*, the diverse phenotypes we observed may have arisen from eliminating different combinations of prions present in different strains. Secondly, the reduction in translation–termination activity that is associated with [*PSI*$^+$] may cause ribosomes to read through naturally occurring stop codons[8–10]. This could alter message stability and/or promote the translation of sequences that are prone to accumulating genetic variation, such as pseudogenes and 3′ untranslated regions (see Supplementary Data and Supplementary Fig. 1). Thirdly, [*PSI*$^+$] prion formation is accompanied by protein aggregation. Therefore, the acquisition and removal of such aggregates could have diverse effects on protein homeostasis and produce distinct phenotypes in different strains[11].

We systematically tested these hypotheses by creating three sets of strain derivatives in several different genetic backgrounds that uncoupled the effects of other prions (set one), translational read-through (set two) and protein aggregation (set three) (Supplementary Table 1). For set one, prions were cured by two different general methods that should eliminate most, if not all, prions (growth on GdHCl and deletion of Hsp104; ref. 5) or by two highly selective methods (mutating the prion-determining domain of the *SUP35* gene (NM) to eliminate [*PSI*$^+$][12,13] and deleting the *RNQ1* gene to eliminate the other known prion present in some of the strains, [*RNQ*$^+$][14]). For set two, we recreated the effects of translational read-through in cells that did not contain the prion ([*psi*$^-$]) either by introducing partial loss-of-function mutations into *SUP35*[15,16] or by introducing mutations that alter the stability of messenger RNAs containing nonsense codons (Δ*upf1*, Δ*ski7*)[17,18]. For set three, prion-like aggregates were recreated in a strain immune to their effects on translation termination. The strains were selectively cured of [*PSI*$^+$] by chromosomal deletion of the prion-forming domain (*sup35*$^{\Delta NM}$) and NM–green fluorescent protein (GFP) was expressed from a strong promoter. We also created other strains that retained Sup35p prion aggregates but had efficient translation termination. This was accomplished by introducing a form of Sup35p that is immune to capture by [*PSI*$^+$] aggregates (extra-chromosomal expression of *sup35C* (without NM)[12] or antisuppressor (ASU) *sup35* variants)[19].

The majority of the phenotypes tested proved to be a simple and direct consequence of [*PSI*$^+$]-mediated nonsense suppression (Table 1; Fig. 1; Supplementary Fig. 2; and data not shown). For example, resistance to 3 mM paraquat was greater in the [*PSI*$^+$] derivative of strain 5V-H19 than in the [*psi*$^-$] derivative (Fig. 1, centre). The [*psi*$^-$] cells acquired resistance to paraquat in the absence of the prion when wild-type *SUP35* was replaced with a mutant that enhanced nonsense suppression (*sup35*^{C653R}). [*PSI*$^+$] cells lost paraquat resistance when [*PSI*$^+$] was selectively cured by deleting the prion-forming domain (ΔNM). Reducing nonsense

©2004 Nature Publishing Group

科学通报 2023 年 第 68 卷 第 11 期: 1330 ~ 1342
京津风沙源区沙化土地治理与生态修复专题 论 文
《中国科学》杂志社 SCIENCE CHINA PRESS

中国北方草地植物补偿性生长与合理放牧强度: 基于放牧实验的整合分析

宋伟江[1,2†], 苏纪帅[2†], 张梦迪[1,2], 赵玉金[2], 王忠武[1], 贾玉山[1*], 白永飞[2,3*]

1. 内蒙古农业大学草原与资源环境学院, 农业农村部饲草栽培、加工与高效利用重点实验室, 草地资源教育部重点实验室, 呼和浩特 010011;
2. 中国科学院植物研究所, 植被与环境变化国家重点实验室, 北京 100093;
3. 中国科学院大学资源与环境学院, 北京 100049
† 同等贡献
* 联系人, E-mail: jys_nm@sina.com; yfbai@ibcas.ac.cn

2022-10-31 收稿, 2022-12-23 修回, 2022-12-26 接受, 2022-12-27 网络版发表
国家自然科学基金重大项目(32192464)和中国科学院野外站联盟项目(KFJ-SW-YW037)资助

摘要 补偿性生长是草地植物对动物采食的一种适应策略, 合理的放牧强度能够促进植物的补偿性生长, 有利于草地生产力和稳定性的维持, 而长期过度放牧则导致草地退化. 因此, 确定合理的放牧强度是科学配置草地生产-生态功能实现草牧业可持续发展的基础. 本文基于各类放牧实验已发表的118篇研究文献, 将放牧家畜的采食率(地上生物量移除量, %)作为放牧强度的测度指标, 对我国北方5种主要草地类型的植物补偿生长特征及其合理放牧强度进行了整合分析, 并结合气候、土壤及植物群落地下生物量和多样性等数据, 厘清了影响植物补偿生长的关键生物和非生物因子. 结果表明, 我国北方草地植物总体处于欠补偿生长状态, 且植物地上部分的补偿性生长主要以牺牲其地下生物量为代价. 其中, 高寒草甸、草甸草原和荒漠草原植物群落均表现为欠补偿生长, 高寒草原和典型草原植物群落表现为等补偿生长. 在区域尺度上, 补偿性生长的绝对值随年降水量和植物物种丰富度的增加而增加. 满足植物群落地上生物量实现等补偿或超补偿, 且对地下生物量不产生负效应, 各类草地的合理利用强度为: 高寒草甸50%、草甸草原48%、典型草原40%、高寒草原37%、荒漠草原31%. 本研究对指导我国北方草地保护与合理利用, 以及退化草地恢复具有重要的理论和实践意义.

关键词 植物补偿性生长, 采食率, 放牧强度, 地下生物量, 生态-生产功能合理配置

草地是全球最大的陆地生态系统, 总面积为 5.25×10^9 hm^2, 约占全球陆地总面积的40.5%(不包括格陵兰岛和南极)[1]. 我国拥有草地近4×10^8 hm^2, 占国土总面积的41.7%[2]. 其中, 北方草地面积为3.1×10^8 hm^2, 占全国草地面积的3/4左右, 构成了我国天然草地的主体和北方重要生态安全屏障, 是欧亚大陆草原的重要组成部分[3,4]. 北方草地分布在新疆、西藏、青海、内蒙古、甘肃、宁夏、四川、陕西、山西、河北、黑龙江、吉林和辽宁13个省份, 覆盖中国11个重点牧区[4]. 长期以来, 草地生态系统不仅为畜牧业生产提供了优质饲草, 还具有调节气候、维持生物多样性、碳固存、防风固沙、涵养水源等重要生态功能[4~6]. 然而, 草地对气候变化和人类干扰, 特别是过度放牧十分敏感[7]. 放牧是天然草地最直接的利用方式, 大量研究表明, 长期过度放牧严重破坏了植物群落和土壤结构, 降低了植被覆盖度、草群高度、生物多样性和初级生产

引用格式: 宋伟江, 苏纪帅, 张梦迪, 等. 中国北方草地植物补偿性生长与合理放牧强度: 基于放牧实验的整合分析. 科学通报, 2023, 68: 1330–1342
Song W J, Su J S, Zhang M D, et al. Plant compensatory growth and optimal grazing intensity of grasslands in northern China: A meta-analysis of grazing experiments (in Chinese). Chin Sci Bull, 2023, 68: 1330–1342, doi: 10.1360/TB-2022-0967

© 2022《中国科学》杂志社

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

力, 进而导致生态系统结构和功能的退化[8,9]. 受过度放牧和气候变化(如气温升高、干旱、降水波动)的共同影响, 我国90%左右的草地发生了不同程度退化, 使草地的生产功能、生态功能和生态系统稳定性降低, 并对我国北方的生态安全构成严重威胁[10]. 因此, 在气候变化的背景下, 确定不同草地类型的适宜放牧强度, 即持续维持草地生态系统生产功能和生态功能协同的最大放牧利用强度, 对科学配置草地生产-生态功能, 恢复退化草地, 减缓气候变化的负面影响, 提升草地生态系统服务, 保障我国的生态安全具有重要意义.

补偿生长(compensatory growth)是植物为保障其生长、生存和繁殖对外界干扰(放牧等)做出的适应策略[11,12]. 从本质上讲, 补偿生长是植物通过叶片光合作用快速积累有机物引起的代谢效应, 即植物受到家畜或动物采食、践踏等干扰后, 改变其生物量和资源分配, 使植物产生更多的新叶, 恢复其光合能力, 从而降低干扰对其生长和繁殖的影响. 根据补偿生长效果可分为欠补偿、等补偿和超补偿[13~15]. 植物被采食后的生长量是衡量其对放牧适应的重要指标, 可作为判断植物是否具有补偿性生长的依据[12]. 放牧既能降低植物的生长速率, 也能促进其生长, 植物在被采食后具体表现出哪种补偿性生长方式, 取决于放牧对其抑制和促进作用的净效应[12]. Orians等人[16]研究表明, 植物受到持续过度采食胁迫时, 通过改变自身原有资源的分配方式, 将更多的光合产物积累于地下部分, 以提高自身生存能力. 而另外一些研究则发现, 放牧降低地上生物量的同时也将引起地下根系的减少[17]. 放牧优化假说认为, 经过优化的管理方式和放牧强度可以增加草地净初级生产力, 使之高于未放牧草地的初级生产力, 表现出超补偿生长[18,19]. 然而, 草地植物往往是通过减少对地下组织的资源分配来实现其地上部分的补偿性生长[14]. 因此, 揭示草地植物补偿生长(包括地上和地下部分)与放牧强度之间的协同和权衡关系与机制是合理配置草地生产-生态功能的科学基础, 可为草地合理利用提供重要的理论支撑.

草地植物补偿性生长的大小和方向受草地类型、降水、温度和土壤肥力等因素的影响. 不同草地生态系统植物群落对环境干扰的适应能力不同, 其生长状况也存在差异[20]. 降水、温度和土壤肥力通过影响植物生长和生物量分配, 影响生态系统初级生产力[21,22]. 我国北方大部分草地存在水分和养分限制, 这使得草地初级生产力对放牧干扰和降水变化更为敏感[23,24]. 一些研究表明, 肥沃的土壤和湿润的气候环境有利于植物发生超补偿生长, 且这种影响在干旱和半干旱区尤其显著[7,25]. 增温对不同草地类型的植物生长产生抑制作用[20]或促进作用[26], 且高寒草原更容易受到增温的影响[27]. 例如, Wang等人[28]通过对高寒草地35年的观测研究发现, 气候变暖缓解了低温对植物生长的限制作用, 促进了植物生长[29]. 此外, 生物多样性对初级生产力的影响同环境因素的影响同等重要[30]. 国内外经典研究认为, 草地生物量先随物种丰富度的增加而增加, 当地上生物量积累到一定程度时, 反而会降低物种丰富度, 两者之间的关系表现出单峰模式[22]. 然而, 许多研究发现, 在外界干扰情况下, 生产力与多样性二者呈正相关[30]、负相关[31]或无明显关系[32], 且在不同群落类型间存在差异[33]. 因此, 厘清植物补偿效应在多大程度上受生物多样性和环境因子影响, 是确定合理放牧强度, 实现草地资源保护与科学利用的基础.

目前, 我国尚缺乏不同草地类型植物补偿生长与放牧强度之间关系的定量研究. 同时, 由于不同草地类型的放牧家畜承载力存在差异, 而现有研究文献中多基于单位面积放牧家畜数量表征放牧强度的大小, 该数值在国家和区域尺度上不具有可比性[34]. 有鉴于此, 本研究以我国北方草地为研究对象, 通过系统收集已发表的放牧实验研究文献, 将放牧强度转化为放牧家畜对草地地上生物量的相对移除量, 即采食率, 以增强不同草地类型间利用强度的可比性. 通过提取和收集不同草地类型植物补偿性生长、采食率、物种丰富度、气象和土壤要素等信息, 分析这些变量之间的关系, 旨在解决以下3个科学问题: (1) 不同草地类型植物群落地上生物量的补偿效应与地下生物量变化存在何种关系? (2) 实现植物群落地上生物量等补偿或超补偿生长, 且不以牺牲地下生物量为代价, 各草地类型的合理利用强度是多少? (3) 北方草地植物群落补偿性生长主要受到哪些生物和非生物因素的影响?

1 材料和方法

1.1 文献选择与数据库建立

2021年12月, 我们以“TS=(grassland OR steppe OR meadow OR pasture OR rangeland OR desert) AND (graz* OR herbivore OR livestock) AND (grazing intensity OR grazing pressure OR grazing gradient)”和

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

“SU=(‘草地’+‘草原’+‘牧场’+‘草场’)*(‘放牧’+‘食草动物’+‘家畜’+‘牲畜’)*(‘放牧强度’+‘牧压’+‘放牧梯度’)”为检索式, 分别在Web of Science和中国知网CNKI数据库, 对我国北方草地已有的放牧实验研究文献进行了检索与系统收集. 采用如下3个标准对文献进行筛选: (1) 文献研究内容为我国北方草地开展的野外原位放牧实验; (2) 实验包括对照组(未放牧草地), 并设置有放牧梯度水平, 同时文献报道了放牧时间和放牧动物类型; (3) 研究包含放牧组和对照组的均值(mean)、标准差(standard deviation, *SD*)或标准误(standard error, *SE*)、重复数(*n*)等信息. 当研究文献未给出标准差或者标准误差时, 采用平均值的1/10作为标准差的估计值[35]. 收集文献中出现的地上生物量、地下生物量(belowground biomass, BGB; 0~30 cm)和植物物种丰富度指标, 直接获取表格形式的数据, 并利用WebPlotDigitizeR-3.8软件提取图片形式的数据. 为确保数据的相对独立性, 将来源于不同文献中的同一站点数据进行合并与剔除. 同时, 我们记录了研究样点位置(经纬度和海拔)、气象因子(多年平均温度, mean annual temperature, MAT; 多年平均降水量, mean annual precipitation, MAP)、放牧家畜种类、实验年份、放牧时间以及草地类型等信息. 当文献中未提供MAT和MAP时, 根据研究样点的经纬度信息, 通过使用全球气候数据库(http://www.worldclim.org/)进行插值补充. 此外, 我们根据经纬度信息插值提取了各研究样点的0~30 cm深度土壤有机质(soil organic matter, SOM)含量, 用于表征土壤肥力[36].

本研究共计收集了118篇有效文献, 提取了534组数据用于后续整合分析. 研究样点覆盖新疆、青海、内蒙古等9个省区(表1), MAT分布范围为–5.3~9.2°C, MAP分布范围为158~742 mm.

1.2 数据分组和分析方法

根据获取数据所属的草地类型, 我们将这些数据归并为高寒草甸、高寒草原(由高寒草甸草原和高寒草原合并而成)、草甸草原、典型草原、荒漠草原和其他草地6种类型[2]. 在统计分析中, 北方草地的整体分析包括了6种类型的所有数据点, 而不同草地类型的比较仅包括前5种类型. 为使不同放牧实验研究的结果具有可比性, 将放牧强度统一转化为家畜采食率指标. 采食率由放牧家畜日食量和放牧天数计算所得[37], 计算公式如下:

$$GR = \frac{I}{I+B_g} \times 100\%, \tag{1}$$

$$I = A \times D, \tag{2}$$

补偿生长计算公式为

$$C = I + B_g - B_c, \tag{3}$$

$$\mathrm{ANPPg} = I + B_g, \tag{4}$$

式中, GR为采食率, I为被采食的牧草生物量, A为放牧家畜日食量[37], D为放牧天数, C为草地植物绝对补偿生长量, ANPPg为放牧草地净地上初级生产力, B_g和B_c分别为放牧草地和未放牧草地的地上现存生物量. 当$C > 0$, 草地植物群落表现为超补偿生长; 当C=0, 草地植物群落表现为等补偿生长; 当$C < 0$, 草地植物群落表现为欠补偿生长.

为确定草地合理利用强度, 我们分别以同一类型草地未放牧地ANPP和BGB的均值及其95%置信区间为参照, 划分不同草地类型的合理采食率. 其中依据放牧地ANPPg与采食率的关系, 并以未放牧地ANPP均值为阈值, 将ANPPg与ANPP均值置信区间下限的交点确定为利用率阈值. 当ANPPg高于ANPP平均值置信区间下限, 即表现为植物等补偿或超补偿生长. 采用类似方法, 当放牧地地下生物量BGBg不低于未放牧地BGB均值的置信区间下限时, 即为合理采食率.

采用Hedges等人[38]提出的效应值(LnRR), 表示地下生物量对放牧的响应特征, 采用标准差计算权重, 效应值LnRR和权重Weight的计算公式如下:

$$\mathrm{Ln}RR = \mathrm{Ln}\left(\frac{X_g}{X_c}\right), \tag{5}$$

$$\mathrm{Weight} = \frac{1}{v}, \tag{6}$$

$$v = \frac{SD_g^2}{n_g X_g^2} + \frac{SD_c^2}{n_c X_c^2}, \tag{7}$$

式中, v为与效应值相对应的研究内方差, SD_g^2、SD_c^2、X_g、X_c、n_g、n_c分别为放牧草地和未放牧草地的标准差、均值和样本量. 观测值权重越大, 表明其对总体效应值的贡献越大[39].

累积效应值RR_{++}和其标准误SE的计算公式如下:

$$RR_{++} = \frac{\sum_{i=1}^{k} w_i \ln RR_i}{\sum_{i=1}^{k} w_i}, \tag{8}$$

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

表 1　中国北方草地放牧试验研究样点信息表

Table 1　Information of grazing study sites in grasslands of northern China

省(自治区)	盟市-旗县	研究点数量	草地类型	纬度(°N)	经度(°E)	年均温 MAT(°C)	年均降水量 MAP(mm)	放牧年限(a)
内蒙古自治区	呼伦贝尔市海拉尔区	6	草甸草原	49.13~49.55	119.35~120.02	−1.86~−0.91	319~354	1~5
	呼伦贝尔市陈巴尔虎旗	1	草甸草原	49.00	119.55	−1.05	324	1
	通辽市扎鲁特旗	1	草甸草原	44.52	120.90	7.31	370	1
	锡林郭勒盟锡林浩特市	10	典型草原	43.43~44.65	116.30~116.70	0.97~3.63	249~311	1~18
	锡林郭勒盟正镶白旗	3	典型草原	42.13~42.92	115.23~115.50	3.37~3.69	341~358	1~6
	锡林郭勒盟太仆寺旗	2	典型草原	41.58~41.78	114.85~115.08	3.85~4.46	369~379	3~4
	锡林郭勒盟东乌珠穆沁旗	1	典型草原	44.67	115.17	2.38	238	1
	锡林郭勒盟苏尼特右旗	3	荒漠草原	41.92~42.27	111.13~112.78	4.83~5.53	209~237	6~9
	乌兰察布市四子王旗	5	荒漠草原	41.17~41.78	110.33~112.02	4.32~4.53	213~325	11~15
	巴彦淖尔市乌拉特后旗	1	荒漠草原	41.42	106.97	5.52	158	4
青海省	西宁市湟中区	1	高寒草甸	37.21	100.04	−0.82	497	2
	果洛藏族自治州达日县	1	高寒草甸	33.62	99.78	−1.36	590	3
	海北藏族自治州门源县	1	高寒草甸	37.53	101.25	−0.82	497	15
	海北藏族自治州刚察县	1	高寒草原	37.35	100.07	−0.60	370	2
	海北藏族自治州海晏县	1	高寒草原	37.12	100.42	1.40	350	1
甘肃省	甘南藏族自治州玛曲县	2	高寒草甸	34.50~35.97	101.88~102.48	2.73~4.29	486~705	3~11
	武威市天祝县	1	高寒草原	34.47	100.2	−0.23	537	4
	庆阳市环县	2	典型草原	37.20	106.83	8.50	348	10~18
	白银市景泰县	1	荒漠草原	37.10	103.52	8.30	185	5
新疆维吾尔自治区	和田地区策勒县	1	高寒草甸	36.13	81.10	−0.20	674	12
	克孜勒苏自治州乌恰县	1	高寒草原	40.45	75.35	−0.31	277	1
	伊犁哈萨克自治州昭苏县	1	草甸草原	42.98	81.05	3.20	314	3
西藏自治区	那曲市安多县	2	高寒草原	32.65	91.17	−3.4	439	4~5
	林芝市工布江达县	1	高寒草原	29.55	92.22	−5.28	402	3
	拉萨市林周县	1	典型草原	29.75	90.85	3.43	501	4
河北省	张家口市沽源县	4	典型草原	41.07~41.77	115.77~115.83	3.88~6.60	391~435	10~14
	承德市丰宁县	1	典型草原	41.73	116.27	3.39	438	1
山西省	朔州市右玉县	1	草甸草原	40.17	112.32	5.31	365	3
	朔州市右玉县	1	典型草原	39.98	112.32	5.48	386	3
四川省	阿坝藏族羌族自治州红原县	6	高寒草甸	31.83~33.08	101.85~102.58	0.34~3.11	644~742	1~18
宁夏回族自治区	吴忠市盐池县	4	荒漠草原	37.07~37.95	106.50~107.50	7.77~9.16	289~321	1~8

$$SE = \sqrt{\frac{1}{\sum_{i=1}^{k} w_i}}. \tag{9}$$

累积效应值的置信区间为95%: $CI=RR_{++}\pm1.96SE$. 当累积效应值的置信区间不包含0时, 表示存在显著效应. 采用类似方法, 我们计算出不同草地类型的植物绝对补偿生长量(C)的累积值. 当累积值显著>0和<0时, 草地植物分别表现为超补偿和欠补偿生长; 当累积值与0无显著差异时, 草地植物表现为等补偿生长.

由于同一研究中的观测数据存在相互不独立问题, 本研究采用混合效应模型, 将“研究”作为随机因子纳入模型分析, 计算累积效应值. 上述分析利用R 4.2.0软

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved.　http://www.cnki.net

件中的“metafor”包的rma.mv函数完成. 采用Meta回归方法, 研究植物补偿性生长与地下生物量效应值、植物多样性效应值、气候因子(MAT、MAP)和土壤养分(SOM)之间的关系. 显著性检验水平为0.05. 上述整合分析及绘图均借助R 4.2.0软件完成.

2 结果

2.1 不同草地类型植物群落补偿生长特征及对地下生物量的影响

放牧影响下, 不同类型草地植物群落补偿性生长的绝对值和地下生物量(BGB)效应值均存在极显著差异(图1). 总体而言, 我国北方草地植物群落地上部分欠补偿生长绝对值为19 g m^{-2}, BGB显著降低. 其中, 高寒草甸植物群落地上生物量欠补偿生长绝对值为32 g m^{-2}, BGB未发生明显变化; 高寒草原植物群落地上生物量表现为等补偿生长; 草甸草原植物群落地上生物量欠补偿生长绝对值为19 g m^{-2}, 且BGB显著降低; 典型草原植物群落地上生物量表现为等补偿生长, BGB显著降低; 荒漠草原植物群落地上生物量欠补偿生长绝对值为24 g m^{-2}, 且BGB显著降低.

Meta回归结果显示, 北方草地放牧系统净地上初级生产力(ANPPg)与BGB效应值呈显著负相关, BGB效应值随着ANPPg的增加而下降, 即随着植物地上部分超补偿生长的增加, 放牧加剧了对BGB的负效应(图2).

2.2 不同草地类型植物群落补偿效应与放牧强度阈值的权衡

家畜采食率对各类草地ANPPg具有显著的影响, ANPPg随着采食率的增加而降低, 即随着放牧强度的增加, 草地植物补偿效应逐渐降低. 放牧条件下, 高寒草甸、高寒草原、草甸草原、典型草原和荒漠草原ANPPg与采食率均呈负相关, 当ANPPg分别低于阈值274、129、242、197和113 g m^{-2}时, 植物群落出现欠补偿生长现象, 相对应的采食率分别为56%、43%、53%、47%和37%(图3). 草甸草原、典型草原和荒漠草原BGB与采食率均呈负相关, 采食率阈值分别为48%、40%和31%(图4), 与以ANPPg划定的采食率阈值相比, 分别降低了5%、7%和6%. 因高寒草甸和高寒草原BGB数据不足, 以其他类型草地采食率阈值降低均值作为参考依据, 其采食率阈值应降低6%左右.

2.3 环境条件和生物多样性对植物群落补偿效应的影响

区域尺度上, 北方草地植物群落地上生物量补偿生长的绝对值与MAT呈显著负相关(图5(a)), 即补偿效应随着MAT的增加而降低; 但典型草原和荒漠草原植物群落补偿生长的绝对值与MAT呈显著正相关, 即随着MAT的增加而增加. 北方草地植物群落地上生物量补偿生长的绝对值与MAP存在极显著非线性关系(图5(b)), 表现为植物补偿生长沿着降水梯度呈先增加

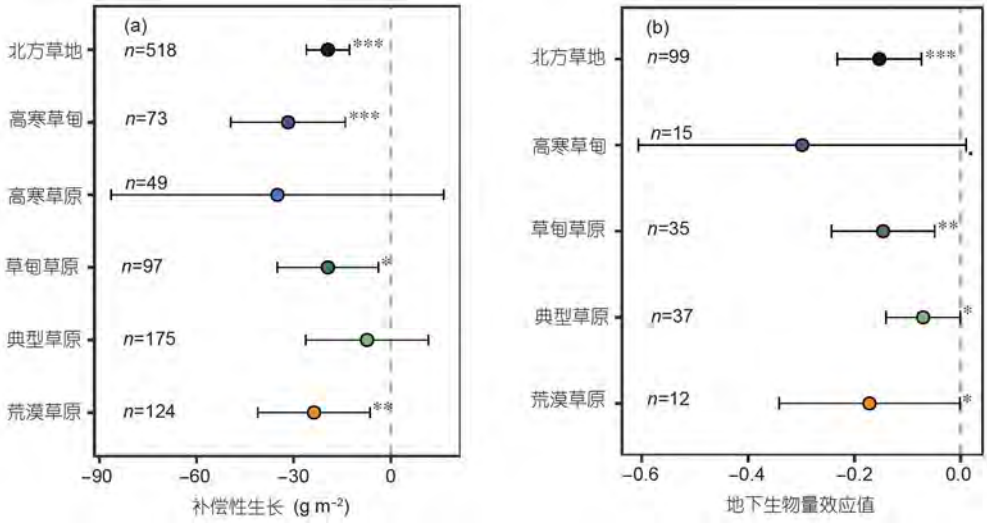


图 1 (网络版彩色)不同草地类型植物补偿生长(a)和BGB(b)对放牧的响应特征. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Figure 1 (Color online) Responses of plant compensatory growth (a) and BGB (b) to grazing in different grassland types. Significance level: *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

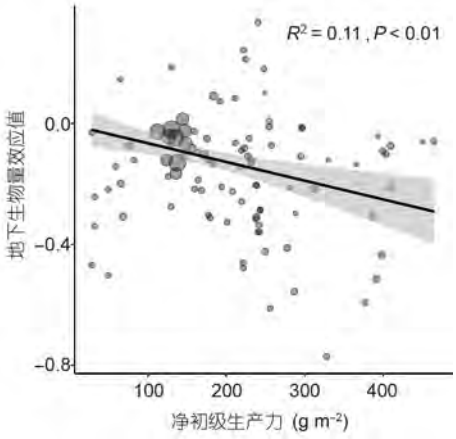


图 2　北方草地生态系统ANPPg和BGB效应值的关系. 点的大小表示权重, 显著性$P < 0.05$, 阴影区域表示95%置信区间

Figure 2　The relationship between ANPPg and effect size of BGB in grasslands of northern China. The size of dots represents the weight, the significance level is $P < 0.05$, and the shaded area represents the 95% confidence interval

后降低的变化规律. 其中, 高寒草原、典型草原和荒漠草原植物群落补偿生长的绝对值均与MAP呈显著正相关, 即随着MAP的增加而增加.

区域尺度上, 群落地上生物量补偿生长的绝对值与SOM呈显著正相关(图5(c)). 然而, 不同草地类型地上生物量补偿生长的绝对值与SOM的关系并不一致. 具体表现为, 荒漠草原和高寒草原地上生物量补偿生长的绝对值与SOM为正相关关系, 但高寒草甸地上生物量补偿生长的绝对值与SOM呈极显著负相关, 即随着SOM含量的增加植物补偿生长呈下降的趋势.

植物群落补偿生长的绝对值与植物物种丰富度效应值呈极显著正相关(图5(d)), 即植物群落补偿生长能力随着植物物种丰富度的增加而提高. 类似地, 典型草原和荒漠草原群落地上生物量补偿生长的绝对值与植物物种丰富度效应值之间也呈正相关关系.

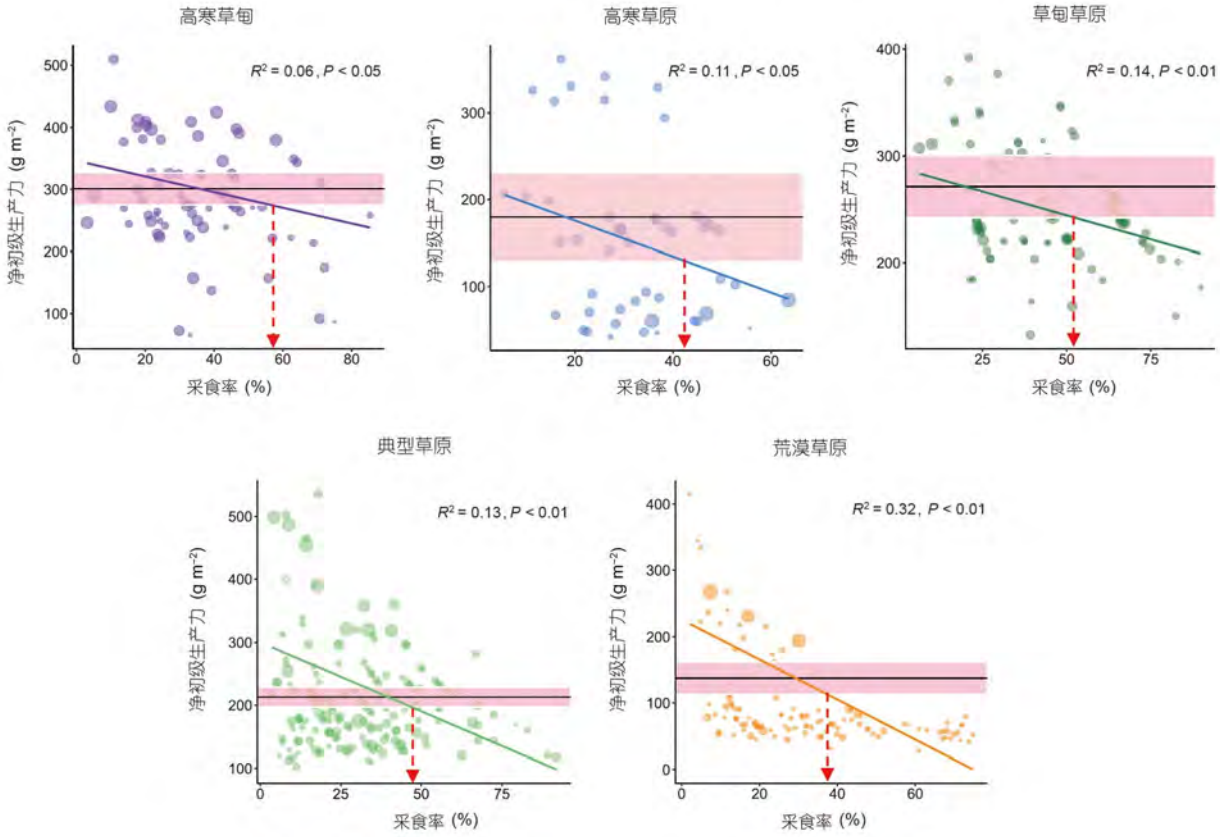


图 3　(网络版彩色)不同草地类型植物补偿生长与采食率的关系. 点的大小表示权重, 显著性$P < 0.05$, 阴影区域表示ANPP平均值95%置信区间, 箭头表示采食率阈值

Figure 3　(Color online) The relationship between plant compensatory growth and forage consumption rate in different grassland types. The size of dots indicates the weight, the significance level is $P < 0.05$, the shaded area indicates the 95% confidence interval of the mean ANPP of ungrazed grasslands, and the arrow indicates the threshold of forage consumption rate

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved.　http://www.cnki.net

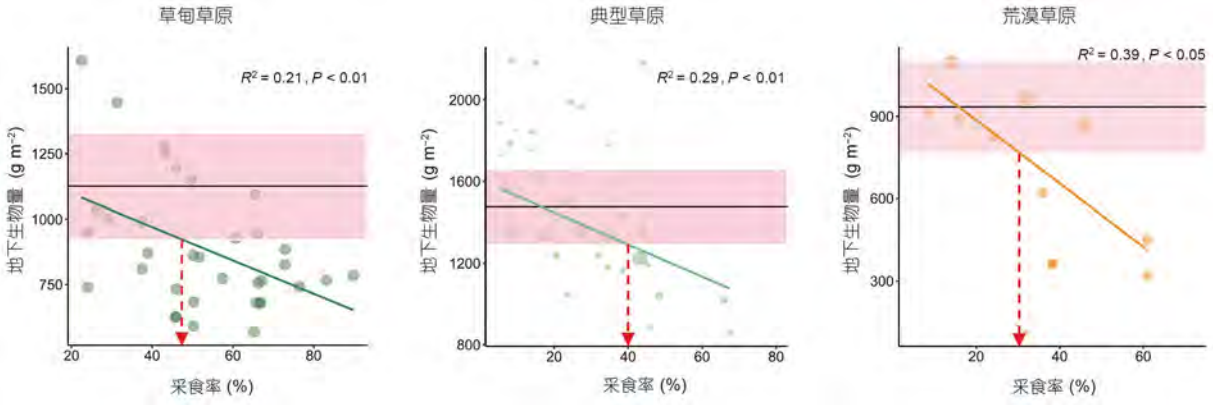


图 4 不同草地类型BGB与采食率的关系. 点的大小表示权重, 显著性P < 0.05, 阴影区域表示BGB平均值95%置信区间, 箭头表示采食率阈值

Figure 4 The relationship between BGB and intake rate in different grassland types. The size of dots indicates the weight, the significance level is P < 0.05, the shaded area indicates the 95% confidence interval of the mean BGB of ungrazed grasslands, and the arrow indicates the intake rate threshold

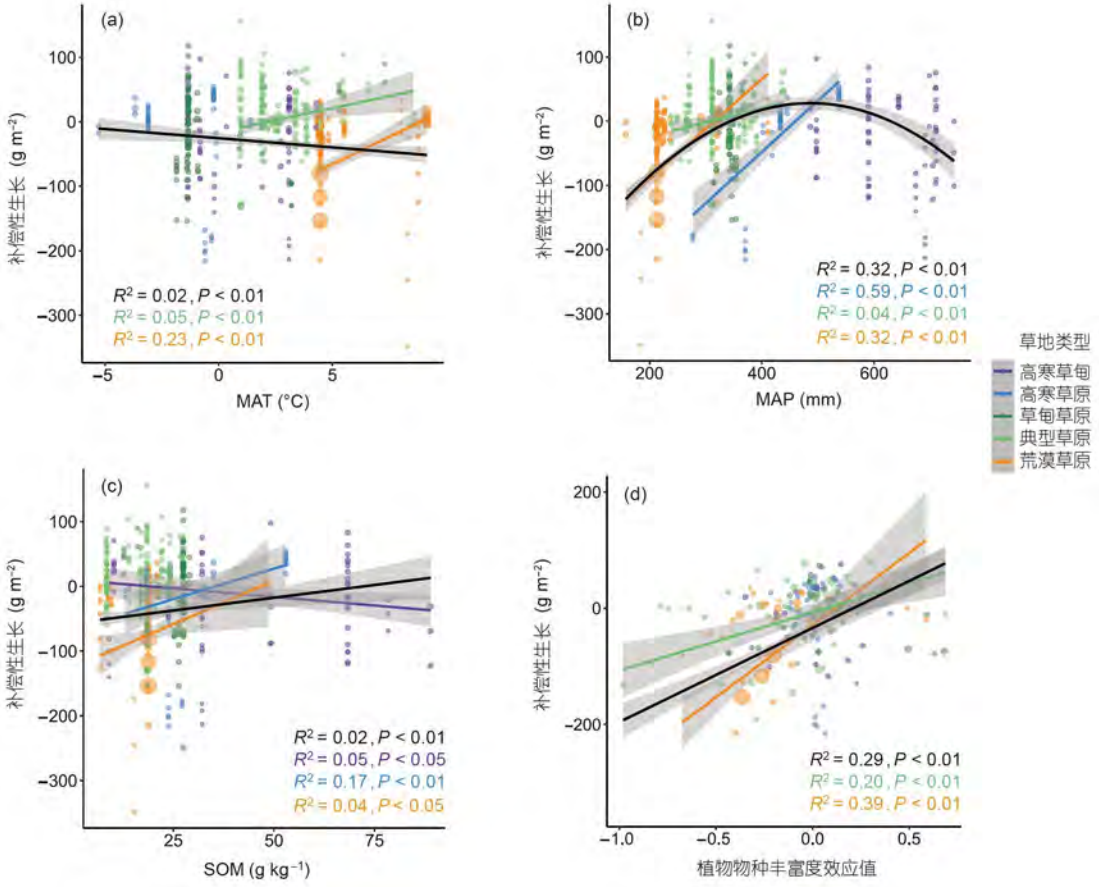


图 5 北方草地植物补偿生长与MAT(a)、MAP(b)、SOM(c)和植物物种丰富度效应值(d)的关系. 点的大小表示权重, 显著性P < 0.05, 阴影区域表示95%置信区间

Figure 5 The relationship between plant compensatory growth, MAT (a), MAP (b), SOM (c) and changes of plant species richness (d) in grasslands of northern China. The size of dots indicates the weight, the significance level is P < 0.05, and the shaded area indicates the 95% confidence interval

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

3 讨论

3.1 草地植物地上部分补偿生长及其对地下生物量的影响

植物补偿生长效应主要取决于受损组织和器官的重建，植物通过增加叶绿素含量、光合酶活性和电子传递能力，改善其光合结构的生理功能，提高CO_2同化能力，从而实现补偿生长[14,40]. 家畜采食一方面有利于去除植物衰老组织，降低群落优势物种的竞争排斥作用，导致消光系数降低，从而提高植物叶片受光面积. 另一方面，家畜采食可促进休眠芽的萌发，新产生叶片的比叶面积、氮磷含量均显著高于老叶，进而使单位叶面积的光合效率提高[11,13,14]. 此外，放牧家畜采食过程中，其排泄物提高了草地土壤肥力[41]，同时其唾液有利于刺激植物的补偿生长[42]. 但随着采食强度的进一步增加，植物活跃的侧生分生组织受损严重，植物光合能力降低，损耗其能量和非结构性碳水化合物的储存，植物再生能力被抑制[43,44]，表现为草地植物由超补偿生长转为欠补偿生长.

植物根系是连接生态系统地上和地下部分的纽带，为植物地上部分提供水分和养分，在面临外界环境变化时，植物地上部分对根系的依赖程度可能更高[45]. 本研究中，不同草地类型地下生物量对放牧的响应存在差异. 其中，放牧未显著影响高寒草甸的地下生物量. 这可能源于其数据样本量相对较少，且存在较大变异，表明未来应更多关注放牧如何影响高寒草甸地下生物量的研究. Yan等人[46]通过Meta分析发现，放牧对我国草地地下生物量负作用的强度高于全球草地平均水平，主要是由长期过度放牧导致草地退化引起的[47]. 本研究发现，在放牧干扰下，我国北方草地整体以及草甸草原、典型草原和荒漠草原的地下生物量均显著下降. 这主要是由于过度放牧降低了植物群落地上生物量，减少了叶片光合产物向根系的输送. 地上生物量的降低还可能会改变植物地上与地下部分的功能平衡，使得植物地下部分呼吸占比增加，消耗根系中更多的碳水化合物[21]. 此外，植物地上部分在受到外界干扰伤害时，会通过改变光合产物的分配格局，将地下器官中储存的碳水化合物更多地运输到地上部分，用于新叶的生长，以补偿干扰引起的伤害，最终导致植物以牺牲地下部分为代价来实现地上部分的补偿性生长[14,16,44,48]. 本研究表明，植物补偿生长与地下生物量效应值之间呈负相关，进而为上述推测提供了直接证据. Bai等人[17]研究发现，适度放牧会提高根系产量及地上生物量，增加采食强度会使植物同化产物更多地分配到地上部分，减少其对地下部分的分配，增加根死亡率，导致地下生物量降低. 在本研究中，当采食率超过各草地类型依据地下生物量划定的放牧强度阈值，且超出幅度不高于6%时，植物地上部分仍存在补偿生长，而地下生物量则显著降低. 同时，家畜高强度践踏导致土壤理化性质改变可能减弱根系对水分和养分的吸收，降低根系生产力，从而影响植物生长，导致地上部分发生欠补偿[8].

3.2 北方草地不同草地类型的合理利用强度

草地植物的补偿生长特征与放牧强度密切相关[49]. 本研究发现，我国北方草地在放牧影响下植物群落总体表现为欠补偿生长，这可能是由于不合理的放牧强度引起的. 在长期重度放牧条件下，植物受光有效性的限制降低，但土壤养分的限制程度加剧，因而放牧对植物生长的抑制作用要强于促进作用[50]，草地植物表现为欠补偿生长[51,52]. 不同草地类型的补偿生长特征存在差异，其中高寒草原和典型草原总体上表现为等补偿生长，表明总体上这两类草地的超载过牧情况不十分突出. 高寒草甸欠补偿生长最为显著，因轻度和中度放牧有利于高寒草甸植物的超补偿生长[19]，可见高寒草甸普遍存在严重过牧情况. 类似地，马红彬和谢应忠[51]研究发现，荒漠草原在轻度和中度放牧干扰下，植物具有补偿或超补偿性生长，而在重度放牧条件下，则表现为欠补偿生长. 我们的研究结果显示，草甸草原群落地上生物量欠补偿生长的绝对值为19 g m^{-2}，荒漠草原地上生物量欠补偿生长的绝对值为24 g m^{-2}，可见这两类草原也存在过度放牧的情况. 综上可知，我国北方草地普遍存在放牧强度不合理的情况，这不仅严重地制约了草原畜牧业的可持续发展，同时也降低了草地的生态功能，长期过度放牧是草地发生大面积退化的最主要和最直接驱动因子. 综合考虑放牧影响下植物群落补偿性生长和地下生物量的变化，不同草地类型的适宜采食率阈值为：高寒草甸50%、高寒草原37%、草甸草原48%、典型草原40%、荒漠草原31%. 这是因为湿润的草甸类草地，植物生长不受水资源限制，其合理放牧强度的阈值更高[49]. 然而不同草地类型植物群落的补偿生长主要取决于其建群种及优势种的生长特性，特别是具有较强耐牧性的建群种和优势种对草地植物群落补偿生长方式和大小具有重要影响. 不同类

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

型草地建群种与优势种详见表S1. 一些研究表明, 在不同放牧梯度下, 羊草(*Leymus chinensis*)、赖草(*Leymus secalinus*)、糙隐子草(*Cleistogenes squarrosa*)、长芒草(*Stipa bungeana*)、针茅(*Stipa capillata*)和紫花针茅(*Stipa purpurea*)表现出不同的补偿生长[14,51,53,54]. 由此可见, 草地植物群落在家畜采食后具体表现哪种补偿生长方式, 与草地类型、气候和土壤条件的制约以及建群种和优势种的耐牧性、生长方式等生物学特征密切相关.

本研究支持放牧优化假说[18], 即在合理采食率范围内, 放牧能够缓解植物间的光竞争强度, 对草地生态系统产生正效应, 提高生物多样性和初级生产力, 有利于草地群落稳定性的维持[7,9]. Li等人[9]对高寒草地生态系统的研究表明, 重度利用对植物群落稳定性产生负效应, 这与我们的研究结果一致. 针对内蒙古典型草原的实验研究表明, 轻度和中度放牧干扰下, 群落地上净初级生产力表现为超补偿生长, 随着采食率的增加, 在重度放牧条件下表现为欠补偿生长, 这也与我们在区域尺度上的研究结果一致[52]. 虽然荒漠草原放牧研究表明, 植物群落在合理放牧利用条件下具有等补偿和超补偿生长情况, 但在过度放牧条件下则表现为欠补偿生长, 因此通过降低放牧强度有利于植物产生超补偿和等补偿生长[51]. 此外, 荒漠草原植被低矮稀疏, 初级生产力较低, 对气候变化和过度放牧更为敏感, 因此更易发生退化, 且一旦遭到严重破坏便很难恢复[55], 这一观点同样体现在本研究中荒漠草原采食率阈值最低. 因此, 我们建议针对过度放牧引起欠补偿程度较为严重的草地类型, 应采取休牧、施肥等恢复措施; 对于欠补偿程度较轻的草地, 应在牧草返青期进行30~60 d的休牧. 因此, 确定合理的放牧强度并将其用于草地可持续管理, 在不牺牲草地地下生物量和生态功能的前提下, 充分利用和发挥植物的超补偿生长潜力, 维持和提升草地的生产功能, 对实现草地资源的可持续利用具有重要意义.

3.3 非生物因素和生物因素对植物补偿效应的影响

本研究发现, 总体上北方草地植物补偿性生长随温度的升高而逐渐降低, 这可能是因为较高的温度会导致蒸散增强, 土壤水分降低, 影响种子萌发和植物生长[56]. 特别是高寒草地由于自然条件严酷、生态系统对气候变化十分敏感, 气候变暖导致永久冻土层融化、蒸散增加和土壤含水量下降, 抑制草地植物生长[20,57]. 相比之下, 本研究中温性草地(草甸草原、典型草原和荒漠草原)对气候变化具有较强的适应性, 气温升高使得春季物候期提前, 植被生长季延长, 植物光合速率增加, 进而有利于植物补偿生长[28,58].

水分是影响草地初级生产力的关键限制因素, 降水主要通过影响植物光合效率和活性, 从而影响初级生产力[59]. 总体上, 北方草地植物补偿生长随降雨量的增加呈先增强后减弱的变化规律, 这主要是因为较高的降雨量导致水分限制的减弱, 但可能使养分的限制增加, 进而导致草地群落降水利用效率降低[60]. 本研究表明, 降雨量的增加有利于典型草原、荒漠草原和高寒草原植物补偿生长, 这与前人的研究结果一致[61].

土壤有机质是衡量土壤肥力的重要指标之一, 土壤有机质含量增加是土壤肥力增加的重要依据[36]. 土壤养分的改善, 对植物生长的促进作用在许多研究中均有报道[62], 且适度的放牧活动会加速营养物质的循环, 促进生态系统土壤肥力对植物生长的正反馈[41]. 本研究发现, 整个北方草地以及高寒草原和荒漠草原植物补偿性生长与土壤有机质存在显著的正相关关系. 土壤养分一方面可直接促进植物生长, 另一方面可通过影响生物多样性来间接影响地上生物量, 从而提高草地初级生产力[22,33]. 然而, 本研究发现, 高寒草甸植物补偿性生长随着土壤有机质增加而降低, 这可能是因为我们的研究样点处于较高海拔地区, 低温使有机质分解较慢, 同时限制植物对养分的利用, 导致植物在放牧干扰下的补偿性生长较低[63].

植物群落初级生产力通常随着物种丰富度的增加而增加[30]. 本研究表明, 放牧条件下, 北方草地补偿生长与植物多样性效应值之间存在正相关关系, 且在典型草原与荒漠草原中具有类似格局. 生物多样性可以显著提高草地生产力. 可能的机制主要包括: (1) 增加草地对气候变化的抵抗力来稳定生态系统初级生产力[64]; (2) 调节生长季提前开始而不是延长生长季的结束[30]; (3) 家畜通过采食可食牧草, 降低群落优势物种的竞争排斥作用, 增强光照对其他物种的供应, 增加杂类草的丰富度[65]. 因此, 适度放牧利用有助于草地维持较高的生物多样性, 进而提高初级生产力和生态系统稳定性[33].

4 结论

本研究基于放牧实验数据, 整合分析了我国北方

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

不同草地类型植物补偿性生长对放牧的响应及其生物和非生物驱动因子, 为该区域制定适宜的放牧强度, 科学配置草地的生态和生产功能, 实现草地资源的可持续利用提供了科学依据. 本研究取得的主要结论包括: (1) 我国北方草地当前的放牧强度不利于草地资源的可持续利用, 植物地上部分的补偿效应主要以牺牲地下生物量为代价. 其中, 高寒草甸、草甸草原和荒漠草原植物均表现欠补偿生长, 高寒草原和典型草原植物则表现为等补偿生长. (2) 北方草地不同类型的适宜利用强度为: 高寒草甸50%、草甸草原48%、典型草原40%、高寒草原37%、荒漠草原31%. (3) 我国北方草地植物补偿生长能力受气温、降水、土壤肥力与植物多样性的影响, 具体影响因草地类型不同而异. 因此, 在实践中应综合考虑不同区域和不同草地类型的适宜利用强度及相关生物与环境因子的变化, 以及草地退化现状和程度, 合理配置草地的生态和生产功能, 加速退化草地的恢复和自我修复, 实现草地资源可持续利用和区域生态安全的双赢.

参考文献

1 White R P, Murray S, Rohweder M. Pilot Analysis of Global Ecosystems: Grassland Ecosystems. Washington DC: World Resources Institute, 2000

2 Department of Animal Husbandry and Veterinary and the General Station of Animal Husbandry and Veterinary Science, the Ministry of Agriculture of the People's Republic of China. Rangeland Resources of China (in Chinese). Beijing: China Science and Technology Press, 1996 [中华人民共和国农业部畜牧兽区司, 全国畜牧兽医总站. 中国草地资源. 北京: 中国科学技术出版社, 1996]

3 Wu J, Zhang Q, Li A, et al. Historical landscape dynamics of Inner Mongolia: Patterns, drivers, and impacts. Landsc Ecol, 2015, 30: 1579–1598

4 Bai Y F, Zhao Y J, Wang Y, et al. Assessment of ecosystem services and ecological regionalization of grasslands support establishment of ecological security barriers in northern China (in Chinese). Bull Chin Acad Sci, 2020, 35: 675–689 [白永飞, 赵玉金, 王扬, 等. 中国北方草地生态系统服务评估和功能区划助力生态安全屏障建设. 中国科学院院刊, 2020, 35: 675–689]

5 Bardgett R D, Bullock J M, Lavorel S, et al. Combatting global grassland degradation. Nat Rev Earth Environ, 2021, 2: 720–735

6 Bai Y, Cotrufo M F. Grassland soil carbon sequestration: Current understanding, challenges, and solutions. Science, 2022, 377: 603–608

7 Li Q, Gao S G, Zhang C L, et al. Assessment of the impacts of climate change and human activities on the dynamic grassland change in Inner Mongolia (in Chinese). Geogr Geo-Inform Sci, 2019, 35: 99–104 [李庆, 高素改, 张春来, 等. 内蒙古草地变化过程中气候变化和人类活动的相对作用评估. 地理与地理信息科学, 2019, 35: 99–104]

8 Zhang X, Zhang W, Sai X, et al. Grazing altered soil aggregates, nutrients and enzyme activities in a *Stipa kirschnii* steppe of Inner Mongolia. Soil Tillage Res, 2022, 219: 105327

9 Li W, Liu C, Wang W, et al. Effects of different grazing disturbances on the plant diversity and ecological functions of alpine grassland ecosystem on the Qinghai-Tibetan Plateau. Front Plant Sci, 2021, 12: 765070

10 Han J. Survey on Ecological Issues of China's Grasslands (in Chinese). Shanghai: Shanghai Yuandong Press, 2011 [韩俊. 中国草原生态问题调查. 上海: 上海远东出版社, 2011]

11 Belsky A J. Does herbivory benefit plants? A review of the evidence. Am Natist, 1986, 127: 870–892

12 Yuan J, Li H, Yang Y. The compensatory tillering in the forage grass hordeum brevisubulatum after simulated grazing of different severity. Front Plant Sci, 2020, 11: 00792

13 Zheng S, Lan Z, Li W, et al. Differential responses of plant functional trait to grazing between two contrasting dominant C_3 and C_4 species in a typical steppe of Inner Mongolia, China. Plant Soil, 2011, 340: 141–155

14 Wang K, Zhong S, Sun W. Clipping defoliation and nitrogen addition shift competition between a C_3 grass (*Leymus chinensis*) and a C_4 grass (*Hemarthria altissima*). Plant Biol, 2020, 22: 221–232

15 Dyer M I, DeAngelis D L, Post W M. A model of herbivore feedback on plant productivity. Math Biosci, 1986, 79: 171–184

16 Orians C M, Thorn A, Gómez S. Herbivore-induced resource sequestration in plants: Why bother? Oecologia, 2011, 167: 1–9

17 Bai W, Fang Y, Zhou M, et al. Heavily intensified grazing reduces root production in an Inner Mongolia temperate steppe. Agric Ecosyst Environ, 2015, 200: 143–150

18 McNaughton S J. Compensatory plant growth as a response to herbivory. Oikos, 1983, 40: 329–336

19 Dong Q M, Zhao X Q, Ma Y S, et al. Influence of grazing on biomass, growth ratio and compensatory effect of different plant groups in *Kobresia parva* meadow (in Chinese). Acta Ecol Sin, 2012, 32: 2640–2650 [董全民, 赵新全, 马玉寿, 等. 放牧对小嵩草草甸生物量及不同植物类群生长率和补偿效应的影响. 生态学报, 2012, 32: 2640–2650]

20 Wu G L, Cheng Z, Alatalo J M, et al. Climate warming consistently reduces grassland ecosystem productivity. Earth Future, 2021, 9: e2020EF001837

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

21 Chandregowda M H, Tjoelker M G, Power S A, et al. Drought and warming alter gross primary production allocation and reduce productivity in a widespread pasture grass. Plant Cell Environ, 2022, 45: 2271–2291

22 Gross K. Biodiversity and productivity entwined. Nature, 2016, 529: 293–294

23 Tian J, Xiong J N, Zhang Y C, et al. Quantitative assessment of the effects of climate change and human activities on grassland NPP in Altay Prefecture. J Resour Ecol, 2021, 12: 743–756

24 Knapp A K, Carroll C J W, Denton E M, et al. Differential sensitivity to regional-scale drought in six central US grasslands. Oecologia, 2015, 177: 949–957

25 Su Y Z, Zhao H L, Zhang T H, et al. Soil properties following cultivation and non-grazing of a semi-arid sandy grassland in northern China. Soil Tillage Res, 2004, 75: 27–36

26 Ma R, Xia C, Liu Y, et al. Spatiotemporal change of net primary productivity and its response to climate change in temperate grasslands of China. Front Plant Sci, 2022, 13: 899800

27 Li L, Zhang Y, Wu J, et al. Increasing sensitivity of alpine grasslands to climate variability along an elevational gradient on the Qinghai-Tibet Plateau. Sci Total Environ, 2019, 678: 21–29

28 Wang H, Liu H Y, Cao G M, et al. Alpine grassland plants grow earlier and faster but biomass remains unchanged over 35 years of climate change. Ecol Lett, 2020, 23: 701–710

29 Park T, Chen C, Macias-Fauria M, et al. Changes in timing of seasonal peak photosynthetic activity in northern ecosystems. Glob Change Biol, 2019, 25: 2382–2395

30 Oehri J, Schmid B, Schaepman-Strub G, et al. Biodiversity promotes primary productivity and growing season lengthening at the landscape scale. Proc Natl Acad Sci USA, 2017, 114: 10160–10165

31 Van Moorsel S J, Hahl T, Wagg C, et al. Community evolution increases plant productivity at low diversity. Ecol Lett, 2018, 21: 128–137

32 Cardinale B J, Duffy J, Gonzalez A, et al. Biodiversity loss and its impact on humanity. Nature, 2012, 489: 59–67

33 Sanaei A, Ali A, Chahouki M A Z. The positive relationships between plant coverage, species richness, and aboveground biomass are ubiquitous across plant growth forms in semi-steppe rangelands. J Environ Manage, 2018, 205: 308–318

34 Liu Y Z, Liu W T, Yang X X, et al. Effects of grazing on the C:N:P stoichiometry in global grassland ecosystems: A meta analysis (in Chinese). Chin J Appl Ecol, 2022, 33: 1251–1259 [刘玉祯, 刘文亭, 杨晓霞, 等. 放牧对全球草地生态系统碳氮磷化学计量特征影响的Meta分析. 应用生态学报, 2022, 33: 1251–1259]

35 Luo Y, Hui D, Zhang D. Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: A meta-analysis. Ecology, 2006, 87: 53–63

36 Mayer M, Rewald B, Matthews B, et al. Soil fertility relates to fungal-mediated decomposition and organic matter turnover in a temperate mountain forest. New Phytol, 2021, 231: 777–790

37 Ministry of Agriculture and Rural Affairs of the People's Republic of China. Calculation of Rangeland Carrying Capacity (in Chinese). Agricultural Industry Standard of the People's Republic of China, NY/T 635-2015 [中华人民共和国农业部. 天然草地合理载畜量的计算. 中华人民共和国农业行业标准, NY/T 635-2015]

38 Hedges L V, Gurevitch J, Curtis P S. The meta-analysis of response ratios in experimental ecology. Ecology, 1999, 80: 1150–1156

39 Peng Y, Wang G, Li F, et al. Unimodal response of soil methane consumption to increasing nitrogen additions. Environ Sci Technol, 2019, 53: 4150–4160

40 Hayashi M, Fujita N, Yamauchi A. Theory of grazing optimization in which herbivory improves photosynthetic ability. J Theor Biol, 2007, 248: 367–376

41 Chapin F S, McNaughton S J. Lack of compensatory growth under phosphorus deficiency in grazing-adapted grasses from the Serengeti Plains. Oecologia, 1989, 79: 551–557

42 Zhang Z, Wang S P, Jiang G M, et al. Responses of *Artemisia frigida* Willd. (Compositae) and *Leymus chinensis* (Trin.) Tzvel. (Poaceae) to sheep saliva. J Arid Environ, 2007, 70: 111–119

43 Fynn R W S, Morris C D, Kirkman K P. Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance. J Ecol, 2005, 93: 384–394

44 Martínez-Vilalta J, Sala A, Asensio D, et al. Dynamics of non-structural carbohydrates in terrestrial plants: A global synthesis. Ecol Monogr, 2016, 86: 495–516

45 Kong X, Zhang M, De Smet I, et al. Designer crops: Optimal root system architecture for nutrient acquisition. Trends Biotechnol, 2014, 32: 597–598

46 Yan L, Zhou G, Zhang F. Effects of different grazing intensities on grassland production in China: A meta-analysis. PLoS One, 2013, 8: e81466

47 Hao Y, He Z. Effects of grazing patterns on grassland biomass and soil environments in China: A meta-analysis. PLoS One, 2019, 14: e0215223

48 Wang H, Dong Z, Guo J, et al. Effects of grazing intensity on organic carbon stock characteristics in *Stipa breviflora* desert steppe vegetation soil

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

systems. Rangel J, 2017, 39: 169–177
49 Ritchie M E, Penner J F. Episodic herbivory, plant density dependence, and stimulation of aboveground plant production. Ecol Evol, 2020, 10: 5302–5314
50 Zhang D, Peng Y, Li F, et al. Above- and below-ground resource acquisition strategies determine plant species responses to nitrogen enrichment. Ann Bot, 2021, 128: 31–44
51 Ma H B, Xie Y Z. Plant compensatory growth under different grazing intensities in desert steppe (in Chinese). Sci Agric Sin, 2008, 41: 3645–3650 [马红彬, 谢应忠. 不同放牧强度下荒漠草原植物的补偿性生长. 中国农业科学, 2008, 41: 3645–3650]
52 Xue R, Zheng S X, Bai Y F. Impacts of grazing intensity and management regimes on aboveground primary productivity and compensatory growth of grassland ecosystems in Inner Mongolia (in Chinese). Biodivers Sci, 2010, 18: 300–311 [薛睿, 郑淑霞, 白永飞. 不同利用方式和载畜率对内蒙古典型草原群落初级生产力和植物补偿性生长的影响. 生物多样性, 2010, 18: 300–311]
53 Ma Z G, Wang Y Q. Improvement and Sustainable Utilization of Grasslands in Northern China (in Chinese). Inner Mongolia: Inner Mongolia University Press, 2013 [马志广, 王育青. 中国北方草原改良与可持续利用. 内蒙古: 内蒙古大学出版社, 2013]
54 Ganjurjav H, Zhang Y, Gornish E S, et al. Differential resistance and resilience of functional groups to livestock grazing maintain ecosystem stability in an alpine steppe on the Qinghai-Tibetan Plateau. J Environ Manage, 2019, 251: 109579
55 Zhu X H, Yang Q, Ding X Y, et al. Ecosystem landscape pattern change and its response to climate in Inner Mongolia desert steppe (in Chinese). Chin J Ecol, 2022, http://kns.cnki.net/kcms/detail/21.1148.Q.20220629.1559.004.html [朱小华, 杨倩, 丁筱悠, 等. 荒漠草原生态系统格局变化及其对气候的响应. 生态学杂志, 2022, http://kns.cnki.net/kcms/detail/21.1148.Q.20220629.1559.004.html]
56 Jacobs A F G, Heusinkveld B G, Holtslag A A M. Long-term record and analysis of soil temperatures and soil heat fluxes in a grassland area, the Netherlands. Agric For Meteorol, 2011, 151: 774–780
57 Yi S, Wang X, Qin Y, et al. Responses of alpine grassland on Qinghai-Tibetan plateau to climate warming and permafrost degradation: A modeling perspective. Environ Res Lett, 2014, 9: 074014
58 Gonsamo A, Chen J M, Ooi Y W. Peak season plant activity shift towards spring is reflected by increasing carbon uptake by extratropical ecosystems. Glob Change Biol, 2018, 24: 2117–2128
59 Gourdji S M, Sibley A M, Lobell D B. Global crop exposure to critical high temperatures in the reproductive period: Historical trends and future projections. Environ Res Lett, 2013, 8: 024041
60 Bai Y, Wu J, Xing Q, et al. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecology, 2008, 89: 2140–2153
61 Chen T, Bao A, Jiapaer G, et al. Disentangling the relative impacts of climate change and human activities on arid and semiarid grasslands in Central Asia during 1982–2015. Sci Total Environ, 2019, 653: 1311–1325
62 Lozano Y M, Hortal S, Armas C, et al. Interactions among soil, plants, and microorganisms drive secondary succession in a dry environment. Soil Biol Biochem, 2014, 78: 298–306
63 Wang Z, Luo T X, Li R C, et al. Causes for the unimodal pattern of biomass and productivity in alpine grasslands along a large altitudinal gradient in semi-arid regions. J Veg Sci, 2013, 24: 189–201
64 Isbell F, Craven D, Connolly J, et al. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature, 2015, 526: 574–577
65 Niu K, Zhang S, Zhao B, et al. Linking grazing response of species abundance to functional traits in the Tibetan alpine meadow. Plant Soil, 2010, 330: 215–223

补充材料

表S1 不同类型草地建群种与优势种

本文以上补充材料见网络版csb.scichina.com. 补充材料为作者提供的原始数据, 作者对其学术质量和内容负责.

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

Summary for “中国北方草地植物补偿性生长与合理放牧强度: 基于放牧实验的整合分析”

Plant compensatory growth and optimal grazing intensity of grasslands in northern China: A meta-analysis of grazing experiments

Weijiang Song[1,2†], Jishuai Su[2†], Mengdi Zhang[1,2], Yujin Zhao[2], Zhongwu Wang[1], Yushan Jia[1*] & Yongfei Bai[2,3*]

[1] *Key Laboratory of Grassland Resources of the Ministry of Education of China, Key Laboratory of Forage Cultivation, Processing and High Efficient Utilization of the Ministry of Agriculture and Rural Affairs, College of Grassland, Resources and Environment, Inner Mongolia Agricultural University, Hohhot 010011, China;*
[2] *State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China;*
[3] *College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China*
† Equally contributed to this work
* Corresponding authors, E-mail: jys_nm@sina.com; yfbai@ibcas.ac.cn

Grassland ecosystems cover a total area of 4 million square kilometers and account for approximately 41% of the total land area in China, providing multiple ecosystem functions and services, such as primary production, carbon sequestration, forage and food production, soil erosion control, and climate change mitigation. About 3/4 of China’s grasslands are distributed in the northern areas, which is an important ecological security barrier in northern China. Grazing is the most dominant land use form in grasslands worldwide; however, overgrazing has resulted in widespread degradation of ecosystem structure and functions. Previous studies indicate compensatory growth is a key adaptive strategy for grassland plants in response to herbivory. Moderate grazing can stimulate plant compensatory growth and enhance primary production and ecosystem stability. Therefore, reasonable grazing intensity is the basis for optimizing ecological and production functions for sustaining the long-term utilization of grasslands in this region. Based on data from 118 studies on field grazing experiments in grasslands of northern China, we conducted a meta-analysis assessing plant compensatory growth and optimal grazing intensity of five dominant grassland types: Alpine meadow, alpine steppe, meadow steppe, typical steppe, and desert steppe. We collected the data of aboveground biomass, belowground biomass, and plant species richness in grazed and ungrazed grasslands. Here, we converted the grazing intensity into forage consumption rate (i.e., percent removal aboveground biomass by domestic animals) for each study to facilitate data analysis and comparisons across different grassland types. Furthermore, we examined the relationships of plant compensatory growth with climatic conditions, soil fertility, and changes in belowground biomass and plant species diversity. Overall, our results showed the under-compensation in plant community biomass production across the northern China grassland and that compensatory growth in plant aboveground biomass frequently occurred at the expense of decreaced belowground biomass. Specifically, plant under-compensations were found in alpine meadow, meadow steppe, and desert steppe, while plant equivalent compensations were found in alpine steppe and typical steppe. The magnitude of plant compensatory growth positively related to mean annual precipitation and plant species richness across the northern China grassland, although the driving factors differed among grassland types. Our study indicates that the sustainable utilization of the northern China grassland requires the equivalent- and/or over-compensation of plant aboveground biomass and, simultaneously, with no substantial reductions in belowground biomass. To achieve these goals, our results suggest that the optimal forage consumption rate is 50% for alpine meadow, 48% for meadow steppe, 40% for typical steppe, 37% for alpine steppe, and 31% for desert steppe. Our findings have important implications for the ecology and management of grassland ecosystems in northern China and beyond.

plant compensatory growth, forage consumption rate, grazing intensity, belowground biomass, optimization of production functions and ecological functions

doi: 10.1360/TB-2022-0967

(C)1994-2023 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

中国北方草地生态系统服务评估和功能区划助力生态安全屏障建设

白永飞[1,2,3*] 赵玉金[1,2] 王 扬[1,2] 周楷玲[1,3]

1 中国科学院植物研究所 植被与环境变化国家重点实验室 北京 100093
2 中国科学院植物研究所 内蒙古草原生态系统定位研究站 北京 100093
3 中国科学院大学 资源与环境学院 北京 100049

摘要 北方草地是我国重要的绿色生态屏障，也是黄河、长江、澜沧江、滦河等江河的发源地和水源涵养区，其对保障我国生态安全，提升生态系统服务和生态系统稳定性具有极其重要的作用。长期以来，我国在畜牧业生产中重视草地的生产功能，而忽视其生态功能，导致生产功能过度利用，以及生态系统服务和生态功能降低，继而严重威胁着我国的生态安全。开展北方草地生态系统服务评估，制定北方草地主体功能区划，是构建和优化生态安全屏障体系，科学配置草地的生态-生产功能，推进生态文明，统筹山水林田湖草一体化保护和修复，建设“美丽中国”，实现人与自然和谐共生的国家重大科技需求。文章基于北方草地生态系统服务和资源环境条件的空间分异规律，将北方草地划分为7个功能区、25个亚区。该生态功能区划将为制定区域国土空间规划，科学布局重要生态系统保护和修复重大工程，统筹推进生态保护和修复工作提供重要的科技支撑。

关键词 中国北方草地，生态系统服务，生态系统服务价值评估，生态功能分区，生态-生产功能合理配置，生态安全屏障

DOI 10.16418/j.issn.1000-3045.20200515003

草地是陆地生态系统的重要组成部分，不仅为人类提供了肉、奶、皮、毛等具有直接经济价值的产品，同时具有调节气候、涵养水源、防风固沙、生物多样性保育、初级生产力和碳固持等极其重要的生态服务功能[1,2]。据统计，世界草地总面积5.25×10^9 hm^2，占地球陆地总面积的40.5%（不包括格陵兰岛和南极）；储存了陆地生态系统总碳量的34%，维持着30%的净初级生产力；提供了全球约30%—50%的

*通讯作者

资助项目：中国科学院野外站联盟项目（KFJ-SW-YW037），国家重点研发计划项目（2016YFC0500804）
修改稿收到日期：2020年5月31日

畜产品[1]。草地主要分布在干旱和半干旱区，占干旱和半干旱区总面积88%，养育了25%的世界人口。

我国是世界草地资源大国，拥有草地总面积近4×10^8 hm^2，占国土总面积的41.7%[3]。其中，中国北方草地总面积约3×10^8 hm^2[4]，主要分布在新疆、西藏、青海、甘肃、四川、宁夏、内蒙古、陕西、山西、河北、辽宁、吉林、黑龙江等13个省份，涵盖了中国11个重点牧区。我国北方草地以内蒙古高原呈连续分布的温性草原为主体，构成了欧亚大陆草原的东翼。根据中国草地分类系统，我国天然草地划分为18个大类。其中，广泛分布于我国北方的温性草原、低地草甸、山地草甸、高寒草原、高寒草甸和温性荒漠等类型，占全国天然草地总面积的85%以上，构成了我国天然草地的主体（图1）；是我国北方地区重要的绿色生态安全屏障，同时也是黄河、长江、澜沧江、滦河等主要江河的发源地和水源涵养区[2,3]。因此，北方草地对保障我国的生态安全，提升生态系统服务和稳定性具有极其重要的作用[2]。

我国约有90%左右的天然草地处于不同程度的退化之中，其中严重退化草地占60%以上。长期过度放牧、草地开垦为农田、气候变化、国家投入不足和牧区政策偏差是导致我国草原大面积退化的主要原因[2,5,6]。长期以来，我国在畜牧业生产中重视草原的生产功能，忽视其生态功能，导致生产功能过度利用，草原超载过牧、滥挖、滥垦等问题十分突出。20世纪60—80年代大面积的优质草场被开垦为农田，这是我国草原退化、生态功能和生态系统服务功能降低的最主要原因。自然因素中，气候变暖、干旱和虫鼠害等也加速了草原退化。同时，草原管理政策的偏差及管理水平相对落后也是导致我国草原退化的重要因素之一[2,5,6]。例如，我国牧区政策和经营管理模式多数照搬和套用农区，但草原牧区环境条件和生产特点与农区有很大不同。草原牧区的环境条件脆弱、气候波动性大、自然灾害多，水分是草地初级生产力最主要限制因子；同农产品生产过程相比，畜产品生产过程更加复杂，既包括植物性生产，又包括动物产品的生产；牧区的生产基础薄弱、经营粗放、利润大量流转；草地管理中需要协调生态功能和生产功能，实现人-草-畜和谐发展。大量研究表明，过度放牧

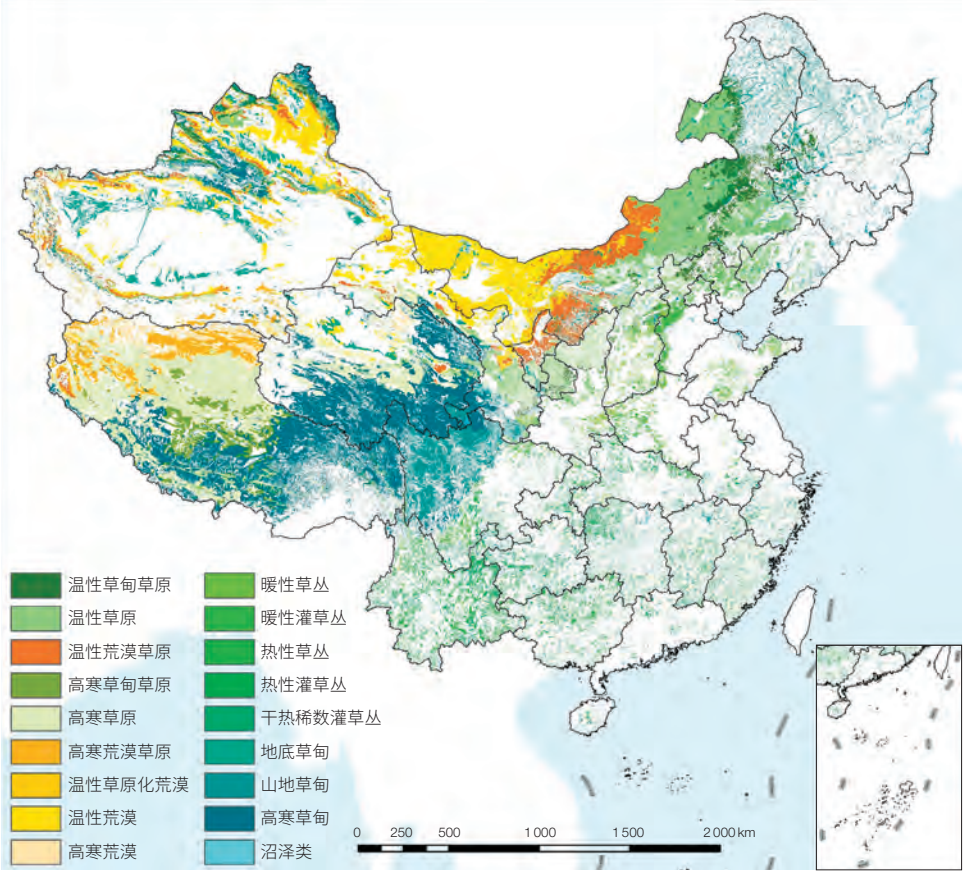


图1　中国草地类型及其分布
（港澳台地区数据缺失）

使植被覆盖度和初级生产力降低，生物多样性减少，土壤养分和水分保持能力下降；土壤侵蚀和水土流失加剧，对气候变化的敏感性增强。从而严重地影响了不同时空尺度上的生态系统功能，加速了草地的退化演替；进而使草地生态系统服务功能日益衰减，虫鼠害和沙尘暴等灾害频繁发生。这严重威胁着我国北方及其周边地区的生态安全[5-7]。2000年以来，我国先后实施了京津风沙源治理工程、退牧还草工程、草原生态保护奖励补助政策等，草原生态明显改善。然而，我国北方草地“局部改善、总体恶化”“治理速度赶不上退化速度”的被动局面亟待从根本上扭转，牧区“人-矿-草-畜”之间的突出矛盾亟待解决，草牧业生产亟待创新发展的理念。

厘清我国北方草地生态系统服务现状和空间格局，开展生态系统服务评估，制定北方草地主体功能区划，是构建和优化生态安全屏障体系，科学配置草地的生态功能和生产功能，推进生态文明、统筹山水林田湖草一体化保护和修复，建设“美丽草原”和“美丽中国”，实现人与自然和谐共生的国家重大科技需求。我国北方草地生态系统服务评估和主体功能区划成果，将为制定区域国土空间规划，科学布局重要生态系统保护和修复重大工程，统筹推进生态保护和修复工作提供重要的科技支撑。

1 生态系统服务及其价值评估

1.1 生态系统服务评估

生态系统服务是指生态系统提供的用以维持和实现人类生存与发展的环境条件和过程，是人类从生态系统获得的惠益，是人类赖以生存和发展的基础[8,9]。生态系统服务包括4个维度：支持服务、供给服务、调节服务和文化服务[9]。生态功能指生态系统各组分（如物质库）的大小及其过程（如物质循环、能量流动）的速率，包括初级生产力、碳固持、水源涵养、防风固沙、生物多样性维持等，其核心内涵是生态系统的支持服务和调节服务。生产功能是指生态系统为人类提供各种消费产品和资源（供给服务），包括家畜产品、牧草产品、食用和药用植物等[2]。

为准确评估我国草地生态系统的碳储量现状和变化，中国科学院战略性先导科技专项“生态系统固碳现状、速率、机制和潜力”（以下简称“碳专项”）设立了“中国草地生态系统的固碳现状、变化和机制”研究课题（2011—2015年）（以下简称“草地课题”）。该课题在全国不同草地类型共设置了4 207个调查样地，采用统一的调查、取样和测试方法，通过数据集成分析并结合遥感和模型手段，估算了我国草地初级生产力、植被和土壤的固碳现状与潜力[10]。本文中，全国草地的初级生产力、植被和土壤碳储量及固碳速率采用了作者主持的碳专项草地课题的部分研究结果。同时，参考其他相关研究的结果，估算了草地生态系统的水源涵养、防风固沙和生物多样性维持服务。

（1）*初级生产力*。全国天然草地植被地上生物量为5.43亿吨，地下生物量为48.36亿吨，其中内蒙古、新疆、青海、西藏、四川、甘肃、黑龙江、吉林、辽宁、河北、山西和陕西13个省份地上和地下生物量分别占全国总地上、地下生物量的68.13%和83.8%。基于植被生产力实测数据，估算出的我国草地植被净初级生产力（NPP）为$1.474\times10^{9}\,t\cdot a^{-1}$，平均为$4.99\,t\cdot hm^{-2}\cdot a^{-1}$，但不同草地类型之间NPP的差异非常大。

（2）*碳固持*。中国草地总碳储量为28.95 Pg C，其中植被碳库储量为1.82 Pg C，土壤有机碳库储量为27.13 Pg C。从空间分布来看，我国草地碳密度和碳储量均呈现从西北向东南逐渐降低的趋势（图2）。其中，内蒙古、新疆、青海和西藏4个省份草地分布面积最广，草地碳储量最大，分别为6.80、6.13、5.68和5.40 Pg C，合计占我国草地总碳储量的60%。其次是四川、黑龙江、云南和甘肃，碳储量分别为

2.97、2.28、1.70 和 1.46 Pg C，贡献了全国草地碳储量的 21%。其他 23 个省份由于草地分布面积较小或总碳密度相对较低等原因，草地碳储量仅占全国草地碳储量的 19%。与森林不同，草地植被碳的绝大部分被储存在地下根系中，根系碳储量占草地植被碳储量的 92%。土壤碳库作为草地生态系统碳储量最主要的组成部分，其碳密度为植被碳密度的 19 倍。我国草地植被平均固碳速率为 250 t C · hm^{-2} · a^{-1}，年固碳量为 1 215 Tg C。这与遥感模型反演结果基本一致——基于 1981—2013 年遥感植被指数（NDVI）数据和 CASA 模型反演估算我国草地植被年固碳量为 1 160 Tg C。从草地类型上，高寒草地植被年固碳量为 734 Tg C，温性草地为 182 Tg C，暖性和热性草丛/灌草丛为 56 Tg C，隐域性草甸类草地等为 233 Tg C。各省份中，草地面积大的省份其年净固碳量也高，其中西藏、青海、四川、内蒙古和新疆分别占全国草地年固碳量的 34%、20%、12%、9% 和 9%。

（3）水源涵养。基于土地覆被、降水、NDVI 等

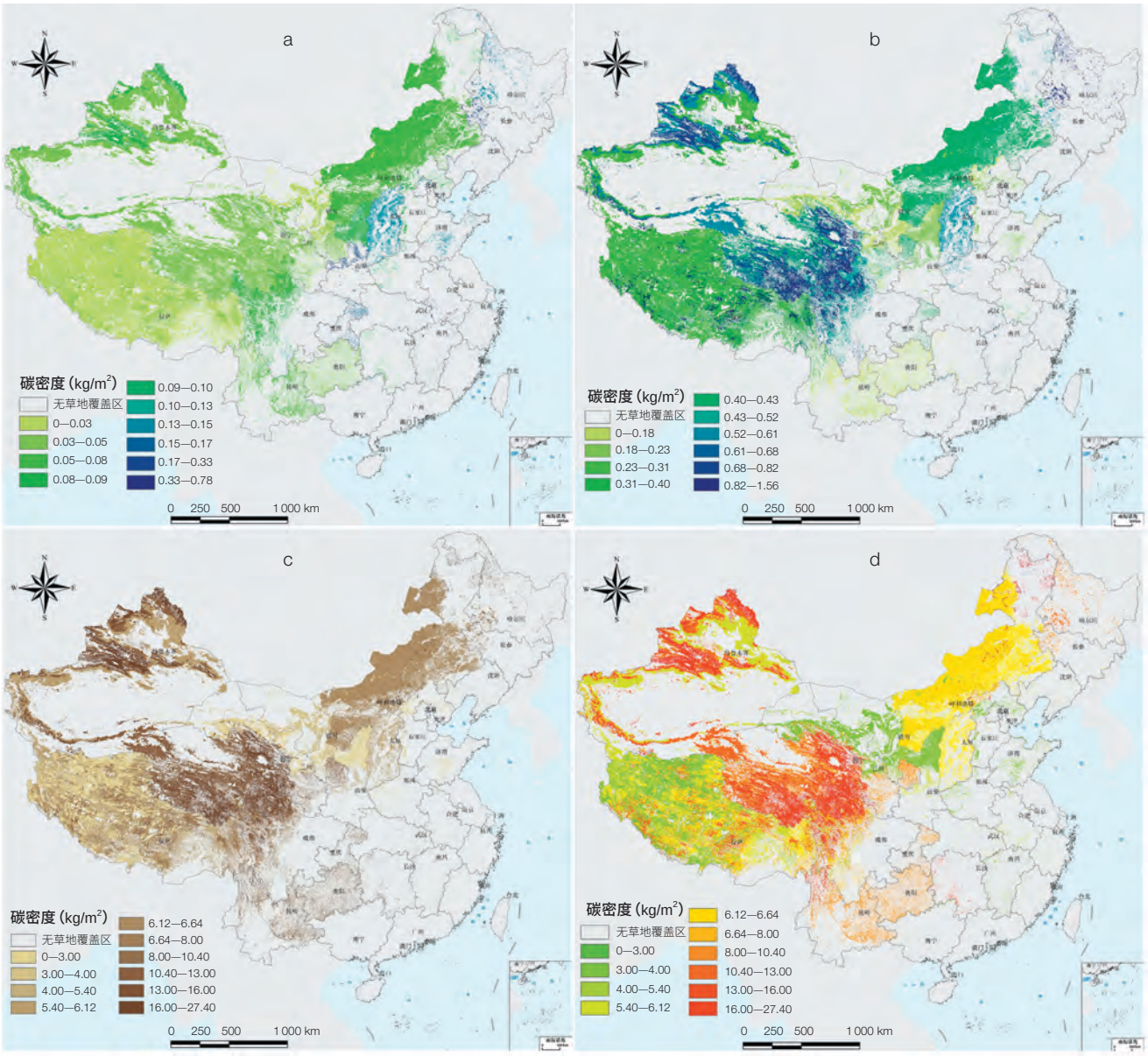


图 2　中国草地植被地上（a）- 地下（b）、土壤（c）和生态系统（d）总碳密度的空间分布
（港澳台地区数据缺失）

数据，采用降水贮存量法估算的中国草地 1980—2000 年平均水源涵养量为 $1.1617\times10^{11}\ m^3\cdot a^{-1}$，其中我国北方草地为 $3.747\times10^{10}\ m^3\cdot a^{-1}$。2000—2010 年中国草地平均年水源涵养量为 $1.1838\times10^{11}\ m^3\cdot a^{-1}$，其中北方草地为 $4.093\times10^{10}\ m^3\cdot a^{-1}$ [11]。北方草地水源涵养服务的空间异质性较大，主要集中在青藏高原和内蒙古高原中东部区域，其中西藏草地 1990—2010 年平均水源涵养量为 $2.749\times10^{10}\ m^3\cdot a^{-1}$ [12,13]；内蒙古锡林河流域草地（9 786 km^2）水源涵养量为 $4\times10^7\ m^3\cdot a^{-1}$ [14]。

（4）防风固沙。防风固沙是干旱与半干旱草地提供的重要生态系统服务，其物质量可以通过风蚀模型，如修正的风蚀方程模型（RWEQ）和土壤流失方程（RUSLE），进行估算。相关研究对我国北方草地部分区域开展了防风固沙量的估算。例如，孙建等 [15]利用修正的通用土壤流失方程估算 1984—2013 年青藏高原草地防风固沙量为 $2.72\times10^7\ t\cdot a^{-1}$；孙文义等[16]估算黄土高原草地 1990—2010 年防风固沙量为 $7.7\times10^9\ t\cdot a^{-1}$；王洋洋等[17]利用 RWEQ 模型估算的宁夏草地 2000—2015 年防风固沙量为 7.298×10^6—$4.120\times10^7\ t\cdot a^{-1}$；江凌等[18]对内蒙古草地的防风固沙量估算值为$5.758\times10^9\ t\cdot a^{-1}$。

（5）生物多样性维持。据不完全统计，全国草地植物共计 254 科、4 000 多属、9 700 多种。其中，有毒植物 52 科、138 属、316 种[19,20]。另外，我国草原区繁衍的野生动物达 2 000 多种，其中国家一级保护动物 14 种、二级保护动物 30 多种。丰富的生物多样性资源构成了我国野生动植物资源基因库，特别是耐旱、耐寒、耐盐和药用植物最重要的基因库。目前，受长期过度放牧、开垦、气候变化、环境污染以及生物入侵等因素的影响，我国草地生物多样性明显降低，进而引起草地生态功能下降和生态系统稳定性的降低[21-23]。

1.2 生态系统服务价值评估

生态系统服务价值评估是制定区域生态环境保护、生态经济核算和生态补偿决策，开展生态功能区划，保护和恢复自然生态系统的重要依据和基础[24]。自 1997 年 Costanza 等[25]首次对全球主要生态系统类型开展服务价值评估以来，国内外研究学者对草地生态系统服务价值开展了大量相关研究工作[26]。我国全国草地生态价值核算可信度较高范围为 0.87 万亿—7.5 万亿元人民币[26]。

依据相关文献值进行估算[27-30]，我国平均单位面积草地生态服务价值为 1 920.5—4 475.8 元/hm^{-2}。按北方草地面积约 $3\times10^8\ hm^2$ 换算，北方草地生态服务价值为 5 764.5 亿—13 452.0 亿元人民币。不同区域和草地类型的生态系统服务价值相差悬殊。其中，沼泽类草地生态系统服务价值最高，其次为暖性灌草丛、暖性草丛、低地草甸、温性草甸草原、温性草原、高寒草甸、高寒草原等，而高寒荒漠价值最低。从区域上看，内蒙古东部的呼伦贝尔、科尔沁和锡林郭勒草原，新疆西北部及青藏高原东部、东北部等地区的单位面积服务价值较高，而内蒙古中西部和青藏高原西部地区单位面积服务价值较低。

2 生态功能区划原则与方法

生态功能区划是根据区域生态系统类型、生态环境敏感性、生态系统受胁迫过程与效应，以及生态系统结构、过程和服务等特征的空间分异规律而进行的地理空间分区。1976 年，美国生态学家 Bailey 首次从生态系统角度提出并编制美国生态区划方案。此后，国内外生态学家和国际组织对生态区划原则、指标体系、分区方法等进行了细化和完善[24,31]。我国生态区划起步相对较晚，最具代表性的是傅伯杰等[31]开展的中国生态功能区划。2008 年，环境保护部和中国科学院联合发布《全国生态功能区划》，将全国划分为 3 类 31 个生态功能一级区，9 类 67 个生态功能二级区，以及 208 个生态功能三级区。该区划明确了保障国家生态安全的重要区域，为我国自然资源合理管理

和可持续利用、经济社会与生态保护协调、健康发展提供了科学指导。2012 年，谢高地等[24]在基于已有三级生态区划方案，以中国县域尺度为最小区划单元，将中国分成 33 个水源涵养功能区、57 个水土保持功能区、19 个防风固沙功能区、11 个沿海防护功能区、62 个产品提供功能区和 86 个生物多样性保护功能区。贾慎修等[3]在 20 世纪 80—90 年代开展的全国首次草原普查的基础上，结合地貌、土壤、植被等生态因素，以草地资源空间分异规律为原则，提出了我国首个草地资源区划。该区划将全国草地分为 7 个区、29 个亚区、74 个小区。然而，该区划以自然区划为主，未考虑人类活动和气候变化对草地生态系统结构、功能和服务的影响。

当前，面向生态文明、“美丽中国”建设和统筹山水林田湖草一体化保护和修复的国家重大战略需求，亟待构建我国草地特别是北方草地的主体功能区划；综合考虑草地生态服务和生态承载力，科学指导和合理配置草地的生态功能和生产功能，进而为制定区域国土空间规划，科学布局北方草地重要生态系统保护和修复重大工程，统筹推进生态保护和修复工作提供重要的科技支撑。

（1）我国北方草地生态功能区划原则。① 生态要素区域分异原则。以气候、地形、土壤、植被等自然要素的地域分异规律为依据。② 主导性原则。以草地类型区域分异为基础，气候、地貌等因素差异服从主要草地类型的分异，同时兼顾不同草地类型的生态系统服务，且非主导功能服从主导功能。③ 生态优先和绿色发展相结合原则。坚持生态优先、因地制宜的原则，兼顾草地生产和社会经济条件、草地利用强度、畜牧业布局和发展方向及草地经营管理、培育技术、自然保护地和国家公园等，合理配置生态功能和生产功能。④ 分级区划原则。照顾行政区界，特别是县域的完整性。

（2）我国北方草地生态功能区划方法。以草地类型、中国草地资源区划和生态服务功能区划为基础，综合考虑气候湿润度、地形、土壤、植被覆盖度等重要生态参数，生态系统服务（包括初级生产力、碳固持、水源涵养、防风固沙、生物多样性维持等），以及土地沙化、盐渍化等生态敏感性评价，兼顾县界完整性确定分区方案和各分区之间的界线（图 3）。

3 生态功能区分区概述与实施措施

3.1 生态功能分区概述

以地名+草地类或亚类为命名方法，根据上述分区原则和方法，将我国北方草地划分为 7 个生态功能区，25 个亚区（图 4），各区的名称、主体生态功能、气候条件、主要问题和生态敏感性详见表 1。

3.2 北方草地各生态功能区实施措施

面向统筹山水林田湖草一体化保护和修复、生态文明和“美丽中国”建设的国家重大需求，依据上述分区方案、各生态区面临的主要问题及其生态和环境敏感性，坚持生态优先的原则，综合考虑生态系统服务和生态承载力的空间分异，以合理配置草地的生态-生产功能为切入点，提出了各生态区应采取的重点措施。

（1）湿润半湿润草甸草原与草甸区。该区生态系统服务和生态功能的核心是水源涵养、碳固持、土壤保持和生物多样性保护。在实施措施上，坚持生态优先，生产-生态有机结合的原则，严格实施以草定畜，从根本上遏制超载过牧和草地退化的势头；采取禁牧、休牧、减牧、轮牧等管理措施，加速退化草地的恢复；严格限制矿产资源开发，保护黑土，禁止开垦草原等行为；采用乡土草种补播、土壤生物修复、施肥、松土、切根等措施，加速严重退化草地的恢复和重建；同时，创新草牧业发展方式，发展高效人工草地、优质草产品加工、草原特色生物种养技术，探索草牧业高质量发展的新模式。

（2）半干旱草原区。该区生态系统服务和生态功

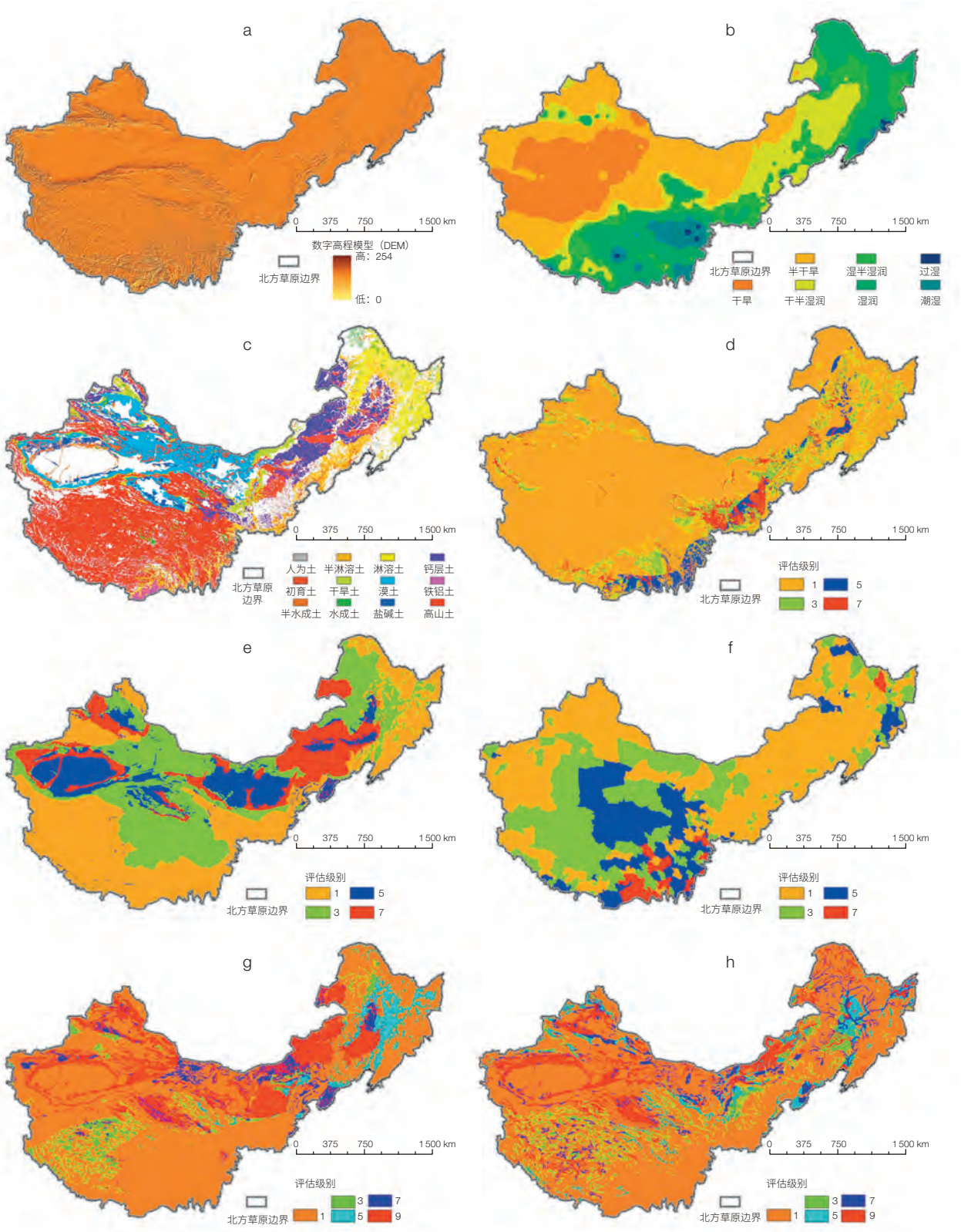


图 3　我国北方草地地形（a）、气候（气候 - 湿润指数，b）、土壤（土壤类型，c；土壤保持重要性等级，d）、生态参数（防风固沙重要性评估，e；生物多样性维持与保护评估，f）及敏感性评估（沙漠化敏感性，g；盐渍化敏感性评估，h）

湿润指数来源于中国气象背景数据集（http://www.resdc.cn/DOI）；土壤类型来源于《1∶100 万中华人民共和国土壤图》；生态系统服务与敏感性评估来源于中国生态系统评估与生态安全数据库（http://www.ecosystem.csdb.cn/ecoass/ecoplanning.jsp）

表1　我国北方草地生态功能区分区概况、主体功能和生态敏感性

I级区	亚区代码	亚区名称	亚区面积（hm^2）	主体功能	国家级自然保护区数量（占该亚区土地面积比）	气候条件			主要问题和生态敏感性
						年平均降水量（mm）	年平均温度（℃）	干燥度	
湿润半湿润草甸草原与草甸区	I-1	三江平原低地草甸亚区	1.0×10^7	水源涵养、碳固持、水文调节	14（17.8%）	558.5	2.9	0.9	湿地和沼泽面积减少，水源涵养和固碳能力降低，水文调节能力下降；气候变化和湿地开垦敏感区
	I-2	大、小兴安岭山地丘陵灌丛与草甸草原亚区	3.3×10^7	水源涵养、土壤保持、生物多样性保护	29（6.5%）	504.2	2.4	0.8	生物多样性减少、原始生态系统受到威胁；水土流失、生物多样性极敏感区
	I-3	长白山山地丘陵灌丛与草甸草原亚区	2.2×10^7	水源涵养、土壤保持、生物多样性保护	25（5.2%）	699.0	3.2	0.8	水土流失、水环境污染，植被退化、景观破碎化严重，土地生产力低；生物多样性、水土流失、气象灾害敏感区
	I-4	松嫩-辽河平原东部草甸与草甸草原亚区	2.0×10^7	土壤保持、水源涵养	17（1.5%）	603.0	5.1	0.9	草原退化、土壤沙化、盐渍化严重，土地生产力低；土壤侵蚀和土地沙化敏感区
	I-5	松嫩-辽河平原西部草甸草原与科尔沁沙地亚区	1.9×10^7	防风固沙、土壤保持	19（4.2%）	440.6	5.5	1.3	草地沙化、盐渍化、退化现象严重；气象灾害、流沙侵蚀、盐渍化敏感区
	I-6	大兴安岭南部丘陵草甸草原亚区	1.6×10^7	土壤保持、生物多样性保护	8（6.3%）	414.2	2.2	1.2	草原退化、沙化严重；生物多样性与土壤侵蚀高度敏感
	I-7	内蒙古高原东部草甸草原与呼伦贝尔沙地亚区	0.6×10^7	防风固沙、土壤保持、生物多样性保护	2（9.6%）	360.2	3.3	1.2	草原退化、沙化严重，土壤侵蚀、风沙危害严重；生物多样性敏感区
半干旱草原区	II-1	内蒙古高原中东部典型草原-浑善达克沙地亚区	2.5×10^7	防风固沙、土壤保持、生物多样性保护	5（7.7%）	307.0	1.8	1.4	草原退化、沙化严重；土地退化、生物多样性极敏感区
	II-2	内蒙古高原西部荒漠草原亚区	1.1×10^7	防风固沙、土壤保持	1（1.4%）	182.5	4.5	3.0	我国沙尘暴风沙源之一，土壤风蚀、流沙危害严重；生物多样性极敏感区
	II-3	黄土高原半干旱草原亚区	2.0×10^7	水土流失控制、防风固沙	8（1.5%）	417.6	6.4	1.4	土地沙化、风蚀和水蚀严重；水土流失、盐渍化和土壤侵蚀敏感区
	II-4	鄂尔多斯高原毛乌素沙地与荒漠草原亚区	1.3×10^7	生物多样性保护、防风固沙、土壤保持	5（7.5%）	238.7	6.0	2.8	草地退化、沙化和水土流失严重；生物多样性敏感区，土壤侵蚀高敏感区
暖性灌草丛区	III-1	燕山-太行山山地丘陵暖性灌草丛亚区	1.0×10^7	水源涵养、土壤保持	8（2.1%）	502.7	6.0	1.2	水土流失重、生态承载力低；土壤侵蚀敏感区
	III-2	华北东部平原丘陵暖性灌草丛亚区	0.5×10^7	生物多样性保护、水源涵养	3（0.6%）	530.7	11.7	1.4	干旱缺水、盐渍化严重；水胁迫高度敏感，地质灾害频发，西北部局部为沙化敏感区
	III-3	华北西部山地丘陵暖性灌草丛亚区	1.6×10^7	土壤保持	15（1.6%）	547.8	8.4	1.2	植被覆盖度低、水土流失严重；土壤侵蚀敏感区

（续表）

干旱荒漠-绿洲-山地草地区	IV-1	阿拉善高原-河西走廊荒漠亚区	4.9×10^7	防风固沙、生物多样性保护	14（12.2%）	105.2	5.5	8.7	草地退化、沙化严重，沙丘活化，威胁绿洲安全和生物多样性保护；土地退化高度敏感
	IV-2	阿尔泰-准噶尔盆地北部荒漠与山地草原亚区	2.0×10^7	防风固沙、土壤保持、生物多样性保护	5（2.0%）	177.0	2.5	5.2	草地退化、沙化严重，虫鼠害频发；生物多样性和生境高度敏感
	IV-3	天山北坡-准噶尔盆地南部荒漠和山地草原亚区	2.9×10^7	生物多样性保护、土壤保持	5（2.2%）	225.3	3.6	5.4	草地退化、沙化、水土流失、局地盐渍化严重；该区西部生物多样性和生境高度敏感，而东部土地退化和土壤侵蚀高度敏感
	IV-4	塔里木-柴达木盆地荒漠-绿洲亚区	16.0×10^7	防风固沙、生物多样性保护	3（6.5%）	66.1	8.5	11.2	草地退化、沙化、虫鼠害严重；土壤盐渍化不断加剧，危及绿洲和生物多样性；土地沙化高度敏感、盐渍化、生物多样性和生境极敏感
高寒草甸区	V-1	甘南高寒草甸亚区	0.4×10^7	水源涵养、生物多样性保护	1（21.0%）	589.7	0.7	1.1	过度放牧、超载严重，草地退化严重；土壤侵蚀和生多样性敏感区
	V-2	祁连山山地高寒草原亚区	1.3×10^7	生物多样性保护、防风固沙	4（7.5%）	336.4	2.9	1.9	草地退化、土地沙化严重，水源涵养能力下降；生物多样性及生境高度敏感，土地沙化与土壤侵蚀中轻度敏感
	V-3	三江源高寒草甸-高寒草原亚区	3.7×10^7	生物多样性保护、水源涵养	国家公园1个（100%）	391.7	5.1	1.0	草地退化、流动沙丘及沙害、荒漠化严重，生物多样性减少，水源涵养能力降低
	V-4	藏东-川西高寒草甸亚区	5.6×10^7	水源涵养、土壤保持	29（7.6%）	625.9	2.0	1.1	草地退化、荒漠化、水土流失和山地灾害严重，土壤侵蚀和野生动物生境高度敏感，沙化中度敏感；生物多样性敏感区
高寒草原区	VI-1	藏西南高寒草原-温性草原亚区	4.9×10^7	生物多样性保护、土壤保持	5（39.6%）	228.1	4.5	1.5	草地退化严重；沙化、盐渍化敏感性较高
	VI-2	藏西高寒草原区	2.4×10^7	生物多样性保护、土壤保持、水源涵养	3（18.8%）	335.5	0.9	1.6	草地退化严重；水土流失和沙化敏感性较高
高寒荒漠区	VII-1	昆仑山西段荒漠区	9.1×10^7	生物多样性保护	1（27.4%）	81.9	4.6	10.8	野生动物生境高度敏感

能的核心是防风固沙和土壤保持。在实施措施上，坚持生态优先、适度利用的原则，严格控制载畜量，遏制超载过牧、草地退化的势头，并将一部分生态空间和承载力还给野生动物；采用乡土草种补播、土壤生物修复等措施，加速修复沙化、风蚀、水蚀、水土流失、盐渍化草地，提升生态系统服务和稳定性；采取禁牧、休牧、减牧、轮牧等管理措施，从根本上解决草-畜矛盾，加速退化草地的恢复；严格限制矿产资源开发，禁止开垦草原；创新草牧业发展方式，适度发展生态旅游业，探索草原生态保护与草牧业高质量发

图 4　我国北方草地生态功能区划图

展的新范式。

（3）暖性灌草丛区。该区生态系统服务和生态功能的核心是水源涵养和土壤保持。在实施措施上，坚持保护优先，限制利用的原则，加大坡耕地退耕还草、还林；根据生态系统内在机理和规律，科学配置植被恢复中草-灌-乔的比例、植物-水分关系和人工植被群落结构，加速植被恢复，有效控制水土流失，提高生物多样性和生态系统稳定性；同时，在植被恢复中坚持以自然修复为主，工程措施为辅，加速退化草地的恢复；严格限制矿产开发；因地制宜适度发展生态旅游业。

（4）干旱荒漠-绿洲-山地草地区。该区生态系统服务和生态功能的核心是防风固沙、水土保持和生物多样性保护。干旱区人类生存和发展依托于绿洲系统，因此在实施措施上，坚持生态优先，根据水资源和生态承载力确定利用方式和利用强度，合理调配流域内的水资源，控制人工绿洲规模，发展节水农业，提高水资源利用效益；严格限制放牧等生产活动，保护荒漠植被；加大力度修复严重沙化、风蚀、水蚀、水土流失、盐渍化的草地；建立和完善以国家公园为主体的自然保护地体系，将大部分荒漠区纳入自然保护地，发展可控的荒漠和绿洲旅游业；探索脆弱荒漠

草原生态保护与沙产业发展的新范式。

（5）高寒草甸区。该区生态系统服务和生态功能的核心是水源涵养、土壤保持和生物多样性保护。在实施措施上，坚持生态优先，生产-生态有机结合的原则，严格实施以草定畜，控制载畜量，从根本上遏制超载过牧；将部分生态空间和承载力还给野生动物，建立和完善以国家公园为主体的自然保护地体系，适度发展特色生态旅游业；采取禁牧、休牧、减牧、轮牧等管理措施，加速退化草地的恢复；采取乡土草种补播、土壤生物修复等措施加速严重退化草地的恢复和重建；探索草牧业高质量发展的新模式。

（6）高寒草原区。该区生态系统服务和生态功能的核心是生物多样性保护和水源涵养。在实施措施上，坚持生态优先的原则，控制人类活动强度和载畜量，将不小于 50% 的生态空间和承载力还给野生动物；建立和完善以国家公园为主体的自然保护地体系，严格限制脆弱高寒草原特色生态旅游业；采取禁牧、休牧、减牧、轮牧及杜绝乱樵滥采野生植物等管理措施，加速退化草地的恢复。

（7）高寒荒漠区。该区生态系统服务和生态功能的核心是生物多样性保护。实施措施上，应限制人类活动对自然生态系统的干扰，严格保护野生动植物资源，建立以国家公园为主体的自然保护地体系，将绝大部分生态空间还给野生动物。

4 实施北方草地生态功能区划的保障措施

实施北方草地生态功能区划对坚持生态优先，科学配置草地的生态功能和生产功能，统筹山水林田湖草一体化保护和修复，构建我国北方生态安全屏障体系，推进生态文明和“美丽中国”建设，实现绿色发展和高质量发展具有重要意义。为此，我们提出了实施北方草地生态功能区划的 8 项保障措施。

（1）划定生态保护红线，科学布局国土生态安全空间。基于各生态功能区的主体功能和生态敏感性，确定生态保护红线，推进和优化以国家公园为主体的自然保护地体系建设，稳步推进国家公园体制试点工作，完善国家级自然保护区空间布局，科学配置草地的生态功能，是实施北方草地生态功能区划、优化国土空间格局、筑牢我国北方生态安全屏障体系的重要举措。同时，加强北方草地生态功能区划实施同《全国重要生态系统保护和修复重大工程总体规划（2021—2035 年）》（以下简称《总体规划》）的衔接，从自然生态系统演替规律和内在机理出发，科学布局北方重要生态系统保护和修复重大工程。目前，我国草地生产功能研究基础较好，但生态功能研究基础薄弱，应依托生态系统野外科学观测研究站网络，加强重要草地生态系统演替规律和内在机理研究，以及生态修复技术体系和试验示范模式研发工作，为实施《总体规划》提供科技支撑。

（2）统筹生态和生产用水比例，创新畜牧业发展模式。水分是北方草地生态系统服务的关键驱动因子。因此，基于水资源承载力及其空间分异和动态变化，统筹和优化生态、生产、生活等用水比例是维持和提升北方草地生态系统服务（包括初级生产力、碳固持、水源涵养、生物多样性保育、防风固沙、土壤保持等）的重要抓手，也是科学配置其生态功能和生产功能的重要基础。在湿润半湿润草原区、农牧交错区及部分绿洲区，根据水资源的承载力，利用部分进行轮作和休闲的耕地，发展适度规模的高效人工草地和营养体农业，从而提升饲草和饲料的生产力水平，减少畜牧业对天然草地的过度依赖，创新畜牧业发展模式，是加速退化草地恢复的有效途径。

（3）缓解牧区草-畜矛盾，提升草地生态功能。超载过牧是当前北方草地面临的突出问题，也是导致草地大面积退化的重要原因。坚持保护优先的原则，根据草地的退化程度和利用状况，因地制宜地采取禁牧、休牧、减牧、轮牧及打草场轮刈休闲等草地管理措施和技术，从根本上减轻长期过度利用对草地的压

力。这是缓解牧区草-畜矛盾，加速退化生态系统自然恢复和自我修复，提升其生态功能的重要抓手。例如，内蒙古自治区从 2001 年开始探索春季休牧，即每年在牧草返青期的 4—5 月进行为期 30—60 天的休牧，加速退化草地的恢复。该项措施已在内蒙古、青海、西藏等省份大面积推广。一些长期坚持春季休牧措施的地区，其草地退化状况已明显好转。2020 年，黑龙江省决定对全省 17 个县（市、区）的草地集中连片进行每年为期 7 个月（4 月 15 日—11 月 15 日）的禁牧，进一步探索禁牧对草原生态修复的作用，推动畜牧业转型发展。

（4）根据草地退化程度和特点制定科学的修复策略。我国北方草地的大面积退化从 20 世纪 70 年代开始，经历了 50 多年的演变和发展过程。其中，90% 左右的天然草地发生了不同程度的退化，其中严重退化草地占 60% 以上。因此，草地生态系统保护和修复是一项长期的任务，应根据草地的退化程度和特点，因地制宜制定科学的修复措施。特别是对于重度退化草地，由于生态系统结构严重退化、功能严重丧失，其生态修复需要经过 3 个关键阶段，即植被建植、结构优化和功能提升（图 5）。① 植被建植阶段。需要解决的关键科技问题是如何构建以先锋植物为主的植物群落，实现由“黄（裸地或沙地）变绿”或由“黑（黑土滩）变绿”的目标，该阶段需要采用生物和工程措施相结合的修复技术。② 结构优化阶段。需要解决的关键科技问题是如何通过免耕补播乡土优势物种等措施，使原生群落的优势物种及其多度显著增加，先锋植物的多度逐渐减少，植物群落结构得到优化。③ 功能提升阶段。其科技目标是植物、土壤和土壤生物群落结构进一步优化，基本实现近自然恢复，其生态系统功能和稳定性显著提升。实现这 3 个关键阶段的修复目标需要十几年甚至几十年的时间，特别是土壤和土壤生物群落的恢复。因此，重度退化草地的生态修复工程，应根据这 3 个关键阶段的特点，制定相应的技术措施、修复目标和草地管理措施。例如，在植被建植阶段需要禁牧，在结构优化阶段只能轻度利

图 5　重度退化草地生态修复的 3 个关键阶段

用，而在功能提升阶段可以合理利用。

（5）提升饲草收获与加工的科技水平。我国草原牧区植物生长季较短，冬季漫长，风雪灾害频发，繁殖母畜的安全越冬很大程度上依赖于秋季收获的干草储备。目前，我国草原牧区饲草收获、打捆、加工和贮藏技术落后，同畜牧业发达国家相比具有很大的差距。牧草收获加工过程中由于干燥时间延长和叶片脱落引起的粗蛋白、维生素损失十分巨大，加上饲草储备设施简陋使干草品质进一步降低，不能满足繁殖母畜对饲草的营养和能量需求，草原畜牧业难以摆脱粗放、落后的经营模式。因此，亟待大力推广饲草收获、压扁、打捆、加工、贮藏等新装备、新工艺和新技术，提升饲草收获与加工的科技水平，实现饲草储备“粮食化”。

（6）实现牧民收入的多元化。探索适合我国草原牧区特点的家庭牧场、牧民协会、牧民合作社等规模化经营模式，创新和完善我国牧区科学发展的体制和机制。同时，适度发展生态旅游、民族文化、特色生物资源产业，实现牧民收入的多元化。

（7）完善草原生态保护补助奖励长效机制。进一步完善草原生态保护补助奖励机制，提高补奖标准，延长奖补年限，增加生态保护补助奖励资金在牧民家庭收入中占比，实现生态保护与牧民增收的“双赢”。同时，建立严格的保护成效监测、检查和考核机制，从根本上遏制超载过牧和草原大面积退化的势头。

（8）发展教育事业，提升牧区文化生活水平。大力发展义务教育、职业教育、高等教育和牧区社会事业，不断提高牧区人口素质、科学文化水平、健康水平和生活质量，实现科技移民、教育移民和发展移民，有效降低生态环境脆弱区的人口压力，促进民族团结和社会稳定。

参考文献

1 White R P, Murray S, Rohweder M. Pilot Analysis of Global Ecosystems: Grassland Ecosystems. Washington: World Resources Institute, 2000.

2 白永飞, 黄建辉, 郑淑霞, 等. 草地和荒漠生态系统服务功能的形成与调控机制. 植物生态学报, 2014, 38(2): 93-102.

3 中华人民共和国农业部兽医司, 全国畜牧兽医总站. 中国草地资源. 北京: 中国科学技术出版社, 1996.

4 李博. 中国北方草地退化及其防治对策. 中国农业科学, 1997, 30(6): 1-9.

5 白永飞, 潘庆民, 邢旗. 草地生产与生态功能合理配置的理论基础与关键技术. 科学通报, 2016, 61(2): 70-81.

6 韩俊. 中国草原生态问题调查. 上海: 上海远东出版社, 2011.

7 杜青林. 中国草业可持续发展战略. 北京: 中国农业出版社, 2006.

8 Daily G C. Nature’s Services Societal Dependence on Natural Ecosystems. Washington DC: Island Press, 1997.

9 Millennium Ecosystem Assessment. Ecosystem and Human Well-being. Washington DC: Island Press, 2005.

10 白永飞, 陈世苹. 中国草地生态系统固碳现状、速率和潜力研究. 植物生态学报, 2018, 42(3): 261-264.

11 吴丹, 邵全琴, 刘纪远, 等. 中国草地生态系统水源涵养服务时空变化. 水土保持研究, 2016, 23(5): 256-260.

12 龚诗涵, 肖洋, 郑华, 等. 中国生态系统水源涵养空间特征及其影响因素. 生态学报, 2017, 37(7): 2455-2462.

13 黄麟, 曹巍, 吴丹, 等. 西藏高原生态系统服务时空格局及其变化特征. 自然资源学报, 2016, 31(4): 543-555.

14 张雪峰, 牛建明, 张庆, 等. 内蒙古锡林河流域草地生态系统水源涵养功能空间格局. 干旱区研究, 2016, 33(4): 814-821.

15 Sun J, Liu Y, Zhou T C, et al. Soil conservation service on the Tibetan Plateau, 1984-2013. Earth & Environmental Science Transactions of the Royal Society of Edinburgh, 2019, 109(3-4): 445-451.

16 孙文义, 邵全琴, 刘纪远. 黄土高原不同生态系统水土保持

服务功能评价. 自然资源学报, 2014, 29(3): 365-376.

17 王洋洋, 肖玉, 谢高地, 等. 基于RWEQ的宁夏草地防风固沙服务评估. 资源科学, 2019, 41(5): 980-991.

18 江凌, 肖燚, 饶恩明, 等. 内蒙古土地利用变化对生态系统防风固沙功能的影响. 生态学报, 2016, 36(12): 3734-3747.

19 徐柱, 闫伟红, 刘天明, 等. 中国草原生物多样性、生态系统保护与资源可持续利用. 中国草地学报, 2011, 33(3): 1-5.

20 赵宝玉. 中国天然草地有毒有害植物名录. 北京: 中国农业科学技术出版社, 2016.

21 Bai Y F, Wu J G, Clark C M, et al. Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. Journal of Applied Ecology, 2012, 49(6): 1204-1215.

22 Bai Y F, Wu J G, Pan Q M, et al. Positive linear relationship between productivity and diversity: Evidence from the Eurasian Steppe. Journal of Applied Ecology, 2007, 44(5): 1023-1034.

23 Bai Y F, Han X G, Wu J G, et al. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature, 2004, 431(7005): 181-184.

24 谢高地, 张昌顺, 张林波, 等. 保持县域边界完整性的中国生态区划方案. 自然资源学报, 2012, 27(1): 154-162.

25 Costanza R, D'Arge R, de Groot R, et al. The value of the world's ecosystem services and natural capital. Nature, 387(6630): 253-260.

26 Xie G D, Zhen L, Lu C X, et al. Applying value transfer method for eco-service valuation in China. Journal of Resources and Ecology, 2010, 1(1): 51-59.

27 陈仲新, 张新时. 中国生态系统效益的价值. 科学通报, 2000, 45(1): 17-22.

28 赵同谦, 欧阳志云, 贾良清, 等. 中国草地生态系统服务功能间接价值评价. 生态学报, 2004, 24(6): 1101-1110.

29 欧阳志云, 王如松. 生态系统服务功能、生态价值与可持续发展. 世界科技研究与发展, 2000, 22(5): 45-50.

30 谢高地, 张钇锂, 鲁春霞, 等. 中国自然草地生态系统服务价值. 自然资源学报, 2001, 16(1): 47-53.

31 傅伯杰, 刘国华, 陈利顶, 等. 中国生态区划方案. 生态学报, 2001, 21(1): 2-7.

Assessment of Ecosystem Services and Ecological Regionalization of Grasslands Support Establishment of Ecological Security Barriers in Northern China

BAI Yongfei[1,2,3*] ZHAO Yujin[1,2] WANG Yang[1,2] ZHOU Kailing[1,3]

（1 State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China;

2 Inner Mongolia Grassland Ecosystem Research Station, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China;

3 College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China）

Abstract Grassland ecosystems of Northern China, the headwaters region and water resource conservation areas for the Yellow River, the Yangzi River, the Lancang River, and the Luanhe River, are important ecological security barriers in China. They play extremely important roles in maintaining multiple ecosystem functions and services and sustaining multinational cultural diversity. However,

* Corresponding author

the grassland ecosystems of Northern China have experienced widespread deterioration in functions and services since the last several decades due to the overexploitation of production functions at the cost of their ecological functions. Therefore, assessment of ecosystem services and ecological regionalization of grasslands in Northern China are needed for optimizing their production functions and ecological functions, establishing ecological security barriers, and achieving ecological civilization. Based on the spatial patterns of key ecosystem services and environmental conditions, we propose seven ecoregions and twenty-five sub-ecoregions across grassland ecosystems in Northern China. The ecological regionalization of grasslands can be used to guide sustainable grassland management, restoration of degraded grasslands, and biodiversity conservation in Northern China.

Keywords grasslands of Northern China, ecosystem services, value of ecosystem services, ecological regionalization, optimizing production functions and ecological functions, ecological security barrier

白永飞 中国科学院植物研究所研究员、博士生导师，中国科学院大学岗位教授，中国科学院内蒙古草原生态系统定位研究站站长。2008年国家杰出青年科学基金获得者，2011年入选内蒙古自治区“草原英才”。主要研究领域：草原生物多样性与生态系统功能的形成和维持机制，生态系统服务对全球变化驱动因子的敏感性和响应机制；退化草原修复与生态系统管理。发表各类研究论文150余篇，其中 *Nature*、*PNAS*、*Ecology Letters*、*Ecology*、*Journal of Applied Ecology*、*Global Change Biology* 等SCI期刊论文120余篇。E-mail: yfbai@ibcas.ac.cn

BAI Yongfei Principle Investigator and Ph.D. Supervisor of Institute of Botany, Chinese Academy of Sciences (CAS), Professor of the University of Chinese Academy of Sciences, and Director of the Inner Mongolia Grassland Ecosystem Research Station, CAS. He won the “Distinguished Young Scholar Program” of the National Natural Science Foundation of China (NSFC) in 2018. He serves as the President of the Plant Ecology Branch of the Chinese Society for Plant Sciences. His main research areas include: relationships between biodiversity and multiple ecosystem functions; sensitivity and responses of ecosystem services to global change drivers; and restoration of degraded grasslands and ecosystem management. He has published more than 150 papers in peer reviewed journals, such as *Nature*, *PNAS*, *Ecology Letters*, *Ecology*, *Journal of Applied Ecology*, and *Global Change Biology*. E-mail: yfbai@ibcas.ac.cn.

■责任编辑：文彦杰

科学通报
评 述
《中国科学》杂志社
SCIENCE CHINA PRESS

放牧对草地生态系统磷循环的调控机制: 研究进展与展望

乌力吉[1,2], 李响[2], 赵萌莉[1], 白永飞[2,3*]

1. 内蒙古农业大学草原与资源环境学院, 呼和浩特 010011;
2. 中国科学院植物研究所植被与环境变化国家重点实验室, 北京 100093;
3. 中国科学院大学资源与环境学院, 北京 100049
* 联系人, E-mail: yfbai@ibcas.ac.cn

2020-03-25 收稿, 2020-05-03 修回, 2020-05-06 接受, 2020-05-07 网络版发表
国家自然科学基金(31630010)资助

摘要 放牧是全球范围内草地生态系统最主要和最直接的利用方式. 磷(P)是植物生长所必需的大量元素, 同时也是草地初级生产力的关键限制性养分元素, 广泛参与植物的光合、呼吸等重要代谢过程. 放牧通过直接和间接作用影响草地植物和土壤各组分的P含量和P库, 进而通过正负两种反馈影响生态系统的P循环. 目前, 国内外有关放牧对草地P循环的影响机制, 特别是P循环的生物学过程和机制尚不十分清楚. 本文总结了有关放牧对植物和土壤各组分P含量及P库的影响及其机制, 并对该领域的几个重要研究方向和亟待回答的科学问题进行了展望. 未来研究中需要重点关注的问题包括: (1)土壤微生物量P组成沿不同放牧强度的变化, 以及放牧对土壤微生物P源和汇关系的影响机制; (2)放牧如何影响土壤磷酸酶的活性(磷酸单酯酶、磷酸二酯酶、三磷酸单酯水解酶等)进而调控土壤中P的矿化过程; (3)放牧如何调控P在植物-土壤-微生物系统中的转化过程; (4)采用分子生物学和组学的手段, 揭示土壤微生物在P循环及生态系统功能中的作用, 以及放牧如何影响植物和根际微生物, 进而调控生态系统P循环; (5)不同放牧强度如何影响植物多样性、菌根真菌多样性及两者之间的关系, 进而影响植物对P的吸收和利用, 以及地上和地下生物量P库; (6)不同家畜种类的食性差异及其对磷循环的影响机制; (7)其他植食动物(植食昆虫、啮齿动物、蚯蚓、植食性线虫等)在草地生态系统P循环中的作用; (8)不同放牧强度如何调控生态系统各营养级组分的N:P化学计量关系, 进而影响N、P循环之间的耦合关系.

关键词 放牧生态系统, 磷循环, 磷含量, 磷库, N:P比, 磷限制

草地是陆地生态系统的重要组成部分, 世界草地总面积为52.5亿公顷, 约占地球陆地总面积的40.5%(不包括格陵兰岛和南极)[1]. 放牧是全球范围内草地生态系统最主要和最直接的利用方式, 放牧对生态系统功能和服务的维持具有重要的调控作用[2]. 据统计, 由于长期超载放牧我国草地90%发生了不同程度的退化, 其中重度退化草地比例达60%左右[3]. 过度放牧引起的草地退化使生态系统功能(如, 初级生产力、养分循环)和服务(如, 水土保持、碳固持)显著降低[4,5]. 磷(P)作为植物生长和繁殖的必需元素, 广泛参与有机体的光合和呼吸等代谢过程, 同时也是组成DNA、RNA、ATP等生物分子以及细胞核和细胞膜的关键元素, 在生态系统物质循环和能量流动过程中起到了重要作用[6].

生态系统养分循环包括生态系统的养分输入和输出以及养分元素在生态系统内生物(植物、微生物和消费者)和非生物组分之间的移动[7]. 陆地生态系统中,

引用格式: 乌力吉, 李响, 赵萌莉, 等. 放牧对草地生态系统磷循环的调控机制: 研究进展与展望. 科学通报, 2020, 65: 1–1
Wu L J, Li X, Zhao M L, et al. Grazing regulation of phosphorus cycling in grassland ecosystems: Advances and prospects (in Chinese). Chin Sci Bull, 2020, 65: 1–1, doi: 10.1360/TB-2020-0321

© 2020《中国科学》杂志社

植被生产力通常受N、P或两者共同限制, N、P循环之间的耦合关系非常密切[7]. 近年来, 生态系统氮(N)循环受到了广泛的重视, 开展了大量的研究工作. 然而, 同N循环相比, P循环的研究相对较少, 尤其是放牧对草地P循环影响的研究十分有限[8]. 例如, 早期研究认为, 水分和氮是干旱、半干旱地区生态系统初级生产力的主要限制因子[9,10], 但近年来一些研究发现, P似乎比N对初级生产力的限制作用更强[8]. 大量研究表明, 施肥、氮沉降、种植固氮植物等人类活动的加剧, 加速了陆地生态系统的N循环[7,11], 使土壤中N的含量及其有效性增加[12], 进而使P的相对限制性增加[8,13,14]. 然而, 与N循环不同, P循环属于相对封闭的沉积型循环, 其周转时间为10^7~10^8年. 在成土过程中, 土壤中的P会随着植物的利用和人类的开采而不断消耗. 因此, 从某种意义上讲P属于地球上的不可再生资源, P必将取代N成为植物生长和生态系统功能和服务维持的主要限制因子[8,15]. 目前, 由于不合理的开发和利用已经造成P资源的相对枯竭, 据初步估计在本世纪中叶地球上50%的廉价P将被耗竭[16].

草地生态系统中, 放牧主要通过采食、践踏和粪尿返还等方式影响养分循环过程[17~22]. 在较短的时间尺度, 磷循环主要发生在生态系统内植物、动物和土壤组分之间, 植物、动物和土壤微生物的生理生态过程控制着磷在土壤和生物体内的移动和形态转化[7]. 目前已有的研究主要集中在放牧对草地土壤和植物P含量及P库的影响, 结果存在较大差异, 影响机制尚不十分清楚(图1). 为此, 本研究在查阅相关文献的基础上, 从三个方面对已有的研究进行总结, 并对未来研究重点进行展望: (1) 放牧对草地生态系统P元素内外循环的影响; (2) 从土壤P的垂直分布、输入与输出、土壤侵蚀和空间异质性四个方面讨论了放牧对土壤P含量和P库的影响; (3) 放牧对不同组织水平(个体、物种、植物功能群、群落)植物P含量和P库的影响机制; (4) 草地磷循环研究展望.

1 放牧对草地生态系统磷元素内外循环的影响

植物在生长发育过程中所需的P主要来源于土壤, 但同C、N等元素相比, 土壤中的P含量很低, 仅占土壤总质量的0.02%~0.2%[23]. 我国土壤P含量为0.17~1.11 g kg^{-1}, 受成土母质的影响我国北方草地属于严重缺P的地区, 土壤中的P绝大部分以无效P形式存在, 土壤有机质是生态系统最主要的磷库[24,25].

草地生态系统中, P的输入方式主要包括大气干沉降[26]、母质风化[27]和降水[28], 输出方式主要包括地表径流[29]、风蚀[30,31]和淋溶[32]等途径. 在放牧系统中, 畜产品的N、P输出往往是不可忽视的重要途径[17,18]. 生态系统中, 磷最初都来源于岩石矿物的风化作用, 但该过程十分缓慢, 一般通过风化作用进入生态系统的磷为0.05~1.0 kg hm^{-2} a^{-1}, 有些地区可以达到5.0 kg hm^{-2} a^{-1}. 风化速率通常与土壤母质、气候、地形、植被覆盖等非生物和生物因素有关, 生态系统中土壤风化主要是风而非水的作用[27]. 在干旱、半干旱草原, 水分是主要的限制因子, 因此通过降雨、淋溶的方式输入和输出生态系统的P均相对较少, 而大气干沉降和风蚀是影响草地生态系统P输入和输出的关键因子[30,33~35]. 研究表明, 干沉降和风蚀往往是同时发生的, 因此土壤P的输入和输出也同时发生, 它们共同受植被

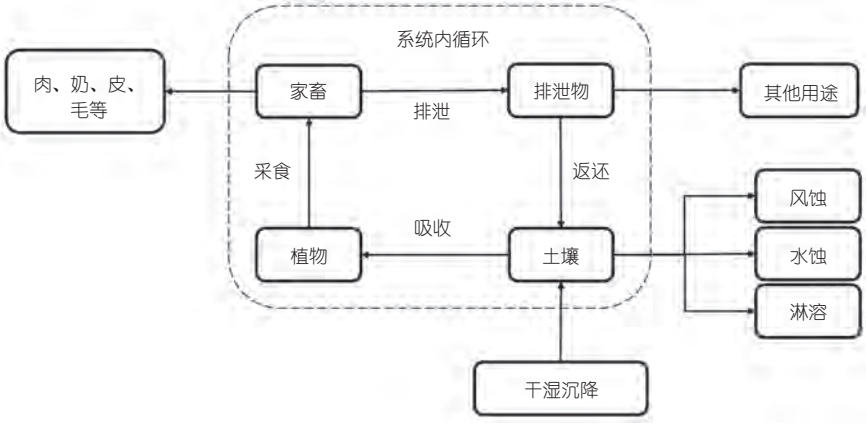


图 1 放牧对草地生态系统磷循环影响的概念图
Figure 1 A conceptual diagram for the influence of grazing on P cycle in grassland ecosystems

盖度和高度[26]、地形[31]、放牧强度等[36]因素影响. 例如, 在内蒙古草原由于春季受到风的强烈影响, 干沉降可达7 kg P ha^{-1} $year^{-1}$[37], 有些地区甚至可以达到9 kg P ha^{-1} $year^{-1}$[38], 其中放牧强度起到关键的调控作用, 甚至可以改变土壤沉降或侵蚀的方向[30]. Zhou等人[39]对全球443篇文献进行Meta分析发现, 草地生态系统中P的输入和输出量分别为0.001~13.9 kg P ha^{-1}和0.001~12.7 kg P ha^{-1}, 二者的变化范围大致相同. He等人[40]进一步研究发现, 在全球尺度上, 放牧显著增加了植物叶片、茎、根系、凋落物P库, 使土壤P库增加了3.6%.

放牧对P在生态系统内循环的影响主要表现为: (1)改变植物群落的物种组成, 植物与菌根真菌之间的互惠共生关系, 影响植物对土壤P的吸收利用, 以及植物对P的重吸收[41~45]; (2)改变群落生物量的大小及其在地上/地下部分的分配比例, 凋落物的数量和质量, 以及放牧家畜的粪尿返还, 影响土壤P的输入和家畜生物量输出, 进而影响生态系统各组分P库的大小以及P循环速率[17,41,43,46]; (3)改变小气候、光的有效性和土壤水分状况, 影响土壤微生物活性, 进而影响土壤有机质的矿化和P循环[6,47~49]. 近期的一个研究发现, 干湿交替增加了土壤磷的有效性, 有利于干旱忍耐型植物对磷的利用[50]; (4)改变生态系统中植物-土壤动物-土壤微生物之间调控与反馈关系, 养分限制和养分平衡[15,51], 特别是P与C、N的化学计量关系以及P循环与C、N循环之间的耦合关系[14,52~54].

2 放牧对土壤磷的影响

2.1 放牧对土壤磷含量垂直分布的影响

土壤P缺乏是我国北方草原面临的共性问题. 汪卫卫[55]对松嫩草地的研究发现, 没有放牧的草地, 土壤全磷的垂直分布格局呈先降低后增加的趋势, 表层土壤的全P含量为0.27 g kg^{-1}, 最小值出现在70 cm土层, 全P含量仅为0.08 g kg^{-1}; 放牧条件下, 只有重度放牧会降低土壤表层全P含量, 轻度和中度放牧的草地土壤P含量随土层深度的增加而降低. 李香真[56]对内蒙古羊草草原的研究发现, 放牧使0~100 cm的土壤P储量降低了21%, P储量随土层深度增加而降低. 李耀等人[57]在内蒙古典型草原的研究也得出了类似的结果, 不同土层中全P含量均表现为禁牧＞自由放牧＞轮牧, 在不同利用方式中P含量均随土层深度增加而降低. 郭颖[58]对青藏高原不同植被类型土壤表层全P含量的研究表明, 全P含量为0.12~1.11 g kg^{-1}, 草地、高寒草甸和高山草原的土壤全P含量一般随土层深度的增加而降低. 尽管放牧对不同草地类型土壤P含量和P库的影响目前仍然没有一致性的结论, 但放牧通过改变风蚀、水蚀、凋落物、植物根系分布、粪尿返还等, 影响表层土壤微生物活性以及植物和微生物对P的吸收和周转[59,60], 进而影响表层土壤的P含量和P库. 特别是长期重度放牧, 使表层土壤的风蚀和水蚀增加, 凋落物显著降低, 植物根系分布浅层化, 粪尿返还量显著增加[26,41,46,61].

放牧草地中, 受植物残体、放牧家畜粪尿返还以及土壤有机质长期积累的影响, 土壤有效P (如Olsen P)含量一般随土层深度的增加而显著降低[62]. 家畜排泄出的P绝大部分以粪便的形式存在, 其P含量远远高于饲草中的P含量. 例如, 绵羊粪便中的全P含量为8 g kg^{-1}, 牛粪便中的全P含量为5.5 g kg^{-1}; 同时, 新鲜粪便中的P含量显著高于干燥粪便中P含量[63]. 粪便中的P大约20%为植物可以利用的无机态P, 而粪便中的有机态P则需要经过微生物分解后才能缓慢地被植物利用[63,64]. Baron等人[46]对人工草地的研究发现, 由于家畜的粪尿返还作用, 放牧显著增加了表层土壤的可提取P含量(extractable P concentration), 0~15 cm土壤的可提取P含量在重度放下最高, 中度放牧下次之, 轻度放牧下最低. 因此, 重度放牧下, 家畜的粪便返还增加了P的流动, 进而加速了表层土壤的P循环.

2.2 放牧对土壤P含量及P输入和输出的影响

在放牧系统中, 家畜对草地的利用驱动着物质循环和能量的流动, 放牧通过采食、粪尿排泄以及畜产品的输出等方式改变了植物-土壤的反馈作用, 对土壤产生正、负两种反馈机制影响土壤P含量. 一些研究发现, 围栏禁牧阻止了家畜采食, 减少了能量和养分从生态系统的输出, 增加了土壤的P含量. 在物质输出方面, 由于植物固定了大量养分, 禁牧可以有效减少物质和能量从土壤-植物系统到消费者的输出[65], 而放牧家畜以皮、毛、肉、奶、粪尿等形式将N、P输出生态系统[17,18], 持续高强度的放牧增加了P的输出量和输出速率, 降低了土壤P含量及其P储量. 在物质输入方面, 放牧通过改变输入系统的凋落物数量和质量进而减缓了养分循环[19]. 许多研究表明, 在干旱、半干旱草原, 放牧对地上生物量和地下生物量均有显著的负效应[41,52,61,66]. 一些研究发现, 放牧改变了植物群落结构

和物种组成[5,41,67]，显著降低了地上生物量的养分含量[68]，进而对凋落物和根系分解产生抑制作用，减缓了P返还生态系统的数量和速率．放牧还可以通过植物-土壤-家畜间的正反馈作用增加土壤的磷含量．研究表明，放牧系统中，家畜从生态系统中获取P，但家畜未能同化吸收的养分绝大部分都以粪尿的形式返还土壤[17,69]．由于P的移动性差，被固定后很少向土壤深层迁移，家畜排泄后P又重新与土壤中的Fe、Al、Ca等元素结合形成难溶性络合物，或吸附于土壤胶体中[8]，使P在土壤表层中富集，增加了土壤表层的P含量．李香真[56]研究认为，放牧家畜的践踏作用使表层土壤容重增加，限制了水分和养分的垂直移动，动物排泄物的输入使表层土壤速效养分增加．这些因素使根系向土壤表层分配的比例增加，表现为根系浅层化现象，因此表层土壤的有机碳、磷在一定的阶段内可以维持原有水平或高于原有水平[56]．进一步研究发现，尽管在干旱、半干旱地区，适度放牧增加了植物群落地上生物量[70]和养分含量[71]，促进了土壤-植物间的正反馈作用[19]，而且适度的践踏，可以加速凋落物的破碎化，减少凋落物的现存量，增加分解的表面积[72]，加速P返还生态系统的速率．

风蚀不仅破坏土壤的结构，对草地初级生产力维持具有负面影响，同时也是引起草地退化的主要机制[31,73]．在放牧系统中，土壤侵蚀是导致表层土壤P含量发生变化的主要因素[35]．放牧主要通过家畜采食影响植被盖度和高度，进而改变土壤风蚀和水蚀过程．由于受到风的强烈影响，我国北方地区土壤风蚀和干沉降往往是同时发生的，这两个过程很难分开[26]，放牧强度对这两个过程起到关键的调控作用，甚至可改变其方向[30]．在放牧强度较低或禁牧状态下，群落具有较高的植被高度和盖度，增加了地表的粗糙度，不仅可以有效地减少风蚀引起土壤侵蚀，而且能够截获风沙中高养分含量的土壤细砂．但重度放牧破坏了土壤团粒结构和土壤结皮，降低了植被高度和盖度，造成了严重的地表裸露，同时增加了近地面的风速，这些因素都会加剧风蚀作用，使土壤表层由养分含量低的粗砂组成，降低了土壤P含量．Li等人[74]从能量角度解释了植被盖度和群落结构对风蚀和土壤养分流失的影响，他们发现当植被盖度较低时，发生土壤侵蚀的风速阈值会降低．这是由于当土壤颗粒跃移过程发生后，已经发生移动的土壤颗粒将部分能量转移到土壤表层颗粒，有效地降低了阈值风速．同时，植被盖度降低特别是草本植物盖度的降低，使植被对风的动力衰减作用降低，导致表层土壤风蚀加剧．另外，凋落物输入减少和丧失使土壤含水量降低，导致表土对风蚀的敏感性增加[74]．因此，过度放牧引起的植被盖度降低、群落物种组成改变(如，多年生禾草被一年生杂类草替代)、凋落物减少，是导致干旱和半干旱草原表层土壤风蚀加剧、生态系统P净输出增加的主要原因．

一些学者认为，放牧在短时间内对土壤P含量的影响不大，而造成的其含量差异的主要因素可能是空间异质性[75~77]．家畜通过粪尿排泄、践踏和选择性采食等方式改变土壤的空间异质性，但目前有关放牧对土壤空间异质性的影响仍没有一致的结论[75,76,78,79]．一些研究认为，家畜的粪尿排泄对土壤养分的空间分布有直接的作用[77,80]．例如，绵羊为了避免牧草被粪尿污染通常会在相对固定的区域排泄，因此在排泄物相对集中的区域形成粪斑和尿斑[81]，植物可利用的N、P在这些斑块的土壤表层富集，增加了土壤养分的空间异质性．同时，家畜的践踏作用直接或间接地改变了土壤的理化性质和植被的分布格局，进而影响土壤N、P的空间异质性．适度的践踏通常可以增加土壤的空间异质性，而重度践踏则降低异质性[82]．家畜的选择性采食对土壤养分(如，N、P)空间异质性的影响具有复杂性，表现为采食作用既可能增加也可能降低土壤养分的空间异质性．家畜的选择性采食减少了可食牧草的盖度和高度，造成不同强度的采食斑块，形成了“肥岛效应”(island of fertility)[79,83,84]，增加了土壤养分的空间异质性[76]．但如果家畜采食降低群落中非优势物种的多度，使优势物种分布更均匀，这可能造成土壤空间格局的同质性[85]．然而，Burke等人[79]在美国矮草草原的研究发现，地形是影响土壤空间变异的主要因素，而放牧和物种则几乎没有影响．Kölbl等人[31]对内蒙古典型草原研究发现，放牧强烈影响着景观尺度上地形控制的土壤颗粒迁移过程，并对地上生物量和与生物量相关的土壤特性具有强烈的影响．上述研究表明，长期放牧可能通过选择性采食、践踏、粪尿排泄等方式改变不同土壤斑块的生物、物理和化学属性，进而影响斑块尺度的P含量和P循环．

3 放牧对植物地上生物量磷含量和磷库的影响

草地生态系统中，植物群落的养分含量受气候、土壤、物种组成和放牧等生物和非生物因素的影

响[41,86~88]. 据最新估算，我国草地生物量P储量为3.31 Tg, 植物叶片平均P含量为1.27 g kg^{-1} (95%的置信区间为0.82~1.98 g kg^{-1}), 根系平均P含量为0.69 g kg^{-1} (95%的置信区间为0.42~1.13 g kg^{-1}), 叶片N:P平均为12.7[89]. 研究表明，放牧通过改变草地生态系统的结构和功能来影响养分循环[18,41,90]. 例如，放牧会改变群落的物种组成和多样性[90]，物种的相对多度和P含量、P输入与输出等影响植物P含量和地上生物量P库[17,18,41,70,91]，进而影响生态系统P循环.

3.1 放牧对植物个体和物种水平磷含量及磷库的影响

植物的资源利用策略、养分权衡分配、表型可塑性等都会影响其P含量和P库，放牧对植物的形态、物候和生理等多方面具有重要的影响[41,71,92]. Li等人[93]研究了放牧对羊草(*Leymus chinensis*)养分分配和个体大小的关系发现，放牧显著增加了羊草茎和叶的P含量，但降低了其叶茎比和个体P库，二者间存在显著的负相关. 这表明放牧改变了羊草个体水平P含量与P库之间的权衡关系, 使养分更多地分配给光合器官, 导致了羊草的矮小化. 生长稀释假说认为, 如果叶生物量的累积增加大于养分获取量的增加, 养分含量将下降[94]. 放牧系统中, 家畜采食养分含量高的叶片组织, 植物为了完成其生活史, 将更多的养分分配给叶片, 增加了叶片的P含量. 但在没有放牧的群落中，植物生物量的增加导致了P的稀释作用. 植物在无牧和放牧条件下养分分配策略的改变，反映了草原植物同草食动物长期协同进化过程中形成的植物个体水平上生长与维持之间的权衡. 在物候方面，可食牧草被家畜采食后的再生，延迟了植物的物候，而幼嫩组织的P含量显著高于成熟组织[68]. 在物种水平，近期的一个研究发现，长期自由放牧使典型草原群落中具有高比根长、高细根比例、根鞘酸性磷酸酯酶活性高的物种多度增加，这些物种具有较高的P获取能力[95]. Smith等人[96]研究发现, 具有较低比根面积和较高根系P含量的物种, 其根系分解速率的更快. 因此, 放牧引起的物种组成的改变将影响植物群落水平P的吸收利用和周转，以及P与碳、氮之间耦合关系.

3.2 放牧对植物功能群水平磷含量和磷库的影响

植物功能群(plant functional group)通常是指对特定或相同环境因子的改变具有相同响应，在生态系统中起相似作用的一类物种的组合. 植物功能群的变化对生态系统功能和服务具有重要影响[90,97]. Zheng等人[71]在内蒙古锡林河流域的研究发现，放牧对植物C、N、P含量的影响随着组织水平的增加而增加(物种-功能群-群落)，放牧改变了不同植物功能群的相对生物量和P含量，进而影响了植物群落地上生物量P库. 在植物功能群组成中，一、二年生植物属于资源获取型(acquisitive resource-use strategy)，为了完成其生活史, 放牧后这类植物将更多的N、P分配给地上组织; 多年生丛生禾草则属于资源保守型策略(conservative resource-use strategy), 由于其适口性较差, 降低了被家畜的采食, 因此其叶片N、P含量变化不显著; 多年生根茎型禾草属于中旱生植物，具有较高的适口性和耐牧性, 放牧后幼嫩器官取代了老旧器官，增加了N、P向叶片的分配；多年生杂类草在资源利用方式、放牧耐受性等方面都介于一、二年生植物和多年生丛生禾草之间, 其对放牧的响应比较温和. Bai等人[41]在蒙古高原草原样带调查中也发现了类似的结论，放牧引起植物功能群组成的改变是生态化学计量关系和生态系统功能发生变化的主要机制. 尽管放牧对草甸草原、典型草原和荒漠草原不同植物功能群的影响大小和方向并不完全一致，但放牧降低了这三类草原群落的地上生物量和凋落物P库，增加了草甸草原和典型草原地下生物量P库，降低了荒漠草原地下生物量P库. 对于草甸草原, 放牧增加了地上生物量N:P比, 降低了土壤N:P比. 对于典型草原和荒漠草原，放牧则增加了土壤N:P比. 这些结果表明, 长期放牧加速了草甸草原的N、P循环, 但可能减缓了典型草原和荒漠草原的P循环，进而改变了N、P循环之间的耦合关系.

3.3 放牧对植物群落水平磷含量和磷库的影响

在群落水平上，放牧主要通过促进和抑制养分循环两个相反的机制影响植物的P含量和P循环. 促进养分循环假说(accelerating nutrient cycling hypothesis)认为, 家畜采食促进了养分含量高的耐牧物种的损失, 这些物种可以通过快速吸收养分、提高相对生长率来进行补偿性生长, 同时具有较高的组织养分含量, 这些变化会引起凋落物分解和养分周转加快，进而促进养分循环[20,21]. 而抑制养分循环假说(decelerating nutrient cycling hypothesis)则认为，家畜优先采食养分含量高的植物，使木质素含量高、养分含量低、适口性差的物种的优势度增加, 进而使凋落物分解速度降低, 减缓

了养分的周转和循环速率[98]. Sitters等人[99]研究发现, 放牧促进了北极冻原生态系统的N循环, 但增加了生物量的P限制. 目前, 大量的研究已经从资源有效性、凋落物分解以及植物-土壤反馈等角度证实了放牧对植物群落P含量或P库有正、负两种效应[17,41,68,100~103].

放牧除了改变植物群落水平的平均P含量外, 还可以通过改变地上生物量, 进而影响生物量P库. 尽管有关放牧对地上生物量的影响目前仍存在很大的争议, 但我国草地的连续多年的控制实验数据表明, 在干旱、半干旱草原, 中度和重度放牧对地上生物量均表现为负效应[41,54,67,104,105]. 这些结果与放牧优化假说相悖, 这一方面可能与目前草地持续较高的放牧强度有关, 另一方面放牧能否促进植物生长主要与资源有效性有关. 在水分条件较好、养分利用率高、竞争低和早期放牧的条件下, 植物会对放牧产生超补偿效应; 而在水分条件差、养分有效性低、竞争强的环境下, 植物对放牧产生等补偿或欠补偿效应[106]. 我国的干旱半干旱草原, 放牧历史悠久, 水分和养分有效性共同限制了放牧对植物生长的促进作用, 因而长期放牧降低了群落地上生物量P库, 特别是大部分的家畜粪尿滞留在畜圈内, 不能返还到草地, 加上畜产品的输出, 加剧了生态系统水平的P输出.

4 放牧对植物根系P含量和P库的影响

4.1 放牧对根系形态和生理特征以及植物与丛枝菌根真菌共生关系的影响

根系不仅为植物地上部分的生长提供了水分和N、P等养分, 同时根系是植物重要的养分库, 植物光合作用固定的碳60%以上被分配到地下根系中[61], 因此根系动态对生态系统碳循环和养分循环具有重要的调节作用[66]. Bardgett等人[103]认为, 在较短的时间尺度家畜采食改变了植物根系分泌物和碳的分配模式, 在较长的时间尺度放牧改变了植物的根系生物量及其形态, 二者共同影响了植物根系的P含量和P库动态. 植物可以通过与丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)共生[107,108], 也可以通过改变自身形态特征[61,109,110]来提高其养分吸收能力. 研究表明, 植物所需90%的P来自AMF[111], AMF在土壤中形成广泛的菌丝网, 能够有效地获取P, 供给宿主植物[112]. 碳限制假说认为, 长期放牧减少了养分向地下部分的分配, 降低了AMF的丰富度[113]. 在资源相对丰富的条件下, 放牧增加了AMF的菌根侵染率及其频度, 维持了更高的生物多样性和地上生产力, 反之, 放牧则降低了菌根侵染率和频度, 对多样性和生产力有一定的负效应[114,115]. 同时, AMF的菌丝长度与放牧后资源有效性及土壤理化性质有很强的相关性[45]. 在生理上, 植物可以通过增加表皮细胞质膜和P的亲和力以及释放有机酸、根系分泌物等活化P, 增加P的吸收效率, 特别是在石灰质土壤中, 酸化有利于释放Ca-P化合物中的P[116].

根系形态(根系直径、根毛长度等)对植物吸收和利用P具有至关重要的作用[117]. 周艳松等人[118]对内蒙古半干旱草原大针茅根系构型的研究发现, 根系分叉数、根表面积和总根长是影响大针茅根系对放牧响应的主要指标, 随着放牧强度的增加, 大针茅根系趋于小型化, 根表面积减少, 植物为了更好地适应环境会分叉产生新的侧根吸收养分和水分. 此外, 重度放牧降低了羊草的总根长、根表面积、根尖数等根系性状, 抑制了根系的吸收作用[119].

4.2 放牧对根系生物量的影响

代谢理论和植物生物量分配理论可以解释放牧后根系生物量的变化[120,121]. 放牧通过改变植物光合产物向地上和地下器官的分配, 使根系生物量及其占总生物量的比例发生变化, 进而影响地下生物量P库和生态系统P循环. 研究表明, 放牧对草地地下生物量的影响主要与气候条件、放牧强度、放牧时间和土壤条件有关. 在干旱、半干旱地区, 大部分研究认为, 放牧对根系生物量有显著的负效应[61,66,71,122]. Gao等人[61]对半干旱典型草原的研究发现, 同不放牧的围封群落相比, 放牧显著降低了群落地下总生物量、活根生物量和净地下初级生产力, 但对根系周转速率没有显著影响. 其中, 重度放牧使群落地下总生物量降低了37%, 活根生物量降低了56%, 地下净初级生产力降低了36%. Yan等人[104]基于全国草地的Meta分析表明, 同全球草地的均值相比, 放牧对我国草地地下生物量具有很大的负效应, 这种负效应主要来源于重度放牧草地. 放牧降低了植物地上生物量, 导致光合产物更多地分配给植物地上器官, 促进其补偿性生长, 导致植物以牺牲地下部分为代价[123]. 此外, 由于家畜的选择性采食, 重度放牧降低了禾本科植物的丰富度, 改变了物种共存, 进而改变了地下生物量[124]. 上述研究表明, 长期过度引起的根系生物量(包括活根和死根)对土壤有机质的输入减少, 可能会降低土壤微生物的活性, 如酸性和碱性磷酸单

酯酶 (phosphomonoesterase)活性, 导致土壤有机P矿化速率的降低, 进而减缓生态系统P循环. 但也有一些研究发现, 放牧显著提高了土壤微生物的活性, 促进了土壤有机质的分解过程, 进而可能加速生态系统P循环[17,125,126].

5 草地磷循环研究展望

草地生态系统中, 放牧家畜是最主要消费者, 对生态系统的磷循环起着关键的调控作用. 尽管放牧对植物和土壤磷的影响已有大量相关报道, 但是大部分研究只关注了放牧对土壤、植物或微生物组分中某一方面或几方面的影响, 很少从整个生态系统水平研究放牧对植物、土壤和微生物P库及P循环的影响, 特别是有关P循环关键生物过程及其机制的研究, 亟待加强[6,60,127]. 因此, 未来需要更多地关注家畜-植物-土壤(包括土壤动物和土壤微生物)等多营养级的研究, 以及放牧强度、气候、地形、土壤和植物群落结构与组成如何影响P循环的关键生物过程(图2). 例如, 草地生态系统中, 土壤微生物量P可达土壤全P的7.5%, 其周转时间仅为几个月, 土壤微生物作为P的源和汇, 对草地土壤P循环关键过程(如P的矿化和固定)具有重要的调控作用[6]. 然而, 有关放牧如何调控土壤微生物(如细菌、古菌、腐生真菌)参与的磷循环过程研究仍较薄弱, 其具体的生物学机制尚不清楚[6,19,111,113,115].

植物多样性与微生物多样性和生态系统功能之间关系是近年来生态学研究的一个热点领域[128]. 植物-根际微生物互惠共生促进磷吸收利用假说认为, 丛枝菌根真菌对植物多样性和生态系统功能的维持具有极其重要的贡献. AMF的多样性及其与植物根系间的互惠共生关系决定了草地群落的物种多样性, 这是因为AMF多样性的增加显著地增加了土壤中的菌丝长度, AMF菌丝与植物根系形成的共生体大大延伸了植物根系的吸收范围, 增加了植物对土壤养分特别是磷的吸收利用, 进而增加了草地初级生产力和稳定性[107,111]. 一些研究表明, AMF与植物根系间的互惠共生关系有利于增强寄主植物对放牧的忍耐性, 但也有研究得出截然相反的结论[113,129].

基于上述分析, 放牧对草地P循环影响机制研究中

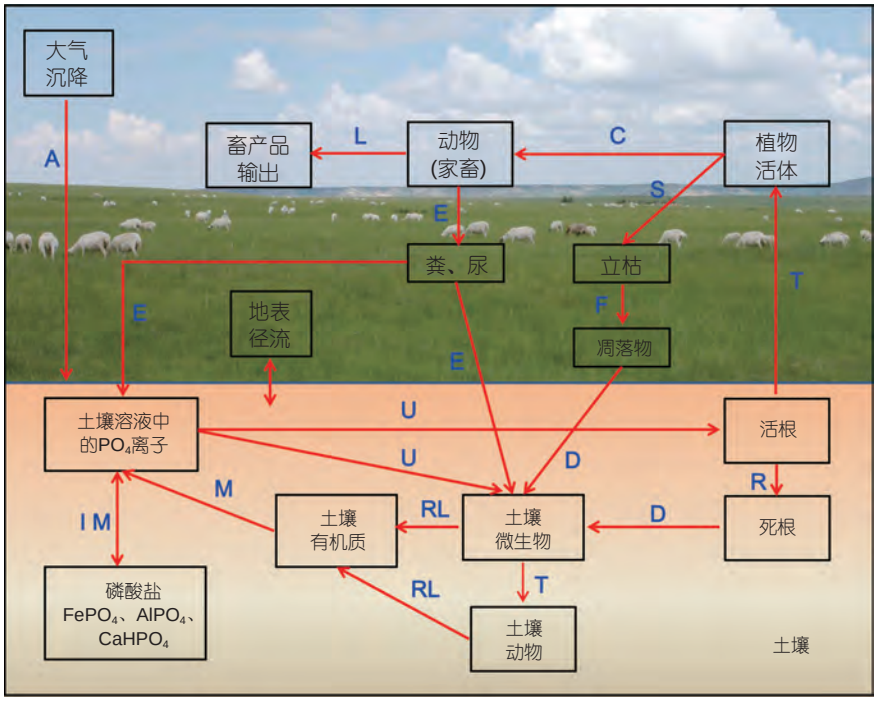


图 2 (网络版彩色)放牧对草地生态系统磷库和磷循环关键生物过程的调控机制. A, 大气湿沉降; C, 食草动物采食; D, 分解; E, 排泄物输出; F, 凋落物脱落; L, 家畜移出; M, 净矿化; R, 根系死亡; S, 植物地上部分衰老; T, 净转移; U, 根系吸收; RL, 土壤动物和微生物释放; IM, 固定与活化

Figure 2 (Color online) Mechanisms underlying the effects of grazing on P pools and key biological processes of P cycling in grassland ecosystems. A, atmospheric wet deposition; C, consumption by herbivores (e.g. domestic livestock); D, decomposition; E, urine and faces excretion; F, litter fall; L, livestock removal; M, net mineralization; R, root death; S, shoot senescence; T, net translocation; U, uptake by roots; RL, release by soil fauna and microbes; IM, immobilization and mobilization

亟待回答的科学问题包括: (1)土壤微生物量P的组成(核酸、磷酯类、细胞质无机P和有机P、多磷酸盐)和含量沿不同放牧强度的变化, 以及放牧对土壤微生物P源和汇的影响机制[130]; (2)放牧如何影响土壤磷酸酶的活性, 包括磷酸单酯酶(phosphomonoesterases)、磷酸二酯酶(phosphodiesterases)、三磷酸单酯水解酶(triphosphoric monoester hydrolases)及作用于含磷酰基酸酐和P–N 键的酶类, 进而调控土壤中P的矿化过程[131]; (3)放牧如何调控P在植物-土壤-微生物系统中的转化过程, 包括: 植物和微生物对P的吸收, 植物根系和微生物分泌物引起的土壤固相中无机P (H_3PO_4、$H_2PO_4^-$、HPO_4^{2-}和PO_4^{3-})的释放, 植物残体向土壤中释放的无机P, 以及微生物和有机质矿化引起的无机P释放等[132]; (4)采用分子生物学和组学的手段在多大程度上能够帮助我们深入理解土壤微生物在P循环及生态系统功能中的重要作用, 以及放牧如何影响植物和根际微生物, 进而调控生态系统P循环的生物过程[133]; (5)不同放牧强度如何影响植物多样性、AMF多样性及两者之间的关系, 进而影响植物对P的吸收和利用, 以及地上和地下生物量P库; (6)已有研究中, 放牧家畜类型比较单一[17], 未来研究中应关注不同家畜种类的食性差异对P循环的影响机制; (7)其他植食动物, 包括植食昆虫(如蝗虫)、啮齿动物、蚯蚓、植食性线虫等在草地生态系统P循环中的作用[134,135]; (8)多数情况下, 草地生态系统中N和P循环是耦合在一起的[60,127]. 因此, 不同放牧强度如何调控生态系统各营养级组分的N:P化学计量关系, 进而影响N和P循环之间的耦合关系, 也是未来研究中的一个新的增长点.

参考文献

1 White R P, Murray S, Rohweder M. Pilot Analysis of Global Ecosystems: Grassland Ecosystems. Washington, D.C.: World Resources Institute, 2000

2 Asner G P, Elmore A J, Olander L P, et al. Grazing systems, ecosystem responses, and global change. Annu Rev Environ Resour, 2004, 29: 261–299

3 Ministry of Environmental Protection of People's Republic of China. The 2005 Report on the State of the Environment of China (in Chinese). Beijing: Ministry of Environmental Protection of People's Republic of China, 2006 [中华人民共和国环境保护部. 中国环境状况公报 2005. 北京: 中华人民共和国环境保护部, 2006]

4 Bai Y F, Huang J H, Zheng S X, et al. Drivers and regulating mechanisms of grassland and desert ecosystem services (in Chinese). Acta Phytoecol Sin, 2014, 38: 93–102 [白永飞, 黄建辉, 郑淑霞, 等. 草地和荒漠生态系统服务功能的形成与调控机制. 植物生态学报, 2014, 38: 93–102]

5 Davidson K E, Fowler M S, Skov M W, et al. Livestock grazing alters multiple ecosystem properties and services in salt marshes: A meta-analysis. J Appl Ecol, 2017, 54: 1395–1405

6 Bünemann E K, Oberson A, Frossard E. Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling. Berlin, Heidelberg: Springer-Verlag, 2011

7 Chapin F S, III, Matson P A, Vitousek P M. Principles of Terrestrial Ecosystem Ecology. 2nd ed. New York: Springer, 2011

8 Vitousek P M, Porder S, Houlton B Z, et al. Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen-phosphorus interactions. Ecol Appl, 2010, 20: 5–15

9 Hooper D, Johnson L. Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation. Biogeochemistry, 1999, 46: 247–293

10 Bai Y, Wu J, Xing Q, et al. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecology, 2008, 89: 2140–2153

11 Schlesinger W H. On the fate of anthropogenic nitrogen. Proc Natl Acad Sci USA, 2009, 106: 203–208

12 Greaver T L, Clark C M, Compton J E, et al. Key ecological responses to nitrogen are altered by climate change. Nat Clim Change, 2016, 6: 836–843

13 Zhan S, Wang Y, Zhu Z, et al. Nitrogen enrichment alters plant N:P stoichiometry and intensifies phosphorus limitation in a steppe ecosystem. Environ Exp Bot, 2017, 134: 21–32

14 Marklein A R, Houlton B Z. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. New Phytol, 2012, 193: 696–704

15 Elser J J, Andersen T, Baron J S, et al. Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science, 2009, 326: 835–837

16 Peñuelas J, Poulter B, Sardans J, et al. Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. Nat Commun, 2013, 4: 2934

17 Chaneton E J, Lemcoff J H, Lavado R S. Nitrogen and phosphorus cycling in grazed and ungrazed plots in a temperate subhumid grassland in Argentina. J Appl Ecol, 1996, 33: 291–302

18 Giese M, Brueck H, Gao Y Z, et al. N balance and cycling of Inner Mongolia typical steppe: A comprehensive case study of grazing effects. Ecol Monographs, 2013, 83: 195–219

19 Bardgett R D, Wardle D A. Herbivore-mediated linkages between aboveground and belowground communities. Ecology, 2003, 84: 2258–2268

20 McNaughton S J. Ecology of a grazing ecosystem: The Serengeti. Ecol Monographs, 1985, 55: 259–294

21 Frank D A, Evans R D. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology, 1997, 78: 2238–2248

22 Zhou G, Zhou X, He Y, et al. Grazing intensity significantly affects belowground carbon and nitrogen cycling in grassland ecosystems: A meta-analysis. Glob Change Biol, 2017, 23: 1167–1179

23 Qin G S, Liu J S, Wang G P. Mechanism of phosphorus availability changing in soil (in Chinese). Chin J Soil Sci, 2006, 37: 1012–1016 [秦胜金, 刘景双, 王国平. 影响土壤磷有效性变化作用机理. 土壤通报, 2006, 37: 1012–1016]

24 Lu R K. General status of nutrients (N, P, K) in soils of China (in Chinese). Acta Pedol Sin, 1989, 26: 280–286 [鲁如坤. 我国土壤氮、磷、钾的基本状况. 土壤学报, 1989, 26: 280–286]

25 Lai L, Hao D M, Peng L F. Development of researches on soil phosphorus (in Chinese). Res Soil Water Conserv, 2003, 10: 65–67 [来璐, 郝明德, 彭令发. 土壤磷素研究进展. 水土保持研究, 2003, 10: 65–67]

26 Hoffmann C, Funk R, Wieland R, et al. Effects of grazing and topography on dust flux and deposition in the Xilingele grassland, Inner Mongolia. J Arid Environ, 2008, 72: 792–807

27 Newman E I. Phosphorus inputs to terrestrial ecosytems. J Ecol, 2006, 83: 713–726

28 López-hernandez D, García M, Niño M. Input and output of nutrients in a diked flooded savanna. J Appl Ecol, 1994, 31: 303–312

29 Green V S, Dao T H, Stone G, et al. Bioactive phosphorus loss in simulated runoff from a phosphorus-enriched soil under two forage management systems. Soil Sci, 2007, 172: 721–732

30 Hoffmann C, Funk R, Li Y, et al. Effect of grazing on wind driven carbon and nitrogen ratios in the grasslands of Inner Mongolia. CATENA, 2008, 75: 182–190

31 Kölbl A, Steffens M, Wiesmeier M, et al. Grazing changes topography-controlled topsoil properties and their interaction on different spatial scales in a semi-arid grassland of Inner Mongolia, P.R. China. Plant Soil, 2011, 340: 35–58

32 Chardon W J, Aalderink G H, van der Salm C. Phosphorus leaching from cow manure patches on soil columns. J Environ Qual, 2007, 36: 17–22

33 Okin G S, Mahowald N, Chadwick O A, et al. Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. Glob Biogeochem Cycle, 2004, 18: GB2005

34 Tsukuda S, Sugiyama M, Harita Y, et al. Atmospheric phosphorus deposition in Ashiu, Central Japan – Source apportionment for the estimation of true input to a terrestrial ecosystem. Biogeochemistry, 2006, 77: 117–138

35 Zhao H L, Yi X Y, Zhou R L, et al. Wind erosion and sand accumulation effects on soil properties in Horqin Sandy Farmland, Inner Mongolia. CATENA, 2006, 65: 71–79

36 Zhao Y, Peth S, Krümmelbein J, et al. Spatial variability of soil properties affected by grazing intensity in Inner Mongolia grassland. Ecol Model, 2007, 205: 241–254

37 Li F. Wind erosion and airborne dust deposition in farmland during spring in the Horqin Sandy Land of eastern Inner Mongolia, China. Soil Tillage Res, 2004, 75: 121–130

38 Yan Y, Xu X, Xin X, et al. Effect of vegetation coverage on aeolian dust accumulation in a semiarid steppe of northern China. CATENA, 2011, 87: 351–356

39 Zhou Q, Daryanto S, Xin Z, et al. Soil phosphorus budget in global grasslands and implications for management. J Arid Environ, 2017, 144: 224–235

40 0 He M, Zhou G Y, Yuan T F, et al. Grazing intensity significantly changes the C:N:P stoichiometry in grassland ecosystems. Glob Ecol Biogeogr, 2020, 29: 355–369

41 Bai Y F, Wu J G, Clark C M, et al. Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. J Appl Ecol, 2012, 49: 1204–1215

42 Faghihinia M, Zou Y, Chen Z, et al. The response of grassland mycorrhizal fungal abundance to a range of long-term grazing intensities. Rhizosphere, 2020, 13: 100178

43 Zhang T R, Li F Y, Shi C J, et al. Enhancement of nutrient resorption efficiency increases plant production and helps maintain soil nutrients under summer grazing in a semi-arid steppe. Agric Ecosyst Environ, 2020, 292: 106840

44 Lü X T, Freschet G T, Kazakou E, et al. Contrasting responses in leaf nutrient-use strategies of two dominant grass species along a 30-yr temperate steppe grazing exclusion chronosequence. Plant Soil, 2015, 387: 69–79

45 Ren H, Gui W, Bai Y, et al. Long-term effects of grazing and topography on extra-radical hyphae of arbuscular mycorrhizal fungi in semi-arid

grasslands. Mycorrhiza, 2018, 28: 117–127
46 Baron V S, Dick A C, Mapfumo E, et al. Grazing impacts on soil nitrogen and phosphorus under Parkland pastures. J Range Manage, 2001, 54: 704–710
47 Faghihinia M, Zou Y, Chen Z, et al. Environmental drivers of grazing effects on arbuscular mycorrhizal fungi in grasslands. Appl Soil Ecol, 2020, 153: 103591
48 Shan Y, Chen D, Guan X, et al. Seasonally dependent impacts of grazing on soil nitrogen mineralization and linkages to ecosystem functioning in Inner Mongolia grassland. Soil Biol Biochem, 2011, 43: 1943–1954
49 Cole C V, Innis G S, Stewart J W B. Simulation of phosphorus cycling in semiarid grasslands. Ecology, 1977, 58: 1–15
50 Bünemann E K, Keller B, Hoop D, et al. Increased availability of phosphorus after drying and rewetting of a grassland soil: Processes and plant use. Plant Soil, 2013, 370: 511–526
51 Frank D A. Ungulate and topographic control of nitrogeN:Phosphorus stoichiometry in a temperate grassland; soils, plants and mineralization rates. Oikos, 2008, 117: 591–601
52 Chen D M, Zheng S X, Shan Y M, et al. Vertebrate herbivore-induced changes in plants and soils: Linkages to ecosystem functioning in a semi-arid steppe. Funct Ecol, 2013, 27: 273–281
53 Chen T, Christensen M, Nan Z, et al. The effects of different intensities of long-term grazing on the direction and strength of plant-soil feedback in a semiarid grassland of Northwest China. Plant Soil, 2017, 413: 303–317
54 Wang B, Wu L, Chen D, et al. Grazing simplifies soil micro-food webs and decouples their relationships with ecosystem functions in grasslands. Glob Change Biol, 2020, 26: 960–970
55 Wang W W. Spatial patterns of soil nutrients and their response to grazing disturbance over the Songnen meadow steppes of NE China (in Chinese). Master thesis. Changchun: Northeast Normal University, 2007 [汪卫卫. 松嫩草地土壤养分空间格局特征及其对放牧干扰的响应. 硕士学位论文. 长春: 东北师范大学, 2007]
56 Li X Z. ffects of grazing on phosphorus stock and forms in chestnut soil (in Chinese). Acta Pratacul Sin, 2001, 10: 28–32 [李香真. 放牧对暗栗钙土磷的贮量和形态的影响. 草业学报, 2001, 10: 2028–2032]
57 Li Y, Wei Z J, Liu H M, et al. Effects of different grazing regimes on total phosphorus and available phosphorus in a typical steppe (in Chinese). Inn Mong Pratacul, 2010, 22: 4–6 [李耀, 卫智军, 刘红梅, 等. 不同放牧制度对典型草原土壤中全磷和速效磷的影响. 内蒙古草业, 2010, 22: 4–6]
58 Guo Y. Distribution characteristics and influencing factors of soil phosphorus under different vegetation types in the Qinghai-Tibet Plateau (in Chinese). Master thesis. Tianjin: Tianjin Normal University, 2017 [郭颖. 青藏高原不同植被类型土壤磷分布特征及影响因素. 硕士学位论文. 天津: 天津师范大学, 2017]
59 Rumpel C, Creme A, Ngo P T, et al. The impact of grassland management on biogeochemical cycles involving carbon, nitrogen and phosphorus. J Soil Sci Plant Nutr, 2015, 15: 353–371
60 Jouany C, Cruz P, Daufresne T, et al. Biological phosphorus cycling in grasslands: Interactions with nitrogen. In: Bünemann E K, Oberson A, Frossard E, eds. Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling. New York: Springer. 2011
61 Gao Y Z, Giese M, Lin S, et al. Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. Plant Soil, 2008, 307: 41–50
62 Haygarth P M, Hepworth L, Jarvis S C. Forms of phosphorus transfer in hydrological pathways from soil under grazed grassland. Eur J Soil Sci, 1998, 49: 65–72
63 McDowell R W, Stewart I. Phosphorus in fresh and dry dung of grazing dairy cattle, deer, and sheep. J Environ Qual, 2005, 34: 598–607
64 Heady H F, Child R D. Rangeland Ecology and Management. Boulder, Colorado: Westview Press, 1994
65 Wu G L, Du G Z, Liu Z H, et al. Effect of fencing and grazing on a Kobresia-dominated meadow in the Qinghai-Tibetan Plateau. Plant Soil, 2009, 319: 115–126
66 Bai W, Fang Y, Zhou M, et al. Heavily intensified grazing reduces root production in an Inner Mongolia temperate steppe. Agr EcoSyst Environ, 2015, 200: 143–150
67 Wan H, Bai Y, Schönbach P, et al. Effects of grazing management system on plant community structure and functioning in a semiarid steppe: Scaling from species to community. Plant Soil, 2011, 340: 215–226
68 Li C, Hao X, Willms W D, et al. Effect of long-term cattle grazing on seasonal nitrogen and phosphorus concentrations in range forage species in the fescue grassland of southwestern Alberta. Z Pflanzenernähr Bodenk, 2010, 173: 946–951
69 Haynes R J, Williams P H. Nutrient Cycling and Soil Fertility in the Grazed Pasture Ecosystem. San Diego: Elsevier Academic Press Inc, 1993
70 Li W H, Xu F W, Zheng S X, et al. Patterns and thresholds of grazing-induced changes in community structure and ecosystem functioning: Species-level responses and the critical role of species traits. J Appl Ecol, 2017, 54: 963–975
71 Zheng S X, Ren H Y, Li W H, et al. Scale-dependent effects of grazing on plant C:N:P stoichiometry and linkages to ecosystem functioning in the

Inner Mongolia grassland. Plos One, 2012, 7: e51750
72 Hou F J, Chang S H, Yu Y W, et al. A review on trampling by grazed l ivestock (in Chinese). Acta Ecol Sin, 2004, 24: 784–789 [侯扶江, 常生华, 于应文, 等. 放牧家畜的践踏作用研究评述. 生态学报, 2004, 24: 784–789]
73 Steffens M, Kölbl A, Giese M, et al. Spatial variability of topsoils and vegetation in a grazed steppe ecosystem in Inner Mongolia (PR China). J Plant Nutr Soil Sci, 2009, 172: 78–90
74 Li J, Okin G S, Alvarez L, et al. Quantitative effects of vegetation cover on wind erosion and soil nutrient loss in a desert grassland of southern New Mexico, USA. Biogeochemistry, 2007, 85: 317–332
75 Zuo X, Zhao H, Zhao X, et al. Spatial pattern and heterogeneity of soil properties in sand dunes under grazing and restoration in Horqin Sandy Land, Northern China. Soil Tillage Res, 2008, 99: 202–212
76 Liu C, Song X X, Wang L, et al. Effects of grazing on soil nitrogen spatial heterogeneity depend on herbivore assemblage and pre-grazing plant diversity. J Appl Ecol, 2016, 53: 242–250
77 Augustine D J, Frank D A. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. Ecology, 2001, 82: 3149–3162
78 Lin Y, Hong M, Han G, et al. Grazing intensity affected spatial patterns of vegetation and soil fertility in a desert steppe. Agr EcoSyst Environ, 2010, 138: 282–292
79 Burke I C. Spatial variability of soil properties in the shortgrass steppe: The relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems, 1999, 2: 422–438
80 Orwin K H, Bertram J E, Clough T J, et al. Short-term consequences of spatial heterogeneity in soil nitrogen concentrations caused by urine patches of different sizes. Appl Soil Ecol, 2009, 42: 271–278
81 Hutchings M R, Gordon I J, Kyriazakis I, et al. Sheep avoidance of faeces-contaminated patches leads to a trade-off between intake rate of forage and parasitism in subsequent foraging decisions. anim Behaviour, 2001, 62: 955–964
82 Liu C. The mechanisms by grazing on grassland plant and soil spatial heterogeneity and their correlation (in Chinese). Doctor thesis. Changchun: Northeast Normal University, 2015 [刘晨. 放牧对草地植被、土壤空间异质性及其相互关系的调控机制. 博士学位论文. 长春: 东北师范大学]
83 Schlesinger W H, Raikes J A, Hartley A E, et al. On the spatial pattern of soil nutrients in desert ecosystems. Ecology, 1996, 77: 364–374
84 Augustine D J, Te Booth D, Cox S E, et al. Grazing intensity and spatial heterogeneity in bare soil in a grazing-resistant grassland. Rangeland Ecol Manage, 2012, 65: 39–46
85 Hirobe M, Kondo J, Enkhbaatar A, et al. Effects of livestock grazing on the spatial heterogeneity of net soil nitrogen mineralization in three types of Mongolian grasslands. J Soils Sediments, 2013, 13: 1123–1132
86 de Mazancourt C, Loreau M, Abbadie L. Grazing optimization and nutrient cycling: When do herbivores enhance plant production? Ecology, 1998, 79: 2242–2252
87 Ren H, Han G, Lan Z, et al. Grazing effects on herbage nutritive values depend on precipitation and growing season in Inner Mongolian grassland. JPECOL, 2016, 9: 712–723
88 Herrero-Jáuregui C, Oesterheld M. Effects of grazing intensity on plant richness and diversity: A meta-analysis. Oikos, 2018, 127: 757–766
89 Tang Z, Xu W, Zhou G, et al. Patterns of plant carbon, nitrogen, and phosphorus concentration in relation to productivity in China's terrestrial ecosystems. Proc Natl Acad Sci USA, 2018, 115: 4033–4038
90 Hooper D U, Vitousek P M. Effects of plant composition and diversity on nutrient cycling. Ecol Monographs, 1998, 68: 121–149
91 Knops J M H, Bradley K L, Wedin D A. Mechanisms of plant species impacts on ecosystem nitrogen cycling. Ecol Lett, 2002, 5: 454–466
92 Fu Y B, Thompson D, Willms W, et al. Long-term grazing effects on genetic variability in mountain rough fescue. Rangeland Ecol Manage, 2005, 58: 637–642
93 Li X, Liu Z, Ren W, et al. Linking nutrient strategies with plant size along a grazing gradient: Evidence from Leymus chinensis in a natural pasture. J Integrative Agr, 2016, 15: 1132–1144
94 Dijkstra F A, Pendall E, Morgan J A, et al. Climate change alters stoichiometry of phosphorus and nitrogen in a semiarid grassland. New Phytol, 2012, 196: 807–815
95 Yu R P, Zhang W P, Yu Y C, et al. Linking shifts in species composition induced by grazing with root traits for phosphorus acquisition in a typical steppe in Inner Mongolia. Sci Total Environ, 2020, 712: 136495
96 Smith S W, Woodin S J, Pakeman R J, et al. Root traits predict decomposition across a landscape-scale grazing experiment. New Phytol, 2014, 203: 851–862
97 Zheng S, Lan Z, Li W, et al. Differential responses of plant functional trait to grazing between two contrasting dominant C3 and C4 species in a typical steppe of Inner Mongolia, China. Plant Soil, 2011, 340: 141–155
98 Ritchie M E, Tilman D, Knops J M H. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology, 1998, 79: 165–177

99 Sitters J, Cherif M, Egelkraut D, et al. Long-term heavy reindeer grazing promotes plant phosphorus limitation in arctic tundra. Funct Ecol, 2019, 33: 1233–1242

100 Li C, Hao X, Zhao M, et al. Influence of historic sheep grazing on vegetation and soil properties of a Desert Steppe in Inner Mongolia. Agr EcoSyst Environ, 2008, 128: 109–116

101 Gao X, Hao X, Marchbank D H, et al. Responses of herbage P, Ca, K and Mg content and Ca/P and K/(Ca + Mg) ratios to long-term continuous and discontinued cattle grazing on a rough fescue grassland. Grass Forage Sci, 2017, 72: 581–589

102 Moretto A S, Distel R A, Didoné N G. Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland. Appl Soil Ecol, 2001, 18: 31–37

103 Bardgett R D, Wardle D A, Yeates G W. Linking above-ground and below-ground interactions: How plant responses to foliar herbivory influence soil organisms. Soil Biol Biochem, 1998, 30: 1867–1878

104 04 Yan L, Zhou G S, Zhang F. Effects of different grazing intensities on grassland production in China: a meta-analysis. Plos One, 2013, 8: e81466

105 Schönbach P, Wan H, Gierus M, et al. Grassland responses to grazing: Effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem. Plant Soil, 2011, 340: 103–115

106 Maschinski J, Whitham T G. The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. Am Natist, 1989, 134: 1–19

107 Heijden M G A. Mycorrhizal fungi reduce nutrient loss from model grassland ecosystems. Ecology, 2010, 91: 1163–1171

108 Tian H, Gai J P, Zhang J L, et al. Arbuscular mycorrhizal fungi associated with wild forage plants in typical steppe of eastern Inner Mongolia. Eur J Soil Biol, 2009, 45: 321–327

109 Lynch J P, Brown K M. Topsoil foraging—An architectural adaptation of plants to low phosphorus availability. Plant Soil, 2001, 237: 225–237

110 Hill J O, Simpson R J, Moore A D, et al. Morphology and response of roots of pasture species to phosphorus and nitrogen nutrition. Plant Soil, 2006, 286: 7–19

111 van der Heijden M G A, Klironomos J N, Ursic M, et al. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature, 1998, 396: 69–72

112 Leake J, Johnson D, Donnelly D, et al. Networks of power and influence: The role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. Can J Bot, 2004, 82: 1016–1045

113 van der Heyde M, Bennett J, Pither J, et al. Longterm effects of grazing on arbuscular mycorrhizal fungi. Agric Ecosyst Environ, 2017, 243: 27–33

114 Guo Y, Du Q, Li G, et al. Soil phosphorus fractions and arbuscular mycorrhizal fungi diversity following long-term grazing exclusion on semi-arid steppes in Inner Mongolia. Geoderma, 2016, 269: 79–90

115 Yang X. Mechanisms of grazing and mycorrhizal fungi affecting plant community diversity in the typical steppe (in Chinese). Doctor thesis. Beijing: China Agricultural University, 2018 [杨鑫. 放牧与菌根真菌影响典型草原植物群落多样性的机制研究. 博士学位论文. 北京: 中国农业大学, 2018]

116 Hinsinger P. Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: A review. Plant Soil, 2001, 237: 173–195

117 Waddell H A, Simpson R J, Ryan M H, et al. Root morphology and its contribution to a large root system for phosphorus uptake by *Rytidosperma* species (wallaby grass). Plant Soil, 2017, 412: 7–19

118 Hou Y-S, Wang L-Q, Zhang P, et al. Responses of the root architecture of *Stipa grandis* to grassland degradation (in Chinese). Pratacult Sci, 2011, 28: 1962–1966 [周艳松, 王立群, 张鹏, 等. 大针茅根系构型对草地退化的响应. 草业科学, 2011, 28: 1962–1966]

119 Song Y-T, Wuyunna, Zhang F-J, et al. Response of Leymus chinesnsis root morphological traits on grazing intensity—Taking Kherlen river basin steppe in Hulunbeir as study region (in Chinese). J Dalian Natl Univ, 2015, 17: 10–14 [宋彦涛, 乌云娜, 张凤杰, 等. 羊草根系形态特征对放牧强度的响应——以呼伦贝尔克鲁伦克流域典型草原为研究区域. 大连民族学院学报, 2015, 17: 10–14]

120 Brown J H, Gillooly J F, Allen A P, et al. Toward a metabolic theory of ecology. Ecology, 2004, 85: 1771–1789

121 Enquist B J. Global allocation rules for patterns of biomass partitioning in seed plants. Science, 2002, 295: 1517–1520

122 Chen Y, Lee P, Lee G, et al. Simulating root responses to grazing of a Mongolian grassland ecosystem. Plant Ecol, 2006, 183: 265–275

123 Brouwer R. Some aspects of the equilibrium between overground and underground plant parts. Jaarboek IBS, 1963, 213: 31–39

124 Onatibia G R, Reyes M F, Aguiar M R. Fine-scale root community structure and below-ground responses to grazing show independence from above-ground patterns. J Veg Sci, 2017, 28: 1097–1106

125 Rui Y, Wang Y, Chen C, et al. Warming and grazing increase mineralization of organic P in an alpine meadow ecosystem of Qinghai-Tibet Plateau, China. Plant Soil, 2012, 357: 73–87

126 Klumpp K, Fontaine S, Attard E, et al. Grazing triggers soil carbon loss by altering plant roots and their control on soil microbial community. J

Ecol, 2009, 97: 876–885
127 Gibson D J. Grasses and Grassland Ecology. Oxford: Oxford University Press, 2009
128 van der Heijden M G A, Bardgett R D, van Straalen N M. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett, 2008, 11: 296–310
129 Bennett A E, Bever J D. Mycorrhizal species differentially alter plant growth and response to herbivory. Ecology, 2007, 88: 210–218
130 Bünemann E K, Prusisz B, Ehlers K. Characterization of phosphorus forms in soil microorganisms. In: Bünemann E K, Oberson A, Frossard E, eds. Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling. New York: Springer, 2011
131 Nannipieri P, Giagnoni L, Landi L, et al. Role of phosphatase enzymes in soil. In: Bünemann E K, Oberson A, Frossard E, eds. Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling. New York: Springer. 2011
132 Frossard E, Achat D L, Bernasconi S M, et al. The use of tracers to investigate phosphate cycling in soil-plant systems. In: Bünemann E K, Oberson A, Frossard E, eds. Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling. New York: Springer, 2011
133 Wasaki J, Maruyama H. Molecular approaches to the study of biological phosphorus cycling. In: Bünemann E K, Oberson A, Frossard E, eds. Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling. New York: Springer, 2011
134 Ibanez S, Millery A, D'ottavio M, et al. Phosphorus-rich grasshoppers consume plants high in nitrogen and phosphorus. Ecol Entomol, 2017, 42: 610–616
135 Lemoine N P, Smith M D. Drought and small-bodied herbivores modify nutrient cycling in the semi-arid shortgrass steppe. Plant Ecol, 2019, 220: 227–239
136 Torsvik V, Øvreås L. Microbial diversity and function in soil: From genes to ecosystems. Curr Opin MicroBiol, 2002, 5: 240–245
137 Dijkstra F A, He M, Johansen M P, et al. Plant and microbial uptake of nitrogen and phosphorus affected by drought using ^{15}N and ^{32}P tracers. Soil Biol Biochem, 2015, 82: 135–142
138 Bünemann E K. Assessment of gross and net mineralization rates of soil organic phosphorus – A review. Soil Biol Biochem, 2015, 89: 82–98

Summary for "放牧对草地生态系统磷循环的调控机制: 研究进展与展望"

Grazing regulation of phosphorus cycling in grassland ecosystems: Advances and prospects

Liji Wu[1,2], Xiang Li[2], Mengli Zhao[1] & Yongfei Bai[2,3*]

[1] *College of Grassland, Resources and Environment, Inner Mongolia Agricultural University, Huhhot 010011, China;*
[2] *State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China;*
[3] *College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China*
* Corresponding author, E-mail: yfbai@ibcas.ac.cn

Grassland ecosystems, which cover a total area of 52.5 million square kilometers and account for 40.5% of the global land surface, are the largest biomes in the world. Grazing is the most dominant and direct land use type in grasslands and a predominant driver regulating multiple ecosystem functions and services, such as primary production, nitrogen (N) and phosphorus (P) cycling, carbon sequestration, forage and food production, and water and soil erosion control etc. Many studies have demonstrated that primary production of grasslands is often limited by water, N and P availability, which interact with grazing to influence the maintenance of ecosystem functions and services. However, compared with numerous studies on the effects of grazing on N cycling and plant water use, fewer studies have explored how grazing influence P cycling of grasslands, particularly the internal cycling of P among main pools within ecosystems. Here we reviewed the advances in grazing effects on soil and plant P pools and biological processes of P cycling. Our review is mainly focused on: (1) grazing effects on internal and external cycles of P in grassland ecosystems; (2) grazing effects on soil P vertical distribution, and P inputs and outputs mediated by soil erosion and spatial heterogeneity; and (3) mechanisms underlying grazing-induced changes in plant P content and P pools across different levels of organization (individual, species, functional group and community). Finally, we proposed a unified framework synthesizing the influence of grazing on P pools and key biological processes of P cycling in grassland ecosystems. We also proposed eight key questions that need to be addressed in future studies: (1) How do the dominant P forms (e.g. nucleic acids, phospholipids, cytoplasmic inorganic P, cytoplasmic organic P, and polyphosphate) and concentration within soil microbial biomass vary with grazing intensity? How does the role of microorganisms as sink and source of P change with increasing grazing intensity? (2) How does grazing affect enzyme activities, including phosphomonoesterases, phosphodiesterases, triphosphoric monoester hydrolases, and enzymes acting on phosphoryl-containing anhydrides and on P–N bonds, and thereby P mineralization in soil? (3) How does grazing regulate the biological processes of P transformation in plant-soil-microbial P cycle? (4) To what degree molecular approaches and omics analyses can improve our understanding of the important role of plants and rhizosphere microorganisms in P cycling? (5) How does grazing affect the relationship between plant diversity and arbuscular mycorrhizal fungi (AMF) diversity, and thereby plant P uptake and utilization? (6) How do grazing animals differ in their effects on the pools and pathways of P cycling due to the interspecific differences in diet and foraging preference? (7) How do other herbivores in terms of grasshoppers, rodents, earthworms, and plant feeding nematodes influence the biological processes of P cycling? (8) How does grazing affect the N:P stoichiometry of key ecosystem compartments, and hence the coupled N and P cycles.

grazing system, phosphorus (P) cycling, P content, P pool, N:P ratio, P limitation

doi: 10.1360/TB-2020-0321

科学通报 2018 年 第 63 卷 第 5-6 期：511 ~ 520
评 述
《中国科学》杂志社
SCIENCE CHINA PRESS

人工草地生产力和稳定性的调控机理研究：问题、进展与展望

白永飞[1,2*]，玉柱[3]，杨青川[4]，万宏伟[1]，黄建辉[1]，纪宝明[5]，李昂[1]

1. 中国科学院植物研究所，植被与环境变化国家重点实验室，北京 100093；
2. 中国科学院大学资源与环境学院，北京 100049；
3. 中国农业大学动物科技学院，北京 100193；
4. 中国农业科学院北京畜牧兽医研究所，北京 100193；
5. 中国林业大学林学院，北京 100083

* 联系人，E-mail: yfbai@ibcas.ac.cn

2017-12-19 收稿，2018-01-04 修回，2018-01-04 接受，2018-02-01 网络版发表

摘要 我国拥有草地总面积60亿亩，占国土面积的41.7%. 长期以来，我国在畜牧业生产中过度利用草地的生产功能，忽视其生态功能，造成草地大面积退化，草-畜关系失衡. 同天然草地相比，建设优质高效人工草地可以使饲草产量提高10~20倍，有望从根本上解决我国肉、奶生产中面临的优质饲草料严重短缺的瓶颈问题，进而遏制过度放牧引起的草地退化，恢复草地生态功能. 目前，我国在人工草地建设中仍面临种植规模小、产量低、利用年限短等问题，草产业发展水平远落后于畜牧业发达国家. 因此，开展人工草地生产力和稳定性调控机理研究是实现以科技为先导，转变畜牧业生产方式，保障我国生态安全、食物安全、生态文明建设的国家重大战略需求. 本文从人工草地生产力和稳定性调控的理论基础、国内外研究现状与进展等方面系统地介绍了近年来该领域取得的最新成果. 在此基础上，对人工草地生产力和稳定性调控机理研究中亟待解决的科学问题以及重要生物学和生态学机制进行了展望.

关键词 草地，生态功能，生产功能，人工草地，生物学和生态学机制，生态安全，饲草安全

我国是草地资源大国，拥有草地总面积60亿亩(1亩=0.067 ha)，约占国土面积的41.7%，是耕地面积的3.2倍、森地面积的2.5倍[1,2]. 长期以来，我国在畜牧业生产中过度利用草地的生产功能，忽视其生态功能，造成了超载过牧、人-草-畜关系失衡和草地大面积退化，并诱发了沙尘暴等生态灾难. 据统计，我国约90%的天然草地发生了不同程度的退化，中度和重度退化草地面积达23亿亩，其中内蒙古、西藏、新疆、青海、四川和甘肃等牧区的退化草地比例高达80%~97%[3,4]. 国务院在2011年发布的《关于促进牧区又好又快发展的若干意见》中明确指出，我国草原生态总体恶化趋势尚未根本遏制，草原畜牧业粗放型增长方式难以为继. 草地畜牧业发达国家的经验表明，在我国广大的农区、农牧交错区和部分牧区因地制宜地发展高产优质人工草地和半人工草地，可以大幅度提高草地的牧草产量和品质，降低畜牧业对农业的依赖，缓解畜牧业与粮食生产争耕地的严峻现实，进而为国家粮食和食物安全做出实质性贡献(草地的概念和定义见表1). 因此，开展人工草地功能调控研究是转变当前粗放型畜牧业生产方式，实现以科技为先导，提升草畜产业的整体生产水平，保障我国粮食和食物安全的重大科技需求.

引用格式：白永飞，玉柱，杨青川，等. 人工草地生产力和稳定性的调控机理研究：问题、进展与展望. 科学通报，2018, 63: 511–520
Bai Y F, Yu Z, Yang Q C. Mechanisms regulating the productivity and stability of artificial grasslands in China: Issues, progress, and prospects (in Chinese). Chin Sci Bull, 2018, 63: 511–520, doi: 10.1360/N972017-00935

© 2018《中国科学》杂志社

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

表 1 草地的基本概念和定义

Table 1 Basic concepts and definitions of grasslands

概念	定义
草地	广义的草地是指可以用于放牧或割草的土地，包括天然放牧地、永久休闲地、5年以上生产草本饲料作物的耕地、疏林地、矮木林、疏灌丛、荒漠、冻原、沿海滩涂、草甸和沼泽湿地[2,6]
天然草地	自然形成的未经人工改良的草地[2,7,8]
人工草地	采用农业技术措施人工种植的草地[2,7,8]
半人工草地	采用松耙、补播、施肥、灌溉等农业技术措施改良后的天然草地，也称为改良草地[2,7,8]

长期以来，发达国家十分重视人工草地和草畜产业的基础研究，依托人工草地大力发展草畜产业，不断提升畜牧业占农业的比重．例如，美国畜牧业占农业的比重为60%左右，德国为70%，法国为57%，加拿大为65%．同时，在这些国家的畜牧业内部结构中，草产业对畜牧业产值的贡献率均超过60%[1]．目前，我国畜牧业占农业的比重为30%左右，而牧区和农牧交错区草原畜牧业仅占全国畜牧业总产值的4%左右[5]．草原畜牧业对农业贡献率低的根本原因在于草地生产力水平低，特别是人工草地基础研究和草产业发展水平均远落后于发达国家．研究表明，建设人工草地可以大大提高草地的生产力和牧草品质．例如，苜蓿(*Medicago sativa* L.)人工草地的产量可达22.5 t/ha，是天然草地的11倍左右，羊草(*Leymus chinensis* (Trin.) Tzvel.)人工草地的产量可达20 t/ha，是天然草地的10倍，燕麦(*Avena sativa* L.)人工草地可达37.5 t/ha，是天然草地的19倍，青贮玉米(*Zea mays* L.)的干物质产量可达45 t/ha，是天然草地的23倍[1]．由此可见，建设优质高效人工草地可以使饲草产量提高10~20倍，有望从根本上解决我国肉、奶生产中面临的优质饲草料严重短缺的瓶颈问题，遏制过度放牧引起的草地大面积退化、生态功能严重衰退等生态安全问题．因此，开展人工草地生产力形成机理与稳定性维持机制研究，建设高产优质人工草地和半人工草地，是实现畜牧业产业方式转变和草地生产与生态功能科学配置的关键，也是保障国家生态安全，践行生态文明建设的重大科学基础．

1 人工草地生产力和稳定性调控的理论基础

1.1 生态化学计量学理论

生态化学计量学(ecological stoichiometry)概念最早由Redfield[9,10]提出，后来由Sterner和Elser[11]建立了生态化学计量学的基本理论和方法体系．其基本原理是通过定量研究基因、个体、种群、群落和生态系统水平生命有机体的元素组成比例及变化，揭示植物、动物、微生物和土壤系统的养分限制与养分平衡，进而阐明不同营养级间的养分转移和循环规律[11~15]．生态化学计量学为定量研究牧草的养分限制和养分平衡，水肥耦合对草地生产力的调控，微生物对牧草和家畜营养元素吸收和利用的调控，牧草-家畜-土壤动物和微生物之间跨营养级的养分转移与循环，以及整个草-畜系统的可持续性提供了强大的理论和方法体系[11,13,16,17]．应用生态化学计量学的基本理论和方法，揭示关键营养元素(如N, P, K, Mo, B, Cu等)及其化学计量平衡对牧草光合速率和同化产物源-库分配的调控机理，水分及水肥耦合作用对牧草产量和品质的调控机制与途径，根瘤菌(*Rhizobium*)和菌根真菌(*Mycorrhizal fungi*)对牧草固氮、氮磷活化和吸收利用的调控机制，刈割对牧草再生性和利用年限的影响机制，以及草-畜复合系统初级生产力的互补增益与草-畜耦合机制，是当前人工草地功能调控和草-畜系统耦合机理研究的前沿[18]．

1.2 生态位分化、补偿和互惠理论

生态位分化(niche differentiation)、补偿(compensation)和互惠(mutualism)理论，为研究牧草功能性状(functional trait)的互补性(complementarity)对草地生产力的调控机制，以及功能性状多样性与草地生产力、稳定性和利用年限的关系，提供了重要的理论基础[19,20]，是当前人工草地生产力和稳定性维持机制的研究热点[21~26]．应用生态位分化、补偿和互惠共生理论，采用稳定性同位素(^{13}C, ^{2}H, ^{18}O, ^{15}N)技术[27,28]，以及野外原位观测与室内分析相结合方法，

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

研究混播人工草地牧草功能性状互补性对草地生产力的调控机制，多草种组合与功能多样性对混播人工草地稳定性的调控机制，半人工草地豆科和禾本科草种配置对草地生产力与牧草品质的调控机理与途径，人工、半人工草地生产功能与生态功能的协同效应和权衡关系，进而阐明牧草功能性状互补性与多样性、草种配置、植物与根际微生物互惠共生对生产力和稳定性调控的生物学和生态学机制，是近年来人工草地功能调控研究的重要领域[29~34].

1.3 放牧优化假说和中度干扰假说

草地资源的科学、合理利用是保护草地的基础，是防止草地退化、实现资源永续利用及草牧业可持续发展最有效的措施[8,35]. 人工草地按利用方式可将其分为割草利用、放牧利用、草田轮作和牧草种子生产等类型. 目前，我国的人工草地大部分为割草和放牧利用型人工草地. 对于割草利用型人工草地，由于连年割草使草地凋落物减少、植被盖度降低、地表裸露增加、表层土壤温度升高、土壤肥力下降，植物群落的种类组成发生变化，生产力降低，草地向旱生化演替[7,8]. 因此，根据不同区域气候、土壤、牧草种类组成及其生物学特性的差异，确定科学合理的牧草刈割时间、刈割次数、留茬高度以及草地轮刈方案是割草利用型人工草地合理利用的重要基础，也是牧草产业体系中亟待解决的重要科学和技术问题[8,35,36]. 对于放牧型人工草地，根据气候和土壤条件、牧草生物学特性、家畜采食习性，科学地确定放牧家畜种类、放牧时期、利用率、放牧强度和放牧制度(连续放牧、轮牧、延迟放牧、季节性休牧)，是我国草牧业生产和生态文明建设中亟待解决的科学和技术问题. 放牧优化假说(grazing optimization hypothesis)认为，经过优化的放牧强度和管理方式可以增加草地的初级生产力[37,38]. 中度干扰假说(intermediate disturbance hypothesis)认为，在中等干扰强度下群落的生物多样性达到最高[39]. 为此，美国把“用一半，留一半”(take half and leave half)作为草地管理的“圣经”[35]. 但许多研究表明，放牧与生物多样性和生态系统功能的关系，还受地形、降水、放牧时间、家畜分布、放牧制度等因素的影响[35,40~42]. 因此，如何科学地确定人工草地的放牧时期、利用率、放牧强度和放牧制度，仍然是当前和今后草业科学的重点研究领域.

2 畜牧业发达国家人工草地现状、研究进展和发展趋势

2.1 人工草地的建设规模和水平是衡量一个国家畜牧业发达程度的重要标志，畜牧业发达国家高度重视人工草地的建设与研究

畜牧业发达国家高产优质人工草地面积占天然草地面积的10%~70%，以人工草地为主的草产业对畜牧业产值的贡献率超过60%[1]. 目前，美国和加拿大的人工草地占天然草地面积的30%，澳大利亚、新西兰人工草地比例达58%~70%，荷兰、丹麦、英国、德国等欧洲国家人工草地的比例达到60%~100% (联合国粮食及农业组织(Food and Agriculture Organization, FAO), 2013). 同时，欧美等畜牧业发达国家十分重视对人工草地生产力和品质调控基础理论及应用研究. 主要包括以下3个方面.（ⅰ）大量元素(N, P, K)和微量元素(B, Mn, Mo, Zn, Se)肥料配比对牧草生长发育(植株分枝、萌蘖和根系发育)、干物质产量和品质(粗蛋白、中性洗涤纤维和酸性洗涤纤维含量)的影响[43]; （ⅱ）根瘤菌(Rhizobia)和丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)对增加牧草氮磷养分供给，提高养分利用效率，地下菌根菌丝体网络对植物间养分再分配的调节机制，以及根际微生物对草地生产力和稳定性的作用机制[18,29,44,45]; （ⅲ）刈割时间、频次、留茬高度对人工草地牧草非结构性碳水化合物的储藏与分配、再生性、产量、品质、牧草种间关系及草地利用年限的影响[31]. 近年来，国外在人工草地研究的最新发展趋势包括：人工草地水分和养分的管理计量化[46]; 更加重视混播人工草地物种配置与草地多功能性[32,34,47~49]; 更加重视人工草地的生产功能与生态功能(碳固持、减少温室气体排放、降低养分淋溶、生物多样性保育)的协同[50~52].

2.2 通过人工草地控制实验，揭示物种多样性与对草地生产力和稳定性的影响机制是近年来的国际研究前沿，并取得了世界瞩目的研究成果

大量研究表明，生物多样性对草地的生产力、稳定性、养分循环及其对干扰的抗性和可恢复性等均具有重要的影响[23,25,53,54]. 20世纪90年代以来，一些发达国家通过人工草地控制实验，对生物多样性与草

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

地生产力、稳定性和水土保持能力关系进行了系统的研究. 在此基础上, 提出了一些具有重要影响力的理论和假说. 其中, 国际上最具代表性和影响力的两个实验研究是: Tilman等人[25,26,53]在美国开展的“草地生产力、生物多样性与生态系统功能关系”长期实验研究; Hector等人[22,51]几十位科学家在欧洲7个国家(德国、英国、希腊、爱尔兰、葡萄牙、瑞典和瑞士)8个地点联合开展的“草地生物多样性与生态系统过程”(BIODEPTH)联网实验研究. 基于上述两个人工草地长期实验及相关研究取得的代表性研究成果包括: (ⅰ) 草地生物多样性对多个生态系统功能和过程(初级生产力、稳定性、养分保持能力、碳固持、抵御外来种入侵)均具有显著的正效应, 这种正效应会随着时间的进程而增强[26,51,55]; (ⅱ) 多样性导致草地初级生产力和养分与水土保持能力增加的主要机制是互补效应(包括生态位分化和互惠效应)和选择效应[22,56]. 多样性导致草地稳定性增加的主要机制是均衡效应和超产效应[26,57]; (ⅲ) 沿着生态系统不同营养级水平, 菌根真菌与植物之间的互惠效应促进了植物对磷的吸收, 菌根真菌多样性进一步增强了植物多样性对草地生产力的正效应[44]. 国际最新研究进展表明, 基于植物功能性状(functional traits)的功能多样性(functional diversity)对多个生态系统功能和过程均具有重要影响[33,54,58]. 这些研究成果为开展混播人工草地和半人工草地中牧草功能性状和功能多样性对草地生产力和稳定性的调控机制研究奠定了重要的理论基础.

2.3 应用生物化学计量学的基本原理和方法, 定量研究牧草养分限制和养分平衡, 以及水肥耦合对人工草地牧草品质、生产力和稳定性的调控机理是当前的热点领域

许多研究表明, 植物叶片的N∶P比可以作为判断植物养分限制的重要指标[59,60]. 例如, Koerselman和Meuleman[61]研究表明, 当植物叶片N∶P比大于16时, 主要受P限制, 当N∶P比小于14时, 主要受N限制, 当N∶P比在14~16范围内, 受N, P共同限制. 我国研究者对中国753种陆地植物的研究表明, 叶片N∶P的质量比为14.4∶1[62]. Elser等人[63]进一步研究发现, 全球陆地和淡水生态系统均受N, P限制, N, P的协同作用对生态系统生产力具有极其重要的影响. 目前, 生物化学计量学的基本理论和方法已经应用到群落组成与稳定性维持、牧草和草食家畜相互作用、植物-根际微生物互惠共生关系、食物网中的物质循环、营养动态等多个领域[13~17].

水分是草原生态系统物种多样性、初级生产力和稳定性维持的最主要限制因子[64~67]. Tilman和Elhaddi[68]研究表明, 严重的干旱使草原植物群落的物种丰富度和生物量分别降低了37%和47%, 干旱后物种丰富度的恢复显著滞后于生物量的恢复. 高生物多样性群落同时具有较高的抗旱性和干旱后的恢复力[69]. 同时, 养分包括N, P等大量元素和Zn, Mn, B, Mo等微量元素, 也是草原生态系统初级生产力和牧草品质的主要限制因子[14,70,71]. 在干旱半干旱地区, 水分和养分对草地初级生产力的限制性是耦合在一起的, 在干旱年份以水分限制为主, 而在多雨年份则转化为养分限制为主[66,72]. 研究表明, 土壤中微量元素Mo含量低可能是导致草原群落中豆科牧草比重低、蛋白产量低的主要原因[73]. 在我国北方牧区和农牧交错区, 水分和土壤养分条件是影响草地生产和生态功能合理配置、人工草地规模化建植和草-畜产业带耦合的主要限制因子. 因此, 阐明水分、养分及其耦合作用对人工草地牧草品质、生产力和利用年限的调控机理与途径是发展优质高效人工草地的重要科学基础.

3 国内人工草地现状与相关研究进展

3.1 草产业发展水平低, 人工草地和半人工草地种植规模小、产量低、品质差、利用年限短, 远落后于畜牧业发达国家

我国作为世界草地大国, 草地资源远未达到科学合理的利用. 据统计, 我国可利用草原面积为49.7亿亩, 人工草地面积1.8亿亩, 仅为天然草地面积的3% (中华人民共和国农业部, 2013). 例如, 2008年, 我国禾本科牧草的种植面积仅为1286.2万亩, 其中多年生牧草为1012.3万亩, 一年生牧草为273.9万亩, 饲草总产量约为1325万 t, 远不能满足现代草产业发展的需求(中国草业统计, 2009). 作为“牧草之王”的苜蓿人工草地, 其种植规模和生产水平是衡量一个国家草地畜牧业现代化程度的重要标志. 据统计, 2000年以来, 全国苜蓿保留面积约为3000万亩, 干草平均亩产为401.4 kg. 同美国相比, 我国苜蓿人工草地种植面积仅为美国的10%左右, 总产量仅为美国的

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

1/100, 品质也远低于美国[74,75]. 近年来, 我国90%以上的苜蓿产品来源于美国[74]. 目前, 我国草畜产业发展仍处于较低水平, 牧区和农牧交错区提供的牛、羊肉, 仅占全国肉类总产量的10%, 相当于美国的1/20, 单位面积草原产肉量仅为世界平均水平的30%, 严重滞后于我国国民经济的发展需求[1], 其根本原因在于人工、半人工草地基础研究和产业发展水平均远落后于发达国家.

3.2 我国人工草地的基础研究发展迅速, 但仍然较薄弱, 对草产业发展的支撑能力低, 不能满足现代草-畜产业发展的科技需求

3.2.1 单播人工草地生产力和品质调控

近年来, 我国单播人工草地生产力和品质方面的研究较多, 主要集中在以下5个方面: (ⅰ) 养分(大量和微量元素)对牧草产量和品质的影响; (ⅱ) 水分对牧草产量的影响; (ⅲ) 收获利用方式和强度对牧草产量、品质、越冬性能的影响; (ⅳ) 苜蓿人工草地根瘤菌固氮; (ⅴ) 人工草地碳固持. 取得的主要进展包括增施K和P肥, 使老芒麦人工草地的地上生物量增加11%~47%[76], 灌溉处理则增加了老芒麦的根长密度、根重密度和地下生物量[77]; 接种根瘤菌增加了苜蓿的根瘤数量, 提高了其固氮能力, 提高了苜蓿的有效分枝数、地上生物量和种子产量. Se, Co配合基肥能够显著提高苜蓿叶面积指数、净光合能力和产草量, 而过量施N则会抑制根瘤菌结瘤, 使苜蓿固氮能力下降[78]; 苜蓿人工草地土壤有机碳和氮积累均随种植年限的延长而增加, 在6~12年左右达到饱和[79,80]. 目前, 我国人工草地的基础研究仍然比较零散, 有关养分限制与养分平衡、水分限制与水肥耦合、植物-根际微生物调控与反馈以及收获利用方式和强度对草地生产力和牧草品质调控机理研究亟待加强[81~85].

3.2.2 混播人工、半人工草地草种配置与生产力和稳定性关系

我国混播人工草地和补播半人工草地的研究起步较晚, 目前主要集中在以下4个方面: (ⅰ) 豆科-禾本科草种配置、混播比例与播种方式对人工草地产量和品质的影响; (ⅱ) 刈割时间和强度对草地生产力和利用年限的影响; (ⅲ) 施肥对草地生产力和品质的影响; (ⅳ) 豆科牧草生物固氮及混播牧草种间关系对产量的影响. 取得的主要进展包括: 合理的豆科-禾本科草种组合可以显著提高草地产量和稳定性, 改善牧草品质[86]; 同撒播、混合条播等方式相比, 禾本科和豆科牧草隔行条播能够更好地减少种间竞争, 有利于混播草地生产力的维持[87]; 刈割时间和强度对不同草种的生理生态、干物质分配和生物量均有影响[88,89]; 合理的肥料种类、比例、水平和时间可以显著提高混播草地牧草的品质和产草量[90]; 豆科牧草根瘤菌的生物固氮可以增加草地氮输入, 提高草地生产力[91]. 上述研究结果为提升我国混播和补播人工草地的研究水平奠定了重要基础. 然而, 现有的工作大多以苜蓿和少数几个禾本科牧草混播组合为对象, 偏重草地建植和收获管理的具体措施, 缺乏草种配置与草地生产力和稳定性维持方面的机理研究.

4 展望

4.1 人工草地生产力和稳定性调控研究亟待解决的重要科学问题

面向保障国家生态安全和食物安全的重大科技需求, 针对我国人工草地规模小、生产力水平低、稳定性差, 草原生产-生态功能缺乏科学配置等问题, 人工草地生产力和稳定性调控研究亟待解决的重要科学问题包括以下两个方面.

4.1.1 优质高效人工草地生产力形成与调控机理

禾本科和豆科牧草人工草地生产力形成与调控机理是优质高效人工草地建设的重要科学基础. 基于生态化学计量学的养分限制和养分平衡理论, 研究重要养分元素(N, P, K和B, Mo, Zn, Cu, Fe, Mn等)及其计量平衡如何对牧草光合速率和同化产物的源-库分配进行调控? 水分及水肥耦合作用如何影响牧草生长发育和刈割后的再生, 进而最终影响牧草的产量和品质? 根际微生物(根瘤菌、菌根真菌)与牧草之间的互惠增益效应(生物固氮和氮、磷吸收利用效率)受哪些生物和非生物因子调控? 在此基础上, 阐明提高牧草养分和水分利用效率以及草地生产力与牧草品质的生物学与生态学机制.

4.1.2 人工和半人工草地物种配置与稳定性的维持机制

依据生态位分化、补偿和互惠理论, 植物功能性状的互补性和多样性是生态系统生产力与稳定性维持的基础. 通过建立多物种配置的混播人工和半人工草地实验研究平台, 研究草种配置(禾本科与豆科、深根型与浅根型、耐旱与喜湿、长寿命与短寿命牧草)如何

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

影响草地N, P的固定与活化、不同土层水分和养分资源利用、气候波动抗性和群落稳定性？牧草功能性状的互补性和多样性如何影响草地初级生产力及其稳定性？多草种组合如何影响草地生产功能(牧草产量与品质)与生态功能(防风固沙、水土保持和碳固持)之间的协同关系？阐明牧草功能性状互补性和功能多样性对草地生产力和稳定性的调控机理以及系统内草地生产功能和生态功能之间的协同与权衡机制.

4.2 人工草地生产力和稳定性调控的重要生物学和生态学机制

针对上述关键科学问题，以单播、混播和补播人工草地为研究对象，通过建立水分、养分协同调控和多物种配置控制实验平台，以5个重要生物学和生态学机制为核心，包括:（ⅰ）基于生态化学计量学的养分限制与养分平衡机制;（ⅱ）基于水分和养分限制的水肥耦合机制;（ⅲ）基于生态位互补理论的资源高效利用机制;（ⅳ）基于牧草功能性状多样性的稳定性维持机制;（ⅴ）基于植物-根际微生物互惠共生关系的植物-土壤调节与反馈机制. 深入研究和阐明这些机制在优质高效人工草地生产力调控，混播人工、半人工草地稳定性维持中的作用方式、相对重要性与调控途径，不断完善和发展我国人工草地功能调控的理论体系.

参考文献

1 Du Q L. Sustainable Development Strategy of Chinese Prataculture (in Chinese). Beijing: China Agriculture Press, 2006 [杜青林. 中国草业可持续发展战略. 北京: 中国农业出版社, 2006]

2 Department of Animal Husbandry and Veterinary and the General Station of Animal Husbandry and Veterinary Science, the Ministry of Agriculture of the People's Republic of China. Rangeland Resources of China (in Chinese). Beijing: China Science and Technology Press, 1996 [中华人民共和国农业部兽医司, 全国畜牧兽医总站. 中国草地资源. 北京: 中国科学技术出版社, 1996]

3 Han J. Survey on Ecological Issues of China's Grasslands (in Chinese). Shanghai: Shanghai Yuandong Press, 2011 [韩俊. 中国草原生态问题调查. 北京: 上海远东出版社, 2011]

4 Ministry of Environmental Protection of People's Republic of China. The 2005 Report on the State of the Environment of China (in Chinese). Beijing: Ministry of Environmental Protection of People's Republic of China, 2006 [中华人民共和国环境保护部. 中国环境状况公报 2005. 北京: 中华人民共和国环境保护部, 2006]

5 Hou X Y. Chinese Grassland Science (in Chinese). Beijing: Science Press, 2013 [侯向阳. 中国草原科学. 北京: 科学出版社, 2013]

6 International Institute for Environment and Development and World Resources Institute. World Resources 1987 (in Chinese). Beijing: Energy Publishing, 1989 [国际环境与发展研究所, 世界资源研究所. 中国科学院自然资源综合考察委员会, 译. 世界资源. 1987. 北京: 能源出版社, 1989]

7 Inner Mongolia College of Agriculture and Animal Husbandry. Grassland Management (in Chinese). 2nd ed. Beijing: China Agriculture Press, 1986 [内蒙古农牧学院. 草原管理学(第二版). 北京: 中国农业出版社, 1986]

8 Teaching and Research Section of Grassland Management, Inner Mongolia College of Agriculture and Animal Husbandry. Grassland Management (in Chinese). Huhhot: Inner Mongolia University Press, 1989 [内蒙古农牧学院草原管理教研室. 草地经营. 呼和浩特: 内蒙古大学出版社, 1989]

9 Redfield A C. On the proportions of organic derivatives in sea water and their relation to the composition of plankton. In: Daniel R J, ed. James Johnstone Memorial Volume. Liverpool: Liverpool University Press, 1934. 176–192

10 Redfield A C. The biological control of chemical factors in the environment. Am Sci, 1958, 46: 205–221

11 Sterner R W, Elser J J. Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere. Princeton: Princeton University Press, 2002

12 Elser J J, Fagan W F, Denno R F, et al. Nutritional constraints in terrestrial and freshwater food webs. Nature, 2000, 408: 578–580

13 Elser J J, Fagan W F, Kerkhoff A J, et al. Biological stoichiometry of plant production: Metabolism, scaling and ecological response to global change. New Phytol, 2010, 186: 593–608

14 Elser J J, Hamilton A. Stoichiometry and the new biology: The future is now. PLoS Biol, 2007, 5: 1403–1405

15 Elser J J, Sterner R W, Gorokhova E, et al. Biological stoichiometry from genes to ecosystems. Ecol Lett, 2000, 3: 540–550

16 Bai Y F, Wu J G, Clark C M, et al. Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. J Appl Ecol, 2012, 49: 1204–1215

17 Yu Q, Chen Q S, Elser J J, et al. Linking stoichiometric homoeostasis with ecosystem structure, functioning and stability. Ecol Lett, 2010, 13: 1390–1399

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

18 Johnson N C. Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. New Phytol, 2010, 185: 631–647
19 Chesson P. Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst, 2000, 31: 343–366
20 Schoener T W. Resource partitioning in ecological communities. Science, 1974, 185: 27–39
21 Tilman D. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton: Princeton University Press, 1988
22 Hector A, Schmid B, Beierkuhnlein C, et al. Plant diversity and productivity experiments in european grasslands. Science, 1999, 286: 1123–1127
23 Loreau M, Naeem S, Inchausti P, et al. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science, 2001, 294: 804–808
24 Hooper D U, Adair E C, Cardinale B J, et al. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature, 2012, 486: 105–108
25 Tilman D, Reich P B, Isbell F. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proc Natl Acad Sci USA, 2012, 109: 10394–10397
26 Tilman D, Reich P B, Knops J M H. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature, 2006, 441: 629–632
27 Dawson T E, Mambelli S, Plamboeck A H, et al. Stable isotopes in plant ecology. Annu Rev Ecol Syst, 2002, 33: 507–559
28 Dawson T E, Siegwolf R T W. Stable Isotopes as Indicators of Ecological Change. Amsterdam: Elsevier Academic Press, 2007
29 Read D J, Perez-Moreno J. Mycorrhizas and nutrient cycling in ecosystems—A journey towards relevance? New Phytol, 2003, 157: 475–492
30 Reynolds H L, Packer A, Bever J D, et al. Grassroots ecology: Plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology, 2003, 84: 2281–2291
31 Tracy B F , Sanderson M A. Productivity and stability relationships in mowed pasture communities of varying species composition. Crop Sci, 2004, 44: 2180–2186
32 Malézieux E, Crozat Y, Dupraz C, et al. Mixing plant species in cropping systems: Concepts, tools and models. A review. Agron Sustain Dev, 2009, 29: 43–62
33 Loreau M. Linking biodiversity and ecosystems: Towards a unifying ecological theory. Philos Trans R Soc B-Biol Sci, 2010, 365: 49–60
34 Goslee S C, Veith T L, Skinner R H, et al. Optimizing ecosystem function by manipulating pasture community composition. Basic Appl Ecol, 2013, 14: 630–641
35 Holechek J L, Pieper R D, Herbel C H. Range Management: Principles and Practices. 5th ed. Upper Saddle River: Prentice-Hall, 2004
36 Barnes R F, Nelson C J, Collins M, et al. Forages, Volume 1: An Introduction to Grassland Agriculture. 6th ed. Iowa: Iowa State Press, 2003
37 McNaughton S J. Grazing as an optimization process: Grass ungulate relationships in the Serengeti. Am Nat, 1979, 113: 691–703
38 McNaughton S J, Banyikwa F F, McNaughton M M. Promotion of the cycling of diet-enhancing nutrients by african grazers. Science, 1997, 278: 1798–1800
39 Connell J H. Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a non-equilibrium state. Science, 1978, 199: 1302–1310
40 Schönbach P, Wan H, Gierus M, et al. Effects of grazing and precipitation on herbage production, herbage nutritive value and performance of sheep in continental steppe. Grass Forage Sci, 2012, 67: 535–545
41 Schönbach P, Wan H W, Gierus M, et al. Grassland responses to grazing: Effects of grazing intensity and management system in an inner Mongolian Steppe ecosystem. Plant Soil, 2011, 340: 103–115
42 Li W H, Xu F W, Zheng S X, et al. Patterns and thresholds of grazing-induced changes in community structure and ecosystem functioning: Species-level responses and the critical role of species traits. J Appl Ecol, 2017, 54: 963–975
43 Berg W K, Cunningham S M, Brouder S M, et al. Influence of phosphorus and potassium on alfalfa yield and yield components. Crop Sci, 2005, 45: 297–304
44 van der Heijden M G A, Klironomos J N, Ursic M, et al. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature, 1998, 396: 69–72
45 Spehn E, Scherer-Lorenzen M, Schmid B, et al. The role of legumes as a component of biodiversity in a cross-european study of grassland biomass nitrogen. Oikos, 2002, 98: 205–218
46 Bell C, Carrillo Y, Boot C M, et al. Rhizosphere stoichiometry: Are C:N:P ratios of plants, soils, and enzymes conserved at the plant species-level? New Phytol, 2014, 201: 505–517
47 Picasso V D, Brummer E C, Liebman M, et al. Crop species diversity affects productivity and weed suppression in perennial polycultures under two management strategies. Crop Sci, 2008, 48: 331–342

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

48 Sanderson M A, Brink G, Ruth L, et al. Grass-legume mixtures suppress weeds during establishment better than monocultures. Agron J, 2012, 104: 36–42
49 Sanderson M A, Brink G, Stout R, et al. Grass-legume proportions in forage seed mixtures and effects on herbage yield and weed abundance. Agron J, 2013, 105: 1289–1297
50 Spehn E M, Hector A, Joshi J, et al. Ecosystem effects of biodiversity manipulations in european grasslands. Ecol Monogr, 2005, 75: 37–63
51 Hector A, Bagchi R. Biodiversity and ecosystem multifunctionality. Nature, 2007, 448: 188–190
52 Kardol P, Van der Wal A, Bezemer T M, et al. Restoration of species-rich grasslands on ex-arable land: Seed addition outweighs soil fertility reduction. Biol Conserv, 2008, 141: 2208–2217
53 Tilman D, Wedin D, Knops J. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature, 1996, 379: 718–720
54 Hooper D U, Chapin F S III, Ewel J J, et al. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr, 2005, 75: 3–35
55 Cardinale B J, Wright J P, Cadotte M W, et al. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proc Natl Acad Sci USA, 2007, 104: 18123–18128
56 Loreau M, Hector A. Partitioning selection and complementarity in biodiversity experiments. Nature, 2001, 412: 72–76
57 Tilman D, Knops J, Wedin D, et al. The influence of functional diversity and composition on ecosystem processes. Science, 1997, 277: 1300–1302
58 Reiss J, Bridle J R, Montoya J M, et al. Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol Evol, 2009, 24: 505–514
59 Aerts R, Chapin F S III. The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. Adv Ecol Res, 2000, 30: 1–67
60 Güsewell S. N:P ratios in terrestrial plants: Variation and functional significance. New Phytol, 2004, 164: 243–266
61 Koerselman W, Meuleman A F M. The vegetation N:P ratio: A new tool to detect the nature of nutrient limitation. J Appl Ecol, 1996, 33: 1441–1450
62 Han W X, Fang J Y, Guo D L, et al. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. New Phytol, 2005, 168: 377–385
63 Elser J J, Bracken M E S, Cleland E E, et al. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett, 2007, 10: 1135–1142
64 Gibson D J. Grasses and Grassland Ecology. Oxford: Oxford University Press, 2009
65 Bai Y F, Wu J G, Pan Q M, et al. Positive linear relationship between productivity and diversity: Evidence from the Eurasian Steppe. J Appl Ecol, 2007, 44: 1023–1034
66 Bai Y F, Wu J G, Xing Q, et al. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecology, 2008, 89: 2140–2153
67 Bai Y G, Broersma K, Thompson D, et al. Landscape-level dynamics of grassland-forest transitions in British columbia. J Range Manage, 2004, 57: 66–75
68 Tilman D, Elhaddi A. Drought and biodiversity in grasslands. Oecologia, 1992, 89: 257–264
69 Tilman D, Downing J A. Biodiversity and stability in grasslands. Nature, 1994, 367: 363–365
70 Vitousek P M, Howarth R W. Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry, 1991, 13: 87–115
71 Vitousek P M, Porder S, Houlton B Z, et al. Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen-phosphorus interactions. Ecol Appl, 2010, 20: 5–15
72 Bai Y F, Wu J G, Clark C M, et al. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: Evidence from inner Mongolia grasslands. Glob Change Biol, 2010, 16: 358–372
73 Sun J H, Tong Y P, Liu Q Y, et al. The important significance of applying molybdenum fertilizer in increasing yield of leguminous crops in agricultural-pastoral economy area (in Chinese). Chin J Ecol Agr, 2001, 9: 77–79 [孙建华, 童依平, 刘全友, 等. 钼肥对农牧交错带豆科作物增产的重要意义. 中国生态农业学报, 2001, 9: 77–79]
74 Yang C, Wang M L, Liu Y Z. Alfafa trade of China, historical changes, future trends and suggestions (in Chinese). Pratacult Sci, 2011, 28: 1711–1717 [杨春, 王明利, 刘亚钊. 中国的苜蓿草贸易——历史变迁、未来趋势与对策建议. 草业科学, 2011, 28: 1711–1717]
75 Yang Q C, Sun Y. The history, current situation and development of alfafa breeding in China (in Chinese). Chin J Grassland, 2011, 33: 95–101 [杨青川, 孙彦. 中国苜蓿育种的历史、现状与发展趋势. 中国草地学报, 2011, 33: 95–101]
76 Han D L, Xu Z M, Ai L, et al. Effect of fertilization on the froage biomass and quality of aged leafy *Elymus sibiricus* (in Chinese). Plant Nutr Fertil Sci, 2009, 15: 1486–1490 [韩德梁, 徐智明, 艾琳, 等. 磷肥和钾肥对老龄多叶老芒麦牧草生物量和品质的影响. 植物营

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

养与肥料学报, 2009, 15: 1486–1490]

77 Li Z Z, Huang D, Wang Z Y. Effects of irrigation regime on growth of *Elymus sibiricus* swards (in Chinese). Sci Agric Sin, 2005, 38: 1621–1628 [李子忠, 黄顶, 王忠彦. 灌溉制度对老芒麦(*Elymus sibiricus*)生长的影响. 中国农业科学, 2005, 38: 1621–1628]

78 Ma X, Wang L L, Li W J, et al. Effects of different nitrogen levels on nitrogen fixation and seed production of alfalfa inoculated with rhizobia. Acta Pratacult Sin, 2013, 22: 95–102 [马霞, 王丽丽, 李卫军, 等. 不同施氮水平下接种根瘤菌对苜蓿固氮效能及种子生产的影响. 草业学报, 2013, 22: 95–102]

79 Jiang H M, Jiang J P, Jia Y, et al. Soil carbon pool and effects of soil fertility in seeded alfalfa fields on the semi-arid Loess Plateau in China. Soil Biol Biochem, 2006, 38: 2350–2358

80 Chang S, Liu N, Wang X, et al. Alfalfa carbon and nitrogen sequestration patterns and effects of temperature and precipitation in three agro-pastoral ecotones of northern China. PLoS One, 2012, 7: e50544

81 Hong F Z. National Planting Zone of Perennial Forage Cultivars (in Chinese). Beijing: China Agricultural Science and Technology Press, 1990 [洪绂曾. 全国主要多年生栽培草种区划. 北京: 中国农业科技出版社, 1990]

82 Hong F Z. Alfalfa Science (in Chinese). Beijing: China Agriculture Press, 2009 [洪绂曾. 苜蓿科学. 北京: 中国农业出版社, 2009]

83 Hong F Z, Hu Z Z, Han J G, et al. Prataculture History of China (in Chinese). Beijing: China Agriculture Press, 2011 [洪绂曾, 胡自治, 韩建国, 等. 中国草业史. 北京: 中国农业出版社, 2011]

84 Lu X S. Grassland, Ranch & Pasture in China (in Chinese). Beijing: Kaiming Press, 2002 [卢欣石. 中国草情. 北京: 开明出版社, 2002]

85 Yang Q C. Guide for Alfalfa Planting Zone and Cultivar (in Chinese). Beijing: China Agricultural University Press, 2012 [杨青川. 苜蓿种植区划及品种指南. 北京: 中国农业大学出版社, 2012]

86 Liu M L, Baoyin T. An experiment on mix-sowing of *Elymus sibiricus* and *Medicargo varia* (in Chinese). Chin J Grassland, 2004, 26: 22–27 [刘美玲, 宝音陶格涛. 老芒麦与草原 2 号苜蓿混播试验. 中国草地, 2004, 26: 22–27]

87 Zheng W, Zhu J Z, Jianaerguli, et al. Effects of different sowing pattens on productive performance of legume-grass mixstures (in Chinese). Chin J Grassland, 2011, 33: 45–52 [郑伟, 朱进忠, 加娜尔古丽, 等. 不同混播方式对豆禾混播草地生产性能的影响. 中国草地学报, 2011, 33: 45–52]

88 Wang W, Miao J X, Chang S H, et al. Effects of cutting on the relationship between community growth and yield, and interspecific competition characteristics in mixed pasture (in Chinese). Pratacult Sci, 2003, 20: 20–23 [王文, 苗建勋, 常生华, 等. 刈割对混播草地种群生长与产量关系及种间竞争特性的影响. 草业科学, 2003, 20: 20–23]

89 Zhang J X, Ma Y S, Shi J J, et al. Effects of clipping on forage yield and quality of mixed-sown artificial grassland in Yantze and Yellow River headwater region (in Chinese). Pratacult Sci, 2010, 27: 92–96 [张金旭, 马玉寿, 施建军, 等. 刈割对江河源区混播草地牧草产量及品质的影响. 草业科学, 2010, 27: 92–96]

90 Zhang Y L, Hu Z Z, Zhao H X, et al. Effect of the seeding-year clipping on the biomass and regrowth rate grass-legume mixed grassland (in Chinese). Acta Agrest Sin, 2004, 12: 308–312 [张永亮, 胡自治, 赵海新, 等. 刈割对混播当年生物量及再生速率的影响. 草地学报, 2004, 12: 308–312]

91 Fan J W, Gao Y G. The role of nitrogen fixation of legume herbage in mixture pasture (in Chinese). Chin J Grassland, 1994, 16: 64–69 [樊江文, 高永革. 混播草地中豆科牧草的固氮作用. 中国草地, 1994, 16: 64–69]

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

Summary for “人工草地生产力和稳定性的调控机理研究: 问题、进展与展望”

Mechanisms regulating the productivity and stability of artificial grasslands in China: Issues, progress, and prospects

Yongfei Bai[1,2*], Zhu Yu[3], Qingchuan Yang[4], Hongwei Wan[1], Jianhui Huang[1], Baoming Ji[5] & Ang Li[1]

[1] *State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China;*
[2] *College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China;*
[3] *College of Animal Science and Technology, China Agricultural University, Beijing 100193, China;*
[4] *Institute of Animal Science of Chinese Academy of Agricultural Sciences, Beijing 100193, China;*
[5] *College of Forestry, Beijing Forestry University, Beijing 100083, China*
* Corresponding author, E-mail: yfbai@ibcas.ac.cn

China has 400 million hectares of grasslands, occupying 41.7% of the country’s total land area. Due to the overexploitation of grassland’s production functions and the neglect of its ecological functions, intensive livestock grazing in recent decades has resulted in widespread grassland degradation, reduction in ecosystem services, and imbalance between forage production and livestock demands in China. Compared to natural grasslands, artificial grasslands can increase forage yield up to 10–20 times. The development of high-quality artificial grasslands could fundamentally ease the severe shortage of forage supply, break the bottleneck in meat and milk production, curb grassland degradation caused by overgrazing, and thereby restore grassland ecological functions. Therefore, understanding the mechanisms that regulate the productivity and stability of artificial grasslands is a major national strategic need in order to transform the practices of sustainable livestock production based on the scientific and technological advancements, and to promote national ecological security, food security, and the development of ecological civilization. In this study, we examined theoretical basis underlying the regulations of artificial grassland productivity and stability, including theories of ecological stoichiometry, niche differentiation, compensation, mutualism, grazing optimization, and intermediate disturbance. Then, we reviewed current research status and the latest progress that has made in this field. Finally, we proposed fundamental research questions that need to be fully addressed in future studies, regarding the effects of stoichiometry of key nutrient elements, coupled water and nutrient availability, mutualism between forage species and soil microbes, and complementarity of functional traits and multiple forage species on plant carbon assimilation, growth, reproduction, forage quality, biomass allocation, primary productivity, and ecosystem stability. We also highlighted several key biological and ecological mechanisms regulating the productivity and stability of artificial grasslands.

grassland, ecological functions, production functions, artificial grassland, biological and ecological mechanisms, ecological security, forage security

doi: 10.1360/N972017-00935

Downloaded to IP: 76.121.120.158 On: 2018-02-13 14:14:45 http://engine.scichina.com/doi/10.1360/N972017-00935

科学通报 2016 年 第 61 卷 第 2 期: 201 ~ 212
专辑: 生态草牧业理论范式与技术体系 评 述
《中国科学》杂志社 SCIENCE CHINA PRESS

草地生产与生态功能合理配置的理论基础与关键技术

白永飞[①], 潘庆民[①*], 邢旗[②]

① 中国科学院植物研究所, 植被与环境变化国家重点实验室, 北京 100093;
② 内蒙古自治区草原勘察规划院, 呼和浩特 010051
* 联系人, E-mail: pqm@ibcas.ac.cn

2015-09-18 收稿, 2015-11-09 修回, 2015-11-10 接受, 2015-12-14 网络版发表
中国科学院重点部署项目(KSZD-EW-Z-012)、中国科学院学部咨询评议项目(2011-4-13-1)和国家科技支撑计划(2012BAD16B0304)资助

摘要 草地生产功能和生态功能的合理配置对于生态草业的可持续发展至关重要. 本文总结了国内外草业发展现状, 特别是我国草地经营管理中存在的主要问题; 介绍了草地生产与生态功能合理配置的6个基础理论: 放牧优化假说、中度干扰假说、放牧促进/减缓生态系统养分循环假说、草畜平衡理论和草地农业系统理论. 在分析生态草业发展面临的主要技术瓶颈基础上, 提出了生态草业建设的核心技术体系, 着重介绍了退化草地恢复与培育的4项技术、天然草地保护与合理利用的2项技术, 以及人工草地建设与管理的技术. 最后介绍了天然草地和人工草地配置的原则, 以及人工草地的类型选择与合理布局的技术. 所述理论和技术对于指导我国生态草业建设和可持续发展具有重要指导意义.

关键词 生态草业, 天然草地, 人工草地, 草地恢复, 草地管理

世界草地总面积为5.25×10^9 hm^2, 约占地球陆地总面积的40.5%[1~4]. 长期以来, 草地生态系统不仅为人类提供了肉、奶、皮、毛等具有直接市场价值的产品, 同时具有维持大气组分、改善区域气候、保持土壤养分、降低水土流失、维系民族文化等重要服务功能. 发达国家的草地畜牧业发展模式主要有4类: 集约化农牧结合型生态畜牧业(美国、加拿大)、草畜平衡型生态畜牧业(澳大利亚、新西兰)、农户饲养型小规模生态畜牧业(日本)和有机集约化人工草地畜牧业(欧洲国家)[5]. 这些发展模式的共同特点是: (ⅰ) 以家庭牧场为主, 实现了草地管理和畜产品生产规模化和集约化, 单位面积草地、家畜单产和商品率水平高; (ⅱ) 高度重视草地畜牧业先进技术的集成应用; (ⅲ) 建立了较完善的公司、农户和科研单位的研发运营机制; (ⅳ) 强化牧场合作组织、专业化生产协会和行业协会在畜牧业发展中的作用.

我国拥有草地近4×10^8 hm^2, 约占国土总面积的41.7%, 是耕地面积的3.2倍、森地面积的2.5倍[6]. 目前, 我国的天然草地有90%左右处于不同程度的退化之中, 其中严重退化草地占60%以上. 人为因素和气候干旱, 特别是草地管理政策的偏差和管理水平的落后是导致我国北方草地退化的主要因素. 研究表明, 长期过度放牧导致草地的植被覆盖度和初级生产力降低, 生物多样性减少, 土壤养分和水分保持能力下降, 土壤侵蚀和水土流失加重, 对气候变化的敏感性增强[6~8]. 这些变化使草地的生态功能日益衰减, 虫鼠害和沙尘暴等自然灾害频繁发生[9,10], 严重威胁了我国北方及其周边地区的生态安全. 同时, 人工草地规模小、建植水平低, 牧草品质差, 肉奶业高度依赖进口牧草. 目前, 草原牧区已成为我国经济可持续发展、边疆稳定和构建和谐社会的关键制约因素.

引用格式: 白永飞, 潘庆民, 邢旗. 草地生产与生态功能合理配置的理论基础与关键技术. 科学通报, 2016, 61: 201–212
Bai Y F, Pan Q M, Xing Q. Fundamental theories and technologies for optimizing the production functions and ecological functions in grassland ecosystems (in Chinese). Chin Sci Bull, 2016, 61: 201–212, doi: 10.1360/N972015-00768

© 2015《中国科学》杂志社

我国草地经营管理存在以下两个问题: (ⅰ) 草地生态功能和生产功能配置不合理, 天然草地退化严重, 生产力水平低. 长期以来, 我国草原牧区过度强调草地的生产功能, 忽视其生态功能, 造成了超载过牧、"人-草-畜"关系失衡和草地的大面积退化. 据统计, 我国中度和重度退化草地面积达1.53×10^8 hm^2, 其中内蒙古、西藏、新疆、青海、四川和甘肃等主要牧区省区的退化草地比例高达80%~97%[7,8]. 温带草原初级生产力下降20%~40%, 高寒草地下降14%~20%[6]. 2012年, 我国牧区牛羊肉总产量274.5万吨、奶类总产量1219.6万吨, 仅占全国总产量的26%和33%[11]. (ⅱ) 人工草地规模小、产量低、品质差、利用年限短, 草-畜产业耦合度低, 肉奶的生产对耕地和进口饲草料的依存度高. 据统计, 我国可利用草原面积为3.31×10^8 hm^2, 人工草地面积1.20×10^7 hm^2, 仅为天然草地面积的3%[12]. 作为"牧草之王"的苜蓿(*Medicago*)人工草地, 其种植规模和生产水平是衡量一个国家草地畜牧业现代化程度的重要标志. 我国苜蓿保有面积约为2.00×10^6 hm^2, 仅为美国的10%左右, 总产量仅为美国的1/100[13,14]. 目前, 我国单位面积草原产肉量仅为世界平均水平的30%, 严重滞后于我国国民经济的发展需求[6], 其根本原因在于人工草地基础研究和产业发展水平均落后于发达国家.

畜牧业发达国家十分重视畜牧业在农业中的比重. 其中, 美国畜牧业占农业的比重为60%左右, 德国为70%, 法国为57%, 加拿大为65%. 同时, 在这些国家的畜牧业内部结构中, 草产业对畜牧业产值的贡献率均超过60%[6]. 目前, 我国畜牧业占农业的比重为30%左右, 远低于发达国家的平均水平[15]. 而且, 我国草-畜产业耦合度低, 突出表现为: (ⅰ) 种间相悖, 即草种与畜种间不协调; (ⅱ) 时间相悖, 即牧草生产的季节性与家畜营养需求失衡; (ⅲ) 空间相悖, 以人工草地为主的牧草生产主要集中在农牧交错区, 而家畜的饲养主要集中在牧区, 地区间草畜供需关系严重失调[16].

1 草地生产与生态功能合理配置的理论基础与基本原则

1.1 发展生态草业的必要性和战略定位

(ⅰ) 我国的传统草原畜牧业难以为继, 迫切需要转型升级. 当前, 我国草原牧区的传统畜牧业模式, 生产力水平低, 抗风险能力差, 效益低, 不仅导致生态环境日益恶化, 而且由于牧民收入的增加赶不上生活支出的增加, 导致牧民的生活水平下降. 近年来, 国家对于草原牧区保护的力度不断加强, 实施了"京津风沙源治理"、"退牧还草"、"天然草地保护"等生态保护和建设工程, 出台了草原生态保护补偿奖励机制. 然而, 这些生态保护和建设工程的实施, 没有和牧区草业发展模式的创新有机结合, 生态补偿没有与生态保护的效果挂钩, 传统畜牧业难以为继的局面没有得到根本扭转. 因此, 亟需探索适宜于牧区特点的生态保护与草业发展新模式, 依靠科技创新推动草业发展.

(ⅱ) 我国草地的生态功能和生产功能均具有巨大的提升潜力. 目前, 我国草原牧区的地上生物量约为3亿吨, 仅为农田的1/4[11,12]. 通过科学配置草地的生态功能和生产功能, 利用约10%优质草地, 建立集约化人工草地, 使优质饲草产量提高10~20倍, 可以从根本上解决草畜矛盾; 进而可以对90%的天然草地进行保护、恢复和适度利用, 提升其生态功能.

(ⅲ) 发展生态草业是实施牧区"科技先导"战略的必由之路. 2012年中央一号文件确立了以"科技为先导"的农业发展新思路; 十八届三中全会指出, 要加快生态文明制度建设, 构建新型农业经营体系, 推进家庭经营、集体经营、合作经营、企业经营等共同发展的农业经营方式创新. 2015年, 中央一号文件又提出了发展生态草牧业的新理念. 这些政策表明, 依靠科技进步, 发展生态草业, 是推进牧区生态文明建设、保障国家食物安全的的必由之路.

1.2 草地生产与生态功能合理配置的理论基础

(ⅰ) 放牧优化假说. 放牧是草地生态系统最主要的利用方式. 放牧优化假说(grazing optimization hypothesis, GOH)认为, 草地初级生产力在中等放牧强度下达到最高, 也就是说, 经过优化的放牧管理方式可以增加草地的初级生产力[17]. 放牧优化理论明晰了放牧对草地生产力的具有正向的调节作用. 但是大量研究表明, 放牧与生态系统功能的关系, 还受到地形因素、降水分布、放牧时间、家畜分布、放牧系统类型(连续放牧、轮牧、延迟放牧、季节性休牧)等因素的影响[18~20]. 最近, Luo等人[21]在新疆天山地区的研究支持放牧优化假说, 他们发现即使在水分限制的条件下, 适度放牧仍然可以促进草地的地上

净初级生产力. 在内蒙古典型草原, 李文怀等人[20]的研究表明, 平地系统的放牧实验支持放牧优化假说, 但坡地系统地结果的并不支持这一假说, 因为地形因素改变了放牧强度与草地生产力的关系. 由此可见, 放牧优化假说的普适性还有待于进一步的验证.

(ⅱ) 中度干扰假说. 人类活动干扰是导致生态系统生物多样性丧失的主要驱动因子. 中度干扰假说(intermediate disturbance hypothesis, IDH)认为, 在中等强度的干扰下群落的生物多样性达到最高[22]. 研究表明, 在环境条件较好的半干旱草原, 植被多样性的变化对放牧干扰的响应支持中度干扰假说[23,24], 例如, 在呼伦贝尔草甸草原的放牧实验发现中等放牧强度下物种多样性最高[25]. 但是, 在锡林郭勒典型草原的放牧实验结果并不支持这一假说, 因为随着放牧强度的增加, 平地和坡地的α多样性均呈逐渐下降的趋势; γ多样性的变化受地形条件的影响, 平地逐渐下降, 而坡地先降后升; 平地的β多样性随放牧强度的增加而逐渐减小, 而坡地的β多样性没有显著变化[26,27]. 由此可见, 草原生态系统生物多样性对放牧的响应还受到气候、地形、土壤等因素的影响[23,24].

(ⅲ) 放牧促进/减缓生态系统养分循环假说. 草地的养分循环是生态系统功能和服务形成与维持的基础[28]. 研究表明, 放牧对草原生态系统具有直接和间接的影响[29~33]. 草食动物对生态系统功能的控制作用, 主要是通过改变优势植物种与生态系统养分循环间的反馈作用来实现[29,30,33,34]. 有关草食动物对生态系统养分循环的调控机理包括两种假说, 即促进养分循环假说(accelerating nutrient cycling hypothesis)和减缓养分循环假说(decelerating nutrient cycling hypothesis). 前者认为, 放牧加快了富含营养的耐牧植物的组织丧失速率, 而这类植物则通过高养分吸收速率、高相对生长速度和组织中的高养分浓度, 对放牧做出补偿性响应. 这种变化加速了凋落物的分解和养分周转, 同动物排泄物的影响一起, 共同提高了生态系统的养分供给速率. 而这种较高的养分供给速率, 更有利于这些耐牧植物同其他物种的竞争. 因而, 放牧通过这种正反馈机制加速了生态系统的养分循环速率[29~42]. 后者则认为, 植食动物对富含营养组织的选择性采食, 导致了那些组织中养分含量低或者含有次生代谢产物的植物在群落中占优势, 这些植物的凋落物分解速率慢, 降低了生态系统养分的周转速率和可利用性. 因而, 通过正反馈作用, 放牧降低了地上初级生产力和养分循环速率[33,37,43~49]. 上述两个假说完全相反的结果表明, 植物生长限制性资源的类型, 可能决定放牧对生态系统氮循环影响的方向[37]. 如果植物群落初级生产力受氮素限制, 放牧可能降低生态系统氮循环速率. 相反, 如果生态系统中氮素的总量很高, 放牧可能提高生态系统氮循环速率[31,32,42,43].

(ⅳ) 气候、放牧、火烧对草原生态系统结构和功能的综合影响. 气候(如水分)、放牧和火烧被认为是草原生态系统结构与功能维持的重要因子[50~52]. Tilman和Elhaddi[53]研究表明, 严重的干旱使草原植物群落的物种丰富度和生物量分别降低了37%和47%. Collins等人[54]研究表明, 施肥和频繁的火烧降低了高草草原的物种丰富度, 但放牧使物种多样性得以恢复和维持. 也有研究表明, 在湿润和肥沃的生境中放牧通常增加了植物多样性, 在干旱和相对肥沃的生境中则降低了植物多样性, 而在干旱和贫瘠的生境中对植物多样性没有影响[55]. Milchunas和Lauenroth[56]对全球263个实验的分析表明, 放牧对物种组成的影响随生产力水平的提高和放牧史延长而增大.

(ⅴ) 草畜平衡理论. 草畜平衡是指在一定区域和时间内, 草原和其他途径提供的饲草料总量与饲养牲畜所需的饲草料总量保持动态平衡. 由于草畜平衡理论兼顾了草原生态安全与畜牧业可持续发展, 在1985年颁布的《中华人民共和国草原法》中成为指导我国草原保护与利用的主要法律依据. 但是由于草原牧区各地自然条件和和会经济发展水平不同, 很难确定一个统一的标准来衡量不同地域是否真正实现了草畜平衡. 对于天然草地, 确定载畜量是草畜平衡的基础[57,58], 但是草场的载畜量年际之间会有很大的变化. 例如, 内蒙古草原的产草量在丰年和欠年之间会相差2~4倍, 因此实际工作中常用5年的平均产草量来估算合理的载畜量. 贾幼陵[59]认为, 在自然生产力条件下的草畜平衡阶段, 主要通过畜群结构的优化、“草库伦”建设以及划区轮牧等措施, 发挥天草地的生产潜力. 在具有规模化人工草地前提下的草畜平衡阶段, 主要通过“以水定草, 以草定畜”, 来实现新的平衡. 在高效集约化的草畜平衡阶段, 通过种植豆科牧草或者草地施肥, 保持草地的氮

素平衡是实现草畜平衡的关键.

(ⅵ) 草地农业系统理论. 我国著名草地学家任继周先生认为, 草地农业生态系统是在自然生态系统的基础上发展起来的, 通过其产业特征和产品属性, 可以将草地农业生态系统归纳为相互联系的4个生产层: 即前植物生产层、植物生产层、动物生产层和后生物生产层[16]. 该理论是草地农业生态系统管理的重要基础, 各生产层之间物质的转换与能量的流动、产品和服务的形成、能量的输入与产出、基本要素间的耦合与调控等过程共同决定了草地农业生态系统的"社会收益"[16].

1.3 草地生产与生态功能合理配置的基本原则

长期以来, 人们片面追求天然草地生产功能而忽视其生态功能是导致我国草原退化的主要原因. 在生态草业建设中, 要实现草地生产功能与生态功能合理配置, 需要遵从以下3条原则: (ⅰ) "生态优先"的原则. 我国的天然草地应该以生态功能为主, 生产生态有机结合, 对生产功能的开发不能以牺牲生态功能为代价; (ⅱ) "功能置换"的原则. 通过在适宜区域发展高产高效人工草地, 替代天然草地的部分生产功能, 使退化天然草地得到恢复和合理利用, 提升其生态功能; (ⅲ) "因地制宜"的原则. 因地制宜确定适宜的载畜率, 适宜的天然草地和人工草地比例以及适宜的家畜种类和品种.

2 生态草业生产与生态功能合理配置的核心技术体系

2.1 生态草业发展的主要技术瓶颈

当前, 我国的草业正经历着由落后的传统模式向集约化模式的转型. 在此过程中, 天然草地的合理利用是基础, 人工草地建设是关键, 而草地生产与生态功能的合理配置是转型成功与否的标志. 在天然草地合理利用方面, 目前的技术瓶颈主要有3个: (ⅰ) 大面积退化草地如何恢复和保育? (ⅱ) 天然草地如何实现可持续合理利用? (ⅲ) 如何对家畜品种进行改良以实现传统放牧模式向集约化养殖模式的转变?

在人工草地方面的技术瓶颈主要有5个: (ⅰ) 我国牧草品种单一, 抵御干旱、低温和病虫害的能力弱; 特别缺乏适合于我国干旱半干旱区的优质高产牧草品种. (ⅱ) 缺乏完善的牧草种子生产体系. 国内自己育成的牧草品种, 其种子数量严重不足. (ⅲ) 缺乏牧草良种良法配套的栽培技术, 导致水分养分利用效率低下, 资源浪费严重. (ⅳ) 牧草收获和贮藏环节养分损失严重, 收获和贮藏技术亟待提升. (ⅴ) 草产品深加工技术亟待突破. 畜牧业发达国家的草产品品质好, 如美国的一级品苜蓿占全部苜蓿产品的70%以上, 而我国80%以上的苜蓿产品质量达不到一级.

所谓生产与生态功能的合理配置, 就是在一定的地理区域内, 通过种植一定比例(1/20~1/10)的高产高效人工草地, 把传统畜牧业对天然草地的依赖转移到人工草地, 使天然草地的功能回归到其本来的自然生态属性, 而人工草地承担起主要的生产功能, 从而实现我国草业的可持续发展. 该领域主要的技术瓶颈主要有3个: (ⅰ) 根据不同草原区域的自然禀赋, 确定合理的人工草地与天然草地的比例. (ⅱ) 根据区域内不同地理单元的水分和热量条件, 进行人工草地的合理布局. (ⅲ) 与之相适应的传统畜牧业模式向集约化畜牧业模式的转变.

2.2 生态草业技术体系的构成

生态草业技术体系是在天然草地合理利用、人工草地建设和草地的生产/生态功能合理配置3个方面, 把已有的先进技术与新研发的技术进行组装配套, 使天然草地以生态功能为主, 生产功能为辅, 人工草地承担主要的生产功能, 从而使我国草原牧区生产功能与生态功能相协调, 草业进入高效可持发展之轨道. 这一技术体系如图1所示.

2.3 退化草地恢复与培育技术

(ⅰ) 退化草地封育技术. 草地封育就是把退化草地通过建设围栏或禁止放牧等措施, 免除草地继续受到家畜采食、践踏等干扰, 依靠其自然修复能力, 使草地群落生产力逐步提高, 优良牧草比例不断增加, 生物多样性和稳定性逐渐恢复. 迄今, 草地封育是最有效的退化草地恢复技术之一, 也是其他恢复技术实施的前提.

退化草地封育技术主要包括围栏封育和禁止放牧两种措施. 前者主要适合于载畜率水平较高, 家畜多而密集的区域, 如草甸草原、典型草原地区; 后者主要是用于载畜率水平低, 家畜少而分散的区域, 如荒漠草原和荒漠地区. 草地封育的效果主要取决于草地退化的程度, 特别是优良牧草所占的比例. 据中

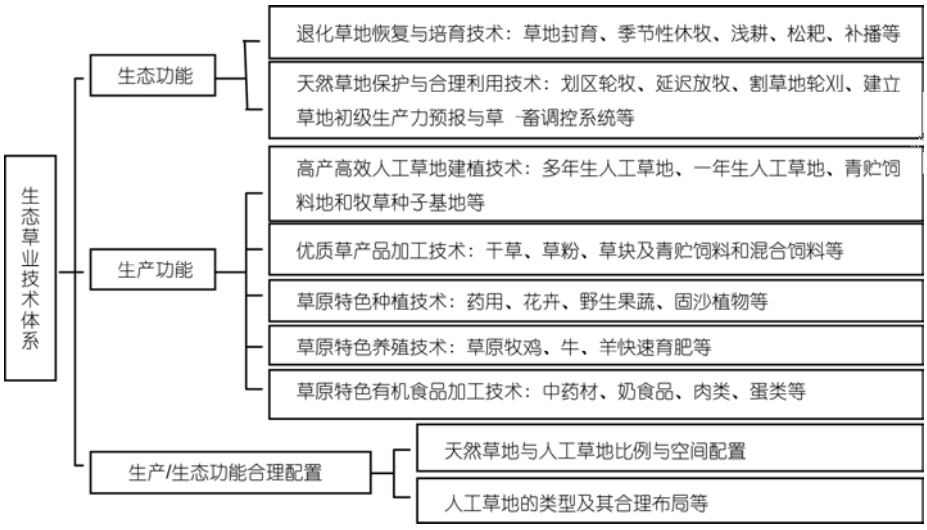


图 1 生态草业技术体系构成
Figure 1 Framework of major technologies for eco-pratacultural systems

国科学院内蒙古草原生态系统定位研究站研究，在轻度(6~9月份的载畜率为3.0 sheep hm^{-2})和中度(6~9月份的载畜率为6.0 sheep hm^{-2})放牧强度下，封育第二年群落的生产力就可以恢复；即使重度放牧区(6~9月份的载畜率为9.0 sheep hm^{-2})，只要羊草(*Leymus chinensis*)和大针茅(*Stipa grandis*)还存在，通过3年的封育，其地上净初级生产力也可以得到恢复[52]. 但是，当群落退化为含小叶锦鸡儿(*Caragana microphylla*)灌丛的冷蒿(*Artemisia frigid*)群落时，尽管封育后羊草、大针茅、冰草(*Agropyron cristatum*)等禾本科优质牧草的比重逐年提高，菊科、蔷薇科和其他杂类草的比重逐年下降[60]，但是群落的生产力恢复很慢，直到封育后5~7年，才能够逐步恢复. 在此过程中，植物种的饱和度逐年下降，而群落多样性和均匀性指数基本上保持稳定[61,62]. 据杨丽娜和宝音陶格涛[63]研究，封育23年的处理区比自由放牧区牧草产量可以提高1倍左右. 在新疆伊犁昭苏盆地，封育5~6年后，群落生物量趋于稳定，禾草和豆科牧草的比例显著增加，而杂类草所占比例下降[64]. 在青海海北地区，封育的效果因放牧的强弱而存在很大差异. 轻牧区封育后，禾草的生物量增加，但优良牧草比例由72%下降为62%；重牧区封育后，禾草及莎草生物量增加显著，优良牧草比例由48%上升为59%[65].

(ⅱ) 退化草地季节性休牧技术. 在我国北方草地，季节性休牧主要包括春季休牧和秋季休牧两种模式. 春季休牧是指每年牧草返青期(4月下旬~6月中旬)禁止放牧，使退化草地得以休养生息. 秋季休牧是指每年秋季牧草进入结实期，停止放牧，使牧草的种子得以成熟入土，以维持草地土壤种子库具有充足的种源. 与常年放牧处理相比较，在呼伦贝尔草原，春季休牧的地上生物量、盖度和高度分别提高87.5%，93%和86%[66]. 在锡林郭勒草原，到生长季结束时，春季休牧处理的牧草产量增产幅度可达1倍，植被盖度和植物多样性也显著提高[67,68].

(ⅲ) 退化草地浅耕和松耙技术. 浅耕或松耙可以改善土壤通气透水性能，提高土壤微生物活性，促进各种养分释放，从而加速退化草地的恢复. 退化草地浅耕的深度一般控制在15~20 cm，耙地的深度在10 cm左右，耙齿间距一般以20~30 cm为宜. 浅耕和松耙的时间均以雨季来临之前为宜[69].

在草地封育的基础上，浅耕和松耙能够促进群落向原生植被演替，从而加速退化草地的恢复[69]. 对于退化的羊草草原，浅耕处理后植被的恢复演替过程可分为4个阶段: (1) 早期恢复阶段: 一般为处理后前3年; (2) 羊草群落阶段: 处理后的4~10年; (3) 过渡性群落阶段: 处理后11~15年; (4) 稳定群落阶段: 处理后16年[69]. 松耙处理后的恢复演替也可以分为4个阶段: (1) 早期恢复阶段: 即处理后的前4年; (2) 羊草小禾草阶段: 处理后的5~14年; (3) 过渡性群落阶段: 处理后的15~18年; (4) 稳定性群落阶段: 处理19年以后[69]. 在农牧交错区的退化羊草草原，

浅耕显著提高植被盖度、高度和地上生物量. 浅耕4年后, 羊草在群落中占绝对优势[70]. 在宁夏盐池的荒漠草原, 浅耕能够有效地抑制猪毛蒿(*Artemisia scoparia*)当季发生数量, 提高退化草地的植被均匀性和多样性[71]. 邵玉琴等人[72]研究表明, 浅耕和松耙能够显著提高土壤微生物类群的数量, 在0~10 cm土层, 真菌和放线菌的数量可以分别提高约50%和40%, 在10~30 cm土层, 细菌和放线菌的数量分别提高40%和30%.

值得一提的是, 浅耕和松耙并不适用于所有的退化草地. 浅耕对于以根茎禾草为主的草地效果良好, 一般耕翻后第1年和第2年不放牧, 第3年可以恢复为较好的草场. 而松耙更适合于相对干旱的大针茅和冷蒿建群的草地[73].

(ⅳ) 退化草地补播技术. 草地补播既可以在不破坏草地植被的情况下通过散播进行, 也可以结合浅耕和松耙进行. 草地补播技术主要包括补播地块的确定、补播品种的选择、补播时期和补播方式、补播量和播种深度、播后管理等技术环节.

补播地块的确定: 综合考虑水分、土壤、地形以及天然群落组成和退化的程度等多个因素来确定补播的地块. 补播一般要在年降水量不低于300 mm的地区实施[15], 或者有灌溉条件, 补播后能够实施灌溉. 地形要相对平坦, 以丘间低地和塔拉(宽谷地)较适宜, 迎风坡、风蚀口都不适合于补播. 土壤水分和养分要好, 严重退化导致土壤水分和养分大量损失的地段也不宜补播. 根据退化程度, 补播时一般要结合浅耕、灌溉、施肥等辅助恢复措施.

补播品种的选择: 对于风蚀沙化草地, 要优先选择防风固沙的植物; 对于盐渍退化草地要优先选择抗盐碱的品种. 割草地可以选择上繁草类, 放牧地应选择下繁草类[15].

补播时期和补播方式: 关于补播时期目前主要有两种观点. 侯向阳[15]认为, 补播应该在植被生长发育最弱的时候进行, 这样可以降低原有植物对补播牧草幼苗的抑制作用. 而陈敏[73]和宝音陶格涛[62]认为在夏季雨季到来之前进行补播为宜, 可以确保补播牧草的萌发有充足的水分和养分供给. 补播方式主要有撒播和条播两种. 条播主要与浅耕和松耙相结合, 用条播机或人工进行播种.

播种量和播种深度: 播种量的确定要考虑牧草种子的千粒重、发芽率、纯净度以及草场的退化程度. 一般禾本科牧草的播种量15~22.5 kg hm^{-2}[15]. 播种深度要考虑土壤状况和种子的大小. 一般土壤质地疏松的沙质土壤, 可播深些, 而土质黏重的土壤可播浅些. 大粒种子相对深些, 小粒种子相对浅些, 但一般播种深度不宜超过3~4 cm.

播后管理: 补播后幼苗能否萌发和正常生长, 播后管理是关键. 对于补播地块, 补播当年应禁止放牧, 因为新生的幼苗地上部分长势较弱, 根系也不发达, 因而对放牧和践踏较敏感. 第2年根据牧草长势可以进行秋季割草或冬季放牧. 播后管理的另一个关键是定期查看地块的病虫鼠害情况, 做好预防, 保证补播草地的快速恢复.

2.4 天然草地保护与合理利用技术

(ⅰ) 划区轮牧技术. 划区轮牧是利用与保护相结合的有计划的放牧利用技术, 是天然草地合理利用的中心环节[74]. 一般是将草地划分为几个轮牧区, 按照一定的次序逐区放牧, 轮替利用草地. 美国早期的延迟轮牧系统(deferred rotation grazing system)是俄勒冈州的Sampson[75]提出的, 他把整片草地划分为两个牧场, 每一块进行隔年放牧, 这样每块牧场都有一年的放牧后恢复期. 后来, 该方法发展为各具地方特色、形式多样的划区轮牧模式: 主要有德克萨斯州的3个畜群/4个牧场系统(three-herd/four-pasture system)[76]、俄勒冈州的季节相适应放牧系统(seasonal-suitability grazing system)、新墨西哥州的最佳草地放牧系统(the best pasture system)和蒙大纳州的休闲轮牧模式(rest-rotation grazing system). 在我国, 根据不同的草地类型, 划区轮牧的模式也不相同. 在草甸草原区, 每个牧户的草地划分为6~8个轮牧小区为宜, 每个小区每次放牧5~7 d, 轮牧周期为40 d左右, 轮牧频次为4次, 每个生长季的轮牧时间是6月4日至11月12日, 放牧时间为160 d. 在典型草原区, 轮牧小区数目以6~10个为宜, 每个小区每次放牧5~8 d, 轮牧周期50 d, 轮牧频次为3次, 轮牧时间是5月28日至10月28日, 放牧时间为150 d左右. 在荒漠草原, 小区数以6~12个为宜, 每小区每次放牧6~12 d, 轮牧周期75 d, 轮牧频次是2次. 每个生长季的轮牧时间是5月20日至11月10日, 放牧时间为160 d左右[77].

与传统的连续放牧相比, 划区轮牧的优点主要体现在以下4个方面: (1) 充分利用了当年长出的牧草, 减少了草料的浪费[74]; (2) 改善了群落结构, 提

高了牧草的产量和品质[78]; (3) 减少了家畜的游走时间, 增加了其休息的时间, 提高了家畜的产量[79]; (4) 减少了对草地的践踏, 降低了水土流失和养分的损失, 提高了草地的质量[80].

(ⅱ) 割草地轮刈技术. 传统的割草地大多采用连年刈割的方式, 导致大量的养分从系统中移出而得不到有效的补充, 破坏了养分平衡, 诱发草原群落的退化演替[81~85], 连年刈割也会影响土壤种子库的密度, 特别是具有生命力的种子数显著降低[86]. 根据16年的定位研究, 仲延凯和包青海[81]指出, 在内蒙古锡林河流域, 最适宜的割草时间为8月中旬, 合理的刈割模式为割1年休1年或割2年休1年[81,82]. 由于割草能够导致草原生态系统养分的失衡, 在割草地轮刈的同时, 通过草地施肥, 补充土壤养分也是有效的管理措施.

2.5 人工草地建植技术

人工草地是草地管理中集约化程度最高的类型, 人工草地的规模和质量是衡量一个国家和地区畜牧业发达程度的重要标志[87]. 人工草地建植的主要技术包括如下5个环节: (ⅰ) 选地与整理; (ⅱ) 牧草品种的选择; (ⅲ) 播种技术; (ⅳ) 田间管理技术; (ⅴ) 收获技术.

选地与整地: 旱作人工草地应该选择在土壤肥沃、降水相对汇集的丘间低地; 而灌溉人工草地最好选择土地平整的弃耕农田. 整地时要深耕细耙, 一般耕深在20 cm左右, 耙平后要镇压, 使地块达到平整、均匀、紧实.

牧草品种的选择: 人工草地的牧草品种一般选择经过区域实验的适合当地水热条件的高产优质的牧草品种. 当前生产上大面积使用的牧草品种主要包括禾本科和豆科两类. 禾本科牧草主要有: 黑麦草(*Lolium perenne*)、青谷子(*Setaria italica*)、羊草、冰草、老芒麦(*Elymus sibiricus*)、披碱草(*Elymus dahuricus*)和无芒雀麦(*Bromus inermis*)等. 豆科牧草主要有: 紫花苜蓿(*Medicago sativa*)、黄花苜蓿(*Medicago falcata*)、沙打旺(*Astragalus adsurgens*)和草木樨(*Melilotus suaveolens*)等.

对于多年生混播人工草地, 要充分考虑牧草产量、牧草品质和草地的利用年限. 根据中国科学院内蒙古草原生态系统定位研究站的实验, 深根系与浅根系牧草搭配、长寿命与短寿命牧草搭配、豆科与禾本科牧草搭配可以很好地实现牧草的高产、优质和长期利用.

播种技术: 由于不同牧草的籽粒大小、发芽率、出苗率不同, 播种前要测定牧草种子的千粒重和发芽率, 在此基础上计算播种量. 根据陈敏和宝音陶格涛[88]研究, 羊草+紫花苜蓿多年生人工草地, 羊草的播种量为30~45 kg hm^{-2}, 紫花苜蓿的播种量为7.5~9 kg hm^{-2}为宜[88]. 播期要根据气候条件和土壤墒情而定, 典型草原区一般在6~7月份为宜[89]. 播种深度一般以2~3 cm为宜, 大粒种子可稍深些, 可以达到3~4 cm. 播种时最好采用精量牧草播种机, 既可以节省种子, 又能保证播种质量. 播种技术的另一个关键环节是播后镇压, 一定要边播种边镇压, 确保种子与土壤密切接触, 着床良好, 同时减少水分的蒸散, 保持墒情, 提高出苗率.

田间管理: 播种后的田间管理主要包括肥水耦合、中耕除草和病虫害防治等环节. 在耕翻前最好施入底肥, 主要包括腐熟的有机肥(或羊粪)和氮磷复合化肥. 在牧草返青期和快速生长期, 根据天气预报进行雨季追肥也是人工草地提高产量和品质的有效措施. 对于灌溉人工草地, 生长季追肥要与浇水相结合. 对于新建植的人工草地, 第一年控制杂草十分重要. 一般播种前通过除草剂除草, 与农田化学除草剂的使用相似. 对于后期出现的杂草, 可以通过机械化中耕进行除草. 人工草地出苗后, 由于牧草幼苗比较鲜嫩富含营养, 是许多昆虫选择性采食的目标, 因此应加强病虫害的防治.

收获技术: 牧草收获是决定牧草品质的关键环节. 长期以来, 我国人工草地牧草的品质一直难以与国外进口草产品竞争, 主要原因就是收获环节牧草养分损失严重. 首先, 牧草要适时收获, 一般苜蓿以初花期收获较为适宜, 此时植株蛋白质含量最高, 饲草的消化率也高. 其次要采用割草压扁技术, 可以使得茎干与叶片同步干燥, 防止叶片的脱落.

2.6 天然草地与人工草地合理配置

天然草地与人工草地的合理配置就是根据不同区域的自然条件, 确定该区域天然草地和人工草地的比例及其空间布局. 一般来说, 建立约10%的高产高效人工草地, 就可以实现天然草地的生产功能, 从而使90%的天然草地得到保护, 恢复其生态功能.

要实现天然草地和人工草地合理配置, 需要进

行如下前期调查工作: (ⅰ) 气象资源调查, 包括辐射、温度、降水、风速、风向、灾害性天气等, 特别是光合有效辐射、年降水量、降水季节分布、蒸发蒸腾、温度的季节变化、无霜期、极端温度、极端灾害等. (ⅱ) 水资源调查, 包括大气降水、地表水、地下水等. (ⅲ) 土壤资源调查, 包括土层厚度、机械组成、有机质含量、土壤氮、磷养分含量等. (ⅳ) 植被结构与生产力调查, 包括植被结构、物种组成、生产力水平等. (ⅴ) 社会经济状况调查, 包括人口情况、草地面积、牲畜种类与数量、农牧民主要经济来源、收入水平和支出水平等.

在上述调查的基础上, 根据生态优先、功能置换和因地制宜原则, 进行天然草地和人工草地的配置. 该项技术主要包括6个环节: (ⅰ) 根据区域自然条件和社会经济情况, 确定天然草地和人工草地的适宜比例, 实现区域范围内的草畜平衡. (ⅱ) 确定人工草地的类型、面积、建设地点和建设周期. (ⅲ) 进行水资源评估. 由于人工草地耗水一般高于天然草地, 因此要进行水分平衡的概算, 要保证水资源的可持续利用. (ⅳ) 进行养分平衡概算. 人工草地产量高而且一年多次刈割, 从土壤中带走大量养分, 导致土壤养分的不平衡, 因此, 需要进行养分平衡的概算, 通过平衡施肥, 确保土壤养分的平衡. 提倡使用有机肥, 提高土壤的保水保肥能力. (ⅴ) 草地生态/生产功能置换的实施. 根据家畜的种类、天然草场的分布与退化程度, 有计划地种植人工草地. (ⅵ) 天然草地的保护和适度利用. 对于大面积的天然草地, 以保护为主, 适度利用, 主要发挥其生态功能, 使之进入良性循环之轨道.

2.7 人工草地的类型选择与合理布局

人工草地类型多样, 按播种牧草的生活型可以分为多年生人工草地和一年生人工草地; 按播种植物的组成可以分为混播人工草地和单播人工草地; 其中单播人工草地又主要分为豆科牧草人工草地和禾本科牧草人工草地. 在人工草地建设中, 要根据区域的气象条件、水资源状况、土壤条件和社会经济条件, 确定人工草地的类型及其面积. 人工草地类型选择的原则如下: (ⅰ) 以多年生人工草地为主、一年生人工草地为辅, 这主要基于我国北方草原牧区干旱少雨的特点. (ⅱ) 豆科人工草地与禾本科人工草地比例要适宜. 不能盲目追求苜蓿人工草地的面积, 应该是豆科与禾本科人工草地相兼顾. (ⅲ) 物种的多样性与品种的多样性相结合. 在物种的选择上要考虑多种牧草, 例如, 禾本科人工草地可以考虑羊草、无芒雀麦、披碱草、青谷子、燕麦草(*Avena sativa*)等. 豆科人工草地可以考虑紫花苜蓿、黄花苜蓿、扁蓿豆(*Melissilus ruthenicus*)、胡枝子(*Lespedeza bicolor* Turcz)和草木樨等. 其中在苜蓿品种的选择上, 以适应性强、高产、优质的国内育成品种为优先, 同时提倡品种的多样化, 避免单一物种或单一品种发生爆发性病、虫、灾害的风险.

人工草地的布局一般根据水热条件和饲养牲畜的种类而定. 在水热条件好, 无霜期长的地块, 可以优先建立高产豆科牧草人工草地(如苜蓿人工草地). 在这样的地块上, 可以实现牧草的一年多茬收获. 在旱作地块上, 可以考虑多年生豆科与禾本科牧草的混播人工草地. 就家畜种类而言, 对于养殖奶牛较多的区域, 可以适当增加苜蓿人工草地的比例, 而对于肉牛和肉羊较多的区域, 可以适当增加禾本科牧草的比例. 此外, 人工草地类型和布局要充分考虑牧草收获过程的机械化水平. 由于我国北方草原牧区雨热同季, 每种牧草的适宜收获期较短, 通过不同成熟期的牧草种类和品种的搭配, 有助于实现不同地块人工草地的错期收获, 保障各类人工草地能够在品质和产量俱佳的时候收获牧草.

综上所述, 本文针对我国草原牧区生态系统管理中存在的问题, 提出了生态功能与生产功能合理配置的理论基础与生态草业建设的核心技术体系, 并就各项技术进行了阐述, 所述理论和技术体系对于我国草原牧区实现生态草业的可持续发展具有指导意义.

参考文献

1 White R P, Murray S, Rohweder M. Pilot Analysis of Global Ecosystems: Grassland Ecosystems. Washington: World Resources Institute, 2000

2 UNEP (United Nations Environmental Programme). World atlas of desertification. In: Middleton N, Thomas D S G, eds. Editorial Commentary. London: Edward Arnold, 1997

3 Reynolds J F, Smith D M S. Global Desertification: Do Humans Cause Deserts? Beilin: Dahlem University Press, 2002
4 Asner G P, Elmore A J, Olander L P, et al. Grazing systems, ecosystem responses, and global change. Annu Rev Environ Res, 2004, 29: 261–299
5 Yan J C, Zhang J B, Luo X F, et al. Present situation, trends and inspiration of the world ecological husbandry (in Chinese). World Agri, 2007, 9: 7–10 [颜景辰, 张俊飚, 罗小锋, 等. 世界生态畜牧业发展现状、趋势及启示. 世界农业, 2007, 9: 7–10]
6 Du Q L. Sustainable Development Strategy of Chinese Prataculture (in Chinese). Beijing: China Agriculture Press, 2006 [杜青林. 中国草业可持续发展战略. 北京: 中国农业出版社, 2006]
7 Ministry of Environmental Protection of People's Republic of China. The 2005 Report on the State of the Environment of China (in Chinese). Beijing: Ministry of Environmental Protection of People's Republic of China, 2006 [中华人民共和国环境保护部. 中国环境状况公报 2005. 北京: 中华人民共和国环境保护部, 2006]
8 Han J. Survey on Ecological Issues of China's Grasslands (in Chinese). Shanghai: Shanghai Far East Publishers, 2011 [韩俊. 中国草原生态问题调查. 上海: 上海远东出版社, 2011]
9 Hong J, Yun X J, Lin J, et al. Pest rodents damages analysis and control in natural grassland of China (in Chinese). Chin J Grassland, 2014, 3: 1–4 [洪军, 贠旭疆, 林峻, 等. 我国天然草原鼠害分析及防控. 中国草地学报, 2014, 3: 1–4]
10 Hong J, Lin J, Wang G J. The occurring and control situation of grasshopper in the grassland of China (in Chinese). Acta Agrest Sin, 2014, 5: 929–934 [洪军, 林峻, 王广君. 我国草原蝗虫发生与防治现状分析. 草地学报, 2014, 5: 929–934]
11 National Bureau of Statistics of the People's Republic of China. China Statistic yearbook 2012. Beijing: China Statistics Press, 2013 [中华人民共和国国家统计局. 中国统计年鉴-2012. 北京: 中国统计出版社, 2013]
12 Ministry of Agriculture of the People's Republic of China. The 2011 Report on the development of Chinese grasslands (in Chinese). Beijing: Chinese Agriculture Press. 2013 [中华人民共和国农业部. 中国草原发展报告 2011. 北京: 中国农业出版社, 2013]
13 Yang C, Wang M L, Liu Y J. Alfalfa trade of China, historical changes, future trends and suggestions (in Chinese). Pratacult Sci, 2011, 28: 1711–1717 [杨春, 王明利, 刘亚钊. 中国的苜蓿草贸易——历史变迁、未来趋势与对策建议. 草业科学, 2011, 28: 1711–1717]
14 Yang Q C, Sun Y. The history, current situation and development of alfalfa breeding in China (in Chinese). Chin J Grassland, 2011, 33: 95–101 [杨青川, 孙彦. 中国苜蓿育种的历史、现状与发展趋势. 中国草地学报, 2011, 33: 95–101]
15 Hou X Y. Chinese Grassland Science (in Chinese). Beijing: Science Press, 2013 [侯向阳. 中国草原科学. 北京: 科学出版社, 2013]
16 Ren J Z. On Pastoral Agriculture Systems (in Chinese). Nanjing: Jiangsu Science and Technology Press, 2012 [任继周. 草业科学论纲. 南京: 江苏科学技术出版社, 2012]
17 McNaughton S J. Grazing as an optimization process: grass ungulate relationships in the Serengeti. Am Nat, 1979, 113: 691–703
18 Holechek J, Pieper R D, Herbel C H. Range Management: Principles and Practices. Fifth edition, New Jersey: Pearson Prentice Hall, 2002
19 Schoenbach P, Wan H W, Gierus M, et al. Grassland responses to grazing: Effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem. Plant Soil, 2011, 340, 103–115
20 Li W H, Zheng S X, Bai Y F. Effects of grazing intensity and topography on species abundance distribution in a typical steppe of Inner Mongolia (in Chinese). Chin J Plant Ecol, 2014, 38: 178–187 [李文怀, 郑淑霞, 白永飞. 放牧强度和地形对内蒙古典型草原物种多度分布的影响. 植物生态学报, 2014, 38: 178–187]
21 Luo G, Han Q, Zhou D, et al. Moderate grazing can promote aboveground primary production of grassland under water stress. Ecol Complex, 2012, 11: 126–136
22 Connell J H. Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained only in a non-equilibrium state. Science, 1978, 199: 1302–1310
23 Briske D D, Fuhlendor S D, Smeins E E. State-and-transition models, thresholds, and rangeland health: A synthesis of ecological concepts and perspectives. Rangel Ecol Manag, 2005, 58: 1–10
24 Sasaki T, Okayasu T, Jamsran U, et al. Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. J Ecol, 2008, 96: 145–154
25 Yan R R, Xin X P, Yan Y C, et al. Impacts of differing grazing rates on canopy structure and species composition in Hulunber meadow steppe. Range Ecol Manage, 2014, 68: 54–64
26 Yang J, Chu P F, Chen D M, et al. Mechanisms underlying the impacts of grazing on plant α, β and γ diversity in a typical steppe of the Inner Mongolia grassland (in Chinese). Chin J Plant Ecol, 2014, 38: 188–200 [杨婧, 褚鹏飞, 陈迪马, 等. 放牧对内蒙古典型草原α、β和γ多样性的影响机制. 植物生态学报, 2014, 38: 188–200]
27 Bai Y F, Huang J H, Zheng S X, et al. Drivers and regulating mechanisms of grassland and desert ecosystem services (in Chinese). Chin J Plant Ecol, 2014, 38: 93–102 [白永飞, 黄建辉, 郑淑霞, 等. 草地和荒漠生态系统服务功能的形成与调控机制. 植物生态学报, 2014, 38: 93–102]

28 Heady H F, Child R D. Rangeland Ecology and Management. Boulder: Westview Press, 1994
29 McNaughton S J. Ecology of a grazing ecosystem: The Serengeti. Ecol Monogr, 1985, 55: 259–294
30 Holland E A, Parton W J, Detling J K, et al. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. Am Nat, 1992, 140: 685–706
31 McNaughton S J, Banyikwa F F, McNaughton M M. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science, 1997, 278: 1798–1800
32 Frank D A, Evans R D. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology, 1997, 78: 2238–2248
33 Ritchie M E, Tilman D, Knops J M H. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology, 1998, 79: 165–177
34 Stark S, Mannisto M K, Eskelinen A. When do grazers accelerate or decelerate soil carbon and nitrogen cycling in tundra? A test of theory on grazing effects in fertile and infertile habitats. Oikos, 2015, 124: 593–602
35 McNaughton S J. Serengeti migratory wildebeest: Facilitation of energy flow by grazing. Science, 1976, 191: 92–94
36 Tilman, D. Resource Competition and Community Structure. Princeton: Princeton University Press, 1982
37 Tilman D. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton: Princeton University Press, 1988
38 DeAngelis D L, Mulholland P J, Palumbo A V, et al. Nutrient dynamics and food-web stability. Ann Rev Ecol Syst, 1989, 20: 71–95
39 Sterner R W, Hessen D O. Algal nutrient limitation and the nutrition of aquatic herbivores. Annu Rev Ecol Syst, 1994, 25: 1–29
40 Hobbs N T. Modification of ecosystems by ungulates. J Wildlife Manage, 1996, 60: 695–713
41 Augustine D J, McNaughton S J. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. J Wildlife Manage, 1998, 62: 1165–1183
42 Schuman G E, Janzen H H, Herrick J E. Soil carbon dynamics and potential carbon sequestration by rangelands. Environ Pollut, 2002, 116: 391
43 Bryant J P, Provenza F D, Pastor J, et al. Interactions between woody-plants and browsing mammals mediated by secondary metabolites. Ann Rev Ecol Syst, 1991, 22: 431–446
44 Pastor J, Binkley D. Nitrogen fixation and the mass balances of carbon and nitrogen in ecosystems. Biogeochemistry, 1998, 43: 63–78
45 Pastor J, Dewey B, Naiman R J, et al. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology, 1993, 74: 467–480
46 Pastor J, Naiman R J. Selective foraging and ecosystem processes in boreal forests. Am Nat, 1992, 139: 690–705
47 Pastor J, Naiman R J, Dewey B, et al. Moose, microbes, and the boreal forest. BioScience, 1988, 38: 770–777
48 Wilson J B, Agnew A D Q. Positive-feedback switches in plant communities. Adv Ecol Res, 1992, 23: 263–336
49 Frank D A, McNaughton S J, Tracy B F. The ecology of the earth's grazing ecosystems. BioScience, 1998, 48: 513–521
50 Gibson D J. Grasses and Grassland Ecology. Oxford: Oxford University Press, 2009
51 Su H, Liu W, Xu H, et al. Long-term livestock exclusion facilitates native woody plant encroachment in a sandy semiarid rangeland. Ecol Evol, 2015, 5: 2445–2456
52 Liu Y S, Pan Q M, Liu H D, et al. Plant responses following grazing removal at different stocking rates in an Inner Mongolia grassland ecosystem. Plant Soil, 2011, 340: 199–213
53 Tilman D, Elhaddi A. Drought and biodiversity in grasslands. Oecologia, 1992, 89: 257–264
54 Collins S L, Knapp A K, Briggs J M, et al. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science, 1998, 280: 745–747
55 Olff H, Ritchie M E. Effects of herbivores on grassland plant diversity. Trends Ecol Evol, 1998, 13: 261–265
56 Milchunas D G, Lauenroth W K. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol Monogr, 1993, 63: 327–366
57 Society for Range Management. A Glossary of Terms Used in Range Management. 3rd ed. Denver: Society for Range Management, 1989
58 Holechek J L, Pieper R D, Herbel C H. Range Management Principle and Practices. Pearson Upper Saddle River: Education, Inc., 2004
59 Jia Y L. On the concepts and practices concerning grassland-livestock balance (in Chinese). Acta Agrest Sin, 2005, 13: 265–268 [贾幼陵. 关于草畜平衡的几个理论和实践问题. 草地学报, 2005, 13: 265–268]
60 Li Z H, Wang W, Liu Z L. Research on the pasture quality of degraded steppe during closed reconvering progress (in Chinese). Acta Sci Natural Unversitatis NeiMonggol, 1995, 26: 334–338 [李政海, 王炜, 刘钟龄. 退化草原围封恢复过程中草场质量动态的研究. 内蒙古大学学报(自然科学版), 1995, 26: 334–338]
61 Li Z H, Pei H, Liu Z L, et al. The research on the dynamics of community characters of degenerate *Leymus chinensis* steppe during recovering succession (in Chinese). Acta Scientiarum Naturalium Unversitatis NeiMonggol, 1995, 25: 88–98 [李政海, 裴浩, 刘钟龄, 等. 羊草草原退化群落恢复演替的研究. 内蒙古大学学报(自然科学版), 1995, 25: 88–98]
62 Baoyin T. The study on dynamic succession of community in degraded steppe of *Leymus chinensis* after different improvement measures (in Chinese). Doctor Dissertation. Hohhot: Inner Mongolia University, 2009 [宝音陶格涛. 不同改良措施下退化羊草(*Leymus chinensis*)草原群落恢复演替规律研究. 博士学位论文. 呼和浩特: 内蒙古大学, 2009]

63 Yang L N, Baoyin T. Study on biomass of Leymus chinensis community after different improving measures (in Chinese). Chin J Grassland, 2010, 32: 86–91 [杨丽娜, 宝音陶格涛. 不同改良措施下羊草群落生物量的研究. 中国草地学报, 2010, 32: 86–91]

64 Li J B, Ma C P, Lu W H, et al. Effects of enclosing spring-autumn grassland on aboveground biomass at Zhaosu horse ranch (in Chinese). Grassland Turf, 2009, 133: 46–50 [李军保, 马存平, 鲁为华, 等. 围栏封育对昭苏马场春秋草地地上植物量的影响. 草原与草坪, 2009, 133: 46–50]

65 Zhou H K, Zhou L, Zhao X Q, et al. Effect of fencing on lightly and heavily grazing *potentilla fruticosa* shrublands (in Chinese). Acta Agrest Sin, 2004, 12: 140–144 [周华坤, 周立, 赵新全, 等. 围栏封育对轻牧与重牧金露梅灌丛的影响. 草地学报, 2004, 12: 140–144]

66 Zhu L B, Zeng Z H, Zhao B P, et al. Effect of spring rest-grazing on steppe vegetation (in Chinese). Acta Agrest Sin, 2008, 16: 278–282 [朱立博, 曾昭海, 赵宝平, 等. 春季休牧对草地植被的影响. 草地学报, 2008, 16: 278–282]

67 Zhao G, Cao Z L, Li Q F. A preliminary study of the effects of deferred spring grazing on the pasture vegetation (in Chinese). Acta Agrest Sin, 2003, 11: 183–188 [赵钢, 曹子龙, 李青丰. 春季禁牧对内蒙古草原植被的影响. 草地学报, 2003, 11: 183–188]

68 Li Q F, Zhao G, Zheng M A, et al. Delay grazing a practical approach to grassland environment protection and sustainable animal production in grassland of northern China (in Chinese). Acta Agrest Sin, 2005, 13: 53–66 [李青丰, 赵钢, 郑蒙安, 等. 春季休牧对草原和家畜生产力的影响. 草地学报, 2005, 13: 53–66]

69 Baoyin T, Li F Y. Can shallow plowing and harrowing facilitate restoration of Leymus chinensis grassland? Results from a 24-year monitoring program. Rangeland Ecol Manage, 2009, 62: 314–320

70 Zhang H S, Shao X Q, Liu G H, et al. Effects of enclosing and shallow ploughing as improvement technologies on the vegetation restoration of degraded *Leymus chinensis* Meadow Grassland (in Chinese). Acta Agrest Sin, 2010, 18: 339–345 [张洪生, 邵新庆, 刘贵河, 等. 围封, 浅耕翻改良技术对退化羊草草地植被恢复的影响. 草地学报, 2010, 18: 339–345]

71 Qu W J, Song N P, Chen L, et al. Responses of two types of desertification grasslands in desert steppe to shallow ploughing (in Chinese). Res Soil Water Conserv, 2014, 21: 85–89 [曲文杰, 宋乃平, 陈林, 等. 荒漠草原两种沙化草地对浅耕翻的响应. 水土保持研究, 2014, 21: 85–89]

72 Shao Y Q, Liu Z L, Jia Z B, et al. Effect of different control measures on the soil cultured microorganisms flora in degraded grassland (in Chinese). Chin J Grassland, 2011, 33: 77–81 [邵玉琴, 刘钟龄, 贾志斌, 等. 不同治理措施对退化草原土壤可培养微生物区系的影响. 中国草地学报, 2011, 33: 77–81]

73 Chen M. Measures for improving degraded grasslands in northern China (in Chinese). China Animal Husbandry Bull, 1996, 6: 29 [陈敏. 北方退化草地改良技术. 中国牧业通讯, 1996, 6: 29]

74 Ren J Z, Mu X D. On the rotational grazing system (in Chinese). Sci Agri Sin, 1964, 1: 21–23 [任继周, 牟新待. 试论划区轮牧. 中国农业科学, 1964, 1: 21–23]

75 Sampson A W. Range improvement by deferred and rotation grazing. U.S. Dept Agr Bul, 1913, 34: 1–16

76 Merrill B L. A variation of deferred rotation grazing for use under southwest range conditions. J Range Manage, 1954, 7: 152–154

77 Xing Q, Shuang Q, Na R, et al. Study on the application of rotational grazing system in grassland (in Chinese). Inner Mongolia Pratacult, 2003, 15: 1–3 [邢旗, 双全, 那日苏等. 草原划区轮牧技术应用研究. 内蒙古草业, 2003, 15: 1–3]

78 Han G D, Xu Z X, Zhang Z T. A comparison of rotation and continuous-seasonal grazing systems (in Chinese). J Arid Land Res Environ, 1990, 4: 85–93 [韩国栋, 许志信, 章祖同. 划区轮牧和季节连续放牧的比较研究. 干旱区资源与环境, 1990, 4: 85–93]

79 Zhang Z T, Xu Z X, Han G D. A comparison of rotation and continuous seasonal grazing systems (in Chinese). Acta Agrest Sin, 1991, 1: 72–77 [章祖同, 许志信, 韩国栋. 划区轮牧和季节连牧的比较试验. 草地学报, 1991, 1: 72–77]

80 Li Q F, Han G D, Ao T, et al. Approach on restoration mechanism of rotational grazing system on desert steppe (in Chinese). Trans CSAE, 2003, 19: 224–227 [李勤奋, 韩国栋, 敖特根, 等. 划区轮牧制度在草地资源可持续利用中的作用研究. 农业工程学报, 2003, 19: 224–227]

81 Zhong Y K, Bao Q H. The study of rational cutting system on the grassland of Xilin river basin (in Chinese). Grassland China, 1999, 21: 28–41 [仲延凯, 包青海. 锡林河流域合理割草制度的研究. 中国草地, 1999, 21: 28–41]

82 Bao Y J, Li Z H, Bao Q H, et al. Influence of mowing for many years on community biomass and the important value of *Leymus chinensis* and *Koeloria cristata* population on *L. chinensis* steppe (in Chinese). Acta Sci Natural Unversitatis NeiMonggol, 2001, 32: 309–313 [鲍雅静, 李政海, 包青海等. 多年割草对羊草草原群落生物量及羊草和洽草种群重要值的影响. 内蒙古大学学报, 2001, 32: 309–313]

83 Baoyin T, Li F Y, Bao Q H, et al. Effects of mowing regimes and climate variability on hay production of *Leymus chinensis* (Trin.) Tzvelev grassland in northern China. Rangeland J, 2014, 36: 593–600

84 Bao Q H, Baoyin T, Zhong Y K, et al. Effects of different cutting system on main typical steppe populations in Inner Mongolia (in Chinese). Chin J Appl Ecol, 2005, 16: 2333–2338 [包青海, 宝音陶格涛, 仲延凯, 等. 不同轮割制度对典型草原主要种群的影响. 应用生态学报, 2005, 16: 2333–2338]

85 Bao Q H, Baoyin T, Yan Q L, et al. The comparison study on community characteristics under mowing treatments in the steppe of *Leymus chinensis*. Acta Sci Natural Unversitatis NeiMonggol, 2003, 34: 74–78 [包青海, 宝音陶格涛, 阎巧玲, 等. 羊草草原割草处理群落特征比较研究. 内蒙古大学学报, 2003, 34: 74–78]

86 Zhong Y K, Bao Q H, Sun W, et al. The influence of mowing on seed amount and composition in soil seed bank of typical steppe Ⅳ The comparing of the compositions of community biomass and seed Amount (in Chinese). Acta Sci Natural Unversitatis NeiMonggol, 2001, 32: 551–556 [仲延凯, 包青海, 孙维, 等. 割草干扰对典型草原土壤种子库种子数量与组成的影响Ⅳ群落生物量的组成与种子数量组成的比较. 内蒙古大学学报, 2001, 32: 551–556]

87 Hu Z Z. A new system of tame grassland classification–The comprehensive and sequential classification (in Chinese). Grassland China, 1995, 17: 1–5 [胡自治. 人工草地分类的新系统——综合顺序分类法. 中国草地, 1995, 17: 1–5]

88 Chen M, Baiyin T. The experimental study of establishing artificial-grassland without irrigation in steppe regions (in Chinese). In: Inner Mongolia Grassland Ecosystem Research Station, Academia Sinica eds. Research on Grassland Ecosystem (2). Beijing: Science Press, 1985. 209–217 [陈敏, 宝音陶格涛. 草原区非灌溉条件下建立人工草地的试验研究. 见: 中国科学院内蒙古草原生态系统定位站编, 草原生态系统研究(2), 北京: 科学出版社, 1988. 209–217]

89 Chen Z Z, Wang S P. Typical Steppe Ecosystem in China (in Chinese). Beijing: Science Press, 2000 [陈佐忠, 汪诗平. 中国典型草原生态系统. 北京: 科学出版社, 2000]

Fundamental theories and technologies for optimizing the production functions and ecological functions in grassland ecosystems

BAI YongFei[1], PAN QingMin[1] & XING Qi[2]

[1] *State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China;*
[2] *Inner Mongolia Autonomous Region Grassland and Planning Institute, Huhhot 010051, China*

Optimizing the production functions and ecological functions in grassland ecosystems is of fundamental importance to grassland ecology and management. Here we summarize the progresses in pratacultural systems worldwide, with an emphasis on major limitations of the pratacultural systems in China. We propose six important hypotheses and theories that can be used to guide grassland management, including grazing optimization hypothesis, intermediate disturbance hypothesis, accelerating nutrient cycling hypothesis, decelerating nutrient cycling hypothesis, forage supply-demand balance theory, and grassland-agriculture system theory. We also propose a framework with three major aspects of technologies in eco-pratacultural systems, including how to restore the degraded grasslands, how to sustainably use the natural grasslands, and how to establish artificial grasslands. Finally, we put forward the rules for establishing eco-pratacultural systems with optimization of the production functions and ecological functions. This review has important implications for the management of eco-pratacultural systems in China and beyond.

eco-pratacultural systems, natural grassland, artificial grassland, restoration of degraded grassland, grassland management

doi: 10.1360/N972015-00768

植物生态学报 2014, **38** (2): 93–102 doi: 10.3724/SP.J.1258.2014.00009
Chinese Journal of Plant Ecology http://www.plant-ecology.com

草地和荒漠生态系统服务功能的形成与调控机制

白永飞[1*] 黄建辉[1] 郑淑霞[1] 潘庆民[1] 张丽霞[1] 周华坤[2] 徐海量[3] 李玉霖[4] 马 健[3]

[1]中国科学院植物研究所植被与环境变化国家重点实验室, 北京 100093; [2]中国科学院西北高原生物研究所, 西宁 810008; [3]中国科学院新疆生态与地理研究所, 乌鲁木齐 830011; [4]中国科学院寒区旱区环境与工程研究所, 兰州 730000

摘 要 生态系统服务功能的形成和维持机制是近年来生态学研究的热点领域。该文从生态系统服务功能的概念与内涵入手, 分析了生态系统服务功能研究的科学前沿和热点领域, 重点介绍了草地和荒漠生态系统服务功能形成与调控机制联网研究的思路、关键科学问题、研究目标、实验设计、观测指标体系, 以及联网研究取得的重要进展。在此基础上, 对未来草地和荒漠生态系统服务功能研究的重点进行了展望。

关键词 荒漠, 联网实验研究, 草地, 生态系统服务功能

Drivers and regulating mechanisms of grassland and desert ecosystem services

BAI Yong-Fei[1*], HUANG Jian-Hui[1], ZHENG Shu-Xia[1], PAN Qing-Min[1], ZHANG Li-Xia[1], ZHOU Hua-Kun[2], XU Hai-Liang[3], LI Yu-Lin[4], and MA Jian[3]

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China; [2]Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China; [3]Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Ürümqi 830011, China; and [4]Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China

Abstract

Examining the drivers and regulating mechanisms of multiple ecosystem services has emerged as a central issue in ecology in recent years. In this paper, we start with the definition of ecosystem services, recent progresses and research priorities in the field. Then, we propose an experimental network to examine the key drivers of ecosystem services and relationships among multiple ecosystem services across grassland and desert ecosystems in northern China. The research network include conceptual diagram, research questions and objectives, field experimental design, ecosystem properties and processes observed across four grassland and desert sites. We review the major findings from the experimental network and future research directions in grassland and desert ecosystem services.

Key words desert, experimental network, grassland, ecosystem services

草地是地球上分布面积最大的一个陆地生态系统, 世界草地总面积为52.5亿hm^2, 约占地球陆地总面积的40.5% (不包括格陵兰岛和南极), 贮存了陆地生态系统总碳量的34%, 其中, 约71%的碳贮存在植物根系和土壤中(White *et al*., 2000)。草地生态系统不仅为人类提供了肉、奶、皮、毛等具有直接经济价值的产品, 同时具有维持大气组分的相对恒定、改善气候、维系生物基因库、固定CO_2、保持水土、抚育和传承多民族文化等极其重要的服务功能(中华人民共和国农业部兽医司和全国畜牧兽医总站, 1996; Sala & Paruelo, 1997; White *et al*., 2000)。

我国是草地资源大国, 拥有草地总面积近4亿hm^2, 约占国土总面积的41.7% (中华人民共和国农业部兽医司和全国畜牧兽医总站, 1996)。据统计, 我国草地上生长的饲用植物共246科1 545属6 704种, 有毒植物49科152属731种, 构成了我国野生植物, 特别是耐旱、耐寒、耐盐和药用植物最重要的种质资源基因库(中华人民共和国农业部兽医司和全国畜牧兽医总站, 1996)。根据中国草地分类系统, 我国天然草地划分为18个大类, 其中, 广泛分布于我国北方的温性草原(温性草甸草原、温性典型草

收稿日期Received: 2014-01-07 接受日期Accepted: 2014-01-17
* E-mail: yfbai@ibcas.ac.cn

原、温性荒漠草原)、高寒草原(高寒草甸草原、高寒典型草原、高寒荒漠草原)、草甸(低地草甸、山地草甸、高寒草甸)和荒漠(温性荒漠、高寒荒漠)等类型占全国草地总面积的66%, 构成了我国天然草地的主体部分, 是我国北方地区重要的绿色生态安全屏障, 同时也是黄河、长江、澜沧江、滦河等主要江河的发源地和水源涵养区(中华人民共和国农业部兽医司和全国畜牧兽医总站, 1996)。目前, 我国90%左右的草地处于不同程度的退化之中, 其中严重退化草地占60%以上(国家环保总局, 2006)。人为因素(过度放牧、开垦)、气候因素(干旱等极端气候)、国家投入不足和牧区政策偏差是导致我国草地大面积退化的主要原因(韩俊, 2011)。许多研究表明, 长期过度放牧是导致草地退化的最主要因素。过度放牧使植被覆盖度和初级生产力降低, 生物多样性减少(White *et al*., 2000; Schönbach *et al*., 2011), 土壤养分和水分保持能力下降, 土壤侵蚀和水土流失加剧(Steffens *et al*., 2008; Reszkowska *et al*., 2011), 对气候变化的敏感性增强, 严重地影响了不同时空尺度上的生态系统功能, 加速了草地的退化演替, 从而使草地的生态服务功能日益衰减, 虫鼠害和沙尘暴等灾害频繁发生, 严重威胁着我国北方及其周边地区的生态安全(国家环保总局, 2006; 韩俊, 2011)。同时, 长期的人类活动干扰和气候变化也是导致荒漠生态系统服务功能下降的重要原因(Reynolds & Stafford Smith, 2002; 慈龙骏, 2005; 张永民和赵士洞, 2008)。因此, 开展草地生态系统服务功能研究, 阐明生态系统服务功能对人类活动干扰和气候波动的响应与适应机制, 揭示草地退化和服务功能降低的直接和间接驱动因子, 对于恢复退化草地, 提升草地的生态服务功能, 具有重要的理论和实践意义。

1 草地生态系统服务功能的概念与内涵

生态系统服务功能是指生态系统提供的用以实现和维持人类生存与发展的环境条件和过程(Daily, 1997), 是人类从生态系统获得的惠益(Millennium Ecosystem Assessment, 2005), 是人类赖以生存和发展的基础(de Groot *et al*., 2002)。生态系统服务功能分为四大类: 支持服务(养分循环、土壤形成、初级生产等)、供给服务(食物、淡水、木材和纤维、燃料等)、调节服务(调节气候、调节淡水、控制疾病)、文化服务(美学、精神、教育、消遣等)(Millennium Ecosystem Assessment, 2005)。关于草地(grassland), 学术界有着多个不同的定义, 可以概括为两大类, 即狭义的草地和广义的草地。狭义的草地等同于植被分类中的草原。联合国教科文组织将草地定义为“由草本植物所覆盖的陆地部分, 灌木和乔木的覆盖度<10%” (Suttie *et al*., 2005)。《牛津植物科学辞典》将草地定义为“水分条件可以满足禾本科草本植物的生长, 但气候和人为因素阻止了乔木的生长, 是介于森林和荒漠之间的一种植被类型, 长期依靠放牧或火来维持” (Allaby, 1998)。《中国植被》一书中, 将草原定义为“由耐寒的旱生多年生草本植物为主(有时为旱生小半灌木)组成的植物群落” (中国植被编辑委员会, 1980)。而广义的草地是从农学范畴进行定义的。按照《世界资源报告1987》和联合国粮农组织(FAO)的定义, 草地是指可以用于放牧或割草的土地, 包括: 天然放牧地、长久休闲地、5年以上生产草本饲料作物的耕地、疏林地、矮木林、疏灌丛、荒漠、冻原、沿海滩涂、湿地沼泽和草甸”(International Institute for Environment and Development and World Resources Institute, 1987)。《中国草地资源》一书采用了与FAO类似的概念, 将草地定义为“草本和木本饲用植物与其所着生的土地构成的具有多种功能的自然综合体” (中华人民共和国农业部兽医司和全国畜牧兽医总站, 1996)。草地生态系统服务功能的本质特征体现为生态功能和生产功能(de Groot *et al*., 2002)。生态功能指其生境、生物学性质和生态过程, 为赖以生存的生命系统提供环境条件, 包括气候调节、养分循环与贮存、固定CO_2、释放O_2、消减SO_2、水源涵养、土壤形成、侵蚀控制、废物处理、滞留沙尘和生物多样性维持等方面(Sala & Paruelo, 1997; White *et al*., 2000; 刘兴元等, 2011)。生产功能是为生命系统提供各种消费资源, 包括家畜生产、牧草产品和药用植物等, 对支撑畜牧业发展具有重要的作用。长期以来, 我国在畜牧业生产中过度利用草地的生产功能, 而忽视了草地的生态功能, 造成了超载过牧、人-草-畜关系失衡和草地的大面积退化, 并诱发了沙尘暴、荒漠化等生态灾难(国家环保总局, 2006; 韩俊, 2011)。

2 生态系统服务功能研究的科学前沿和热点领域

近年来, 生态系统服务功能研究已成为国际生态学研究的前沿和热点。国际上围绕生态系统服务功能的内涵和类型划分, 生态系统服务功能的现状、受威胁程度和变化趋势评估, 服务价值化评估, 以及服务功能的关键驱动因子与相互作用机制等方面开展了大量的研究工作(Daily, 1997; Daily *et al*., 2000; Kremen, 2005; Millennium Ecosystem Assessment, 2005; Bennett *et al*., 2009; Perrings *et al*., 2010; Chisholm & Wintle 2012; Bateman *et al*., 2013)。目前, 生态系统服务功能研究的科学前沿和热点领域包括以下4个方面:

2.1 生态系统服务功能的关键驱动因子及多个服务功能之间的相互作用机制是生态系统服务功能研究的科学前沿

生态系统为人类的生存和发展提供了多种服务, 包括支持服务、供给服务、调节服务和文化服务等。许多研究表明, 人类对一些服务功能的过度利用(例如供给服务)可能会导致另一些服务功能(如支持和调节服务)的显著下降、衰退甚至丧失, 特别是当许多服务功能之间存在非线性关系时, 其变化更加难以预测(Millennium Ecosystem Assessment, 2005)。揭示管理措施(如放牧、割草、施肥)和环境变化是如何对生态系统的多个服务功能产生影响, 以及多个生态系统服务功能之间的关系与相互作用机制是当前生态系统服务功能研究的科学前沿(Carpenter *et al*., 2006; Bennett *et al*., 2009; Perrings *et al*., 2010)。在草地生态系统中, 定量评估初级生产力、碳固定、防风固沙、保持水土和生物多样性维持功能之间的相互依赖性(interdependency)、弹性(resilience)和权衡关系(tradeoff), 可以帮助我们深入理解各种服务功能之间的依存关系及其生态学机制, 同时为草地资源的保护、管理和可持续利用提供详实的科学依据。

2.2 生态系统“结构－过程－服务”的相互作用机理及其反馈与调控机制是当前生态系统服务功能研究的热点

生态系统服务依赖于生态系统的结构和过程, 土地利用变化、气候变化和管理措施通过改变生态系统的结构和过程而影响其服务功能(Bennett *et al*., 2009; Carpenter *et al*., 2009)。进入后千年生态系统评估时代, 基于不同区域和生态系统类型的比较研究, 揭示生态系统“结构－过程－服务”的相互作用机理及其反馈调节机制, 成为当前乃至今后若干年内生态系统服务功能研究的热点领域(Palmer *et al*., 2004; Carpenter *et al*., 2006, 2009; 傅伯杰等, 2009; Fu *et al*., 2013)。

2.3 生态系统服务的尺度特征与多尺度关联是生态系统服务功能研究的重点和难点

生态系统服务功能的形成依赖于一定的时间和空间尺度上的生态系统结构与过程, 只有在特定的时空尺度上才能表现其显著的主导作用和效果(Peterson & Parker, 1998; Millennium Ecosystem Assessment, 2005; 傅伯杰等, 2009; Perrings *et al*., 2010; Scholes *et al*., 2013)。近年来, 对生态系统服务功能的时空特征、尺度效应和多尺度关联的研究已引起越来越多的关注(Power, 2010; Dearing *et al*., 2012; Quijas *et al*., 2012; Seppelt *et al*., 2013)。

2.4 生物多样性与生态系统服务功能的关系是生态系统服务功能研究的重要内容

生物多样性与生态系统服务功能的关系成为近20年来全球范围内备受关注的重要领域, 是生态学研究的热点(Sala *et al*., 2000; Loreau & Hector, 2001; Hooper *et al*., 2005; Reiss *et al*., 2009; Midgley, 2012; Turnbull *et al*., 2012)。尽管国内外学者围绕生物多样性与生态系统服务功能开展了大量研究, 但由于两者的关系非常复杂, 目前仍存在着很大的不确定性(Kremen, 2005; 傅伯杰等, 2009; Feld *et al*., 2010; Bullock *et al*., 2011; Isbell *et al*., 2011; Perrings *et al*., 2011; Larigauderie *et al*., 2012; Fu *et al*., 2013)。生物多样性与生态系统服务功能的实验研究是阐明生物多样性与生态系统服务功能关系的重要手段(Mertz *et al*., 2007; 傅伯杰等, 2009; Geijzendorffer & Roche, 2013; Vihervaara *et al*., 2013)。在草地生态系统中, 依托大型野外控制实验平台, 结合长期实验观测数据, 从植物、动物和土壤微生物3个营养级水平, 研究植物多样性、食草动物和土壤微生物之间的相互作用, 及其对生态系统过程与服务功能的反馈与调控机制, 进而阐明生物多样性与生态系统生产力、稳定性和养分、水分保持能力等服务功能的内在联系, 是草地生态系统生物多样性与服务功能关系研究的重要领域(Sala *et al*., 2000; Reiss *et al*., 2009)。

doi: 10.3724/SP.J.1258.2014.00009

3 草地和荒漠生态系统服务功能形成与调控机制联网研究

在国家重点基础研究发展计划(“973”)项目“中国主要类型生态系统服务功能与生态安全”第二课题“草地和荒漠生态系统服务功能形成与调控机理”的资助下，我们选择我国典型草原、高寒草甸、沙化草地和荒漠的代表性类型为对象，依托4个国家野外科学观测研究站，建立了联网研究实验平台，采用统一的实验设计、统一的观测内容与指标和统一的实验研究方法，开展了水分、养分和动物采食及其耦合作用对生态系统过程和服务功能调控机制的研究。开展联网实验研究的4个国家野外科学观测研究站包括：位于青海省海北藏族自治州门源回族自治县的青海海北高寒草地生态系统国家野外科学观测研究站(海北站, 101°19′ E, 37°37′ N)，位于内蒙古自治区通辽市奈曼旗的内蒙古奈曼农田生态系统国家野外科学观测研究站(奈曼站, 120°42′ E, 42°55′ N)，位于内蒙古自治区锡林郭勒盟锡林浩特市的内蒙古锡林郭勒草原生态系统国家野外科学观测研究站(内蒙古站, 116°42′ E, 43°38′ N)，以及位于新疆维吾尔自治区阜康市的新疆阜康荒漠生态系统国家野外科学观测研究站(阜康站, 87°93′ E, 44°29′ N)(图1)。

3.1 拟回答的关键科学问题和研究目标

本联网实验研究拟回答的关键科学问题包括：(1)沿水分梯度，降水量及其季节分配是如何影响草地和荒漠生态系统结构与功能的？(2)多种限制性养分(氮(N)、磷(P)、钾(K))是如何并在多大程度上影响生态系统生物多样性、初级生产力和服务功能的？其主要调控机制是什么？(3)沿不同的组织水平和空间尺度，水分与养分的耦合作用是如何自下而上地影响生态系统过程和服务功能的？(4)水分、养分和动物采食是如何影响生态系统各组分(植物地上部分、凋落物、植物根系、土壤和土壤微生物)之间的化学计量关系的？不同组分之间相互作用的强度有多大？它们是如何对生态系统格局、过程和服务功能进行调控的？

联网研究的目标为：通过草地和荒漠生态系统关键限制因子的联网实验研究，揭示水分、养分和动物采食及其耦合作用对生态系统结构与功能的多营养级水平和多尺度调控机理，阐明生态系统结构、过程和服务功能之间的内在联系及其对放牧和环境扰动的响应与适应机制。

3.2 实验设计

联网实验包括3个养分(N、P、K)添加处理，每种养分设2个水平(添加和对照)，采用三因子设计，共8个处理；实验还包括1个草食动物剔除处理，2个水平(N、P、K添加和完全对照)，共2个处理，合计10个处理。N、P、K添加处理分别为10 g N·m^{-2}(施用72.9 g·m^{-2} $CaNO_3$)、10 g P·m^{-2} (施用44.4 g·m^{-2} $Ca(H_2PO_4)_2·H_2O$) 和 10 g K·m^{-2}(施用 48.2 g·m^{-2} K_2SO_4)，每年的施肥时间为4月10日(阜康站)和7月1–3日(其他站)。将10个处理的每个实验小区进一步划分为4个亚区：A为对照区；B为预留实验区；C为夏季增雨区；D为冬春增雪区，具体增雨(雪)量和处理时间安排见表1。将每个亚区进一步划分为永久观测区(1 m × 1 m)、稳定性同位素标记及凋落物与根系分解实验区(1 m × 1 m)和生物量测定与土壤采样区(2.5 m × 1 m)三部分。实验采用完全随机区组设计，共10个一级处理(30个二级处理)，每个处理6次重复，共计60个小区，每个小区面积为6 m × 6 m (草地)或8 m × 8 m (荒漠)(图2)。

3.3 观测指标体系

3.3.1 生态系统属性

根据草原生态系统的地上、地下组分，选取了9项生态系统属性指标进行观测，包括：植物种类组成，地上净初级生产力(*ANPP*)，地下生物量，生态系统净气体交换(*NEE*)，土壤呼吸，氮矿化作用，微生物生物量、C:N及群落结构，凋落物分解，氮素吸收、分配和利用。

3.3.2 植物功能性状

植物功能性状的观测指标分为5类：整株性状(株高、茎和叶生物量、茎叶比、叶片密度、个体生物量和根冠比)，叶片形态性状(叶片面积、叶干物质含量和比叶面积)，叶片生理性状(光合速率，叶寿命，水分和氮素利用效率，叶片C、N、P含量)，根系性状(根直径，根表面积，根长密度，比根长，根系生物量，根系C、N、P含量)和种子性状(种子质量)，共计26个性状指标。

3.4 取得的主要研究成果

本课题将来自联网实验研究取得的部分成果集合成为“草地和荒漠生态系统服务功能形成与调控机理”专辑发表。这一专辑共收录了11篇研究论文，内容涉及水分和养分添加以及动物采食对草地和荒漠生态系统植物群落结构和初级生产力、植物

图1 联网控制实验平台(野外实验设置)。**A,** 锡林郭勒草原生态系统国家野外科学观测研究站。**B,** 海北高寒草地生态系统国家野外科学观测研究站。**C,** 奈曼农田生态系统国家野外科学观测研究站。**D,** 阜康荒漠生态系统国家野外科学观测研究站。

Fig. 1 Field setup of the experimental network across four national ecosystem observation and research stations. **A,** National Grassland Ecosystem Observation and Research Station of Xilin Gol. **B,** National Alpine Meadow Ecosystem Observation and Research Station of Haibei. **C,** National Agricultural Ecosystem Observation and Research Station of Naiman. **D,** National Desert Ecosystem Observation and Research Station of Fukang.

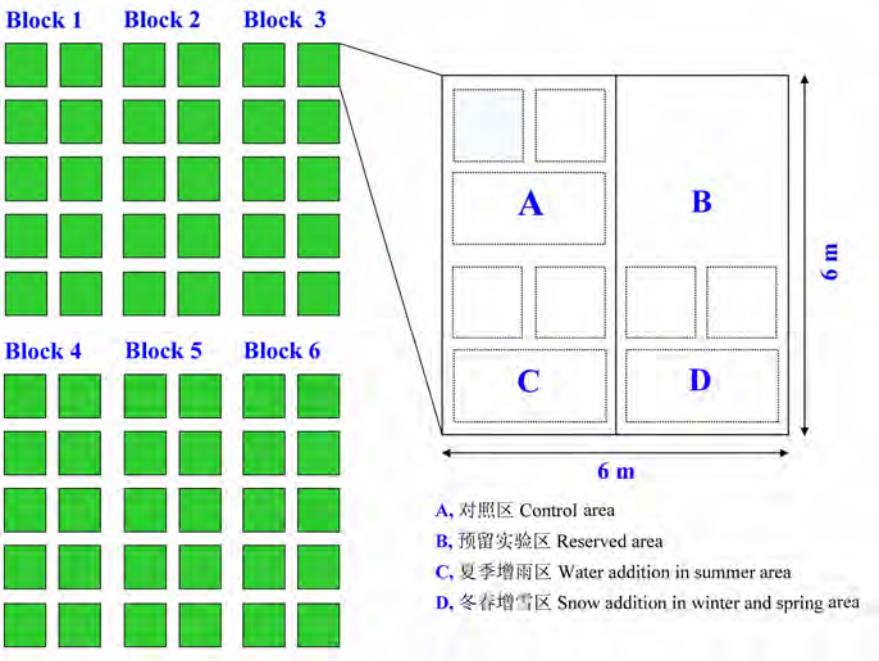


图2 联网实验完全随机区组设计一级与二级实验处理方案。**Block 1–6**表示6个实验区组重复。

Fig. 2 The first and second treatment schemes of the randomized complete-block design in each site. **Blocks 1** to **6** denote six replicates.

doi: 10.3724/SP.J.1258.2014.00009

表1 4个野外台站夏季增雨和冬季增雪量及时间安排

Table 1 Snow addition amount and schedule in winter and water addition amount and schedule in summer at four field stations

野外台站 Field station	冬季增雪 Snow addition in winter (mm)			夏季增雨 Water addition in summer (mm)									
	1月5日 Jan. 5	2月5日 Feb. 5	3月5日 Mar. 5	6月5日 June 5	6月15日 June 15	6月22日 June 22	6月29日 June 29	7月6日 July 6	7月13日 July 13	7月20日 July 20	7月27日 July 27	8月2日 Aug. 2	8月9日 Aug. 9	8月15日 Aug. 15
Fukang	15	15	10	10				10						
Haibei	20	15	15		14	14	14	14	14	14	14	14	14	14
Naiman	10	10	5		10	10	10	10	10	10	10	10	10	10
Xilin Gol	10	10	5		10	10	10	10	10	10	10	10	10	10

Fukang, 阜康荒漠生态系统国家野外科学观测研究站; Haibei, 海北高寒草地生态系统国家野外科学观测研究站; Naiman, 奈曼农田生态系统国家野外科学观测研究站; Xilin Gol, 锡林郭勒草原生态系统国家野外科学观测研究站。

Fukang, National Desert Ecosystem Observation and Research Station of Fukang; Haibei, National Alpine Meadow Ecosystem Observation and Research Station of Haibei; Naiman, National Agricultural Ecosystem Observation and Research Station of Naiman; Xilin Gol, National Grassland Ecosystem Observation and Research Station of Xilin Gol.

功能性状、氮素吸收分配、土壤呼吸以及微生物组成的影响等方面。基于这些研究成果，可以进一步开展不同植被类型的对比研究，以及区域尺度的集成与整合分析。

3.4.1 养分和水分添加对高寒草地植物群落结构和服务功能的影响

通过在青藏高原高寒草甸连续4年(2009–2012年)的养分、水分添加和^{15}N稳定性同位素示踪实验，揭示了养分和水分添加对高寒草甸植物群落结构和生产力、植物N吸收与分配策略及物候特征的影响机制，发现：1) N、P添加提高了高寒草甸植物群落地上生物量，P添加提高了群落地下生物量，而N添加对地下生物量无显著影响；N、P添加改变了植物功能群组成，使禾草的多度增加，杂类草的多度降低(杨晓霞等, 2014)。2)养分和水分添加改变了不同功能群植物的物候特征。N、P添加使莎草科、禾本科、杂类草植物的返青期和枯黄期推迟，而增雪处理使杂类草的返青期提前，使大多数植物的开花期提前，增水处理使杂类草的枯黄期提前(叶鑫等, 2014)。3)不同植物种对N素的吸收和分配策略具有明显的生态位分化和资源分配策略的权衡(邓建明等, 2014)。4)对三江源区不同退化阶段草地土壤呼吸的研究发现，土壤温度和湿度对土壤呼吸具有重要影响，中度退化草地生长季的土壤呼吸速率最高，重度退化草地的土壤呼吸速率最低，土壤呼吸与地上生物量存在显著正相关关系(温军等, 2014)。

3.4.2 养分、水分添加和放牧对典型草原群落结构和服务功能的影响

以内蒙古典型草原为研究对象，通过N、P添加实验和放牧控制实验，研究了养分添加、降水波动和放牧强度对典型草原群落物种多样性、初级生产力和植物功能性状的影响，发现：1)群落净初级生产力受N、P元素共同限制。建群种羊草对N、P添加的响应因组织水平而异，同时受年际间降水波动的影响。羊草通过增加比叶面积、叶片大小和叶片N含量，提高整体光合能力，促进个体生长(白雪等, 2014)。2)植物多样性对放牧的响应受降水波动和地形因素的调节，丰水年份群落α、β和γ多样性均高于平水年份，平地对放牧的缓冲能力强于坡地，干旱会加剧重度放牧对植物多样性的影响(杨婧等, 2014)。3)生态位分化机制对草原群落物种多度分布起着主导作用，常见种和稀有种通过不同的响应方

式共同维持了群落的物种多样性(李文怀等, 2014)。4)对群落中常见植物的根际和非根际土壤中细菌和真菌数量及群落结构的研究发现, 根际土壤中的细菌和真菌数量普遍高于非根际土壤, 尤其以真菌更为明显; 大多数物种的根际细菌及真菌的群落结构与非根际存在显著差异(王纳纳等, 2014)。

3.4.3 养分和水分添加对沙化草地和荒漠群落结构和服务功能的影响

通过在荒漠和沙化草地设置养分(N、P、K)与水分(夏季增雨、冬春增雪)添加实验, 研究了养分与水分添加对荒漠和沙化草地群落物种多样性和生物量分配格局、植物功能性状的影响, 发现: 1)养分和水分添加降低了荒漠群落的物种多样性, 改变了植物功能群组成, 使禾草类植物增加, 十字花科植物减少。而水分添加、肥水交互作用对物种丰富度均无显著影响(赵新风等, 2014a)。2)施氮、增水的交互作用对荒漠建群种植物钠猪毛菜(*Salsola nitraria*)的功能性状具有显著的影响, 施氮+冬春增雪处理使钠猪毛菜的株高、个体生物量、叶面积和比叶面积显著增加, 钠猪毛菜通过形态可塑性提高其适应能力(赵新风等, 2014b)。3)施氮+夏季增雨(冬季增雪)显著提高了一年生植物向叶片和果实的生物量分配, 而对多年生植物无明显影响; 施氮+冬季增雪使群落的叶生物量分配增加, 而施氮+夏季增雨使群落的茎生物量分配增加(毛伟等, 2014)。

4 未来展望

今后我国草地和荒漠生态系统服务功能的研究重点应集中于以下几个方面: 1)草地和荒漠生态系统初级生产力形成和维持机制; 2)生物多样性与生态系统稳定性和服务功能的关系; 3)生态系统服务功能对环境扰动的响应与适应机理; 4)生态系统重要服务功能之间的相互依赖性、弹性、可逆性、权衡关系和尺度效应; 5)水分、养分等关键限制因子及其耦合作用对生态系统结构与功能的多营养级水平和多尺度调控机理。

基金项目 国家重点基础研究发展计划项目(2009CB421102)。

致谢 感谢参加“草地和荒漠生态系统服务功能形成与调控机理”课题的所有科研骨干和研究生对课题顺利完成做出的努力和贡献; 感谢“973”项目组的首席科学家和研究骨干在本课题开展和实施过程中给予的建议和帮助; 感谢贺金生研究员在联网实验方案设计与实施中给予的建议和指导。

参考文献

Allaby M (1998). *Oxford Dictionary of Plant Sciences*. Oxford University Press, Oxford, UK.

Bai X, Cheng JH, Zheng SX, Zhan SX, Bai YF (2014). Eco-physiological responses of *Leymus chinensis* to nitrogen and phosphorus additions in a typical steppe. *Chinese Journal of Plant Ecology,* 38, 103–115. (in Chinese with English abstract) [白雪, 程军回, 郑淑霞, 詹书侠, 白永飞 (2014). 典型草原建群种羊草对氮磷添加的生理生态响应. 植物生态学报, 38, 103–115.]

Bateman IJ, Harwood AR, Mace GM, Watson RT, Abson DJ, Andrews B, Binner A, Crowe A, Day BH, Dugdale S, Fezzi C, Foden J, Hadley D, Haines-Young R, Hulme M, Kontoleon A, Lovett AA, Munday P, Pascual U, Paterson J, Perino G, Sen A, Siriwardena G, van Soest D, Termansen M (2013). Bringing ecosystem services into economic decision-making: land use in the United Kingdom. *Science,* 341, 45–50.

Bennett EM, Peterson GD, Gordon LJ (2009). Understanding relationships among multiple ecosystem services. *Ecology Letters,* 12, 1394–1404.

Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-Benayas JM (2011). Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends in Ecology & Evolution*, 26, 541–549.

Carpenter SR, De Fries R, Dietz T, Mooney HA, Polasky S, Reid WV, Scholes RJ (2006). Millennium ecosystem assessment: research needs. *Science,* 314, 257–258.

Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Diaz S, Dietz T, Duraiappah AK, Oteng-Yeboah A, Pereira HM, Perrings C, Reid WV, Sarukhan J, Scholes RJ, Whyte A (2009). Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. *Proceedings of the National Academy of Sciences of the United States of America,* 106, 1305–1312.

Chisholm RA, Wintle BA (2012). Choosing ecosystem service investments that are robust to uncertainty across multiple parameters. *Ecological Applications,* 22, 697–704.

Ci LJ (2005). *Desertification and Its Prevention and Control in China*. Higher Education Press, Beijing. (in Chinese) [慈龙骏 (2005). 中国的荒漠化及其防治. 高等教育出版社, 北京.]

Compiling Committee of the Vegetation of China (1980). *The Vegetation of China*. Science Press, Beijing. (in Chinese) [中国植被编辑委员会 (1980). 中国植被. 科学出版社, 北京.]

Daily GC (1997). *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington DC.

Daily GC, Soderqvist T, Aniyar S, Arrow K, Dasgupta P,

Ehrlich PR, Folke C, Jansson A, Jansson BO, Kautsky N, Levin S, Lubchenco J, Maler KG, Simpson D, Starrett D, Tilman D, Walker B (2000). Ecology—the value of nature and the nature of value. *Science,* 289, 395–396.

de Groot RS, Wilson MA, Boumans RMJ (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics,* 41, 393–408.

Dearing JA, Yang XD, Dong XH, Zhang EL, Chen X, Langdon PG, Zhang K, Zhang WG, Dawson TP (2012). Extending the timescale and range of ecosystem services through paleoenvironmental analyses, exemplified in the lower Yangtze basin. *Proceedings of the National Academy of Sciences of the United States of America,* 109, E1111–E1120.

Deng JM, Yao BQ, Zhou HK, Zhao XQ, Wei Q, Chen Z, Wang WY (2014). Nitrogen uptake and allocation characteristics of alpine meadow main species under nitrogen and water additions based on ^{15}N isotope. *Chinese Journal of Plant Ecology,* 38, 116–124. (in Chinese with English abstract) [邓建明, 姚步青, 周华坤, 赵新全, 魏晴, 陈哲, 王文颖 (2014). 水氮添加条件下高寒草甸主要植物种氮素吸收分配的同位素示踪研究. 植物生态学报, 38, 116–124.]

Department of Animal Husbandry and Veterinary, the General Station of Animal Husbandry and Veterinary, the Ministry of Agriculture, P. R. China (1996). *Rangeland Resources of China*. China Science and Technology Press, Beijing. (in Chinese) [中华人民共和国农业部兽医司, 全国畜牧兽医总站 (1996). 中国草地资源. 中国科学技术出版社, 北京.]

Feld CK, Sousa JP, da Silva PM, Dawson TP (2010). Indicators for biodiversity and ecosystem services: towards an improved framework for ecosystems assessment. *Biodiversity and Conservation,* 19, 2895–2919.

Fu BJ, Wang S, Su CH, Forsius M (2013). Linking ecosystem processes and ecosystem services. *Current Opinion in Environmental Sustainability,* 5, 4–10.

Fu BJ, Zhou GY, Bai YF, Song CC, Liu JY, Zhang HY, Lü YH, Zheng H, Xie GD (2009). The main terrestrial ecosystem services and ecological security in China. *Advances in Earth Science,* 24, 571–576. (in Chinese with English abstract) [傅伯杰, 周国逸, 白永飞, 宋长春, 刘纪远, 张惠远, 吕一河, 郑华, 谢高地 (2009). 中国主要陆地生态系统服务功能与生态安全. 地球科学进展, 24, 571–576.]

Geijzendorffer IR, Roche PK (2013). Can biodiversity monitoring schemes provide indicators for ecosystem services? *Ecological Indicators,* 33, 148–157.

Han J (2011). *Survey on Ecological Issues of China's Grasslands*. Shanghai Far East Publishers, Shanghai. (in Chinese) [韩俊 (2011). 中国草原生态问题调查. 上海远东出版社, 上海.]

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs,* 75, 3–35.

International Institute for Environment and Development and World Resources Institute (1987). *World Resources 1987: an Assessment of the Resource Base that Supports the Global Economy*. International Institute for Environment and Development and World Resources Institute, New York.

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M (2011). High plant diversity is needed to maintain ecosystem services. *Nature,* 477, 199–202.

Kremen C (2005). Managing ecosystem services: What do we need to know about their ecology? *Ecology Letters,* 8, 468–479.

Larigauderie A, Prieur-Richard AH, Mace GM, Lonsdale M, Mooney HA, Brussaard L, Cooper D, Cramer W, Daszak P, Díaz S, Duraiappah A, Elmqvist T, Faith DP, Jackson LE, Krug C, Leadley PW, Le Prestre P, Matsuda H, Palmer M, Perrings C, Pulleman M, Reyers B, Rosa EA, Scholes RJ, Spehn E, Turner II BL, Yahara T (2012). Biodiversity and ecosystem services science for a sustainable planet: the DIVERSITAS vision for 2012–20. *Current Opinion in Environmental Sustainability,* 4, 101–105.

Li WH, Zheng SX, Bai YF (2014). Effects of grazing intensity and topography on species abundance distribution in a typical steppe of Inner Mongolia. *Chinese Journal of Plant Ecology,* 38, 178–187. (in Chinese with English abstract) [李文怀, 郑淑霞, 白永飞 (2014). 放牧强度和地形对内蒙古典型草原物种多度分布的影响. 植物生态学报, 38, 178–187.]

Liu XY, Long RJ, Shang ZH (2011). Evaluation method of ecological services function and their value for grassland ecosystems. *Acta Prataculturae Sinica,* 20, 167–174. (in Chinese with English abstract) [刘兴元, 龙瑞军, 尚占环 (2011). 草地生态系统服务功能及其价值评估方法研究. 草业学报, 20, 167–174.]

Loreau M, Hector A (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature,* 412, 72–76.

Mao W, Li YL, Cui D, Zhao XY, Zhang TH, Li YQ (2014). Biomass allocation response of species with different life history strategies to nitrogen and water addition in sandy grassland in Inner Mongolia. *Chinese Journal of Plant Ecology,* 38, 125–133. (in Chinese with English abstract)

[毛伟, 李玉霖, 崔夺, 赵学勇, 张铜会, 李玉强 (2014). 沙质草地不同生活史植物的生物量分配对氮素和水分添加的响应. 植物生态学报, 38, 125–133.]

Mertz O, Ravnborg HM, Lövei GL, Nielsen I, Konijnendijk CC (2007). Ecosystem services and biodiversity in developing countries. *Biodiversity and Conservation,* 16, 2729–2737.

Midgley GF (2012). Biodiversity and ecosystem function. *Science*, 335, 174–175.

Millennium Ecosystem Assessment (2005). *Ecosystem and Human Well-being*. Island Press, Washington DC.

Palmer M, Bernhardt E, Chornesky E, Collins S, Dobson A, Duke C, Gold B, Jacobson R, Kingsland S, Kranz R, Mappin M, Martinez ML, Micheli F, Morse J, Pace M, Pascual M, Palumbi S, Reichman OJ, Simons A, Townsend A, Turner M (2004). Ecology for a crowded planet. *Science,* 304, 1251–1252.

Perrings C, Duraiappah A, Larigauderie A, Mooney H (2011). The biodiversity and ecosystem services science-policy interface. *Science,* 331, 1139–1140.

Perrings C, Naeem S, Ahrestani F, Bunker DE, Burkill P, Canziani G, Elmqvist T, Ferrati R, Fuhrman J, Jaksic F, Kawabata Z, Kinzig A, Mace GM, Milano F, Mooney H, Prieur-Richard AH, Tschirhart J, Weisser W (2010). Ecosystem services for 2020. *Science,* 330, 323–324.

Peterson DL, Parker VT (1998). *Ecological Scale: Theory and Applications*. Columbia University Press, New York.

Power AG (2010). Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society B—Biological Sciences,* 365, 2959–2971.

Quijas S, Jackson LE, Maass M, Schmid B, Raffaelli D, Balvanera P (2012). Plant diversity and generation of ecosystem services at the landscape scale: expert knowledge assessment. *Journal of Applied Ecology*, 49, 929–940.

Reiss J, Bridle JR, Montoya JM, Woodward G (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution,* 24, 505–514.

Reszkowska A, Krümmelbein J, Peth S, Horn R, Zhao Y, Gan L (2011). Influence of grazing on hydraulic and mechanical properties of semiarid steppe soils under different vegetation type in Inner Mongolia, China. *Plant and Soil,* 340, 59–72.

Reynolds JF, Stafford Smith DM (2002). *Global Desertification: Do Humans Cause Deserts?* Dahlem University Press, Berlin.

Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000). Global biodiversity scenarios for the year 2100. *Science,* 287, 1770–1774.

Sala OE, Paruelo JM (1997). Ecosystem services in grasslands. In: Daily GC ed. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington DC.

Schönbach P, Wan HW, Gierus M, Bai YF, Müller K, Lin LJ, Susenbeth A, Taube F (2011). Grassland responses to grazing: effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem. *Plant and Soil,* 340, 103–115.

Scholes RJ, Reyers B, Biggs R, Spierenburg MJ, Duriappah A (2013). Multi-scale and cross-scale assessments of social-ecological systems and their ecosystem services. *Current Opinion in Environmental Sustainability,* 5, 16–25.

Seppelt R, Lautenbach S, Volk M (2013). Identifying trade-offs between ecosystem services, land use, and biodiversity: a plea for combining scenario analysis and optimization on different spatial scales. *Current Opinion in Environmental Sustainability,* 5, 458–463.

State Environmental Protection Administration of China (2006). *Report on the State of the Environment in China: 2005*. Beijing. (in Chinese) [国家环保总局 (2006). 2005年中国环境状况公报. 国家环保总局, 北京.]

Steffens M, Kölbl A, Totsche KU, Kögel-Knabner I (2008). Grazing effects on soil chemical and physical properties in a semiarid steppe of Inner Mongolia (P. R. China). *Geoderma,* 143, 63–72.

Suttie JM, Renolds SG, Batello C (2005). Grasslands of the World. Food and Agriculture Organization of the United Nations, Rome.

Turnbull LA, Levine JM, Loreau M, Hector A (2012). Coexistence, niches and biodiversity effects on ecosystem functioning. *Ecology Letters,* 16, 116–127.

Vihervaara P, D'Amato D, Forsius M, Angelstam P, Baessler C, Balvanera P, Boldgiv B, Bourgeron P, Dick J, Kanka R, Klotz S, Maass M, Melecis V, Petřik P, Shibata H, Tang JW, Thompson J, Zacharias S (2013). Using long-term ecosystem service and biodiversity data to study the impacts and adaptation options in response to climate change: insights from the global ILTER sites network. *Current Opinion in Environmental Sustainability,* 5, 53–66.

Wang NN, Chen Y, Ying JY, Gao YS, Bai YF (2014). Effects of typical plant on soil microbial communities in an Inner Mongolia grassland. *Chinese Journal of Plant Ecology,* 38, 201–208. (in Chinese with English abstract) [王纳纳, 陈颖, 应娇妍, 高勇生, 白永飞 (2014). 内蒙古草原典型植物对土壤微生物群落的影响. 植物生态学报, 38, 201–208.]

Wen J, Zhou HK, Yao BQ, Li YK, Zhao XQ, Chen Z, Lian LY, Guo KX (2014). Characteristics of soil respiration in different degraded alpine grassland in the source region of Three-River. *Chinese Journal of Plant Ecology,* 38,

doi: 10.3724/SP.J.1258.2014.00009

209–218. (in Chinese with English abstract) [温军, 周华坤, 姚步青, 李以康, 赵新全, 陈哲, 连利叶, 郭凯先 (2014). 三江源区不同退化程度高寒草原土壤呼吸特征. 植物生态学报, 38, 209–218.]

White R, Murray S, Rohweder M (2000). *Pilot Analysis of Global Ecosystems: Grassland Ecosystems*. World Resources Institute, Washington DC.

Yang J, Chu PF, Chen DM, Wang MJ, Bai YF (2014). Mechanisms underlying the impacts of grazing on plant α, β and γ diversity in a typical steppe of the Inner Mongolia grassland. *Chinese Journal of Plant Ecology,* 38, 188–200. (in Chinese with English abstract) [杨婧, 褚鹏飞, 陈迪马, 王明玖, 白永飞 (2014). 放牧对内蒙古典型草原α、β和γ多样性的影响机制. 植物生态学报, 38, 188–200.]

Yang XX, Ren F, Zhou HK, He JS (2014). Responses of plant community biomass to nitrogen and phosphorus additions in an alpine meadow on the Qinghai-Xizang Plateau. *Chinese Journal of Plant Ecology,* 38, 159–166. (in Chinese with English abstract) [杨晓霞, 任飞, 周华坤, 贺金生 (2014). 青藏高原高寒草甸植物群落生物量对氮、磷添加的响应. 植物生态学报, 38, 159–166.]

Ye X, Zhou HK, Liu GH, Yao BQ, Zhao XQ (2014). Responses of phenological characteristics of major plants to nutrient and water additions in *Kobresia humilis* alpine meadow. *Chinese Journal of Plant Ecology,* 38, 147–158. (in Chinese with English abstract) [叶鑫, 周华坤, 刘国华, 姚步青, 赵新全 (2014). 高寒矮生嵩草草甸主要植物物候特征对养分和水分添加的响应. 植物生态学报, 38, 147–158.]

Zhang YM, Zhao SD (2008). Desertification: current state and trends, scenarios and response options. *Advances in Earth Science,* 23, 306–311. (in Chinese with English abstract) [张永民, 赵士洞 (2008). 全球荒漠化的现状、未来情景及防治对策. 地球科学进展, 23, 306–311.]

Zhao XF, Xu HL, Zhang P, Tu WX, Zhang QQ (2014a). Effects of nutrient and water additions on plant community structure and species diversity in desert grasslands. *Chinese Journal of Plant Ecology,* 38, 167–177. (in Chinese with English abstract) [赵新风, 徐海量, 张鹏, 涂文霞, 张青青 (2014). 养分与水分添加对荒漠草地植物群落结构和物种多样性的影响. 植物生态学报, 38, 167–177.]

Zhao XF, Xu HL, Zhang P, Zhang QQ (2014b). Influence of nutrient and water additions on functional traits of *Salsola nitraria* in desert grassland. *Chinese Journal of Plant Ecology,* 38, 134–146. (in Chinese with English abstract) [赵新风, 徐海量, 张鹏, 张青青 (2014). 养分与水分添加对荒漠草地植物钠猪毛菜功能性状的影响. 植物生态学报, 38, 134–146.]

责任编委: 贺金生 责任编辑: 谢 巍

生物多样性 2013, **21** (6): 639–650 Doi: 10.3724/SP.J.1003.2013.12134
Biodiversity Science http: //www.biodiversity-science.net

中国草地生物多样性监测网络的指标体系及实施方案

万宏伟 潘庆民 白永飞*

(中国科学院植物研究所植被与环境变化国家重点实验室, 北京 100093)

摘要: 建立生物多样性监测网络是生物多样性保护和研究的基础, 在一些发达国家相关的工作已经比较完善, 我国森林生物多样性监测的网络也已经初具规模(http://www.cfbiodiv.org/), 而国家尺度上的草地生物多样性监测网络尚未建设。我国草地面积广, 野生动植物资源丰富, 对环境因子变化响应敏感且受人类活动干扰的影响较为强烈。建立国家尺度上的草地生物多样性监测网络, 对于揭示我国草地生物多样性资源现状, 研究其变化规律与机制, 监督和指导保护实践至关重要。作者在借鉴国外监测指标体系的基础上, 结合我国的草地资源和利用现状, 从整合政策和科学两方面的需求, 并考虑监测指标遴选及其空间异质性和检出概率, 结合拟探讨的具体科学问题, 提出了我国草地生物多样性监测与研究网络的指标体系和具体监测方案。该方案以草地植物多样性研究为核心, 兼顾草地生态系统健康和功能, 包含3类27项82个具体指标, 并给出了监测样地选取与设置的方案, 以及每个指标的野外监测方法与数据获取途径。最后, 作者以2012年在内蒙古的一个调查样地为例, 简要阐述了野外工作流程和注意事项, 并展示了部分野外调查结果。

关键词: 草原生态系统, 生物多样性, 监测网络, 指标体系, 监测方法

China grassland biodiversity monitoring network: indicators and implementation plan

Hongwei Wan, Qingmin Pan, Yongfei Bai*

State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093

Abstract: A biodiversity monitoring network is fundamental to biodiversity research and successful conservation practice. Many developed countries have established national or even continental scale biodiversity monitoring networks, covering a wide range of natural and semi-natural ecosystems. In China, the only biodiversity monitoring network that currently exists is the Chinese Forest Biodiversity Monitoring Network (CForBio, http://www.cfbiodiv.org/), which was founded in 2004. Grassland ecosystems, which cover 41.7% of the total land area of China, are most sensitive to environmental changes and have long been subject to overgrazing and other human disturbances, resulting in widespread deterioration of biodiversity and ecosystem services. It is essential, therefore, to establish a Chinese grassland biodiversity monitoring network to investigate the current status of Chinese grasslands, the pressure and/or drivers of changes in biodiversity, and to provide guidance on their restoration and conservation practices. Based on the successful experiences of other international biodiversity monitoring networks and the natural grassland conditions in China, we propose a national grassland biodiversity monitoring and research network, which includes the overarching objectives and scientific questions, indicators, methodology issues, and a case study in the Inner Mongolia grassland.

Key words: grassland ecosystem, biodiversity monitoring and research network, indicators, methodology

收稿日期: 2013-06-02; 接受日期: 2013-11-20

基金项目: 中国科学院知识创新工程重要方向项目“中国生物多样性监测与变化机理研究(KSCX2-EW-Z-5)”和国家自然科学基金重点项目“蒙古高原草原生物多样性的格局与维持机制研究: 控制实验与野外调查相整合的多尺度途径(31030013)”。

* 通讯作者 Author for correspondence. E-mail: yfbai@ibcas.ac.cn

丰富多彩的生命世界是地球在浩瀚宇宙中最具魅力之处。各种生命形式息息相关，彼此作用，一起维系着生态系统的结构和功能。然而，由于人类活动的干扰不断加剧，大量生物正在以前所未有的速度灭绝。据估计，目前物种灭绝的速率是物种自然灭绝速率的1,000–10,000倍(WWF, http://wwf.panda.org/about_our_earth/biodiversity/biodiversity/)。生物多样性与多种生态系统服务功能密切相关。生物多样性的丧失以及生态系统服务功能和可持续性的下降，将最终威胁到人类的福祉和生存。因此，生物多样性的保护已经刻不容缓。

建立生物多样性监测网络是生物多样性保护和研究的基础工作。从1992年《生物多样性公约》(Convention on Biological Diversity)签署至今，已经有越来越多的发达国家致力于生物多样性监测，国家尺度的生物多样性监测网络正在不断壮大(Gilbert *et al.*, 1998; Olsen *et al.*, 1999; Plattner *et al.*, 2004; Pellikka *et al.*, 2005)，而发展中国家在国家尺度上的生物多样性监测相对薄弱，并明显滞后于发达国家(Pereira *et al.*, 2013)。例如，瑞士的生物多样性监测网络(FOEN-Biodiversity Monitoring Switzerland)、美国繁殖鸟类多样性监测网络(USGS-North American Breeding Bird Survey)及英国的两栖爬行类多样性监测网络(National Amphibian & Reptile Recording Scheme)已经比较成熟。但是，不同监测网络服务于不同监测需求，并有着各自不同的监测目标和侧重点，如有的专门针对鸟类和两栖爬行类，有的是针对所有生物多样性组分的。最近，Pereira等30位科学家在*Science*上发表文章，联合倡导通过确立基本生物多样性变量(essential biodiversity variables)来推动全球生物多样性联合监测(Pereira *et al.*, 2013)。

生物多样性的测度与空间和时间尺度密切相关(Whittaker, 1972; Whittaker *et al.*, 2001; Yoccoz *et al.*, 2001; Adler & Lauenroth, 2003)。在特定群落内，物种多样性随着调查面积增加而逐渐增高，并最终趋于饱和，这就是经典的种–面积关系，它形象地刻画了物种多样性对于空间尺度的依赖性(Connor & McCoy, 1979)。在时间序列上，物种多样性随时间的推移也不断变化，其经典例子有群落原生演替、次生演替(Connell & Slatyer, 1977)、放牧干扰下植物群落的演替和状态转化(Briske *et al.*, 2005)。强烈的时空尺度依赖性和多层次性决定了生物多样性现状的分析需要在不同组织水平上进行多空间尺度、全面和连续的监测(Noss, 1990; Dengler, 2009)。而这需要大量的人力和物力投入，数据获取极为困难。特别是植物多样性的监测，需要在单个监测点设置多个观测样方，加之植物样方的调查本身就是一项比较耗时的工作，从这个意义上讲，相对于动物(例如鸟类和蝴蝶)种类和数量的调查要困难得多，导致目前大多数生物多样性监测网络中，草本植物群落多样性监测相对薄弱。

我国是世界草地资源大国，拥有草地总面积近4亿公顷，约占国土总面积的41.7%(中华人民共和国农业部兽医司和全国畜牧兽医总站, 1996)。据统计，我国草地上生长的饲用植物共246科1,545属6,704种，有毒植物49科152属731种(中华人民共和国农业部兽医司和全国畜牧兽医总站, 1996)，构成了我国野生植物，特别是耐旱、耐寒、耐盐和药用植物最重要的种质资源基因库。但是，由于从传统游牧到定居放牧的草地利用方式的转变、野生动物栖息地的丧失，再加上过度放牧，大部分草地植被发生了不同程度的退化，狼(*Canis lupus*)、黄羊(*Procapra gutturosa*)、蒙古驴(*Equus hemionus*)等宝贵的野生动物资源已在我国绝大部分草地区域消失。就广泛分布于我国北方的天然草地而言，目前有90%左右处于不同程度的退化之中，其中严重退化的草地占60%以上(Wu & Loucks, 1992)。

伴随人类干扰活动的加剧，我国北方草地还正经受着前所未有的全球气候变化的强烈影响(Xiao *et al.*, 1995; Gao *et al.*, 2000)。在过去几十年中，该区域生长季温度平均升高了近2°C，大气CO_2浓度升高了50 ppm，降水量及降水的季节分配均发生了显著变化(Blunden & Arndt, 2013)，是受全球变暖影响最为强烈的区域之一(Chase *et al.*, 2000; Yu *et al.*, 2003)。在过去几十年中，蒙古高原C_4植物的分布区在温度驱动下向北迁移了近1个纬度，约80 km(Wittmer *et al.*, 2010)，而且氮沉降和降雨格局的变化也均会对草地群落的物种多样性造成极为显著的影响(Auerswald *et al.*, 2012; Lan & Bai, 2012; Ren *et al.*, 2012)。

综上所述，随着人类活动干扰和全球环境变化的不断加剧，我国草地野生动植物资源的生存将面临前所未有的挑战和威胁。那么，我国草地生物多

样性资源现状如何？未来会朝着怎样的方向发展？变化的主要驱动力是什么？如何有效地保护草地上生长的珍贵的野生动植物资源以减缓其灭绝的速度？这些问题的解答, 都离不开国家尺度草地生物多样性的连续监测。

在我国, 针对森林生态系统进行多样性监测的网络已经初具规模(http://www.cfbiodiv.org/), 然而对于分布广泛的草地生态系统, 国家尺度上的多样性监测网络尚未建设。迄今, 我国尚未对草地生态系统进行过全面的植物群落组成清查(方精云等, 2009)。因此, 如何构建一个符合我国国情的、国家尺度的草地生物多样性监测网络是我们当前的重要任务之一。我国草地生态系统多样性监测和研究的重点是草本植物的多样性, 那么如何设计和构建一个切实可行的以草地植物多样性监测为主的草地生物多样性监测与研究网络是本文拟探讨的核心问题。

本文中, 我们以植物的多样性为中心, 并兼顾其他关键生态系统健康指示指标, 提出了一套监测与研究草地生物多样性的指标、方法体系及实施方案。希望通过对我国国家尺度上的草地生物多样性尤其是植物多样性的连续监测, 来研究我国草地生物多样性的现状、格局(空间异质性)、变化(时间异质性)及其驱动机制, 进而为我国的草地生物多样性保护和管理提供第一手的基础数据和科学支撑。具体目标包括: (1)明确多样性监测与研究所针对的具体科学问题; (2)确立多样性监测的指标体系; (3)选取和设置野外监测样点; (4)统一调查方法; (5)野外调研取样和室内测量分析; (6)数据的录入、整理和存档; (7)历史、环境及其他相关资料的收集整理; (8)数据的集成分析、成果发表和推广应用; (9)根据研究和应用的需要调整和完善草地生物多样性监测网络。同时，我们以2012年调查的样地为案例, 简要阐述了野外观测方法和注意事项, 并展示了部分野外调查结果。

1　建立我国草地生物多样性监测体系的基本原则

首先, 必须考虑如何整合政策和科学两方面的需求。生物多样性监测一般要同时满足两种需求: 一种是政策需求, 服务于管理和保护政策的制定; 一种是科学需求, 服务于揭示生物的共存和变化机制, 并预测未来的变化趋势。现实中, 大多数生物多样性监测网络仅仅服务于一方面的需求(Yoccoz *et al*., 2001)。只有兼顾两方面的要求才能使长期的监测数据更有价值(Krebs, 1991)。

其次, 必须进行多样性监测指标的遴选和取舍。已有的研究表明, 监测指标的数量和质量各有利弊, 应进行权衡选择。针对某个特定类群生物多样性的监测, 如美国的繁殖鸟类和英国的两栖爬行类动物多样性监测网络, 监测指标相对较少, 监测工作可以做得非常具体深入, 所获得的数据也能满足研究的要求, 但其缺点在于无法全面反映生物多样性的整体现状和变化。而针对整体生物多样性的监测, 如瑞士生物多样性监测网络, 虽然可以对整体生物多样性的现状和变化作出量化评估, 但由于监测指标多任务重, 监测网络的维持和运行需要投入大量的人力和财力, 而且针对单个类群的监测内容不得不简化, 导致监测数据的精度无法满足对单个类群的多样性研究的要求。因此, 在服务于多样性整体监测目标的前提下, 建立草地多样性监测网络指标体系需要对监测指标进行遴选和取舍。

第三, 必须考虑监测指标的空间异质性和检出概率(Yoccoz *et al*., 2001)。不同物种具有不同的空间分布范围, 并且各物种的丰富度在其分布区内也存在很大的时空异质性。因此, 监测样地的面积、位置及观测时间和方法均与监测指标的检出概率密切相关。另外, 样地的位置(山谷还是山顶, 阴坡还是阳坡)、野外观测的时间(生长季初期、中期还是末期)及观测所采取的方法(样方的大小或者样线的长度)也会对监测指标造成影响。所以, 如何通过样地数量、面积和位置的合理设置及监测方法的正确应用, 尽量提高各个监测指标的检出概率和准确度, 同时兼顾监测指标的时空异质性, 是建立多样性监测指标体系应遵循的第三个原则。

2　我国草地生物多样性监测体系拟解决的科学问题

我们分别从生物多样性的研究和保护两个层面提出了我国草地生物多样性监测与研究应解决的科学问题。从生物多样性保护层面来看, 拟通过历史及待建设草地多样性网络监测数据的集成整合分析, 揭示草地生物多样性变化的关键驱动因子, 并探讨其变化的机理, 进而为草地生物多样性

保护实践提供理论指导, 具体问题包括下文的1–5项。从研究的层面来看, 本方案主要解决我国草地植物多样性的形成和维持机制、尺度依赖性及多样性和生态系统功能关系等问题, 具体包括下文的6–10项。

(1)我国草地植物组成和多样性现状如何？哪些物种濒临灭绝？哪些区域是生物多样性和生物多样性保护的热点？

(2)我国草地植物组成和多样性在过去几十年内发生了多大程度的变化?哪些区域对于人类活动干扰和环境变化的响应最为敏感？

(3)我国各类型草地的植物组成和多样性的变化轨迹怎样？人类活动干扰对草地生物多样性丧失的驱动作用如何？

(4)在当前草地管理模式和未来可能的环境变化情景下, 各类型草地植物组成和多样性会怎样变化？我们该如何应对？

(5)指示草地生态系统健康的关键生态系统功能(地上净初级生产力、碳固持等)及其他营养级生物的多样性(哺乳类、鸟类、蝴蝶、蝗虫)的现状如何, 是否受到人类活动干扰和环境变化的胁迫？该如何保护？

(6)我国草地植物的α、β、γ多样性具有怎样的空间格局特征？形成、维持和变化的机制是什么？

(7)不同类型草原群落构建的内在机制是什么？是以中性理论的随机过程为主导, 还是以生态位分化(例如环境筛选、限制相似性)的确定性过程为主导？

(8)种–面积关系具有怎样的时空格局特征和尺度依赖性？决定因子是什么？

(9)优势植物种具有怎样的空间分布格局？驱动因子是什么？种间的消长关系是否受生境、环境因子以及人类活动干扰等因素的影响？

(10)植物多样性与其他营养级多样性(哺乳类、鸟类、蝴蝶、蝗虫)及关键生态系统功能(地上净初级生产力、碳固持等)间存在怎样的内在联系？机制是什么？

3 我国草地生物多样性监测指标体系及各指标的调查方法

目前国际上的多样性监测网络大都从生物多样性保护的视角出发, 采取压力–状态–响应(Pressure-State-Response)指标体系, 根据监测区域特点筛选和确立相应的指标体系(de Bello *et al*., 2010)。监测的核心指标则多关注濒危物种、受胁迫较严重的物种及对人类活动干扰和全球变化响应敏感的物种(Landsberg & Crowley, 2004)。然而, 这些监测网络大都服务于政策的需求, 侧重服务于生物多样性保护, 而对于多样性格局、变化、过程和机制的研究较少, 且很少考虑尺度依赖性的问题。

本方案与国际上已有的多样性监测网络的区别在于侧重点为草原植物多样性。根据本方案的总体目标和具体科学问题, 我们提出了一个以草地植物多样性研究为核心, 兼顾草地生态系统健康和功能的包含 3 类 27 项 82 个具体指标的监测指标体系, 详见表 1。其中 1–8 项为植物组成多样性野外调查内容, 9–19 项为生态系统健康和关键生态系统功能指标, 20–27 项为关键环境和人类活动干扰指标。各个具体指标数据的获取途径、调查空间尺度也在表 1 中进行了说明。

参考国内外生物多样性网络监测与研究方法, 并结合具体问题, 我们确定了本方案涉及的所有监测指标野外调研和数据获取方法。各指标的测定方法详见附录 I。

4 监测样地选取、设置和调查规划

4.1 监测样地的设置原则

生物多样性监测网络样点的设置常用的方法有两种: 一种是按照群落类型进行布设, 另外一种是系统随机布设。第一种方案的前提是要有近期详尽的植被图作为依据。我国现有的草地植被图是基于20世纪80年代之前的草地植被调查数据构建的, 而这段时期恰恰是我国草地受人类活动干扰尤其是过度放牧影响最为严重的时期, 大部分草地后来发生了不同程度的退化。因此, 这样的植被图可能已经不能够真实地反映我国草地现有的植被分布状况。而按照后一种方案采用系统随机的方法, 不需要植被图作为依据, 可以不考虑植物类型及其分布。瑞士的生物多样性监测网络就是按照这种方法构建的。使用该方法进行样点选取和布设的优点有两个: 一是所有观测点的数据均可以作为随机样本进行统计学分析; 二是均匀的网络监测点数据可以通过插值的方法对不同空间尺度的指标(例如植物多样性、某物种的多度)的空间分布进行回溯和重

表1　草地生物多样性监测指标体系、测度尺度和数据获取途径

Table 1　Indicators of China grassland biodiversity monitoring, their measurement scale and sources

序号 No.	监测项 Parameters	具体指标 Indicators	获取途径 Sources	空间尺度 Spatial scale/level
1	植物群落的物种组成 Species composition of plant community	植物物种名录 Plant species list	野外观测(样方) Field observation (quadrats)	样地和景观尺度 Plot (1 ha) and landscape (25 ha)
2	植物物种多度 Abundance	物种的地上生物量和个体密度 Aboveground biomass and species density		景观尺度 Landscape
3	植物群落的盖度 Coverage	冠层盖度 Canopy coverage		景观尺度 Landscape
4	种–面积关系 Species–area relationship	物种名录 Species list	野外观测 Field observation	样地尺度 Plot
5	物种的点格局分析 Point pattern analysis	个体的空间位置 Position of individuals	野外观测 Field observation	样地尺度 Plot
6	植物功能性状 Plant functional traits	植株高度、茎叶比、比叶面积、单叶重、单叶面积、叶干物质含量、叶氮含量、叶磷含量 Height, leaf stem ratio, specific leaf area, leaf weight, leaf area, leaf dry matter content, leaf nitrogen content, and leaf phosphorus content	野外取样和室内分析 Field sampling and laboratory analysis	物种水平 Species
		生长型、生活史策略、光合途径、固氮能力、克隆生长特性、根系结构和子叶类型 Growth form, life history strategies, photosynthetic pathways, nitrogen fixation ability, clonal growth characteristics, root structure and cotyledon types	文献检索 Literature	物种水平 Species
7	植物种库 Plant species pool	物种名录 Species list	野外观测(样带) Field observations (transects)	景观尺度 Landscape
8	植物多样性 Plant diversity	α、β、γ多样性, 物种丰富度、物种均匀度、物种多样性、功能多样性、谱系多样性 α, β, γ diversity, species richness, species evenness, species diversity, functional diversity, and phylogenetic diversity	基于本表1、2、6、7项计算获得 Calculated based on parameters 1, 2, 6, 7	样地、景观、区域到国家尺度 Plot, landscape, regional to national
9	哺乳动物多样性 Mammal diversity	珍稀、濒危动物的有无 Presence or absence of rare and endangered species	社会调研 Social investigation	区域尺度 Regional
10	微生物多样性 Microbial diversity	分类操作单元 Operational Taxonomic Units (OTUs)	野外取样和室内分析 Field sampling and laboratory analysis	样地尺度 Plot
11	昆虫多样性 Insect diversity	种数和个体数 Number of species and individuals	野外取样和室内分析 Field sampling and laboratory analysis	样地尺度 Plot
12	鸟类的多样性 Bird diversity	种数和个体数 Number of species and individuals	野外观测 Field observation	景观尺度 Landscape
13	蝴蝶的多样性 Butterfly diversity	种数和个体数 Number of species and individuals	野外观测 Field observation	景观尺度 Landscape
14	蝗灾的状况 Locust outbreak	蝗虫个体的数量 Number of locust individuals	野外观测 Field observation	样地尺度 Plot
15	鼠害的状况 Rodent damage	鼠洞和土丘的密度 Density of rat holes and mounds	野外观测 Field observation	景观尺度 Landscape
16	净初级生产力 Net primary production	地上、地下净初级生产力 Aboveground and belowground net primary production	野外取样和室内分析 Field sampling and laboratory analysis	样地尺度 Plot
17	土壤碳、氮、磷储量 Soil carbon, nitrogen, phosphorus stocks	土壤容重、土壤碳氮磷含量 Soil bulk density and soil C, N, P content	野外取样和室内分析 Field sampling and laboratory analysis	样地尺度 Plot
18	水土保持力 Soil and water conservation	裸地面积、凋落物量及凋落物覆盖度、植被盖度 Bare soil proportion, litter mass and coverage, and vegetation coverage	野外观测、取样和室内分析 Field observation, sampling and laboratory analysis	样地和景观尺度 Plot and landscape scale
19	地下水供给 Groundwater supply	地下水水位及水质 Groundwater level and quality	野外测量、取样和室内分析 Field observation, sampling and laboratory analysis	景观到区域尺度 Landscape to regional
20	气象因子 Meteorological factors	降水、气温、年潜在蒸散量、年实际蒸散量、年总太阳辐射、年光和有效辐射、积温 Precipitation, temperature, annual potential evapotranspiration, annual actual evapotranspiration, annual total solar radiation, annual effective radiation, and annual accumulated temperature	气象站实测、模型插值 Meteorological station measurement and model interpolation	景观尺度 Landscape

表1 (续) Table 1 (continued)

序号 No.	监测项 Parameters	具体指标 Indicators	获取途径 Acquisition channels	空间尺度 Spatial scale
21	其他环境变化因子 Other environmental change factors	大气CO_2分压、氮沉降量、酸沉降量 CO_2 partial pressure, acid and nitrogen deposition	地面实测、模型计算和预测 Direct measurement and Interpolation	景观到区域尺度 Landscape toregional
22	土壤理化性质 Soil physical and chemical properties	土壤类型、质地、酸碱度、有机质含量、持水量 Soil type, texture, pH, organic matter content, water holding capacity	野外取样和室内分析 Field sampling and laboratory analysis	样地尺度 Plot
23	地形因素 Topography	坡向、坡度、地表起伏度、地表粗糙度 Aspect, slope, surface waviness and roughness	通过DEM数据计算获得 Derived from DEM data	样地和景观尺度 Plot and landscape
24	土地利用 Land use	土地利用类型、土地利用强度、土地利用历史 Types, intensity and history of land use	遥感、社调和文献检索 Remote sensing, social investigation and literature	景观到区域尺度 Landscape to regional
		家畜(牛马羊)粪便密度 Livestock (sheep, horse, cattle) manure density	野外观测 Field observation	景观尺度 Landscape
25	社会经济因素 Socio-economic factors	人口数量、生活来源、人均收入 Population, source of income, per capita income	社会调研和年鉴统计资料检索 Social investigation and annual books	区域尺度 Regional
26	景观因素 Landscape factors	生境破碎化程度 Degree of habitat fragmentation	遥感 Remote sensing	区域尺度 Regional
27	地史进化因素 Geohistory and evolutionary factors	地质历史和进化历史 Geological and evolutionary history	文献检索、谱系分析 Literature, phylogenetic analysis	区域尺度 Regional

建。然而该方法也有局限性: 一是对于监测指标的空间分辨率低于调查样点的粒度, 为使监测指标达到一定的精确度, 往往需要设置大量的野外监测点; 二是这种样点选取和布设的方法忽略了交通是否便利的问题, 野外调研难度大、代价高、可行性差。

综合考虑上述两种方法的利弊和我国国情, 我们提出了我国草地生物多样性监测的样点选取和布设方案: 首先, 按照系统布点原则, 将我国陆地生态系统分成100 km×100 km的方格, 这是因为空间上两点的气候条件具有明显差异的最小距离是100 km(O'Brien, 1993)。然后, 通过植被图、近年的高分辨率遥感图和行政区划图信息的整合, 在每个方格内综合考虑植被类型、遥感植被信息和空间位置(行政区域、交通便利程度)等信息, 选取适当数量的监测样点。每个方格内及相邻方格内的监测样点在空间上要尽量分散, 以覆盖较大的空间异质性。单个方格内监测样点数量越多, 多样性监测网络的精确度和辨识度就越高, 取样的代表性越强。但是, 由于人力物力投入的限制, 样点设置的数量可根据具体情况调整, 我们建议选取5–10个点为佳。

另外, 样点的设置还需考虑不同方格间地形因素的差异: 对于空间异质性大的方格可多设几个监测点, 而对于空间异质性较小的方格可少设一些监测点, 但数量差别不宜过大, 以保证监测点在大空间尺度上分布均匀。监测网络还应是开放的, 监测样点的数量可以通过实地考察调研以及知识经验的积累进行调整。按此方式, 整个网络监测点的布设在空间上既具有系统随机性, 又可确保每个监测点的区域代表性和整体方案的可行性。

除系统随机布设外, 监测样点还应包括在多样性保护和生态系统功能方面具有重要功能和意义的单元, 即保护区和具有重要生态服务功能的隐域性生境。从20世纪70、80年代至今, 我国已经陆续建立一批草地自然保护区, 但目前对于这些保护区生物多样性的监测和研究工作还相当薄弱。保护区的生物多样性监测和分析不仅是衡量多样性保护效果、指导多样性保护实践的重要依据, 同时也为评估人类活动干扰所导致的同类型生境中多样性的变化提供了重要的参考, 因而需加强长期连续监测。传统生态学研究大都以面积大、分布广的代表性植被类型作为研究对象, 而对于面积小、空间上相对隔离的隐域性生境关注较少。这些生境由于水分、养分条件好, 生产力较高, 具有丰富的生物多样性资源, 但同时又是人类活动干扰较为严重的区域, 因此也应该是草地生物多样性监测和保护重点考虑的对象。此外, 监测样点的选取要结合考虑生境的生态功能, 优先在具有重要生态系统服务功能的生态系统中设置监测样点, 例如湿地、河流源头地, 以及上文提到的隐域性生境。

根据上述原则及我国草地分布和利用情况, 我

们建议将野外调研分成四个部分逐步开展, 分别是: (1)我国重点牧区的11片连片草地; (2)青藏高原高寒草地; (3)荒漠和沙地; (4)湿地、河流源头地等具有重要生态学意义的生境及其他生物多样性较高的隐域性生境和天然草地自然保护区。

4.2 监测样地的确定

样地的精准定位、清晰界定和统一的调研方法是保证各个监测指标在不同的时空序列上具有可比性的关键因素。

(1)精准定位。目前的高精度手持GPS还无法十分精准地定位一个点, 误差一般在几米到十几米不等。为提高定位精度, 建议在每个调查样地的中心点埋设不锈钢金属地标, 通过金属探测器和高精度手持GPS的配合使用, 实现对每个调查样地中心点的精确定位。然后以该中心点为参照, 使用罗盘、测量绳和标杆, 准确确定样地内设置的所有样方和样线, 进而减少空间异质性所带来的误差。样地内样线样方定位的具体操作方法见5.1节野外考察工作流程。需要注意的是, 因为金属地标的面积、形状、重量都会对金属探测器的灵敏度造成影响, 根据我们过去几年的工作经验, 建议地标大小控制在500 g左右, 直径控制在10 cm左右, 埋设的深度在30–40 cm左右。

(2)空间尺度。包括两个方面: 一是调查取样的空间范围, 由于不同类型生物的分布范围和密度具有差别, 因此需要设置不同的空间观测范围以提高检出的概率。例如, 目前国际上对鸟类、蝴蝶多样性监测多采用1 km^2的样地作为一个基本调查单元(如北美和英国繁殖鸟类多样性监测网络); 对于森林(乔木)多样性的监测一般在几十公顷(一般小于100 ha)的尺度上进行, 如巴拿马热带雨林和我国森林多样性监测大样地(Hubbell & Foster, 1983; 马克平, 2011); 而对于灌木和草本植物多样性的调查单元面积一般在100 m^2以下(方精云等, 2009)。二是调查取样的面积和空间分布。调查空间分布相同而取样面积不同则大样方调查获取的物种数会高于小样方调查获取的物种数; 如果取样面积相同而调查空间分布不同, 空间异质性可能导致调查在空间上分布越离散的物种多样性越高, 这两种情况均会导致监测数据不具可比性。为保证各个监测指标取样的代表性, 并确保不同样地间以及同一样地不同时间序列上的监测数据具有可比性, 需要根据不同指标设置不同的调查空间范围, 并对既定空间范围内调查样方样线的空间分布和大小进行统一的设置。

目前, 已有的多样性监测网络大都以1 km^2为基本调查单元, 且侧重于动物种类和数量的监测, 对于植物特别是草本植物种类和数量的监测相对不足, 大都无法满足研究所需的调查精度。例如处于国际领先水平的瑞士生物多样性监测网络, 对于草本植物, 在1 km^2内仅有1个面积为10 m^2的样方(Hintermann *et al.*, 2002)。而对于植物群落而言, 1 km^2通常会跨越不同的生境, 1个10 m^2样方的数据对于1 km^2景观单元的植物物种组成和多样性并不具备代表性, 并且基于单个样方的调查数据也无法反映植物群落的空间变异。根据我们2012年在内蒙古地区开展的草地生物多样性野外考察经验, 发现以1 km^2作为一个基本调查单元进行动植物多样性调查的确耗时过多, 无法在面上展开野外工作, 因而将景观尺度多样性调查的空间范围缩减一半, 定为500 m × 500 m, 样地尺度的空间范围定为100 m × 100 m。

尽管尺度是生态学上一个十分重要的概念, 且目前的生态学研究中学者们在理论层面对于群落、生态系统、景观等组织层次大都有比较一致的认识, 但在实践调查层面, 对于每个组织层次的空间范围和边界却并没有很清晰的界定(Whittaker *et al.*, 2001)。目前, 比较常用的解决办法是对空间调查的范围和粒度进行清晰地定义。本方案中将0.25 km^2作为一个基本景观单元, 0.01 km^2作为一个基本样地单元。每个基本景观调查单元的样方、样线布设方法如图1所示, 图中两条垂直实线为样线, 黑色实线方格和虚线圆圈为草本和灌木样方, 带点的实线圆圈为种–面积曲线和草本植物点格局调查的空间位置, 虚线正方形表示从100 m × 100 m到500 m × 500 m五个空间尺度。

5 野外考察的工作流程和注意事项

根据上述监测指标体系及实施方案, 2012年3–8月, 由中国科学院植物研究所植被与环境变化国家重点实验室草原生态系统功能生态学研究组筹划并组织了我国首次草地植物多样性野外实地调研工作。考察人员包括研究人员、博士和硕士研究生、动植物分类学专家和在校大学生志愿者等48人, 历时43天, 共完成内蒙古地区142个草地生物

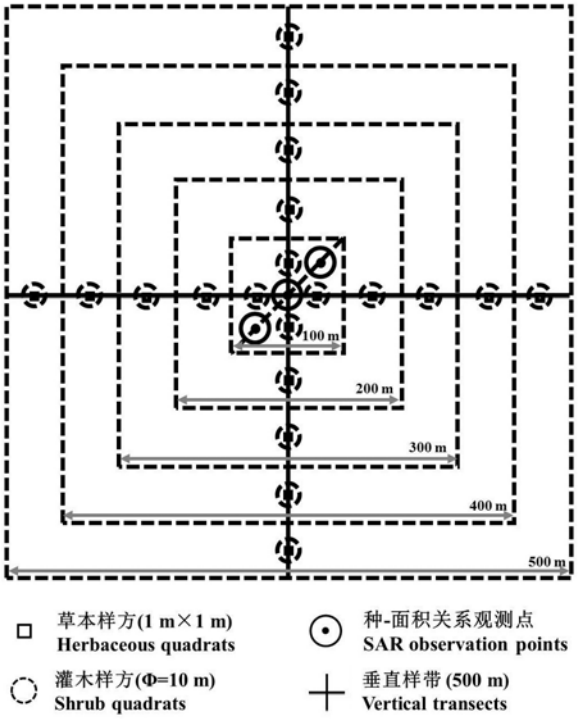


图1 单个监测样地上样线、样方、种–面积关系及点格局调查点的空间布局示意图。
Fig. 1 Layout of the transects, quadrats, species–area relations and point pattern observation positions within each monitoring plot.

图2 2012年内蒙古草地生物多样性野外考察样点分布图
Fig. 2 Grassland biodiversity surveyed plots from the field campaign of 2012 in Inner Mongolia

多样性监测样点的调研(图2)。下面我们以此次考察实践为例，简要介绍草地生物多样性野外考察的工作流程和注意事项。

5.1 野外考察工作流程

野外考察工作开展之前，首先要确定计划考察样点的总数，然后根据考察样点的空间位置结合Google地图信息规划考察路线和食宿地点，制定详细的野外考察工作计划，并准备考察需要的各种实验工具和耗材。野外考察开始前需对调研队伍进行动植物分类及具体调查技术的培训。考察流程如下:

第一步，将事先规划好的路径信息导入GPS，寻找和定位监测样地。

第二步，到达样地后，根据样地的地形、植被和土地利用情况，确定考察的中心点，并通过标杆进行标记。样地中心点的确定要尽量保证500 m×500 m调查样地在空间上是连续分布的，并且100 m×100 m样地位于所调查植被的代表性地段。

第三步，以中心点标杆为依据，通过罗盘(确定方向)和米绳(测量距离)确定东南西北4条250 m的样线(每25 m插1根旗杆)，以及位于东北和西南对角线上距离中心点45 m的两个种–面积和点格局考察点的位置，并用旗杆作标记；同时，进行植物多样性调查的人员开始种–面积曲线的调查和记录。

第四步，植物、鸟类、蝴蝶多样性相关调查人员从中心点开始沿标记好的样线开始样带考察和记录工作，昆虫、土壤微生物多样性、点格局及植物性状调查人员开始在样地尺度上开展相关实验布设和调查取样工作；与此同时，野外调查工作组组长进行样地中心点地标的埋设、样地位置及天气信息的记录、景观和工作照片的拍摄，并协调各组之间的工作；另外，社调人员开始在调查样地周边村落进行社会调研和地下水位的测量和取样工作。

第五步，完成调查取样后，收集、整理并清点标杆、旗杆、样方、剪刀等实验工具，赶赴下个考察点继续当天的考察工作。

第六步，完成当天野外工作任务返回驻地后，须对当天调查的数据、照片和标本进行整理存档并检查完成质量，对昆虫样品进行分类和鉴定，并将植物性状样品转交内业人员进行室内测定。

第七步，样地考察和社调人员开始新一轮的野外调查和取样工作，内业人员进行植物性状的测定，循环往复，从一个驻地转移到下一驻地，直到完成当年的考察任务。

第八步，野外考察工作结束后，须尽快对采集的植物、土壤和地下水样品进行室内分析和测定，

图3　2012年内蒙古草原生态系统定位研究站(IMGERS)周边的一个监测样地内各植物物种的频度和排序

Fig. 3　Rank of the plant species according to frequency in a surveyed plot for monitoring grassland biodiversity around the Inner Mongolia Grassland Ecosystem Station (IMGERS) of the Chinese Academy of Sciences in 2012

以及数据的录入和分析。注意要妥善保管原始数据、照片资料和野外工作笔记, 因为这些资料是录入数据质量控制的重要依据。

5.2　数据整理分析

数据的集成分析和相关成果的整理是本方案中草地生物多样性研究部分的工作重点。下面我们以内蒙古草原生态系统定位研究站(IMGERS)周边的一个监测样地为例, 简单展示各类数据的处理分析方法及初步的统计结果。

案例分析样地位于116°40'33.330" E、43°37'49.416" N, 海拔1,182.9 m。年均降水量300.9 mm, 年均气温3.38°C, 年潜在蒸发量590.2 mm, 年总太阳辐射5,406 mJ/m^2, 年光合有效辐射753.54 mJ/m^2, 零摄氏度以上积温2,776.1°C·日。调查样地为全年放牧地。根据家畜粪斑密度判断, 该样地为牛羊混牧, 羊粪和牛粪粪斑的平均密度分别为5.19个/m^{2}和0.19个/m^2。样地没有发生明显鼠害, 两条500 m×10 m样带上共发现鼠洞9个、鼠丘2个。该样地植物群落以小叶锦鸡儿(*Caragana microphylla*)、木地肤(*Kochia prostrata*)、糙隐子草(*Cleistogenes squarrosa*)、双齿葱(*Allium bidentatum*)、冰草(*Agropyron cristatum*)、冷蒿(*Artemisia frigida*)等多年生植物和刺穗藜(*Chenopodium aristatum*)、猪毛菜(*Salsola collina*)等一年生植物为主(图4), 植被平均盖度65%, 裸地面积约占20%。

植物样方、样带及种–面积调查数据, 可以用于分析不同空间尺度上植物群落α、β、γ多样性的变化规律及其空间尺度依赖性, 构建不同空间尺度上及不同调查粒度下的种–面积关系曲线。而结合面上多点的调查数据, 以及人类活动干扰和环境因子数据, 可进一步分析草地植物多样性的空间分布格局和驱动因素, 以及种–面积关系的时空尺度依赖性和决定因素。

我们通过对前文样地的调查数据整理计算发现: (1)在500 m×500 m的空间尺度上, 基于20个样方调查数据得出, 该样地植物的α多样性为10, β多样性约为3.6, γ多样性为36, 而基于两条垂直500 m×5 m样带(每100 m×5 m为一个基本调查单位)的调查数据得出, 该样地植物的α多样性为24, β多样性约为2.375, γ多样性为57; (2)在100 m×100 m的空间尺度上, 基于3个种–面积调查数据, 该样地植物的α多样性为27, β多样性约为1.481, γ多样性为40。

通过3组数据的对比可以发现: (1) α多样性随取样面积或者调查的粒度增加而增大, β多样性则表现出相反的变化趋势, 这说明随着取样面积的增大, 群落的相似度在逐渐增加; (2) 基于25 ha测得的β多样性明显高于基于1 ha测得的β多样性, 是何种因素驱动植物群落在如此小的空间尺度上(500 m×500 m)发生变化？其内在机制有待进一步探讨。

通过种–面积调查数据的计算分析我们发现, 即使在1 ha的空间尺度上, 基于不同取样点构建的种–面积关系也存在明显差异(图4)。根据图4中d、e、

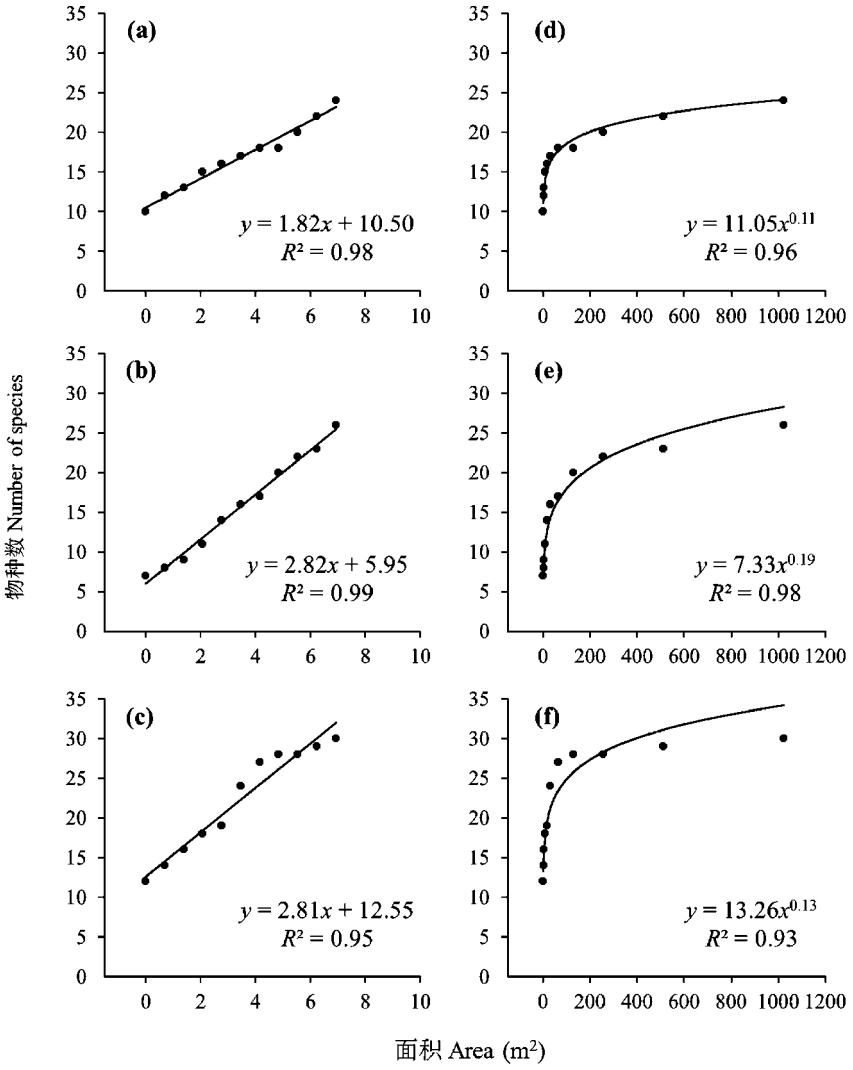


图4 2012年内蒙古草原生态系统定位研究站(IMGERS)周边的一个监测样地植物物种基于调查取样面积对数转换值(a–c)和实际调查取样面积(d–f)的种–面积关系

Fig. 4 Species–area relationship of the plant species based on both logarithm transformed area (a–c) and actual investigation area (d–f) from a grassland biodiversity monitoring plot around the Inner Mongolia Grassland Ecosystem Station (IMGERS) of the Chinese Academy of Sciences in 2012

f各自的曲线方程，我们计算获得1 ha和25 ha样地的物种数分别为31、44、46和45、83、72，这与样带调查所获取的1 ha和25 ha样地的物种总数35和57相比均有较大差异，而景观尺度上(25 ha)预测值和实测值的差别则更为显著。这种差异可能主要是由两方面的原因所致：一是基于小空间尺度获取的种–面积关系对较大空间尺度多样性的预测并不适用；二是样带调查本身有可能低估了景观尺度上的植物多样性。但真正的原因还有待于进一步考证。

对蝴蝶和鸟类的分析结果如下：(1)该样地有7种蝴蝶，共计87只，以玄灰蝶(*Tongeia fischeri*)和牧女珍眼蝶(*Coenonympha amaryllis*)为主，二者合计占据了整个蝴蝶群落的85%(图5A)；(2)鸟类共计7种15只，以蒙古百灵(*Melanocorypha mongolica*)为主，戴胜(*Upupa epops*)、家燕(*Hirundo rustica*)和麻雀(*Passer montanus*)等伴人鸟只统计种类，没有计数(图5B)。

生物多样性和生态系统功能是生态学领域的研究热点之一，也是本监测方案拟研究的关键问题之一。本方案计划通过对各类生态系统健康指标及

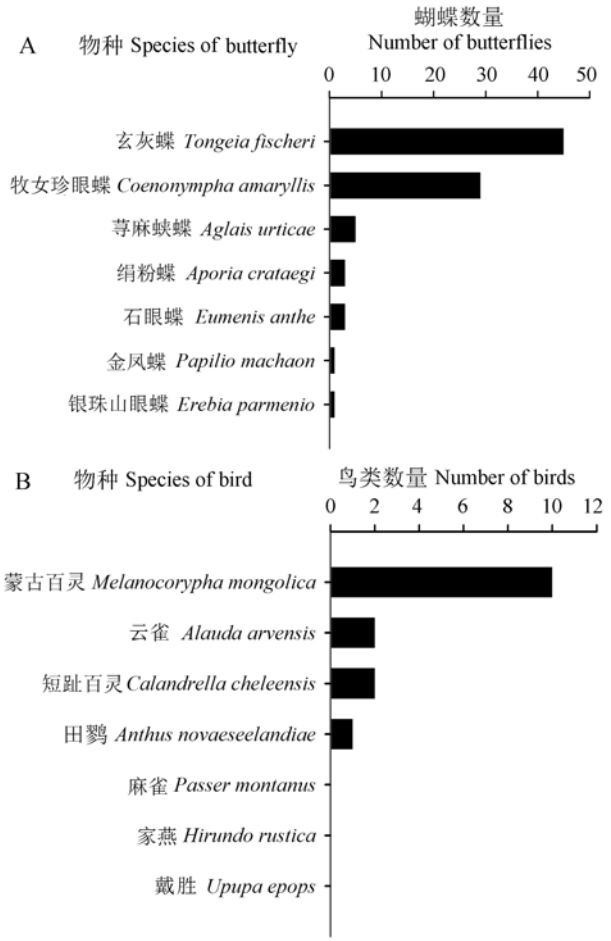


图5　2012年内蒙古草原生态系统定位研究站(IMGERS)周边的一个监测样地内蝴蝶(A)和鸟类(B)的种类、数量和排序
Fig. 5　Rank of the butterfly (A) and bird (B) species according to numbers in a grassland biodiversity monitoring plot around the Inner Mongolia Grassland Ecosystem Station (IMGERS) of the Chinese Academy of Sciences in 2012

关键生态系统功能的同步调查, 一方面从大的空间尺度上分析二者之间的联系和机制, 另一方面通过各个样地长期连续的监测, 沿时间序列分析草地多样性及其主要服务功能在人类活动干扰和全球气候环境变化影响下的响应、变化趋势及驱动力。上面简单展示了几个核心调查指标的结果, 希望对理解本监测方案有所帮助。

致谢: 特别感谢马克平研究员对本项工作的大力支持, 感谢雷富民研究员、周红章研究员和王艳芬教授对方案提出了宝贵建议, 感谢刘书润教授、杨贵生教授、郝树广博士、于晓东博士、陈彬博士对2012年青年志愿者培训和野外考察工作的支持, 感谢王扬、黄银、蒋宏志和所有来自高校在校大学生青年志愿者对2012年草地生物多样性野外考察工作的参与和支持, 感谢程军回、李文怀对该方案谱系分析和点格局分析方法的总结。

参考文献

Adler PB, Lauenroth WK (2003) The power of time: spatiotemporal scaling of species diversity. *Ecology Letters*, **6**, 749–756.

Auerswald K, Wittmer MHOM, Bai Y, Yang H, Taube F, Susenbeth A, Schnyder H (2012) C_4 abundance in an Inner Mongolia grassland system is driven by temperature–moisture interaction, not grazing pressure. *Basic and Applied Ecology*, **13**, 67–75.

Blunden J, Arndt DS (2013) State of the climate in 2012. *Bulletin of the American Meteorological Society*, **94**, S1–S258.

Briske DD, Fuhlendorf SD, Smeins FE (2005) State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology and Management*, **58**, 1–10.

Chase JM, Leibold MA, Downing AL, Shurin JB (2000) The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*, **81**, 2485–2497.

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization.*The American Naturalist*, **111**, 1119–1144.

Connor EF, McCoy ED (1979) The statistics and biology of the species–area relationship. *The American Naturalist*, **113**, 791–833.

de Bello F, Lavorel S, Gerhold P, Reier Ü, Pärtel M (2010) A biodiversity monitoring framework for practical conservation of grasslands and shrublands. *Biological Conservation*, **143**, 9–17.

Dengler J (2009) A flexible multi-scale approach for standardised recording of plant species richness patterns. *Ecological Indicators*, **9**, 1169–1178.

Department of Animal Husbandry and Veterinary of the Ministry of Agriculture of the People's Republic of China (中华人民共和国农业部兽医司), General Station of Animal Husbandry and Veterinary of the People's Republic of China (全国畜牧兽医总站) (1996) *Rangeland Resources of China* (中国草地资源). China Science and Technology Press, Beijing. (in Chinese)

Fang JY (方精云), Wang XP (王襄平), Shen ZH (沈泽昊), Tang ZY (唐志尧), He JS (贺金生), Yu D (于丹), Jiang Y (江源), Wang ZH (王志恒), Zheng CY (郑成洋), Zhu JL (朱江玲), Guo ZD (郭兆迪) (2009) Methods and protocols for plant community inventory. *Biodiversity Science* (生物多样性), **17**, 533–548. (in Chinese with English abstract)

Gao Q, Yu M, Yang X (2000) An analysis of sensitivity of terrestrial ecosystems in China to climatic change using spatial simulation. *Climate Change*, **47**, 373–400.

Gilbert G, Gibbons D, Evans J (1998) *Bird Monitoring*

Methods: A Manual of Techniques for Key UK Species. RSPB, Sandy, UK.

Hintermann U, Weber D, Zangger A, Schmill J (2002) *Biodiversity Monitoring in Switzerland BDM*. Swiss Agency for the Environment, Forests and Landscape (SAEFL), Berne.

Hubbell SP, Foster RB (1983) Diversity of canopy trees in a neotropical forest and implications for conservation. In: *Tropical Rain Forest: Ecology and Management* (eds Sutton SL, Whitmore TC, Chadwick AC), pp. 25–41. Blackwell Scientific Publication, Oxford.

Krebs CJ (1991) The experimental paradigm and long-term population studies. *Ibis*, **133**, 3–8.

Lan ZC, Bai YF (2012) Testing mechanisms of N-enrichment-induced species loss in a semiarid Inner Mongolia grassland: critical thresholds and implications for long-term ecosystem responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 3125–3134.

Landsberg J, Crowley G (2004) Monitoring rangeland biodiversity: plants as indicators. *Austral Ecology*, **29**, 59–77.

Ma KP (马克平) (2011) Assessing progress of biodiversity conservation with monitoring approach. *Biodiversity Science* (生物多样性), **19**, 125–126. (in Chinese)

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355–364.

O'Brien EM (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography*, **20**, 181–198.

Olsen AR, Sedransk J, Edwards D, Gotway CA, Liggett W, Rathbun S, Reckhow KH, Young LJ (1999) Statistical issues for monitoring ecological and natural resources in the United States. *Environmental Monitoring and Assessment*, **54**, 1–45.

Pellikka J, Rita H, Lindén H (2005) Monitoring wildlife richness: Finnish applications based on wildlife triangle censuses. *Annales Zoologici Fennici*, **42**, 123–134.

Pereira HM, Ferrier S, Walters M, Geller GN, Jongman RHG, Scholes RJ, Bruford MW, Brummitt N, Butchart SHM, Cardoso AC, Coops NC, Dulloo E, Faith DP, Freyhof J, Gregory RD, Heip C, Höft R, Hurtt G, Jetz W, Karp DS, McGeoch MA, Obura D, Onoda Y, Pettorelli N, Reyers B, Sayre R, Scharlemann JPW, Stuart SN, Turak E, Walpole M, Wegmann M (2013) Essential biodiversity variables. *Science*, **339**, 277–278.

Plattner M, Birrer S, Weber D (2004) Data quality in monitoring plant species richness in Switzerland. *Community Ecology*, **5**, 135–143.

Ren HY, Schönbach P, Wan HW, Gierus M, Taube F (2012) Effects of grazing intensity and environmental factors on species composition and diversity in typical steppe of Inner Mongolia, China. *PLoS ONE*, **7**, e52180.

Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon*, **21**, 213–251.

Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.

Wittmer MHOM, Auerswald K, Bai Y, Schäufele R, Schnyder H (2010) Changes in the abundance of C_3/C_4 species of Inner Mongolia grassland: evidence from isotopic composition of soil and vegetation. *Global Change Biology*, **16**, 605–616.

World Wildlife Fund (WWF) (2013) Biodiversity: the magic of our planet! How many species are we losing? http://wwf.panda.org/about_our_earth/biodiversity/biodiversity/ (2013.11.13)

Wu JG, Loucks O (1992) *Grasslands and Grassland Sciences in Northern China.* U.S. National Research Council edition. National Academy Press, Washington, DC.

Xiao X, Ojima DS, Parton WJ, Chen Z, Chen D (1995) Sensitivity of Inner Mongolia grasslands to climate change. *Journal of Biogeography*, **22**, 643–648.

Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution*, **16**, 446–453.

Yu FF, Price KP, Ellis J, Shi PJ (2003) Response of seasonal vegetation development to climatic variations in eastern central Asia. *Remote Sensing of Environment*, **87**, 42–54.

(责任编委: 贺金生　责任编辑: 周玉荣)

附录I　草地生物多样性监测各指标的野外调研方法和数据获取途径

Appendix I　Indicators and methods for monitoring China grassland biodiversity

http://www.biodiversity-science.net/fileup/PDF/w2013-134-1.pdf

附录I　草地生物多样性监测各指标的野外调研方法和数据获取途径
Appendix I　Indicators and methods for monitoring China grassland biodiversity

一、植物群落物种组成和多样性

1–3　植物群落的物种组成、相对多度及冠层盖度

调查时间和频度：在植物生长旺盛期(6–8月)各地区打草之前进行调查；每5年进行1次。

调查方法：在每个调查样点，首先按照正文中图1所示，确定草本和灌木样方的中心点位置。然后以该点为中心设置1 m×1 m草本样方，目测植物群落的冠层盖度，记录样方内出现的所有植物物种的学名，并对每个物种的株丛数、株丛大小(丛茎和分蘖数)、营养枝和生殖枝高度等几个指标进行测量和记录。如果调查样地内有灌木，则须以每个中心点为圆心设置半径为5 m的灌木样方，然后调查并记录样方内出现的所有灌木的种类、数量、冠幅和高度。植物的相对多度用密度或基于密度、高度、丛幅计算获得的综合优势度来表征。

注：(1)草本样方清查之前须对其进行拍照并命名存档，以备后用；(2)如果样方的中心点恰好在灌木丛里，草本样方的设置须做适当的调整，可将其设置在离中心点最近的以草本植物为主的地方，灌木样方仍以该点为中心，无需调整；(3)丛生草本植物的丛径要从茎的基部测量，其丛大小、高度以及灌木的冠幅、高度均选代表性植株进行测定。

4　种–面积关系

调查时间和频度：与植物样方调查同步进行。

调查方法：在每个调查样点，首先按照图1所示，以样地中心点为参照，通过罗盘和测量绳的结合使用，确定样点中心点外的另外两个种–面积调查中心点(与样地中心点的距离为45 m)的位置并做标记。然后，以种–面积调查的中心点为圆心，采取同心圆的方式对种–面积关系进行调查。此方法仍然基于巢式样方法(Bonham, 1989)，但为方便野外调查，我们稍作调整，以不断扩大同心圆直径的方式来增加调查面积。具体的调查面积仍然与巢式样方取样面积相对应，分别为2^0、2^1、2^2、…、2^{10} m^2。在此基础上，按照巢式样方调查面积扩增原则，我们新增了4个更小的调查面积，分别为2^{-1}、2^{-2}、2^{-3}、2^{-4} m^2。野外观测时，我们以事先在测量绳上长度为0.1410、0.1995、0.2821、0.3989、0.5642、0.7979、1.1284、1.5958、2.2568、3.1915、4.5135、6.3831、9.0270、12.7662、18.0541 m处做好明显标记，然后以测量绳为半径，以种–面积调查中心点为圆心，调查并记录随半径增加新增调查面积内出现的所有新物种。

5　物种的点格局分析

调查时间和频度：与植物样方调查同步进行。

调查方法：在每个种–面积关系调查中心点的附近设置1个正南正北的2.5 m×2.5 m点格局调查样方。将事先制作的进行了25等分的2.5 m×2.5 m样方框置于草本植物之上，调整框的四角使其四边分别指向东南西北四个方向，并固定好框的四角，然后从西南角的0.5 m×0.5 m样方开始拍照，依次向东拍摄，到最后一个样方后，从其上方折返向西拍摄，依次类推，对25个0.5 m×0.5 m的样方进行拍照存档。每个样地设置3个点格局分析样方，野外拍摄时从北边的样方开始，然后是中间的样方，最后是南边的样方，以确保照片的编号不会出错。

注：(1)拍摄的照片需要进行植物物种的鉴定和空间位置读取等后期工作，因此照片一定要足够清晰；(2)拍摄时从样方的正上方垂直拍摄，要避免拍摄者的阴影出现在所拍摄的样方内；(3) 当天获取的照片数据要当天导入电脑并整理编号[样地号+空间位置(北、中、南)+照片编号(1–25，起始于西南角的一张为1，然后按照拍照顺序依次类推)]，以一个样地一个文件夹的方式存档。

格局照片数据提取方法：植物坐标位置的提取使用AutoCAD2004软件完成。(1)首先将拍摄的照片以光栅图像格式导入到软件中，将左下角定为插入点，并且以1:1的大小插入图片；(2)将图片调整至适合窗口大小，通过UCS命令把坐标原点重新定位到样方的左下角；(3)通过功能栏中的坐标位置标注功能，对植物的空间位置进行确定，标注时以植物的

中心位置作为其坐标; (4) 最后, 通过输出功能将所有标注的X、Y坐标值导出到Excel表格中, 进行后续的数据分析。

点格局分析方法: 主要是通过Programita软件完成(Wiegand & Moloney, 2004)。采用软件中的*O-ring O(t)*函数进行统计分析, 这种方法可以消除*Ripley K(t)*函数分析方法中存在的积累效应(Ripley, 1981), 理论上可以提高格局分析的精确度。

针对种群分布格局分析, 其定义式为:

$$O(t) = \lambda g(t) \tag{1}$$

其中, $g(t) = \frac{dK(t)}{dt} / 2\pi(t)$。在完全随机的情况下 $O(t) = \lambda$; 若 $O(t) > \lambda$, 表示空间聚集; 而当 $O(t) < \lambda$ 时, 表示空间均匀分布。

针对种间或种内关系分析, 其定义式为:

$$O_{12}(t) = \lambda_2 g_{12}(t) \tag{2}$$

其中, $g_{12}(t) = \frac{dK_{12}(t)}{dt} / 2\pi(t)$。若 $O_{12}(t) = \lambda_2$, 说明两个种在该尺度下无关联; 若 $O_{12}(t) > \lambda_2$, 表明二者正关联; 当 $O_{12}(t) < \lambda_2$ 时, 表明二者负关联。

6 植物功能性状

调查时间和频度: 与植物样方调查同步进行。

调查指标和方法: 植物功能性状数据获取包括两部分: 一部分是野外直接测定, 包括植株高度、茎叶比、比叶面积、单叶重、单叶面积、叶干物质含量、叶氮含量、叶磷含量、叶型(周长/面积比); 另一部分通过文献查阅获取, 包括生长型、生活史策略(多年生/一二年生)、光合途径(C_3/C_4/CAM)、固氮能力(有或无)、克隆生长特性、根系结构(须根或轴根)和子叶类型(单子叶或双子叶)。

植物功能性状测定集中在样地尺度上进行。在每个调查点随机选取优势种和常见种个体30个, 贴地面剪取每个植株的地上部分, 然后卷入湿毛巾放置到冷藏箱内以转移到室内进行处理。内业人员将取回的植物样品在室内逐个进行茎叶分拣、叶片图像扫描, 并称量鲜重、烘干(60°C, 24 h)称干重并做记录。称完干重的样品以物种为单位混合为一个样品, 并将每种植物的茎叶分装到信封内保存, 以备后期进行植物氮磷元素含量的测定。为保证空间取样范围的一致性, 植物性状测定的个体分别集中在种–面积和点格局测定的3个点上进行, 每个点剪取10个个体。叶片性状测定可参考Cornelissen等(2003)编写的植物功能性状测定手册。

注: (1)用于功能性状测定的植株需区分营养株和繁殖株, 因为二者的茎叶比有极大差异, 另外, 对繁殖株所处的物候期要单独记录; (2)进行植物干物质含量测定时须保证植物吸水时间不少于6 h, 以确保植物叶片达到水分饱和; (3)因植物叶片存在叶龄差异, 建议将叶片简单分为幼叶、绿叶(最上部充分展开叶到最下部全绿叶)、老叶(部分干枯的叶片)、枯叶(完全干枯的叶片)4个龄组; 绿叶用于叶面积测定; 各部分叶片须单独计数、称重、分装, 以备后期单独进行元素含量测定。

7 植物种库

调查时间和频度: 与植物样方调查同步进行。

调查方法: 在每个调查样点, 首先按照图1所示, 以样地中心点为参照, 通过罗盘和测量绳确定东南西北4个方向上的4条250 m样线, 每隔25 m插1根标杆。然后从中心点开始调查, 并记录每条样线上左右5 m范围内出现的所有植物物种, 按0–50 m、50–100 m、100–150 m、150–200 m、200–250 m分段记录数据。

注: (1)当调查样地有明显地形起伏时, 要对样线的方向进行调整, 确保有一条样线沿坡面布设; (2)样带调查的主要目的是进行景观尺度上种库的调查, 因此如果发现样带调查范围外(5 m外)有新植物种出现也须记录。

8 植物多样性

数据获取方法: 基于群落清查数据计算获得。植物多样性包括物种多样性、功能多样性、谱系多样性3个方面。

(1)物种多样性。包括物种丰富度、均匀度、综合多样性指数、α、β和γ多样性。物种丰富度(*S*)即为群落清查样方中出现的植物物种的总数。物种均匀度(*E*)以Pielou均匀度指数(Pielou, 1975)表征, 物种多样性以Shannon-Wiener多样性指数(*H*)表征。α多样性等于特定空间范围内所有调查样方的物种丰富度的均值, γ多样性为这些样方内所出现的所有不同物种的总和, β多样性等于γ/α或者γ–α。

Pielou均匀度指数和Shannon-Wiener多样性指数的计算公式分别如下:

$$E = H / Ln(S) \tag{3}$$

$$H = -\sum_{i=1}^{S} P_i Ln(P_i) \tag{4}$$

式中，其中 $P_i = \frac{N_i}{N}$，为样区内第i类植物的个体数(N_i)与群落所有植物的总个体数量(N)的比值(Shannon, 1948; 马克平和刘玉明, 1994)。

(2)功能多样性。目前关于物种功能多样性的指标众多，按测度的方法大致可以归为3类：基于植物功能性状数值(trait values)的功能多样性直接测度；基于距离矩阵(distance matrix)的功能多样性测度；基于功能系统树(functional dendrogram)的功能多样性测度(Petchey *et al.*, 2009)。基于样方调查数据和植物功能性状数据，通过免费开源软件Fdiversity可以很方便快捷地实现对各类功能多样性指标的计算，具体计算方法请参考文献Casanoves等(2011)。

(3)谱系多样性。谱系多样性整合了物种的进化信息，其值等于群落内物种间的谱系距离总和(Srivastava *et al.*, 2012)。谱系多样性常用的指数有：谱系α多样性(群落内进化亲缘关系)、谱系β多样性(群落间进化亲缘关系)、谱系丰富度和谱系均匀度等(Kembel *et al.*, 2010)。计算时，首先根据被子植物分类系统，对物种名称进行核对和正确分类(Bremer *et al.*, 2009)；其次，将核对好的植物名称以科/属/种的顺序排列，通过在线Phylomatic软件(http://phylodiversity.net/phylomatic/ html/pm2_form.html)生成相关物种的谱系树；然后，通过Phylocom软件中的BLADJ运算模块，对已生成的谱系树的进化枝长进行估算(Webb *et al.*, 2008)；最后，将带有进化枝长估算的谱系树，导入R软件，通过picante包可计算出谱系α多样性、谱系β多样性(Kembel *et al.*, 2010)。

二、生态系统健康及关键生态系统功能

9 哺乳动物多样性

调查方法：哺乳动物多样性拟通过红外相机陷阱(camera trapping)法和社会调研两种方法进行调查。红外相机陷阱法是目前大型哺乳类动物种类和数量的监测中较为先进的方法(Yasuda, 2004)。但由于相机在野外比较容易丢失，使用该方法进行哺乳动物多样性监测局限于管理较好的草地自然保护区内。保护区内红外相机的具体设置方法可参考文献Yasuda(2004)。由于红外相机一旦装好后，只需定期取数据和更换电池，因此调查的时间和频度可根据实际情况进行调整。原则上，监测时间越连续，监测数据越可靠，价值越高。

社会调研与野外样地考察可结合进行，主要是针对珍稀、濒危、受威胁的保护动物的有无进行问卷调查。在每个植物多样性调查样点周边按照不同年龄段(20、30、…、70岁)，每个年龄段选取1–3个当地牧户作为社调对象。然后通过问卷的方式，了解当地在不同时间段上大型野生哺乳动物的种类和丰富度的状况。

10 微生物多样性

调查时间和频度：与植物样方调查同步取样。

调查方法：用于土壤微生物多样性测定的土壤样品在1 ha样地内的4个植物样方中采集。为增加样品的代表性，每个样方内用土钻，钻取0–10 cm、10–20 cm、20–40 cm 3个土层，每个土层取5钻土壤样品。将每层的5钻土样充分混匀，利用4分法取出足量样品放置于冷藏箱转运到实验室冷冻保存，以备后期土壤微生物多样性测定。

微生物多样性测定采用目前最为先进的宏基因组学(metagenomics)方法，从土壤样品中提取基因组DNA，通过第二代高通量测序技术直接对土壤样品中所提取出来的基因片段进行测序分析。然后，将所得序列(通常为16S/18S rRNA等兼具保守及高变特性的序列)与专业数据库(Silva、RDP等)进行比对，得出样品中所含物种的信息，并通过对所得序列(通常为16S/18S rRNA等兼具保守及高变特性的序列)进行进一步的聚类，得到相应的分类操作单元(OTUs)。OTUs的数量即为微生物多样性的表征指标。具体的土壤样品DNA提取和基因序列的分析方法参见Delmont等(2011)。

11 昆虫多样性

调查时间和频度：与植物多样性调查同步。

调查指标和方法：昆虫多样性调查分为两部分：一部分与蝗虫数量的调查相结合进行，另一部

分专门针对步甲进行调查。与蝗虫数量调查相结合的部分将在蝗灾状况调查中进行详述，这里仅介绍步甲的野外取样调查方法。地栖型鞘翅目步甲的种类和数量的调查采用常规的陷阱诱捕法(Greenslade, 1964)，调查范围在样地(1 ha)尺度上进行。野外调查时在东南西北4条样线的5 m、15 m、25 m、35 m、45 m处，将高10.4 cm、口径7 cm的玻璃罐头瓶埋入地表下，瓶口与地面齐平。24 h后收集玻璃罐头瓶中诱捕到的步甲并带回驻地进行种类鉴定和数量统计并记录。为防止小型哺乳动物和两栖动物掉入陷阱，可在瓶口覆盖具13 mm×20 mm筛眼的筛网。

12　鸟类的多样性

调查时间和频度：与植物多样性调查同步。

调查方法：繁殖鸟类的种类和数量调查采用样带法，具体方法参考英国环境变化监测网络关于鸟类监测的草案(UK-ECN Birds Portocols)和北美繁殖鸟类监测网络(North American Breeding Birds Survey)的鸟类监测的方法体系。野外观测时，沿东西南北4条250 m样线，以均匀的步速，识别和记录所有看到和听到的鸟类的种类和数量。野外观测须对每条样线调查的起止时间、发现鸟类时观测者所处样线的位置以及鸟类距离观测者的距离等信息进行记录。4条样线的总调查时间应控制在1 h左右。鸟类距观测者距离分为4个类别：25 m范围内、25–100 m范围内、100 m以外以及飞行中的鸟类。

13　蝴蝶的多样性

调查时间和频度：与植物多样性调查同步。

调查方法：蝴蝶多样性的调查同样采取样带法，参考英国蝴蝶多样性监测方案(United Kingdom Butterfly Monitoring Scheme)和英国环境变化监测网络(UK-Environmental Change Network)确立的蝴蝶监测草案。野外观测时，沿东南西北4条样线，按照0–50 m、50–100 m、100–150 m、150–200 m、200–250 m分段记录样线左右各5 m范围内出现的所有蝴蝶种类和数量，以及发现蝴蝶时观测者所处的样线位置和蝴蝶距离样线的垂直距离。每条样线的调查时间控制在15 min左右，4条样线合计控制在60–90 min内。无法直接识别的蝴蝶可先用捕网抓捕，对照蝴蝶图鉴进行种类鉴定。另外，野外观测时需对每条样线调查的起始时间进行记录。

14　蝗灾的状况

调查时间和频度：与蝴蝶多样性调查同步。

调查指标和方法：蝗虫的种类繁多，并且不同种类有很明显的时间上的生态位分化，在单个时间点上捕获的蝗虫通常是很多不同龄期的混合体，种类难以鉴定。因此，我们建议蝗灾的状况仅以蝗虫的数量来表征，野外调查仅对不同龄期蝗虫的数量进行调查和分析，不进行种类鉴定。在蝗虫数量调查的同时进行昆虫多样性调查。

蝗虫数量和昆虫多样性的调查采取扫网法，在样地尺度的4条50 m样线上，每条样线上两步扫一网(一个往复)，合计扫25网。将搜集到的所有昆虫装到带有编号的网袋中置于工业酒精中暂存。回到驻地后，将当天扫集到的昆虫样品进行处理，分离出所有蝗虫，按龄期计数并记录，其他类型昆虫仅记录种类，不进行数量统计。无法识别的昆虫通过装有甲醛的塑管进行保存，留待后期鉴定。

注：(1)标准扫网直径为33 cm，洞口到网底为66 cm，网眼40目，手柄长1.2 m；(2)为避免植物调查人员对昆虫取样的干扰，扫网操作可偏离样线一定距离(建议10 m左右)，但平行于样线进行。

15　鼠害的状况

调查时间和频度：与植物种库调查同步进行。

调查指标和方法：鼠害的状况这里采用鼠洞和土丘的数量进行表征。调查按照500 m×500 m的景观尺度，方法为基于样带的土丘和洞口统计法。土丘和洞口的计数调查与植物物种种库样线调查相结合进行：从样地中心点出发到样线终点的过程中进行植物物种的调查，从终点返回时按照与植物调查相同的分段(0–50 m、50–100 m、100–150 m、150–200 m、200–250 m)分别进行洞口和土丘数量的统计和记录。土丘和洞口调查的样带宽度为10 m，沿样线左右各5 m。

16　净初级生产力

调查时间和频度：调查时间为生物量高峰期，具体时间根据各调查样地的实际情况确定，调查频度应与多样性调查一致。

调查指标和方法：净初级生产力分为地上和地下两部分。鉴于生产力指标野外测定相对困难，仅在样地尺度上进行。地上净初级生产力(ANPP)在无放牧样地，其值等于生物量高峰期的群落地上总生物量；在有放牧的情况下，其值等于家畜采食量+

地上牧草现存量, 家畜采食量通过移动围栏法进行测定, 具体测定方法可参考McNaughton等(1996)。地上生物量的调查采取1 m×1 m的样方法, 每个样地设置5个样方, 其中4个与多样性调查样方一致, 另外一个设置在样地的中心点。植物地下净初级生产力的测定采取改进的内生长法, 在生长季初期先用直径10 cm的根钻, 按照0–10 cm, 10–20 cm, 20–40 cm, 40–60 cm和60–100 cm取出土壤, 移除根系后, 将土壤按层次回填, 并标记好根钻的准确位置。生长季末期, 用直径7 cm的根钻, 在10 cm旧根钻中心按照0–10 cm, 10–20 cm, 20–40 cm, 40–60 cm和60–100 cm取出土壤, 拣出新增根系后回填。生长季末期所获取的植物根系数据即为当季的净地下初级生产力(BNPP)。BNPP的测定样点与ANPP样点应保持一致。植物根系的空间异质性很大, 为增加取样的代表性, 减少数据间的变异, 建议每个取样点增加根钻取样的重复。重复数的设置可参考Taylor等(2013)。

17 土壤碳、氮、磷储量

调查时间和频度: 在生物量高峰期进行取样调查, 每5年调查一次。

调查指标和方法: 碳、氮、磷储量包括地上生物量、地下生物量、凋落物量和土壤总碳、氮、磷几部分。地上生物量、地下生物量、凋落物量的调查可与ANPP、BNPP的调查结合进行, 其值等于每块样地的地上、地下(0–100 cm)根系及凋落物的现存量。通过样方法和根钻法一次测定即可获取这几个参数, 测量重复数与生产力测定相同。用于植物地下生物量测定的土壤根钻样品, 过2 mm筛后的土壤风干后用于土壤总碳、氮、磷的测定; 根系和砾石部分水洗后分开, 烘干后测定根系和砾石重量。所有植物、土壤样品烘干称重后带回实验室粉碎并进行碳、氮、磷含量的测定。土壤容重是进行土壤碳储量计算必须的系数, 应在每个样地进行一次测定。测量的方法采用常规的环刀法, 每个样地重复5次, 取样点位置及测定土层分类与土壤碳、氮、磷含量测定保持一致。

18 水土保持力

调查指标和方法: 水土保持能力以植被盖度、裸地面积、凋落物量和地上生物量几个间接指标来表征。这些指标的测定方法参照前文相应介绍。

此外, 还有两个用来表征草地水土保持能力的间接指标, 分别是归一化植被指数(NDVI)和积雪覆盖度。这两个指标可以通过遥感数据的分析获取。为提高样地间的可比性, 用于NDVI计算的遥感数据要尽量保持时间上的同步性。考虑到植被地上生物量空间分布格局最明显的时间段应该在植物生长旺盛期, 因此建议最好采用这个时期的遥感数据进行NDVI的计算。积雪覆盖度的遥感分析则以融雪初期的遥感影像数据为最佳, 因为这个时候雪层较薄的地方冬雪已融化, 而雪层较厚的地方还留有积雪, 通过遥感影像可以清晰地分辨出草地的积雪覆盖状况。根据积雪覆盖状况我们可以进一步对每个观测样地的固雪能力进行评估。

19 地下水供给

调查时间和频度: 与哺乳动物多样性社会调研同步进行。

调查指标和方法: 地下水的供给状况以地下水的水位和水质两个指标来表征。在进行社调的居民点选取饮水井2–3个, 进行地下水水位的测量, 并取井水样带回实验室进行水质分析。如果调查居民点有用于农田灌溉的机井, 需额外选取2–3个机井进行地下水水位的测量和井水取样。

三、气候、土壤、地质历史环境和人类活动干扰

20–21 气象因子和其他环境变化因子

年均降水量、年均气温、年潜在蒸散量、年实际蒸散量、年总太阳辐射、年光和有效辐射、CO_2分压、氮沉降量、酸沉降量等气象和环境指标可通过多样性监测样地附近(几公里范围内)的气象监测站直接获取, 如附近无气象站则通过模型插值计算获得。

22 土壤理化性质

土壤类型数据可通过文献查阅获得; 土壤质地、酸碱度(pH)、有机质含量、持水量几个指标通

过对各个样地所取的土壤样品进行室内测定分析获得。各指标的测定方法参考Paul (2007)。

23 地形因素

地形因素主要测定坡向、坡度、地表起伏度和地表粗糙度, 这几个指标对与植物生长密切相关的水分、养分、温度和光照条件都会造成不同程度的影响, 进而影响植物群落的空间结构和多样性。具体数据可基于ASTER GDEM(Version 2, released at 2011.10.03)通过ArcGIS计算获得。

24 土地利用

土地利用类型、土地利用强度、土地利用历史是影响草地生物多样性和生态系统功能的3个关键指标。这些指标的数据获取途径主要有4种: (1)社会调研, 即通过对调查样地归属者的问卷调查获取相关数据; (2)遥感影像分析, 即通过对每个监测样地时间序列上植被状况、牧民住房建筑面积等指标的变化来判断土地利用的类型和强度, 进而反演样地的土地利用历史; (3)野外观测, 即通过调查样地的牧草采食情况、有无家畜粪便及其密度判断调查样地是否存在放牧、放牧的类型及强度。家畜粪便密度的调查与草本灌木样方的调查结合进行, 羊粪密度的调查在1 m×1 m的草本样方中进行, 马、牛等大型家畜的粪便密度调查在直径为10 m的灌木样方中进行; (4)通过草地监测部门发布的年鉴及草地资源类文献资料的检索获取不同级别行政单元内的土地利用状况信息。

25 社会经济因素

社会经济发展的需要是草地开发利用的主要驱动力因素, 本方案拟对监测样地附近居民的数量、经济来源和人均收入水平等几个社会经济指标进行调研。社会调研方法、时间和频度与本监测方案涉及到其他调研指标(例如哺乳类动物多样性)同步进行。另外较大的空间尺度上(例如以行政单元区划为基本调查单位)的社会经济指标可通过检索年鉴等统计资料获得。

26 景观因素

人类活动干扰除直接影响草地生态系统结构和功能外, 其造成的生境破碎化会进一步对草地生物多样性及其他生态系统服务功能造成影响(Saunders *et al*., 1991; Fahrig, 2003)。因此本方案将生境破碎化程度作为一个重要的景观因素进行监测和分析, 以帮助我们更好地分析我国草地生物多样性变化的驱动机制。随着景观生态学发展, 目前关于生境破碎化的分析技术已经比较成熟。本研究方案计划利用我国现有的最新的植被类型图及土地利用类型图, 通过空间分析软件包FRAGSTATS, 对区域尺度的生境破碎化程度进行量化分析。FRAGSTATS 的详细介绍可参考网页www.umass.edu/landeco/research/fragstats/fragstats.html。

27 地史进化因素

关于草地生物多样性现有格局的形成和维持机制有现代成因和历史成因两类假说, 前者强调现代环境因素的作用, 而后者着重强调地质和进化史的作用(Gaston, 2000; Mittelbach *et al*., 2007)。因此, 除对 20–26 几个现代环境因子进行调查外, 本方案计划通过对我国草地地质和进化历史方面已有研究资料进行的检索和整理, 探索和揭示地史和进化因素在我国草地生物多样性格局的形成和维持中的作用。

参考文献

Bonham CD (1989) *Measurements for Terrestrial Vegetation*. John Wiley & Son, New York.

Bremer B, Bremer K, Chase MW, Fay MF, Reveal JL, Soltis DE, Soltis PS, Stevens PF, Anderberg AA, Moore MJ, Olmstead RG, Rudall PJ, Sytsma KJ, Tank DC, Wurdack K, Xiang JQY, Zmarzty S (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society*, **161**, 105–121.

Casanoves F, Pla L, Di Rienzo JA, Díaz S (2011) FDiversity: a software package for the integrated analysis of functional diversity. *Methods in Ecology and Evolution*, **2**, 233–237.

Cornelissen JHC, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Delmont TO, Robe P, Cecillon S, Clark IM, Constancias F, Simonet P, Hirsch PR, Vogel TM (2011) Accessing the soil metagenome for studies of microbial diversity. *Applied and Environmental Microbiology*, **77**, 1315–1324.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, **34**, 487–515.

Greenslade PJM (1964) Pitfall Trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*, **33**, 301–310.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon

H, Ackerly DD, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.

Ma KP (马克平), Liu YM (刘玉明) (1994) Quantifying biodiversity I: measurement of alpha diversity (part 2). *Chinese Biodiversiy* (生物多样性), **2**, 231–239. (in Chinese)

McNaughton SJ, Milchunas DG, Frank DA (1996) How can net primary productivity be measured in grazing ecosystems? *Ecology*, **77**, 974–977.

Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA, McPeek MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM, Turelli M (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.

Paul EA (2007) *Soil Microbiology, Ecology and Biochemistry*, 3rd edn. Academic Press, Oxford.

Petchey OL, O'Gorman E, Flynn DFB (2009) A functional guide to functional diversity measures. In: *Biodiversity, Ecosystem Functioning, and Human Wellbeing* (eds Naeem S, Bunker DE, Hector A, Loreau M, Perrings C). Oxford University Press, Oxford.

Pielou EC (1975) *Ecological Diversity*. Wiley, New York.

Ripley BD (1981) *Spatial Statistics*. John Wiley & Sons, Incorporated, New York.

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.

Shannon CE (1948) A mathematical theory of communication. *Bell System Technical Journal*, **27**, 623–656.

Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirotchnick N (2012) Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters*, **15**, 637–648.

Taylor BN, Beidler KV, Cooper ER, Strand AE, Pritchard SG (2013) Sampling volume in root studies: the pitfalls of under-sampling exposed using accumulation curves. *Ecology Letters*, **16**, 862–869.

Webb CO, Ackerly DD, Kembel SW (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.

Wiegand T, Moloney KA (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos*, **104**, 209–229.

Yasuda M (2004) Monitoring diversity and abundance of mammals with camera traps: a case study on Mount Tsukuba, central Japan. *Mammal Study*, **29**, 37–46.

(责任编辑: 周玉荣)

02草地.pdf 1 2024/3/25 16:12:39

(SCPC-20240315-1665)

国家野外科学观测研究站观测技术规范

第一卷

生态系统与生物多样性

总　　则	于贵瑞 何洪林 李庆康 张雷明 苏　文
森林生态系统	刘世荣 王辉民 戴晓琴 等
草地生态系统	白永飞 王　扬 辛晓平 张　琳 高天明 等
农田生态系统	李发东 张文菊 马　力 等
荒漠生态系统	李新荣 谭会娟 潘颜霞 等
湿地生态系统	于秀波 宋长春 韩广轩 夏少霞 等
湖泊生态系统	朱广伟 秦伯强 谢　平 等
海洋生态系统	王　凡 孙晓霞 郑　珊 等
城市生态系统	周伟奇 任玉芬 王效科 等
生物多样性	陈　磊 高连明 米湘成 等
地球关键带与地表通量	于贵瑞 张雷明 刘丛强 王艳芬 黄　辉 等
喀斯特区域	王克林 张　伟 陈洪松 彭　韬 罗为群 等
数据管理	何洪林 苏　文 郭学兵 等

科学出版社　生物分社
联系电话：010-64012501
E-mail：lifescience@mail.sciencep.com
网　址：https://life.sciencereading.cn

销售分类建议：生态学

科学出版社
互联网入口

生命科学订阅号
赛拉艾芙

www.sciencep.com

ISBN 978-7-03-078220-5
9 787030 782205 >

定价：899.00元
（全十三册）

国家野外科学观测研究站观测技术规范 — 第一卷 — 生态系统与生物多样性 — 草地生态系统

科学出版社

编写委员会　主编

国家野外科学观测研究站
观测技术规范

第一卷

生态系统与生物多样性

草地生态系统

白永飞 王　扬 辛晓平 张　琳 高天明 等

科学出版社

编写委员会　主编

国家野外科学观测研究站观测技术规范

第 一 卷

生态系统与生物多样性

草地生态系统

白永飞　王　扬　辛晓平　张　琳　高天明 等

科学出版社
北　京

内 容 简 介

开展长期的、规范化的科学观测是国家野外科学观测研究站的首要任务，也是获取高质量科学数据和开展联网研究的基础与保障。本系列规范以国家战略需求和长期生态学研究为导向，指出了生态系统与生物多样性领域野外站观测技术规范的基本任务与内容，提出了野外站长期观测与专项观测相结合的技术体系，明确了本领域不同类型野外站的观测指标体系、观测技术方法和观测场地建设要求，制定了明确的数据汇交与管理要求，以保证观测数据的长期性、稳定性和可比性，从而推动开展全国和区域尺度的联网观测与研究。本系列规范适用于指导生态系统与生物多样性领域国家野外科学观测研究站以及相关行业部门野外站开展观测研究工作。

本系列规范可供生态学、生物学、农林科学、环境科学和地球科学等领域科研人员开展野外观测研究工作参考使用。

图书在版编目（CIP）数据

国家野外科学观测研究站观测技术规范. 第一卷，生态系统与生物多样性/编写委员会主编. —北京：科学出版社，2024.3

ISBN 978-7-03-078220-5

Ⅰ. ①国… Ⅱ. ①编… Ⅲ. ①野外作业–观测–试验基地–中国–技术规范 ②生态系–观测–中国–技术规范 ③生物多样性–监测–中国–技术规范 Ⅳ. ①N24-65 ②Q147-65 ③Q16-65

中国国家版本馆 CIP 数据核字（2024）第 053422 号

责任编辑：李 迪 高璐佳 / 责任校对：郑金红
责任印制：肖 兴 / 封面设计：北京美光设计制版有限公司

科学出版社 出版
北京东黄城根北街 16 号
邮政编码: 100717
http://www. sciencep. com
北京捷迅佳彩印刷有限公司 印刷
科学出版社发行 各地新华书店经销
*
2024 年 3 月第 一 版 开本：720×1000 1/16
2024 年 3 月第一次印刷 印张：76
字数：1 500 000

定价：899.00 元（全十三册）

（如有印装质量问题，我社负责调换）

“国家野外科学观测研究站观测技术规范”丛书

指导委员会

主　任：张雨东

副主任：兰玉杰　苏　靖

成　员：黄灿宏　王瑞丹　李　哲　刘克佳　石　蕾　徐　波　李宗洋

科学委员会

主　任：陈宜瑜

成　员（按姓氏笔画排序）：

于贵瑞　王　赤　王艳芬　朴世龙　朱教君　刘世荣
刘丛强　孙和平　吴孔明　张小曳　张劲泉　张福锁
陈维江　周广胜　侯保荣　姚檀栋　秦伯强　徐明岗
唐华俊　黄　卫　崔　鹏　康世昌　康绍忠　葛剑平
蒋兴良　傅伯杰　赖远明　魏辅文

编写委员会

主　任： 于贵瑞

副主任： 葛剑平　何洪林

成　员（按姓氏笔画排序）：

于秀波　马　力　马伟强　马志强　王　凡　王　扬
王　霄　王飞腾　王天明　王兰民　王旭东　王志强
王克林　王君波　王彦林　王艳芬　王铁军　王效科
王辉民　卢红艳　白永飞　朱广伟　朱立平　任　佳
任玉芬　邬光剑　刘文德　刘世荣　刘丛强　刘立波
米湘成　孙晓霞　买买提艾力•买买提依明　苏　文
杜文涛　杜翠薇　李　新　李久乐　李发东　李庆康
李国主　李晓刚　李新荣　杨　鹏　杨朝晖　肖　倩
吴　军　吴俊升　吴通华　辛晓平　宋长春　张　伟
张　琳　张文菊　张达威　张劲泉　张雷明　张锦鹏
陈　石　陈　继　陈　磊　陈洪松　罗为群　周　莉
周广胜　周公旦　周伟奇　周益林　郑　珊　赵秀宽
赵新全　郝晓华　胡国铮　秦伯强　聂　玮　聂永刚
贾路路　夏少霞　高　源　高天明　高连明　高清竹
郭学兵　唐辉明　黄　辉　崔　鹏　康世昌　彭　韬
斯确多吉　韩广轩　程学群　谢　平　谭会娟
潘颜霞　戴晓琴

第一卷　生态系统与生物多样性
编写委员会

主　任： 于贵瑞

副主任： 葛剑平 何洪林

成　员（按姓氏笔画排序）：

于秀波　马　力　王　凡　王　扬　王天明　王志强
王克林　王艳芬　王铁军　王效科　王辉民　白永飞
朱广伟　任玉芬　刘世荣　刘丛强　米湘成　孙晓霞
苏　文　李　新　李发东　李庆康　李新荣　辛晓平
宋长春　张　伟　张　琳　张文菊　张雷明　陈　磊
陈洪松　罗为群　周伟奇　郑　珊　赵新全　秦伯强
聂永刚　夏少霞　高天明　高连明　郭学兵　黄　辉
彭　韬　韩广轩　谢　平　谭会娟　潘颜霞　戴晓琴

草地生态系统编写组

白永飞　王　扬　辛晓平　张　琳　高天明　张雷明
郭小伟　闫瑞瑞　杜　娟　吴冬秀　张扬建　曹广民
辛晓平　王　堃　郭建英　王德利　马妙君　赵　亮

第一卷　生态系统与生物多样性
资助项目及单位

1. 科技基础资源调查专项“我国典型生态系统状况本底调查和历史数据整编”课题：生态系统观测指标规范制定及关键带生态系统状况本底调查和数据集成（2021FY100701）

2. 科技部基础研究司科技工作委托任务“国家野外站观测技术规范研究”

3. 国家生态科学数据中心（NESDC）

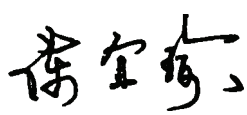
序

国家野外科学观测研究站作为“分布式野外实验室”，是国家科技创新体系组成部分，也是重要的国家科技创新基地之一。国家野外科学观测研究站面向社会经济和科技发展战略需求，依据我国自然条件与人为活动的地理分布规律进行科学布局，开展野外长期定位观测和科学试验研究，实现理论突破、技术创新和人才培养，通过开放共享服务，为科技创新提供支撑和条件保障。

2005 年，受科技部的委托，我作为“科技部野外科学观测研究站专家组”副组长参与了国家野外科学观测研究站的建设工作，见证了国家野外科学观测研究站的快速发展。截至 2021 年底，我国已建成 167 个国家野外科学观测研究站，在长期基础数据获取、自然现象和规律认知、技术研发应用等方面发挥了重要作用，为国家生态安全、粮食安全、国土安全和装备安全等方面做出了突出贡献，一大批中青年科学家依托国家野外科学观测研究站得以茁壮成长，有力提升了我国野外科学观测研究的国际地位。

通过长期野外定位观测获取科学数据，是国家野外站的重要职能。建立规范化的观测技术体系则是保障野外站获取高质量、长期连续科学数据、开展联网研究的根本。科技部高度重视国家野外站的标准化建设工作，并成立了全国科技平台标准化技术委员会野外科学观测研究标准专家组，启动了国家野外站观测技术规范的研究编制工作。我全程参加了技术规范的高水平专家研讨评审会，欣慰地看到通过不同领域的野外台站站长、一线监测人员和科研人员的共同努力，目前国家野外站五大领域的观测技术规范已经基本编制完成，将以丛书形式分领域出版。

面对国家社会经济发展的科技需求，国家野外站也亟须从顶层设计、基础能力和运行管理等方面，进一步加强体系化建设，才能更有效实现国家重大需求的科技支撑。我相信，“国家野外科学观测研究站观测技术规范”丛书的出版一方面将促进国家野外站管理的规范化，另一方面将有效推动国家野外站观测研究工作的长期稳定发展，并取得更高水平研究成果，更有效地支撑国家重大科技需求。



中国科学院院士　陈宜瑜

前　　言

当前我国经济已由高速增长阶段转向高质量发展阶段，资源环境约束日渐增大。推动经济社会绿色化、低碳化发展是生态文明建设的核心，是实现高质量发展的关键。依托野外站开展长期观测与研究，推动生态系统与生物多样性、地球物理与地表动力灾害、材料腐蚀降解与基础设施安全等五大领域的学科发展，是支撑国家社会经济高质量发展和助力新质生产力的重要基础性保障。

标准化和规范化的观测技术体系是国家野外站开展协同观测，并获取高质量联网观测数据的前提与基础。国家野外站由来自于不同行业部门的观测站组成，在台站定位、主要任务和领域方向等方面存在不同程度的差异，对野外站规范化协同观测和标准化数据积累的影响日益明显。目前国家野外站存在观测体系不统一、部分野外站类型规范化技术体系缺乏的突出问题，亟须在现有野外站观测技术体系基础上，制定标准化的观测技术规范，以保障国家野外站长期观测和研究的科学性，观测任务实施的统一性与规范性，更有效地服务于国家重大科技需求和学科建设发展。

2021 年 6 月，科技部基础司和国家科技基础条件平台中心启动了国家野外站观测技术规范的研究编制工作，并成立了全国科技平台标准化技术委员会“野外科学观测研究标准专家组”，组织不同领域技术骨干开展野外站观测技术规范的编写工作。两年多来，数百名野外站一线科研人员开展全力协作，围绕技术规范的编制进行了百余次不同规模的研讨和修改。作为野外科学观测研究标准专家组组长，我参与了技术规范编制工作的整个过程，也见证了野外站科研精神的传承，很欣慰地看到一支甘心扎根野外、勇于奉献和致力于野外科学观测研究科技队伍的成长。随着国家野外站五大领域的观测技术规范编制工作的完成，该成果将以丛书形式陆续出版，并将很快开展相应的野外站宣贯工作，从而有效推动国家野外科学观测研究站的规范化建设与运行管理，为更好地发挥国家野外站科技平台作用，助力实现我国高水平科技自立自强提供基础性支撑。

中国科学院院士　于贵瑞

目　　录

1　引言……1
2　范围……3
3　规范性引用文件……4
4　术语与定义……6
4.1　草地……6
4.2　草地生态系统……6
4.3　综合观测场……6
4.4　辅助观测场……6
4.5　长期观测场地系统……6
4.6　专项观测场地系统……7
4.7　站点尺度观测……7
4.8　区域尺度观测……7
4.9　防风固沙……7
4.10　碳汇功能……7
4.11　遥感产品……8
4.12　生态系统空间格局……8
5　观测任务与内容……9
5.1　长期观测任务与内容……9
5.2　专项观测任务与内容……10
6　观测指标体系……12
6.1　长期观测指标……13
6.1.1　背景信息……13
6.1.2　生物群落……14
6.1.3　大气环境……16
6.1.4　水环境……18

6.1.5 土壤环境……20
6.2 专项观测指标……23
6.2.1 生物多样性……23
6.2.2 草地利用……23
6.2.3 碳汇功能……24
6.2.4 生态修复……25
6.2.5 生态遥感……26
7 观测场地组成与设置……27
7.1 长期观测场地系统……27
7.1.1 综合观测场……27
7.1.2 辅助观测场……28
7.1.3 调查点……28
7.1.4 地表径流观测场……28
7.1.5 气象观测场……29
7.2 专项观测场地系统……29
7.2.1 生物多样性观测系统……29
7.2.2 草地利用观测系统……30
7.2.3 碳汇功能观测系统……31
7.2.4 生态修复观测系统……32
7.2.5 生态遥感观测系统……32
8 观测技术方法……34
8.1 长期观测指标的测定方法……34
8.1.1 背景信息……34
8.1.2 生物群落指标……36
8.1.3 大气环境指标……45
8.1.4 水环境指标……48
8.1.5 土壤环境指标……52
8.2 专项观测指标的技术方法……56
8.2.1 生物多样性……56

8.2.2　草地利用……57
8.2.3　碳汇功能……58
8.2.4　生态修复……59
8.2.5　生态遥感……59
参考文献……63
附录……64

1 引　　言

国家野外科学观测研究站（以下简称“国家野外站”）是我国重要的国家科技创新基地之一，是我国创新体系的重要组成部分。国家野外站旨在面向国际前沿科学问题和国家重大需求，在坚持生态系统长期观测的基础上，开展生态系统过程、结构、功能和生态系统优化管理的研究与示范，深刻揭示问题本质，提出明确的科学指导思想，为科技创新和社会经济可持续发展提供科技支撑。随着国家野外站的不断建设发展，为了更好地推动和实现野外站观测研究工作的开展，结合当前学科领域科技发展趋势和国家科技创新需求，建立统一的野外科学观测研究指标体系和技术规范，是国家野外站获取长期连续、高质量观测数据，支撑野外站长期科学目标和国家需求的重要保障。

草地是陆地生态系统的重要组成部分，其主要指以草本或半灌木为主，或兼有灌木和稀疏乔木，植被覆盖度大于 5%、乔木郁闭度小于 0.1、灌木覆盖度小于 40%的土地，以及其他用于放牧和割草的土地。我国现有草地面积 2.65 亿 hm^2，占国土总面积的约 27.6%。作为我国重要的生态系统和自然资源，草地不仅是我国传统的畜牧业基地，同时也是黄河、长江、澜沧江、滦河等主要江河的发源地和水源涵养区，是我国重要的生态安全屏障，在调节气候、涵养水源、防风固沙和生态固碳等方面发挥着极其重要的生态功能，在维护国家生态安全、边疆稳定、民族团结和促进经济社会可持续发展、农牧民增收等方面具有基础性、战略性作用。长期以来，由于不合理的人为利用，加之气候变化的影响，致使我国 90%左右的天然草地处于不同程度的退化中。开展草地生态系统的长期观测研究，认识草地生态系统结构、过程和功能变化规律，研究其对人为管理和全球变化的响应，对制定科学的草地生态系统管理政策与措施，促进我国草地生态系统的保护与可持续利用具有重要意义。

当前，随着生态学研究由注重生态系统结构、功能和生产力维持向关注生态系统服务的维持与调控机制转变，由生态系统不同组织层次水平结构研究向多营养级垂直结构研究转变，生态系统观测的手段也由传统站点尺度的地面监测为主向基于天空地一体化的跨尺度生态系统多要素立体观测转变。通过获取高频、跨尺度生态系统空间分布和动态变化信息，结合长期地面观测和模型模拟，实现区

域尺度生态系统生产力、群落结构组成等重要生态系统参量的反演，以及时识别和监测自然干扰及人为活动对生态系统的影响范围和强度，已成为当前生态系统观测领域的重要发展方向。在此基础上，构建更为系统、先进、统一和兼具创新性的观测指标体系与规范，对促进国家野外站运行的规范化、长期化、稳定化，获取长期连续观测数据，推动联网研究具有重要意义。本规范以促进草地生态系统长期观测研究和服务国家地方重大需求的双重目标为导向，在参考国内外生态系统观测技术规范的基础上，遵从科学性、系统性、前瞻性和可操作性的原则，系统编制了草地生态系统结构、过程和功能等方面的观测指标，拓展补充了草地生物多样性、放牧割草利用、碳汇功能、生态修复和生态遥感等内容的专项观测，以科学认知气候变化和人类活动对自然生态系统的影响，为草地资源的科学利用、区域可持续发展以及国家生态安全屏障建设提供基础数据和科学依据。

本规范的编写经历了野外站调研、规范编写、多轮意见征询和规范完善等阶段。2021 年 6 月 26 日，全国科技平台标准化技术委员会野外科学观测研究标准专家组（以下简称专家组）成立，于贵瑞院士任组长；同期举行的第一次专家组工作会议对推进各领域国家野外观测研究站长期监测规范的编写提出了指导意见。2021 年 12 月 27 日，中国科学院植物研究所白永飞研究员组织草地类国家野外站站长和监测人员，以及中国生态系统研究网络生物分中心成员，对在系统梳理国内外生态系统长期观测技术规范进展基础上编写的初稿进行了讨论；会议同期成立草地类国家野外站观测规范编写组，组长由白永飞研究员担任，成员为多个草地国家野外站和中国生态系统研究网络生物分中心工作人员。2022 年 1～2 月，根据各草地国家站反馈的意见，编写组对初稿进行了修改。2022 年 2 月 17 日，专家组召开会议，在系统评阅第一批野外站的观测技术体系的基础上，确立了新增专项观测指标的重要意见。2022 年，专家组先后组织专家对修订后的草地规范进行了审阅，并提出了进一步的修改意见，编写组对本规范的专项观测指标、观测场地设置及观测技术方法等进行了讨论与修改。经过一年的编写征询和专家组的多次研讨审议，2022 年 11 月 1 日，本规范通过了全国科技平台标准化技术委员会野外科学观测研究标准专家组的审议和讨论，并在进一步修改完善后提交科技部基础研究司和国家科技基础条件平台中心，作为指导本领域国家野外站开展长期观测、数据管理汇交的依据。本规范将在野外实地试用和接收反馈问题的基础上，继续修改完善。

2 范　　围

本规范明确了草地生态系统长期观测的目标任务、观测内容、观测指标体系、观测场地体系和观测技术方法。

本规范适用于国家草地生态系统野外站的长期定位观测，也适用于其他相关类型生态系统的长期观测工作。

生态系统过程与变化丛书

孙鸿烈　陈宜瑜　秦大河　主编

内容简介

本书依托中国科学院中国生态系统研究网络（CERN）的 9 个草地和荒漠类野外台站近 40 年来的主要科研进展和成果，从植物生理生态响应、生态系统结构与功能、退化生态系统修复与适应性管理等方面，阐述了我国北方干旱和半干旱生态系统在全球变化、人为活动干扰等自然和人为因素影响下的关键生态学过程与变化机理，以及在应对地区社会经济发展和环境变化等过程中，野外台站基于基础研究开展的大量试验示范工作。另外，本书还对野外台站未来的发展方向进行了展望。

本书内容丰富，资料翔实，可供从事地学、生命科学、环境科学等相关领域的科学研究、教学和生产管理部门的科技人员及高等院校师生参考。

策划编辑　柳丽丽　　责任编辑　柳丽丽　　封面设计　王凌波　　版式设计　童　丹
插图绘制　于　博　　责任校对　　责任印制

出版发行　高等教育出版社
社　　址　北京市西城区德外大街 4 号
邮政编码　100120
印　　刷
开　　本　787mm × 1092mm　1/16
印　　张
字　　数　　千字
购书热线　010-58581118
咨询电话　400-810-0598
网　　址　http://www.hep.edu.cn
　　http://www.hep.com.cn
网上订购　http://www.hepmall.com.cn
　　http://www.hepmall.com
　　http://www.hepmall.cn
版　　次　　年　月第 1 版
印　　次　　年　月第　次印刷
定　　价　　元

本书如有缺页、倒页、脱页等质量问题，请到所购图书销售部门联系调换
版权所有　侵权必究
物 料 号　　-

WBS 要素：11-00654-004（正式出版前务必删除此项）

生态系统过程与变化丛书编委会

主编：孙鸿烈　陈宜瑜　秦大河
编委（按姓氏笔画排序）：
于贵瑞　马克平　刘国彬　李　彦　张佳宝
欧阳竹　赵新全　秦伯强　韩兴国
秘书：于秀波　杨　萍

主要作者

第 1 章　王扬
第 2 章　曹广民
第 3 章　张扬建
第 4 章　李玉霖
第 5 章　黄振英
第 6 章　李新荣
第 7 章　何志斌
第 8 章　李彦
第 9 章　曾凡江

丛书总序

生态系统是地球生命支持系统。我国人多地少，生态脆弱，人类活动和气候变化导致生态系统退化，影响经济社会的持续发展。如何实现生态保护与社会经济发展的双赢，是我国可持续发展面临的长期挑战。

20 世纪 50 年代，中国科学院为开展资源与环境研究，陆续在各地建立了一批野外观测试验站。在此基础上，80 年代组建了中国生态系统研究网络（CERN），从单个站点到区域和国家尺度上对生态环境开展了长期监测研究，为生态系统合理利用、保护与治理提供了科技支撑。

CERN 由分布在全国不同区域的 44 个生态系统观测试验站、5 个学科分中心和一个综合中心组成，分别由中国科学院地理科学与资源研究所等 21 个研究所管理。CERN 的生态站包括农田、森林、草原、荒漠、沼泽、湖泊、海洋和城市等生态系统类型。学科分中心分别管理各生态站所记录的水分、土壤、大气、生物等数据。综合中心则针对国家需求和学科发展适时地组织台站间的综合研究。

CERN 深入揭示了各类生态系统的结构、功能与变化机理，促进了我国生态系统的研究，实现了生态学研究走向国际前沿的跨越发展。“中国生态系统研究网络的创建及其观测研究和试验示范”项目获得了 2012 年度国家科学技术进步一等奖，并被列为中国科学院“十二五”期间的 25 项重大科技成果之一。同时，CERN 已成为我国生态系统研究的人才培养和国际合作交流的基地，在国内外产生了重要影响。

2015 年，CERN 启动了《生态系统过程与变化》丛书的编写，以期系统梳理 CERN 长期的监测试验数据，总结生态系统理论研究与实际应用的成果，预测各类生态系统变化的趋势与前景。

孙鸿烈

目　录

绪论……（ 1 ）
第 1 章　内蒙古典型草原生态系统过程与变化……（ 3 ）
1.1　内蒙古站概况 ……（ 3 ）
1.1.1　区域代表性……（ 3 ）
1.1.2　基本情况……（ 4 ）
1.1.3　研究方向与建设目标……（ 5 ）
1.1.4　研究样地与实验平台……（ 5 ）
1.1.5　台站成果简介……（ 7 ）
1.2　植物对环境胁迫的生理生态响应 ……（ 7 ）
1.2.1　植物的光合作用和水分利用效率……（ 7 ）
1.2.2　植物性状对放牧和环境的适应……（ 9 ）
1.3　内蒙古典型草原的生态系统结构、功能及其维持机制 ……（ 10 ）
1.3.1　典型草原的生态系统结构与功能……（ 10 ）
1.3.2　放牧对典型草原生态系统结构和功能的影响……（ 12 ）
1.3.3　氮沉降对典型草原生态系统结构和功能的影响……（ 15 ）
1.4　区域生态系统重要生态学问题及其过程机制 ……（ 19 ）
1.4.1　内蒙古草原区生物多样性和生态系统功能的维持机制……（ 19 ）
1.4.2　草地生态系统的适应性管理……（ 25 ）
1.5　退化草地生态系统修复与生态系统管理 ……（ 26 ）
1.5.1　草地生产与生态功能的合理配置……（ 26 ）
1.5.2　沙化草地生态系统修复技术与示范……（ 27 ）
1.5.3　人工草地种植技术与示范……（ 28 ）
1.5.4　天然草原的放牧适应性管理……（ 29 ）
1.6　展望 ……（ 29 ）
参考文献 ……（ 30 ）
第 2 章　海北高寒草地生态系统过程与变化……（ 37 ）
2.1　海北站概况 ……（ 37 ）
2.1.1　海北站地貌特征和历史沿革……（ 37 ）
2.1.2　学科定位、研究方向与研究目标 ……（ 40 ）
2.1.3　台站基础设施及研究平台……（ 41 ）
2.1.4　代表性研究项目……（ 43 ）

2.2 高寒草地在地球碳、水循环中的作用 …… (46)
2.2.1 青藏高原高寒草地的碳收支 …… (46)
2.2.2 高寒草地土壤碳对放牧的响应 …… (47)
2.2.3 青藏高原高寒草地的碳增储潜力 …… (48)
2.2.4 高寒草地水分收支基本特征 …… (49)
2.3 高寒草地对模拟气候变化响应的生物学机制 …… (50)
2.3.1 碳素的外源添加对高寒草地碳转化的激发效应 …… (50)
2.3.2 气候变化对高寒草地生态系统碳、氮循环的影响 …… (51)
2.3.3 天然草地的开垦对青藏高原氧化亚氮排放的影响 …… (52)
2.3.4 高寒湿地温室气体通量对水位降低和氮添加的分子机理响应 …… (53)
2.3.5 “铁门”机制：湿地旱化引起的亚铁氧化减缓了土壤碳组分的降解 …… (53)
2.3.6 高寒植物物候序列对气候变化的响应 …… (54)
2.3.7 高寒植物果实期对增温和降温的反应相对稳定 …… (55)
2.3.8 三江源区高寒草地对气候变化响应空间分异 …… (56)
2.4 高寒草地稳定性的维持及其弹性 …… (57)
2.4.1 气候变化对青藏高原高寒草地稳定性的影响 …… (57)
2.4.2 高寒草地生态系统植物功能群及生产力对气候变化的响应 …… (57)
2.4.3 高寒草甸植物类群对氮素添加的响应 …… (58)
2.4.4 放牧作用对高寒草甸氮素养分的影响 …… (59)
2.4.5 影响高寒草地生态系统多功能性的因子 …… (59)
2.4.6 高寒嵩草草甸对放牧干扰的响应与适应 …… (60)
2.5 高寒嵩草草甸的适应性管理及功能的提升技术 …… (63)
2.5.1 高寒嵩草草甸退化演替状态的量化判别 …… (63)
2.5.2 高寒小嵩草草甸退化演替状态的量化判别 …… (65)
2.5.3 不同退化演替状态高寒草甸功能提升的瓶颈分析 …… (66)
2.5.4 放牧制度的改革是高寒草地功能提升最有效和经济的手段 …… (67)
2.5.5 放牧强度对土壤速效养分的影响 …… (67)
2.5.6 老化草毡表层破解 …… (68)
2.5.7 人工草地的建植 …… (71)
2.6 展望 …… (72)
参考文献 …… (73)
第 3 章 藏北高寒草地生态系统过程与变化 …… (77)
3.1 那曲站概况 …… (78)
3.1.1 区域生态系统概况 …… (78)
3.1.2 区域代表性 …… (79)
3.1.3 台站的历史发展沿革 …… (79)
3.1.4 学科定位、研究方向与目标 …… (80)
3.1.5 台站基础设施 …… (80)

3.1.6　成果简介……（84）
3.2　藏北高寒草地对环境胁迫的生理生态的响应和适应 ……（84）
3.2.1　高寒草地生态系统对增温的生理生态响应……（85）
3.2.2　高寒草地生态系统对水分的响应和适应……（86）
3.2.3　高寒草地生态系统对养分的响应和适应……（87）
3.3　藏北高寒草地生态系统结构、功能及其维持机制 ……（89）
3.3.1　增温对植物群落结构的影响……（89）
3.3.2　氮沉降对植被群落结构的影响……（91）
3.3.3　放牧对植被群落结构的影响……（93）
3.4　退化生态系统修复与生态系统管理 ……（96）
3.4.1　高原生态系统退化成因认知……（96）
3.4.2　高原生态系统退化表征及监测……（96）
3.4.3　高原退化生态系统修复和管理……（98）
3.5　展望 ……（100）
参考文献 ……（101）
第 4 章　科尔沁沙地生态系统过程与变化……（107）
4.1　奈曼站概况 ……（107）
4.1.1　台站区域生态系统特征……（107）
4.1.2　区域代表性……（108）
4.1.3　台站的历史发展沿革……（109）
4.1.4　学科定位、研究方向与目标 ……（109）
4.1.5　台站基础设施……（109）
4.1.6　成果简介……（110）
4.2　植物对环境胁迫的生理生态的响应和适应 ……（111）
4.2.1　风和风沙流……（111）
4.2.2　沙埋……（113）
4.2.3　干旱胁迫……（115）
4.3　生态系统结构、功能及其维持机制 ……（117）
4.3.1　科尔沁沙地植被格局及其影响因素……（117）
4.3.2　科尔沁沙地土壤生物及其影响因素……（120）
4.3.3　科尔沁沙地生态系统功能及其驱动因素……（122）
4.4　区域生态系统重要生态学问题及其过程机制 ……（125）
4.4.1　科尔沁沙地土地沙漠化……（125）
4.4.2　科尔沁沙地植被 – 水分关系 ……（129）
4.5　退化生态系统修复与生态系统管理 ……（133）
4.5.1　科尔沁沙地退化土地治理措施及其效应……（133）
4.5.2　技术模式……（138）
4.6　展望 ……（140）

参考文献 ……（141）
第 5 章 鄂尔多斯沙地草地生态系统过程与变化……（145）
5.1 鄂尔多斯生态站概况 ……（146）
5.1.1 区域代表性……（146）
5.1.2 台站的历史发展沿革……（146）
5.1.3 学科定位与研究方向……（147）
5.1.4 台站基础设施……（148）
5.1.5 台站成果简介……（149）
5.2 植物对环境胁迫的生理生态的响应和适应 ……（149）
5.2.1 植物对干旱胁迫的响应和适应……（149）
5.2.2 植物对沙埋胁迫的响应和适应……（152）
5.2.3 植物对风致机械刺激的响应和适应……（153）
5.2.4 植物对盐分胁迫的响应和适应……（153）
5.3 生态系统结构、功能及其维持机制 ……（158）
5.3.1 鄂尔多斯高原植物群落对沙埋和降水的适应与响应……（158）
5.3.2 毛乌素沙地油蒿群落不同演替阶段的油蒿种群动态……（160）
5.3.3 毛乌素沙地主要植物种凋落物分解特性……（161）
5.4 区域生态系统重要生态学问题及其过程机制 ……（164）
5.4.1 北方荒漠化带植物性状变异……（164）
5.4.2 北方蒿属植物及近缘种化学计量学……（166）
5.4.3 北方蒿属植物及近缘种的表现性状与物种分布……（168）
5.4.4 温带草原物种和功能多样性……（168）
5.4.5 北方干旱半干旱区凋落物分解……（169）
5.5 退化生态系统修复与生态系统管理 ……（171）
5.5.1 克隆植物在毛乌素沙地植被风蚀斑块修复中的应用……（172）
5.5.2 沙地生态系统基于碳储存功能的不同土地利用方式的选择……（172）
5.5.3 沙地蔬菜沙葱的资源收集与沙地种植技术……（174）
5.6 展望 ……（176）
参考文献 ……（177）
第 6 章 腾格里沙漠 – 阿拉善荒漠生态系统过程与变化 ……（181）
6.1 沙坡头站概况 ……（181）
6.1.1 台站区位……（181）
6.1.2 台站的历史发展沿革……（182）
6.1.3 学科定位和研究方向……（182）
6.1.4 基础设施……（182）
6.1.5 成果简介……（183）
6.2 植物对环境胁迫的生理生态响应与适应 ……（184）
6.2.1 植物逆境适应的分子机理……（184）

6.2.2　植物逆境适应的生理机制……（186）
6.2.3　植物对环境胁迫的生态适应对策……（190）
6.3　固沙植被结构、功能及其维持机制……（191）
6.3.1　固沙植被系统结构及其维持机制……（192）
6.3.2　固沙植被系统功能及其维持机制……（193）
6.4　中国北方沙区植被稳定性维持的生态水文阈值及生态系统管理……（201）
6.4.1　固沙植被生态水文阈值模型构建……（202）
6.4.2　模型模拟……（205）
6.4.3　固沙植被的生态水文阈值……（208）
6.4.4　固沙植被的调控和管理……（210）
6.5　展望……（211）
参考文献……（212）
第 7 章　黑河流域中游荒漠生态系统过程与变化……（219）
7.1　临泽站概况……（219）
7.1.1　区域生态系统特征……（219）
7.1.2　区域代表性……（220）
7.1.3　台站的历史发展沿革……（220）
7.1.4　学科定位、研究方向与目标……（220）
7.1.5　台站基础设施……（221）
7.1.6　台站成果简介……（221）
7.2　荒漠生态系统的结构、功能及其维持机制……（221）
7.2.1　荒漠生态系统的植物群落及物种多样性特征……（222）
7.2.2　荒漠植物的生态调节功能与植物间相互作用……（229）
7.2.3　荒漠生态系统物种多样性与初级生产力的时空变化特征……（232）
7.2.4　荒漠土壤动物分布特征及其生态功能……（234）
7.3　植物对环境胁迫的生理生态响应和适应……（236）
7.3.1　荒漠植物对降水的响应……（237）
7.3.2　荒漠植物对土壤营养元素的响应……（242）
7.3.3　风沙活动对荒漠植物的影响……（245）
7.4　区域生态系统重要生态学问题及其过程机制……（252）
7.4.1　风沙活动对绿洲的危害……（252）
7.4.2　荒漠生态系统水文过程变化对植被稳定的影响……（253）
7.5　退化生态系统修复与生态系统管理……（255）
7.5.1　绿洲边缘区固沙植被的建设……（255）
7.5.2　绿洲防护体系生态水文调控管理……（257）
7.6　展望……（258）
参考文献……（259）

第 8 章 准噶尔盆地荒漠生态系统过程与变化……（263）
8.1 阜康站概况 ……（263）
8.1.1 区域生态系统特征……（263）
8.1.2 区域代表性……（264）
8.1.3 台站的历史发展沿革……（264）
8.1.4 学科定位、研究方向与目标 ……（265）
8.1.5 台站基础设施……（265）
8.1.6 主要成果……（267）
8.2 准噶尔盆地荒漠植物对环境胁迫的生理生态响应与适应 ……（268）
8.2.1 多枝柽柳与梭梭对降水变化的生理生态响应……（268）
8.2.2 荒漠植物群落个体对降水变化的响应与适应……（270）
8.2.3 荒漠植物群落对降水变化的响应与适应……（272）
8.3 准噶尔盆地荒漠生态系统结构、功能及其维持机制 ……（275）
8.3.1 准噶尔盆地荒漠生态系统类型……（275）
8.3.2 准噶尔盆地荒漠生态系统植物群落结构及其组成变化……（275）
8.3.3 荒漠生态系统水分来源研究……（281）
8.3.4 梭梭的生物量分配与死亡机制……（284）
8.4 区域生态系统重要生态学问题及其过程机制 ……（286）
8.4.1 干旱内陆河小流域山地 – 盆地垂直带生态系统 ……（286）
8.4.2 人工绿洲安全与外围自然荒漠的关系……（288）
8.4.3 水盐运移与植被演替过程……（289）
8.5 退化生态系统修复与生态系统管理 ……（292）
8.5.1 耐盐小麦的选育及其在盐碱地改良利用中的示范推广……（292）
8.5.2 免灌荒漠植被种植技术在准噶尔盆地生态修复中的应用……（293）
8.6 展望 ……（294）
参考文献 ……（295）
第 9 章 塔里木盆地荒漠生态系统过程与变化……（299）
9.1 策勒站概况 ……（299）
9.1.1 概况与区域环境特征……（299）
9.1.2 区域代表性……（300）
9.1.3 总体目标和研究方向……（300）
9.1.4 台站基础设施……（301）
9.1.5 台站成果简介和人才队伍……（302）
9.2 植物对环境胁迫的生理生态响应和适应 ……（302）
9.2.1 植物对水分胁迫的生理生态响应与适应……（302）
9.2.2 植物对盐分胁迫的生理生态响应和适应……（305）
9.2.3 植物对弱光胁迫的生理生态的响应和适应……（308）
9.3 生态系统结构、功能及其维持机制 ……（311）

9.3.1　绿洲外围植被的分布与地下水……（311）
9.3.2　绿洲外围植被的水分来源……（312）
9.3.3　植物群落的更新与维持……（315）
9.3.4　植物群落生产力关键种的生物量和产量……（317）
9.4　区域生态系统重要生态学问题及其过程机制 ……（319）
9.4.1　绿洲水资源变化特征与综合管理……（319）
9.4.2　沙漠－绿洲不同下垫面地表风沙活动特征及其规律 ……（323）
9.4.3　绿洲化过程中农田土壤粒径分异性特征……（323）
9.4.4　绿洲小气候效应及其对降尘作用的影响……（324）
9.5　退化生态系统修复与生态系统管理 ……（325）
9.5.1　荒漠－绿洲过渡带生态屏障可持续管理技术体系与模式构建 ……（326）
9.5.2　不同区域类型的试验示范区和技术推广区建设与效益分析……（327）
9.6　展望 ……（328）
参考文献 ……（329）

绪　　论

我国的草原、沙地和荒漠面积约占国土面积的 50%。这些区域是我国少数民族的主要聚居区和重要的畜牧业基地，也是关系国家生态安全的重要资源和能源区，在我国北方绿色生态屏障建设、牧区社会经济可持续发展和民族团结与社会稳定等方面具有极为重要的作用。近几十年来，人类活动引发的快速全球变化，特别是气候变暖、极端气候事件、生物多样性丧失、草地退化、土地沙漠化等重大生态环境问题极大地影响着草原、沙地和荒漠生态系统的结构、生态系统功能和区域社会经济及生态安全，严重威胁和困扰着人类的生存和社会的可持续发展。因此，开展草原、沙地和荒漠生态系统格局与过程的长期监测、研究和示范，对于推进陆地生态系统对全球变化的响应与适应性研究具有重要的科学意义。

中国生态系统研究网络（Chinese Ecosystem Research Network, CERN）成立于 1988 年，肩负着对中国各类生态系统开展长期监测、科学研究和试验示范的重大使命，是国家创新体系的重要组成部分。目前，生态系统研究网络包括 9 个草地荒漠类生态站，分布在 31–44° N, 80–120° E 的范围内，其中草地生态系统站 3 个，分别位于我国的内蒙古高原、青藏高原东北部和藏北高原等全国主要草原分布区；沙地站 2 个，分别位于我国北方农牧交错带的科尔沁沙地和毛乌素沙地；荒漠站 4 个，位于腾格里沙漠、巴丹吉林沙漠、准噶尔盆地和塔里木盆地等主要荒漠生态系统。自上世纪 50 年代以来，这些生态站面向国家和区域社会经济和科技发展需求，开展了一系列科学观测和研究工作，取得了许多重大原创性基础研究成果和显著的试验示范成效，对于深入认知我国草原、沙地和荒漠生态系统的结构与功能变化，及其对环境变化的响应与适应具有重要的科学意义，同时，为保障国家粮食安全、生态文明建设和重大生态工程建设等提供了重要的科技支撑。

适逢中国生态系统研究网络成立 30 周年，本书以集中展示的方式，系统梳理和总结了近 30 年来，我国草地、荒漠生态系统研究领域在长期监测、基础研究和试验示范等方面的研究进展。本书重点关注了不同草地、荒漠生态系统下植物对环境适应的生理生态学机制，生态系统结构、功能的变化及其维持机制，放牧管理、碳水耦合、风沙活动等关系区域生态系统的重要生态学问题，以及退化生态系统修复与管理方面的研究进展。本书对我国干旱和半干旱区、以及青藏高原的草地、荒漠生态系统的理论发展、科学管理、保护利用具有重要的推动作用和参考价值。

当前，我国正处于实施创新驱动发展战略的关键时期，我国的生态安全和区域可持续发展也面临着更严峻的挑战。生态站作为国家创新基地的重要组成之一，应进一步面向国际前沿科学问题和国家重大需求，结合区域发展中面临的新问题，以提升国家自主创新能力为目标，从监测、研究和示范等方面增强生态站的科学观测研究综合能力。

（1）坚持长期监测：短期观测研究难以建立未来人类活动和气候变化背景下自然生态系统过程和功能变化的预警机制；准确量化生态系统服务功能，综合评估生态服务功能的区域特征

和空间格局，以及生态系统承载力依赖于长期观测研究的支持。同时，加强生态系统要素监测手段由以传统地面监测为主向天—空—地一体化的立体监测转变，构建生态要素监测数据云平台，提升台站的长期监测能力和共享服务能力。

（2）加强科学研究和平台建设：围绕我国草原、沙地和荒漠生态系统，面向全球变化、生态系统过程和功能、生物多样性等国际科学前沿和粮食安全、生态文明建设等重大国家需求，开展生态系统生态学、全球变化生态学、生物多样性、生态水文学、流域生态学、生物地球化学循环等方面的研究工作，同时加强地学、生物学、生态学等领域的跨学科交叉研究与学科融合，促进原创性重大科学理论和科技成果产出。

（3）加强科研示范和示范试验推广：围绕生态系统保护和修复、生态系统服务功能评估、生态补偿政策等国家重大科技需求，实现生态修复和合理利用由单项技术示范为主，向多项技术集成示范转变，建立生态保护与可持续利用技术体系和示范体系；同时，应充分理解自然—社会系统互馈与耦合关系，将“水、土、气、生”为主要研究内容的恢复生态学理论和经济增长、人类福祉提升等社会经济要素结合在一起，推进“生态－社会－经济”三者之间的协同增长，实现“绿水青山就是金山银山”这个可持续发展目标。

第 1 章　内蒙古典型草原生态系统过程与变化*

探求草地生态系统过程与变化，是当代干旱半干旱地区生态学的重要问题之一。内蒙古草原是欧亚大陆草原的重要组成部分，是我国重要的畜牧业基地和重要的水源涵养区，同时也是我国北方的重要生态屏障。由于近几十年的过度利用，该区域有 90%左右的草地处于不同程度的退化之中，其中严重退化草地占 60%以上。人为因素和气候干旱，特别是长期的过度放牧是导致内蒙古草地退化的主要原因。长期过度放牧严重地影响了不同时空尺度的草地生态系统功能，加速了草地的退化演替，致使虫鼠害和沙尘暴等自然灾害频繁发生，从而使草地的生态服务功能日益衰减，严重威胁我国北方及其周边地区的生态安全，成为实现区域经济可持续发展、边疆稳定和构建和谐社会的关键制约因素。

中国科学院内蒙古草原生态系统定位研究站（以下简称内蒙古站），是我国在温带草原区建立的第一个草原生态系统长期定位研究站。长期以来，内蒙古站围绕草原生态系统生态学基础研究、生态系统长期监测以及生态系统管理等应用研究开展了大量的试验工作，在草原生物多样性与生态系统稳定性的维持机制、放牧对生态系统生产力和生物地球化学循环的影响以及草地生态系统服务对全球变化的响应等方面取得了众多的研究成果。本章围绕内蒙古典型草原生态系统的过程与变化，对内蒙古站近 40 年的研究成果进行介绍，旨在回顾和总结以往的研究成果，进一步促进草原生态科学的发展。

1.1　内蒙古站概况

1.1.1　区域代表性

我国草地总面积 4 亿 hm^2 左右，约占我国国土面积的 40%。其中，北方草地约 3.13 亿 hm^2，约占我国草地总面积的 78%。内蒙古站所在的锡林郭勒草原面积 20.3 万 km^2，位于内蒙古自治区中部，是我国中温带半干旱典型草原的核心分布区，由于该区域的植被地貌特征能够较好地反映温带草原的特征与面貌，因而是我国北方草地最具典型性和代表性的区域。锡林郭勒草原可利用的天然草地 1783 万 hm^2，居我国 11 片重点牧区之首，是全国 4 亿 hm^2 草地中自然条件较好且大面积集中分布的地区，因而也是我国草地畜牧业最具代表性的区域。长期以来，锡林郭勒

* 本章作者为中国科学院植物研究所王扬、陈迪马、郑淑霞、应娇妍、陈世苹、白永飞。

草原作为我国北方地区重要的绿色生态屏障之一，有效阻止了草原腹地土壤侵蚀、沙化以及来自中亚和我国西部的沙尘侵害，对于维持整个华北地区，特别是京、津地区的生态环境安全起着极其重要的作用。然而，近几十年来，由于人类活动干扰和环境自然演变相互交织，锡林郭勒草原发生了严重退化，生产力不断下降，干旱化与荒漠化进程不断加剧，草原的生态服务功能日益衰减，自然灾害事件频繁发生，成为华北地区沙尘暴和扬沙的主要沙源。锡林郭勒草原是我国北方天然草地生态环境问题最为严重也最具代表性的区域，因此国家“沙源治理”工程、“退耕还林（草）”工程、“退牧还草”工程、科技部“防沙治沙”十五攻关项目、中国科学院“西部行动”计划等都把该区域确定为重点实施区域。由此可见，内蒙古站的研究区域在我国北方草地的植被地貌特征、社会经济问题和生态环境问题方面均具有极强的区域代表性。

1.1.2　基本情况

内蒙古站所在的锡林河流域位于 43°26′N—44°08′N，116°04′E—117°05′E，是我国中温带半干旱典型草原最具典型性和代表性的区域（图 1.1）。该区域特定的地理位置和复杂的地貌条件为地带性草原植被和草原动物种群的形成与分布提供了条件，构成了典型的草原生态系统类型。该区域气候属于半干旱草原气候，年平均气温 0.9℃（1982—2015 年），最高气温 38.7℃，最低气温 −51.0℃（1988 年），7 月平均气温 19.3℃，1 月平均气温 −21.2℃，年降水量 330 mm，无霜期约 200 天。地带性土壤为栗钙土，包括典型栗钙土和暗栗钙土两个亚类。本区种子植物约 625 种，分属于 74 科、291 属。本区植被以草原植被为主，群落中主要植物种类组成有羊草（*Leymus chinensis*）、大针茅（*Stipa grandis*）、克氏针茅（*Stipa krylovii*）、洽草（*Koeleria cristata*）、冰草（*Agropyron cristatum*）、糙隐子草（*Cleistogenes squarrosa*）、变蒿（*Artemisia commutate*）和冷蒿（*Artemisia frigida*）等。本区的动物也反映了草原区系的特点。兽类有黄羊、狍、狐、狼、獾、刺猬、蛇和多种啮齿类动物（黑线仓鼠、达乌尔黄鼠、莫氏田鼠、达乌尔鼠兔、五趾跳鼠等）。鸟类物种主要有百灵、田鹨、云雀、伯劳、鹌鹑和鹰等，多为食虫鸟类。昆虫主要有蝗虫、黏虫、瓢虫、蚜虫、金龟子、叶蜂蝶和蚊蝇等 22 种，分属于 4 亚科、13 属，是草原生态学研究的重要对象。

图 1.1　中国科学院内蒙古草原生态系统定位研究站（参见书末彩插）

内蒙古站始建于 1979 年，是我国在温带草原区建立的第一个草原生态系统长期定位研究站。1982 年内蒙古站被接收为国际“人与生物圈计划”（MAB）重点项目示范站，1989 年被批准为中国科学院院级开放站，1992 年被确定为中国生态系统研究网络的重点站，2005 年晋升为国家野外科学观测研究站（暨内蒙古锡林郭勒草原生态系统国家野外科学观测研究站）。2007 年被国家人事部和中国科学院授予“中国科学院先进集体”；2009 年被科技部授予“中国野外科技工作先进集体”；2001—2005 年、2006—2010 年、2011—2015 年连续三次获得中国生态系统研究网络综合评估“优秀野外台站”称号。

1.1.3　研究方向与建设目标

内蒙古站研究方向主要包含以下三个方面：① 草原生态系统结构与功能、生物多样性与生态系统稳定性、全球变化等方面的生态学基础研究；② 草原生态系统水、土、气、生要素的长期监测和资料积累；③ 生态系统管理特别是退化草地恢复、放牧地和割草地管理、人工草地建设、生物多样性保育等方面的应用研究。

内蒙古站的建设目标是建成国际一流的国家野外科学观测研究站，成为我国温带草原区具有国际先进水平的科学研究基地、培养造就高科技人才的人才基地和高新技术产业化示范的创新基地，为我国草原生态学、资源学、环境科学等相关学科的发展提供野外试验和研究平台，为我国草原生态系统优化管理提供示范模式和配套技术，为我国北方草原地区社会和经济的可持续发展提供决策依据。

1.1.4　研究样地与实验平台

（1）主要研究样地

内蒙古站的试验观测场主要包括综合观测场、辅助观测场和气象观测场。综合观测场设在羊草样地，辅助观测场设在大针茅样地，气象观测场设在站区西侧。综合观测场所在的羊草样地于 1979 年围封，面积 24 hm^2。辅助观测场所在的大针茅样地于 1979 年围封，面积 25 hm^2。综合观测场内主要设置了小气候梯度仪、自动气象站、涡度相关系统、生物节律自动观测系统、土壤温湿盐自动观测系统、径流场、中子仪水分观测点、地下水采样点、土壤监测采样区、生物监测采样区、蝗虫种群动态观测场等。辅助观测场主要设置了生物监测采样区、土壤监测采样区、蝗虫种群动态观测场等。

除了试验观测场的主辅样地外，内蒙古站还设有多个研究样地，主要包括：① 羊草群落系列研究样地（1979 年围封区、1999 年围封区、2001 年围封区和自由放牧区）；② 退化草地恢复生态学研究样地（1983 年围封区和外侧自由放牧区）；③ 浑善达克沙地大样地（建于 2013 年，位于锡林郭勒盟正蓝旗桑根达来镇以北 30 km 的浑善达克沙地腹地，样地面积为 1000 m × 1000 m）。

（2）主要实验平台

随着生态学研究的不断深入，野外长期定位研究的实验生态学受到各国生态学家的高度重视。以科学问题为导向的大型野外控制试验平台，已经成为内蒙古站基础研究和开展试验示范的主要基地。2000 年以来，内蒙古站设计实施了多个大型生态学实验平台（图 1.2）。

长期养分添加实验平台：自 2000 年开始实施，包括不同水平、不同时期氮素、磷素和有机肥添加的处理 50 个，每个处理 9 次重复，共 450 个实验小区。该实验对于揭示养分驱动的生态系统的响应机理以及草原生态系统的元素生物地球化学循环具有重要意义。

图 1.2 内蒙古站主要实验平台

注:(a)长期养分添加实验平台;(b)因子调控实验平台;(c)生物多样性与生态系统功能实验平台;(d)长期放牧实验平台;(e)降水实验平台;(f)凋落物实验平台(参见书末彩插)

退化草地生态系统火因子调控实验平台:该实验平台建于 2005 年,包括 81 个处理,每个处理 8 次重复,共 648 个实验小区。其研究结论有助于了解草原的退化机理、退化草地恢复的驱动因子、并为阐明火因子在草地生态系统结构和功能维持中的作用提供重要的实验依据。

生物多样性与生态系统功能实验平台:该实验平台是由内蒙古站与美国哥伦比亚大学、亚利桑那州立大学等单位的科学家共同设计的,包括 96 个处理,每个处理 8 次重复,共 768 个实验小区,2005 年启动。该实验不仅可以检验现有的众多生态学的重要理论,而且可以深入揭示草原生态系统结构、功能、过程相互之间的关系,特别是对于回答生物多样性与生态系统功能的关系这一颇具争议的科学热点问题具有重要意义。

长期放牧实验平台:长期放牧实验平台是由中国和德国双方科学家于 2004 年共同建成的。平台包括不同地形条件下(平地和坡地)的传统利用(只进行放牧或打草处理)和混合利用(放牧和打草处理隔年交替进行)两种土地利用方式。实验设置 7 个放牧梯度,36 个实验处理,74

个实验小区，总面积 200 多 hm^2，是迄今世界上最大的长期受控放牧实验平台。该平台主要用于研究不同放牧率对草地生态系统生产力和物质通量的影响，其研究结论对于指导我国北方典型草原生态系统的适应性管理具有重要理论价值。

降水实验平台：该实验平台建于 2013 年，包括大型防雨棚试验区和遮雨架试验区。该实验平台主要用于研究内蒙古典型草原生态系统对极端降水事件的响应阈值和应答机理以及对长期干旱的适应机制。

凋落物实验平台：该实验平台建于 2013 年，设置凋落物移除和添加两种实验处理，每种处理下设置 0、50% 和 100% 三个处理梯度，共计实验小区 126 个。该实验平台主要研究凋落物在维持草地生态系统生物多样性和生态系统功能稳定性方面的机制，为改善草地生态系统以及退化草地恢复提供理论依据。

1.1.5　台站成果简介

建站以来，内蒙古站共发表各类研究论文 2100 余篇，其中在 *Nature*、*Science*、*Ecology Letters*、*Ecological Monographs*、*Ecology*、*Global Change Biology* 等 SCI 期刊发表论文近 700 篇，出版论著 30 余部，研究成果获得国家科技进步一等奖 1 项，国家和中国科学院自然科学奖 10 项。取得的重大原创性基础研究成果包括：① 基于近 40 年的长期监测和实验数据，揭示了内蒙古草原生物多样性与生态系统稳定性的维持机制；② 通过长期放牧控制实验，阐明了放牧对生态系统生产力、碳氮循环、温室气体排放和草原蝗虫爆发的调控机理；③ 基于 20 年的控制实验和长期监测数据，揭示了草地生态系统服务对全球变化关键驱动因子的敏感性及其响应和适应机制。

另外，内蒙古站始终坚持把研究成果服务于社会，服务于内蒙古草原的生态环境保护和社会经济的可持续发展。2001 年以来，先后建立了沙地综合治理、退化草地恢复、天然草场合理利用、人工草地建植等多个试验示范区，受到了国家和相关部门及内蒙古自治区的高度重视。取得的重要技术研发和试验示范成果包括：① 围封休牧、延迟放牧与划区轮牧技术体系；② 多年生混播人工草地草种配置与建植技术；③ 浑善达克沙地和沙化草地“三分之一治理，三分之二封育自然恢复”模式。这些试验示范成果为国家“京津风沙源治理工程”、“退牧还草”工程、“草原生态保护奖励补助机制”提供了重要的科技支撑。

1.2　植物对环境胁迫的生理生态响应

1.2.1　植物的光合作用和水分利用效率

陆地生态系统通过植物光合作用从大气中固定 CO_2 并形成糖类，植物的光合作用是生态系统生产力形成的生理基础。内蒙古站自 20 世纪 80 年代以来较为系统地开展了锡林郭勒典型草原优势物种和群落光合生理过程的研究。杜占池和杨宗贵（1988，1992，1997）描述了典型草原优势物种羊草、大针茅和冷蒿叶片光合速率的日动态和季节动态，发现了干旱所导致的叶片光合午休现象。戚秋慧等（1989）发现典型草原群落的水平光合作用呈现出与个体光合相似的日变化和季节变化。Chen 等（2005b）研究了放牧对典型草原 6 个主要优势物种光合生理特征的影

响，发现放牧显著降低了植物的光合速率，且植物的光合速率与其对群落生物量的贡献明显相关。近年来，利用改进的红外分析仪－静态箱法，内蒙古站科研人员陆续开展了典型草原群落水平碳交换过程对氮沉降、降水格局变化及物种多样性改变等全球变化因子的响应研究。基于内蒙古站氮沉降实验平台的研究表明氮添加显著提高了生态系统的光合速率和呼吸速率，随着氮添加强度的增加，生态系统光合和呼吸均表现出饱和现象，阈值出现在 10.5 g N m^{-2}·年 $^{-1}$ 的氮添加处理（Tian et al.，2016），这与生产力的研究非常类似（Bai et al.，2010）。相似的非线性响应过程也出现在降水格局控制实验中，研究发现，生态系统碳通量对降水变化的响应是非线性的，对减水响应的敏感性显著大于增水（Zhang et al.，2017）。植物光合碳固定对降水变化的响应显著高于呼吸过程，并决定了生态系统资源利用效率和生产力。基于春季增雪、夏季增雨和氮添加对生态系统碳交换过程的研究表明，春季增雪对生态系统水平碳交换量的影响是非常有限的，夏季增雨显著提高了生态系统光合与呼吸，氮添加仅在夏季增雨和湿润年份才显著促进生态系统碳通量（Zhang et al.，2015）。在多样性与生态系统功能控制实验平台上的研究发现，功能群数量的减少显著降低了生态系统碳交换速率，不同功能群间存在明显的互补效应（Pan et al.，2016）。以上研究结果对预测未来全球变化背景下，草原生态系统结构和功能稳定性的响应格局具有重要意义。

水分是我国北方干旱－半干旱草原生产力的主要限制因子，研究植物光合生理过程对水分可利用性的响应对了解并预测未来全球变化背景下草原生态系统生产力的变化趋势具有重要作用。水分利用效率（water use efficiency，WUE）是生态系统碳水循环耦合关系的重要指标，是连接陆地生态系统碳循环和水循环的关键环节。WUE 是指消耗一定的水量，植物光合作用所固定的 CO_2 或生产的干物质量（或净初级生产力 NPP），大多数情况下应用于叶片水平上的研究。在实际应用中常通过光合速率和蒸腾速率的比值计算瞬时水分利用效率（WUEi）。作为叶片长期水分利用效率的指示指标，叶片稳定性碳同位素比值也被广泛应用于 WUE 的研究。陈世苹等（Chen et al.，2002，2003，2005a）从植物种、功能群和群落三个尺度研究了内蒙古锡林河流域主要草原群落中植物对氮、水资源的利用和适应策略及其生理生态学机制。结果表明，随着土壤水分可利用性的下降，羊草、大针茅和黄囊苔草等优势物种的 $\delta^{13}C$ 值显著增大，水分利用效率明显提高，表现出对干旱生境的生态适应性（Chen et al.，2002；陈世苹等，2004）。在不同植物组织和空间尺度上，C_4 植物糙隐子草叶片的碳稳定性同位素判别（$\delta^{13}C$ 值）呈现显著差异（Yang et al.，2011）。

以上个体 WUE 的研究表明，随着降水的增多或水分条件的改善，植物的 WUE 明显下降，而生态系统水平上的 WUE 对环境条件变化的响应并没有一致的结论。近几年来，随着生态系统水平碳通量研究方法的改进，对生态系统水平 WUE（WUEe）的研究越来广泛。目前，WUEe 的研究主要是通过静态箱法和涡度相关法对碳水通量进行直接测量。自 2004 年起，作为 ChinaFLUX 加盟站，内蒙古站在不同围封时间的草原生态系统中陆续建立了多套涡度相关系统，迄今为止，已经收集了 14 年的碳水通量连续监测数据。WUEe 主要通过生态系统总初级生产力（GPP）和生态系统蒸发散（ET）的比值进行估算。长期数据表明，2006—2013 年内蒙古站长期围封的羊草样地平均 WUEe 为 0.72 ± 0.19 g C·mm^{-1}，年际变异从 0.40 g C·mm^{-1} 至 1.01 g C·mm^{-1}。退化恢复羊草样地表现出更高的 WUEe，多年平均值为 1.00 ± 0.27 g C·mm^{-1}，年际变异从 0.66 g C·mm^{-1} 至 1.34 g C·mm^{-1}。

1.2.2　植物性状对放牧和环境的适应

近年来，植物功能性状的研究为功能生态学，特别是为生物多样性与生态系统功能关系的机理研究注入了新的活力（Diaz and Cabido，2001；McGill et al.，2006；Kraft et al.，2015）。通过植物功能性状，研究植物对气候变化和人类干扰的响应与适应机制，有助于揭示物种替代和群落演替的机理，对于探明草原退化过程和机制具有重要意义（Diaz et al.，2007）。内蒙古大学的王炜教授团队通过分析 1983—1993 年内蒙古退化草原群落（退化草地恢复生态学研究样地）中 8 个主要植物种群的个体性状变化，揭示了个体小型化是过度放牧下群落生产力衰退的重要表现。个体小型化表现为植株变矮、叶片变小、节间缩短以及植物根系分布浅层化等性状的集合。个体小型化是植物对过度放牧的负反馈机制，是从个体水平上认识退化演替机理的关键（王炜等，2000；王鑫厅等，2015）。此外，植物性状是影响物种对放牧响应的关键。基于放牧实验平台的研究发现，植物的比叶面积和叶片氮含量能够较好地预测植物对不同放牧强度的响应（Li et al.，2017）。

植物功能性状之间的权衡（trade-offs）关系，反映了植物通过自身内部结构与功能的调整，为适应胁迫环境，在资源获取、利用和分配方面的策略，也反映了群落内物种的竞争和共存机制（Sterck et al.，2011）。基于锡林河流域草甸、草甸草原和典型草原三种不同类型草原中植物叶片、个体、物种、功能群（生活型和水分生态型）和群落多个组织水平的研究发现，随着组织水平的上升，放牧对草甸中植物功能性状的影响逐渐减弱，而对典型草原植物性状的影响逐渐增强（图 1.3）。叶片大小和数量之间的权衡关系，以及植物采用躲避型策略和忍耐型策略，是放牧对不同类型草原影响差异的主要原因（Zheng et al.，2010）。

关于物种共存格局和机制的研究，多从地上性状来考虑，往往忽略了根系性状对群落构建的影响。由于叶片和根系所面临的选择压力和在养分竞争中的作用不同，同时分析叶片和根系性状对物种共存作用的异同点，可以丰富我们对半干旱草原物种共存机制的理解（Geng et al.，2017；Ma et al.，2018）。基于蒙古高原样带调查的研究发现，沿着东北－西南方向养分和水分可利用性逐渐减少的环境梯度，植物的比叶面积和比根长在物种水平上表现为适应旱生环境的特征，随着水分减少，比叶面积和一级根的比根长均降低；在群落水平上，根系性状对环境筛选更为敏感，而

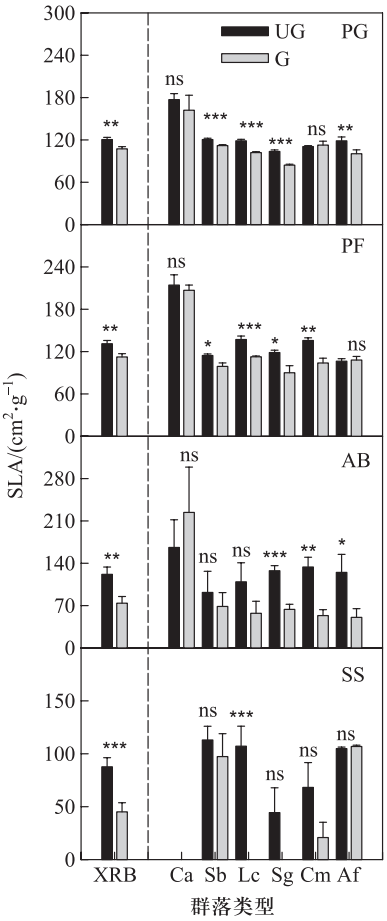


图 1.3　放牧对 6 个群落中不同功能群植物比叶面积（SLA）的影响。

PG，表示多年生禾草；PF，表示多年生杂类草；AB，表示一二年生植物；SS，表示半灌木和灌木。Ca，*Carex appendiculata*，灰脉薹草草甸；Sb，*Stipa baicalensis*，贝加尔针茅草甸草原；Lc，*Leymus chinensis*，羊草典型草原；Sg，*Stipa grandis*，大针茅典型草原；Cm，*Caragana microphylla*，小叶锦鸡儿典型草原；Af，*Artemisia frigida*，冷蒿典型草原。XRB，指六类群落的平均值。（引自 Zheng et al.，2010）

地上性状主要由群落组成和环境因子的交互作用所决定（Cheng et al.，2016）。物种性状之间的权衡与协同关系不仅受环境因子影响，还与其进化过程有关。比叶面积和根系性状均表现出显著的谱系信号，且根系性状的谱系信号高于地上性状。当消除物种谱系关系的影响后，比叶面积与一级根的比根长呈正相关关系，而与二级根和三级根的比根长均呈负相关关系（Cheng et al.，2016）。该研究对于从谱系发育的角度重新认识植物性状间的关系，以及保护我国干旱和半干旱草原的物种多样性和生态系统功能具有重要意义。

养分重吸收是植物营养器官枯萎过程中养分再转移的过程，是植物适应不同养分条件生境的重要策略。养分重吸收的改变，不仅影响植物生长及物种之间的竞争作用，还可以通过对凋落物质量的影响改变生态系统的养分循环。中国科学院沈阳应用生态研究所吕晓涛研究团队通过对内蒙古站长期围封样地内优势物种的研究发现：从叶片中重吸收的氮素占植物地上部分氮素重吸收总量的 64%～83%，从茎中重吸收的氮素占 17%～36%，保留在枯茎中的氮素占地上立枯总氮量的 25%～52%，表明茎秆的枯萎过程对于植物养分保持和凋落物分解具有重要意义，且非叶器官的养分重吸收率明显高于前人的预期。另外，受土壤资源可利用性的影响，凋落物质量在微尺度内也存在较大的变异，凋落物质量可能反馈于土壤资源条件并维持土壤养分的异质性（Lü et al.，2012）。进一步基于氮、磷添加控制实验的研究发现：随着氮添加量的增多，优势物种羊草和大针茅的叶片氮、磷的重吸收率降低，N/P 与氮添加量呈负相关，表明植物与土壤之间可能存在由养分重吸收介导的正反馈作用（Lü et al.，2013）。该研究说明，草地生态系统中氮素和磷素在吸收与周转的循环过程中处于动态耦合状态，植物氮、磷重吸收对氮沉降的趋同性响应，意味着养分重吸收是植物和生态系统面对氮沉降增加而进行主动调节的重要机制。

1.3 内蒙古典型草原的生态系统结构、功能及其维持机制

1.3.1 典型草原的生态系统结构与功能

内蒙古站所在的锡林河流域是我国中温带半干旱典型草原最具典型性和代表性的区域。区内的代表性群落为羊草草原和大针茅草原。内蒙古站的综合观测场即建立在羊草草原群落。群落的优势物种为根茎类禾草羊草和大针茅、冰草、洽草等密丛型禾草。这些禾草的生物量之和占群落总生物量的 60% 以上（姜恕等，1985）。基于 1981—2011 年内蒙古站长期围封样地的观测发现，植物多样性呈现明显的变化，其中 1981—1991 年间呈增加趋势，1992 年后多样性呈下降趋势。植物多样性的变化趋势主要由多年生杂类草的变化引起，占群落生物量主体的禾草类物种的数量保持稳定。不同功能群的相对生物量也呈现明显的时间变化，自 1992—2011 年，C_3 植物的相对生物量显著降低，而 C_4 植物的相对生物量不断增加（Li et al.，2015）。相比自然围封群落，内蒙古站的退化恢复样地经过 10 年（1983—1993 年）的围封恢复，群落的植物多样性没有明显变化，但群落的均匀度随着恢复年数的增加不断降低，趋向于综合观测场代表的顶级群落（Li et al.，2008）。

内蒙古典型草原地处半干旱区，水分是草地生态系统初级生产力的主要限制因子。基于内蒙古站的羊草（*Leymus chinensis*）草原和大针茅（*Stipa grandis*）草原连续 24 年的长期定位监测发现，1—7 月的降水量是影响草原生态系统初级生产力的主要因子（Bai et al.，2004），但其水分利用效率随年降水量的增加而降低（图 1.4）（Bai et al.，2008）。在区域尺度上，生态系统初级生产力随年平均降水量的增加而增加，但其变异性则逐渐降低，稳定性逐渐增加；另外，降水利用效率（rain-use efficiency，RUE）在空间和时间尺度上呈相反的变化趋势，沿空间尺度降水利用效率随降水量的增加而增加，与同一生态系统的降水利用效率随年降水量的增加而降低相反；此外，内蒙古高原植物群落的降水利用效率，在最干旱年份和最湿润年份均表现出显著的趋同，分别为 1.08 $g \cdot m^{-2} \cdot mm^{-1}$ 和 0.51 $g \cdot m^{-2} \cdot mm^{-1}$（Bai et al.，2008）。这些结果对预测未来全球变化背景下草原生态系统结构和稳定性响应格局具有重要的意义。

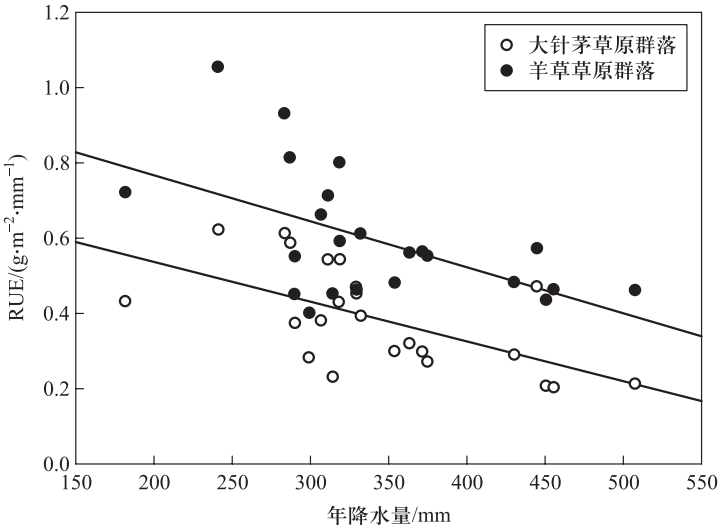


图 1.4　内蒙古站大针茅草原和羊草草原群落的降水利用效率（RUE）与年降水量的关系
（重绘自 Bai et al.，2008）

甲烷作为仅次于二氧化碳的第二大温室气体，其温室效应是单位质量二氧化碳的 25 倍（IPCC，2007）。传统观点认为，陆地植物的甲烷释放是由地下微生物分解产生的甲烷从植物茎部释放到大气中的，植物本身并不释放甲烷。中国科学院植物研究所的王智平研究员通过稳定性碳同位素标记的方法，首次在内蒙古草原证明植物可以释放甲烷，但释放甲烷的植物仅限于木本灌木，所有草本植物均不释放甲烷（Wang et al.，2008）。进一步对内蒙古锡林河流域的甲烷收支估算表明：虽然锡林河流域的草地面积分布很广，但其吸收的甲烷却远低于该区域湿地和动物的释放量。其中放牧和非放牧草地的甲烷吸收速率分别为 3.3 kg $CH_4 \cdot hm^{-2}$ 和 4.8 kg $CH_4 \cdot hm^{-2}$，而湿地和放牧家畜的甲烷释放速率分别为 791.0 kg $CH_4 \cdot hm^{-2}$ 和 8.6 kg $CH_4 \cdot hm^{-2}$。基于放牧草地、未放牧草地和湿地分布面积的推算，锡林河流域每年甲烷释放量约为 7.29 Gg CH_4。从实现甲烷收支平稳的角度分析，当前的放牧强度已超过甲烷零释放的 8 倍。因此，从我国北方草地的整体状况来看，过去几十年快速增长的放牧压力，已经把我国北方温带草地转变为甲烷的释放源（Wang et al.，2009）。

1.3.2 放牧对典型草原生态系统结构和功能的影响

放牧是我国温带典型草原最主要的土地利用方式。自 20 世纪 50 年代以来，内蒙古地区的人口不断增加，畜牧业生产迅速发展，长期过度利用带来的生物多样性丧失和生态系统功能退化已经严重影响了区域的社会经济发展。研究放牧对生态系统结构和功能的影响，是草地资源可持续利用的重要前提和基础。

（1）放牧对植物多样性的影响及其机制

过度放牧是导致世界范围内草地生物多样性丧失的主要原因之一（Milchunas et al.，1988；Olff and Ritchie，1998）。内蒙古草原地处干旱和半干旱区，具有较长的放牧历史，尤其是在当前的重度利用情况下，放牧在很大程度上造成物种多样性的降低。基于内蒙古站放牧实验平台（杨婧等，2014；Li et al.，2015；Li et al.，2017）的研究发现，放牧降低了草原的植物物种多样性（α 多样性和 γ 多样性），而放牧对多样性的促进作用仅在小尺度（李永宏，1993）或轻度利用（杨婧等，2014；Li et al.，2015）情况下才会发生。在内蒙古典型草原区域，放牧往往降低物种多样性，这与部分草甸草原（Liu et al.，2015）以及欧洲、美洲等其他地区（Olff and Ritchie，1998）放牧对物种多样性显著的正效应不同。另外，放牧对物种多样性的影响还受地形和降水条件调控，平地对放牧的缓冲能力强于坡地，干旱会加剧过度放牧对生物多样性的影响（杨婧等，2014）。因此，在确定合理的放牧强度时，应结合地形和降水条件，有针对性地加强不同生境系统下植物多样性的保护。

（2）放牧对生态系统功能的影响

放牧是影响草地生产力的重要因素。基于内蒙古站长期放牧实验平台的研究发现，中度和重度放牧降低了从物种、功能群到群落三个组织水平的地上生物量（Wan et al.，2011），但轻度放牧有助于增加地上生物量（李永宏和汪诗平，1999；Li et al.，2017）。此外，生态系统结构和功能往往对放牧强度存在非线性响应（Diaz et al.，2007）。基于内蒙古站的长期放牧实验平台研究发现：当放牧强度超过 3.0 只羊 · hm^{-2} 时，典型草原生态系统的生产力下降，群落结构也发生明显改变（图 1.5），其中优势物种组成的变化是引起群落结构和功能改变的主要原因（Li et al.，2017）。根系是植物重要的养分和水分吸收系统。在内蒙古典型草原生态系统中，草地的地下生产力受降水和放牧共同影响（Gao et al.，2011；Bai et al.，2012），其中气候对地下生产力的影响达 25%，放牧的影响达 35%，相比于长期土地利用，地下生物量在面对气候变异时具有更高的弹性。放牧显著降低了草地的地下生物量（放牧群落，1490 ~ 1670 g · m^{-2}；围封群落，2390 ~ 2530 g · m^{-2}），且随着放牧强度的增加，地下根系的分布呈现浅层化现象，但放牧没有改变根系周转速率（Gao et al.，2008）。

不同利用强度下草地群落的空间结构存在差异，其中围封禁牧区和过度放牧下的群落结构均趋向于同质化，而轻度利用下的草地群落结构趋向于非均质，表现为斑块状分布的过度啃食区和拒食区共存，且这种异质性的群落结构只有在轻度利用的情况下才稳定存在（Ren et al.，2015）。传统放牧区呈斑块状分布的群落结构并不一定会降低草地的生态系统功能。基于 6 年的放牧实验发现，具有斑块状结构的群落呈现出更高的生物多样性和更大的凋落物与土壤环境变异，由此形成具有较高水分和养分的沃岛，有助于草地生态系统功能的恢复和最大化（Ren et al.，2015）。

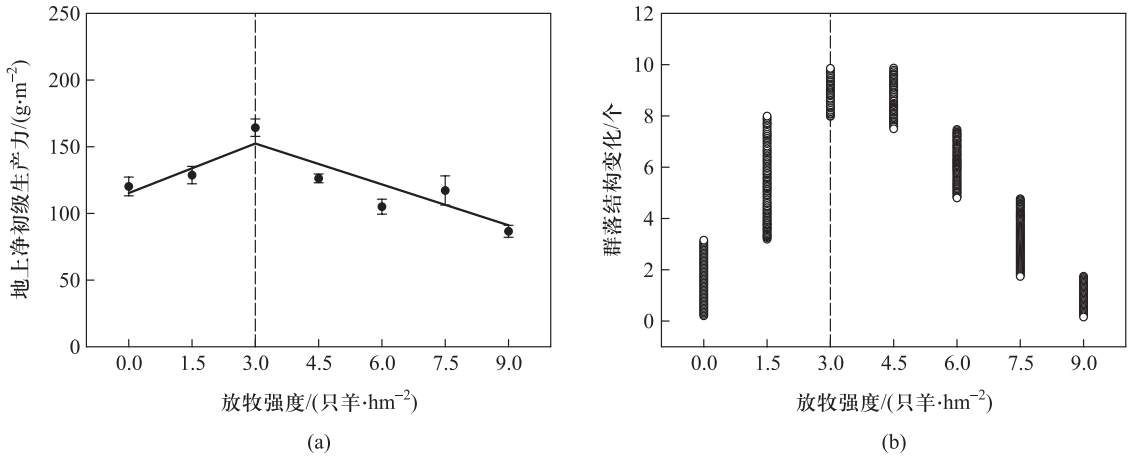


图 1.5　内蒙古站长期放牧实验平台中地上净初级生产力（a）和群落结构变化（b）与放牧强度的关系（2009 年）（改自 Li et al., 2017）

注：群落结构阈值的变化用群落中物种多度均值和方差的变化表示。通过 *R* 软件包 TITAN 的非参数拐点分析（nonparametric change-point analysis, nCPA）计算群落结构的阈值。拐点被定义为某个特定的放牧强度，它可以将物种多度数据分为两组并且组间的均值或方差的差异最大

放牧不仅改变了草地生态系统的生产力和结构，对生态系统的氮循环也产生了深刻的影响。中德合作项目成员德国霍恩海姆大学 Marcus Giese 研究团队基于放牧实验平台三年（2014—2016 年）的连续野外实验，通过测定不同放牧强度（长期重度放牧、冬季放牧和围封未利用）下草地的氮通量和氮库，首次系统深入地研究了放牧对内蒙古草原氮收支和氮循环的影响（Giese et al., 2013）。研究发现：影响内蒙古草原氮收支的主导因素是大气氮沉降、风蚀和水蚀。其中，长期重度放牧造成风蚀加剧引起的氮流失（0.4 ± 0.4 g N · m^{-2}）和打草（1.13 ± 0.15 g N · m^{-2}）与夜间羊圈留存的排泄物（0.57 g N · m^{-2}）是草地氮损失的主要途径，而气体形式（N_2O、NO_x、N_2 和 NH_3）的氮损失和以羊毛、肉产品输出的氮损失的量则非常小（表 1.1）。基于氮平衡的计算发现，在重度放牧区，氮的年平均损失量为 0.9 ± 0.8 g N · m^{-2}，而长期围封区则表现为氮汇，氮的年输入量为 1.8 ± 1.1 g N · m^{-2}，其中氮的主要输入来源为干沉降。另外，重度放牧不仅减少了表层土壤有机氮的氮库，还降低了与植物氮吸收、分解、总微生物氮周转和生物固氮有关的氮通量。气候变化带来的大气氮沉降能显著改变氮库的源汇途径以及氮通量。

表 1.1　2004—2006 年间内蒙古典型草原不同放牧强度下草地的年平均氮收支　（单位：g N · m^{-2}）

氮平衡组分	长期重度放牧	冬季放牧	围封未利用
氮增加			
净干沉降 †	§	0.3 ± 0.2	1.2 ± 0.8
湿沉降 †	0.6 ± 0.2	0.6 ± 0.2	0.6 ± 0.2
N_2 固定 ‡	0.05 ± 0.03	0.05 ± 0.03	0.05 ± 0.03
氮流失			
净尘土流失 †	0.4 ± 0.4	§	§

续表

氮平衡组分	长期重度放牧	冬季放牧	围封未利用
N_2O 排放 †	0.01 ± 0.006	0.01 ± 0.006	0.02 ± 0.005
NO_x 排放 †	0.03 ± 0.006	0.03 ± 0.006	0.03 ± 0.006
反硝化作用（N_2 丧失）‡	0.01 ± 0.006	0.01 ± 0.006	0.02 ± 0.005
NH_3 挥发（来自尿斑）‡	0.09 ± 0.02	0.001	0
土壤毛细上升和淋溶	§	§	§
湿沉降后的地表径流 ‡	0.06 ± 0.02	§	§
有机氮流失（水蚀和风蚀）‡	0.3 ± 0.1	§	§
输出到羊圈的排泄物（尿、粪便）	0.57	0.06	0
羊肉输出	0.08	0	0
羊毛输出	0.05	0.02	0
干草生产（占地上生产力的 60%）	0	1.13 ± 0.15	0
总收入	0.7 ± 0.2	1.0 ± 0.4	1.9 ± 1.0
总流失	1.6 ± 0.6	1.3 ± 0.2	0.05 ± 0.0
收支总量	−0.9 ± 0.8	−0.3 ± 0.6	1.8 ± 1.1

注：对于通过计算或估算所得的氮通量，用 † 和 ‡ 标注，其他与绵羊有关的氮平衡组分的估算由于是基于定量放牧率的实验所得，所以相对稳定。† 表示平均值 ± 标准差；‡ 表示平均值 ± 不确定性的范围；§ 表示没有相关过程（改自 Giese et al.，2013）。

牲畜数量的不断增加和施肥被认为是自工业革命以来大气温室气体 N_2O 浓度增加的主要原因。但传统方法中对 N_2O 的估算，多是基于生长季的测量结果，致使不同研究之间存在较大差异。基于中德合作项目连续两年的研究发现：冻融交替期是 N_2O 排放的一个重要时期，其中围封禁牧区在冻融交替时期的 N_2O 的排放占全年的 72%，但重度放牧区的排放量仅占全年排放量的 8%。相比于围封群落，放牧显著地减少了冻融交替时期 N_2O 的排放量，且随着放牧利用强度的增加，草地 N_2O 的排放量减少（Holst et al.，2008；Wolf et al.，2010）。另外，相较于放牧场，在锡林河流域的典型草原生态系统，N_2O 的排放源更多来自羊圈（Hoffmann et al.，2016）。基于牧户的定点研究发现，羊圈的 N_2O 排放量比放牧场的排放量高出三个数量级（Holst et al.，2007，2009；Chen et al.，2011）。当生长季的放牧率超过每公顷 1.5 只羊单位的时候，羊圈的 N_2O 排放量超过区域总排放量的 31%，而散落在放牧场粪尿的 NO_2 排放量仅占区域 N_2O 总排放量很小的一部分（Holst et al.，2007）。

（3）放牧对牧草养分的影响

牧草是放牧家畜最重要的食物来源，牧草的产量和质量是关系畜牧业发展的基础。放牧和水热条件的变化都会影响牧草的养分状况。基于放牧实验平台的研究发现，作为牧草品质的主要指标，粗蛋白质（CP，crude protein）含量和纤维素酶可消化有机物（CDOM，cellulase digestible organic matter）含量无论是在传统放牧还是混合利用情况下，均随放牧强度的增加而增加，而中性洗涤纤维（NDF）和木质素（lignin）在部分年份随利用强度增加而降低（Schönbach et al.，

2009，2012；Muller et al.，2014；Ren et al.，2016a，2016b）。虽然放牧会影响牧草的养分含量，但不同物种的养分含量受放牧的影响存在差异。基于 2008 年和 2010 年两个干湿年份的研究发现，放牧显著增加了羊草（*Leymus chinensis*）、根茎冰草（*Agropyron michnoi*）和糙隐子草（*Cleistogenes squarrosa*）的养分（CP、CDOM）含量，但对大针茅的影响很小（Ren et al.，2016）。另外，牧草养分含量受生长季的水热分配调控，具有明显的年际和季节变异，大部分植物的养分在湿润年份要高于干旱年份，而且每年生长季早期（7 月）的养分含量最高，生长季末期（9 月）的养分含量最低。由于牧草的生产力主要受优势种而不是物种多样性的影响，所以牧草的养分产量主要由优势物种的 ANPP 决定，而养分含量和物种多样性的影响较小（Ren et al.，2016b）。

（4）过度放牧加剧蝗虫的爆发

在内蒙古草原，蝗虫灾害始终是生产中的一个重要问题。特别是 20 世纪 80 年代以后，随着放牧活动的增加，草地退化严重，蝗虫灾害发生频度有明显增加的趋势。美国亚利桑那州立大学 James Elser 研究组和中国科学院动物研究所康乐院士团队通过分析亚洲小车蝗（*Oedaleus decorus asiaticus*）的饮食结构，发现高氮食物会显著降低亚洲小车蝗的大小和生存能力，而重度放牧由于导致植物含氮量降低而有利于蝗虫的生长和发育（Cease et al.，2012）。该研究证明了过多的蛋白质可能不利于亚洲小车蝗的生长，提出了新观点：过度放牧降低了植物氮素浓度从而加剧了蝗虫爆发的频率，这一成果颠覆了传统的氮浓度增加导致蝗虫爆发的观点（William and Mattson，1980）。该研究部分解释了内蒙古草原退化与蝗虫成灾的关系，不仅对内蒙古草原蝗虫的控制具有意义，对世界其他地区草原蝗虫的控制也具有启发和借鉴意义。

1.3.3　氮沉降对典型草原生态系统结构和功能的影响

氮沉降导致的自然生态系统养分增加是全球变化的重要内容。研究表明，氮沉降显著影响干旱区和半干旱区的植物多样性、群落生产力、土壤生物结构和土壤碳氮循环等多个陆地生态系统过程和功能（Suding et al.，2005；Clark and Tilman，2008；Yang et al.，2012；Hautier et al.，2014）。研究氮沉降对内蒙古典型草原的影响对于我们认识草原生态系统结构和功能至关重要。

（1）氮沉降对植物生物多样性的影响

氮沉降往往降低群落的物种多样性（Hillebrand et al.，2007），但其效应在成熟群落和退化群落中存在差异。中国科学院植物研究所白永飞等研究人员基于长期养分添加实验平台（包括 6 个氮素添加梯度：0.00 g N·m^{-2}·年$^{-1}$、1.75 g N·m^{-2}·年$^{-1}$、5.25 g N·m^{-2}·年$^{-1}$、10.50 g N·m^{-2}·年$^{-1}$、17.50 g N·m^{-2}·年$^{-1}$、28.00 g N·m^{-2}·年$^{-1}$），研究了氮素添加对内蒙古典型草原成熟和退化群落不同组织水平（植物种、功能群、群落）上植物多样性的影响，结果发现：氮素添加显著降低成熟自然群落的物种多样性，其中多年生禾草和杂类草被一年生植物替代，而对退化群落植物多样性的影响较小（Bai et al.，2010）。深入研究引起物种丧失的机制发现，造成物种丧失的氮素添加阈值与物种的丰富度有关，稀有种丧失的阈值低于常见种；氮素添加后，资源消耗型物种（叶片氮素含量高、光合速率高、根冠比低、繁殖输出高等，如灰绿藜、轴藜等）的相对优势度增加，并逐渐取代资源保守型物种（如大针茅、冰草等），而土壤酸化对物种多样性的影响小于竞争作用（图 1.6）（Lan and Bai，2012）。

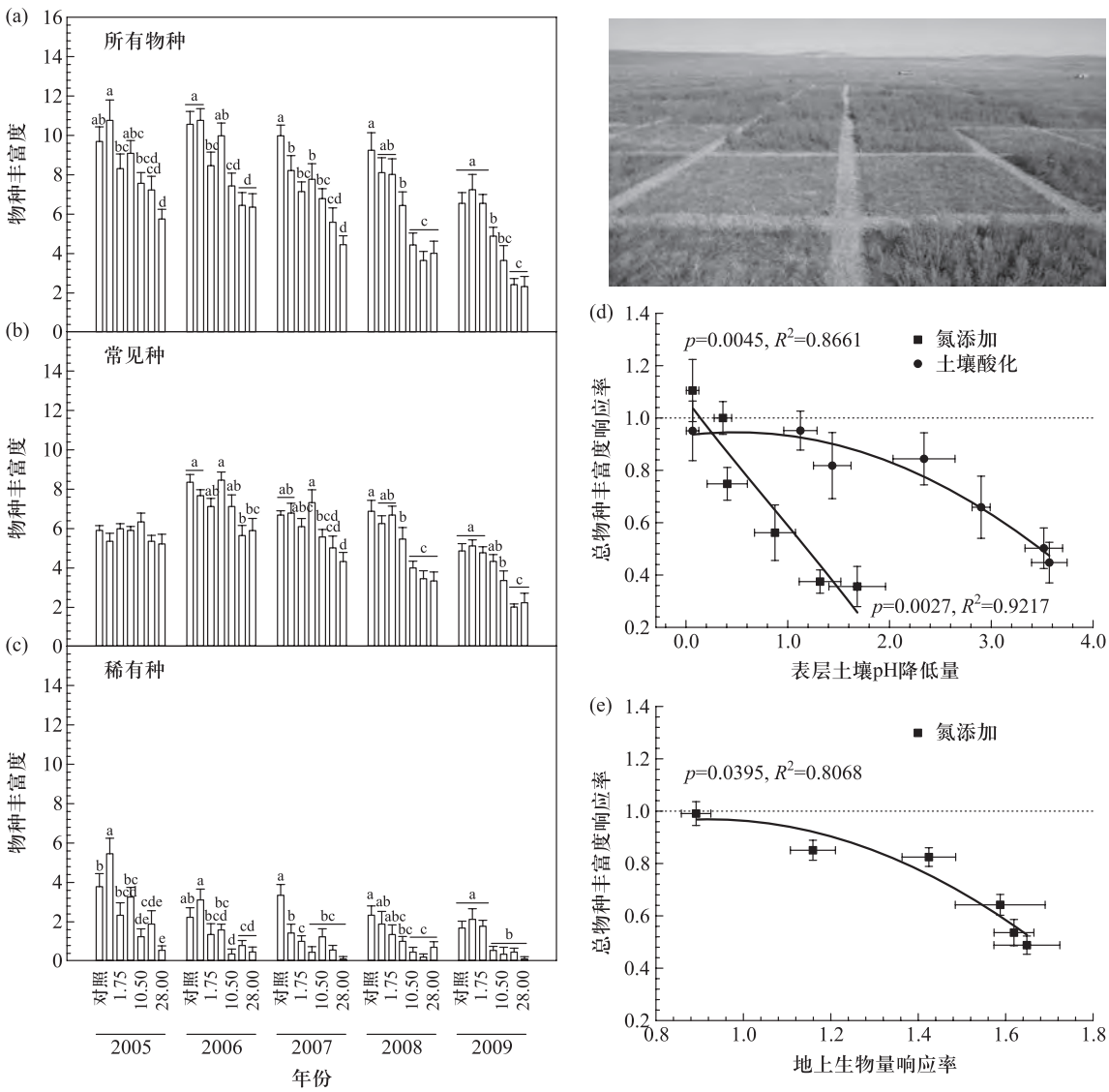


图 1.6　（a）–（c）长期养分添加实验平台（2005—2009 年）的群落所有物种丰富度、常见种丰富度及稀有种丰富度对氮素添加的响应；（d）–（e）氮素添加和酸添加实验引起的表层土壤酸化及地上生物量增加对总物种丰富度响应率的影响（改自 Lan and Bai，2012）

此外，以往有关氮沉降对物种多样性的影响多基于样方尺度（0.5 m^2 ~ 4 m^2），而氮沉降的影响往往发生于区域水平。对于氮沉降背景下生物多样性保护和生态系统管理，在不同空间尺度下氮素增加对生物多样性的影响非常必要。在不同空间尺度下氮素增加对植物多样性影响的研究表明：氮素增加导致物种多样性降低的程度随着取样面积增加而减小，而导致物种多样性降低的氮素添加阈值随着取样面积增加而增加，其中 1 m^2 下的阈值为 1.1 g N · m^{-2} · 年 $^{-1}$，25 m^2 下的阈值为 1.7 g N · m^{-2} · 年 $^{-1}$（Lan et al.，2015）。

（2）氮沉降对生态系统功能的影响

通过长期氮素添加实验发现，氮沉降有助于提高典型草原的地上生物量，且群落初级生产

力对氮素添加响应主要受土壤水分有效性和水分与氮素的耦合作用共同决定（Bai et al.，2010）。氮素添加可以显著地提高植物群落的降水利用效率，其值可以超过自然状态下群落降水利用效率的两倍以上（Bai et al.，2008）。该实验结论修正了 Travis Huxman 等（2004）关于提出的最大降水利用效率（RUE_{max}）不可超越的结论。虽然氮素添加能够提高草地的生产力，但其对生态系统稳定性的影响仍存在很大不确定性。基于内蒙古站两个氮添加平台的研究发现，氮素添加会导致群落生物量对干旱的敏感性增加，从而降低群落生物量的稳定性（包括增加生物量空间的异质性和年际的变异性）（Lan and Bai，2012），此外氮素增加也会通过降低物种丰富度和种间的异质性，导致群落稳定性下降（Zhang et al.，2017）（图 1.7）。

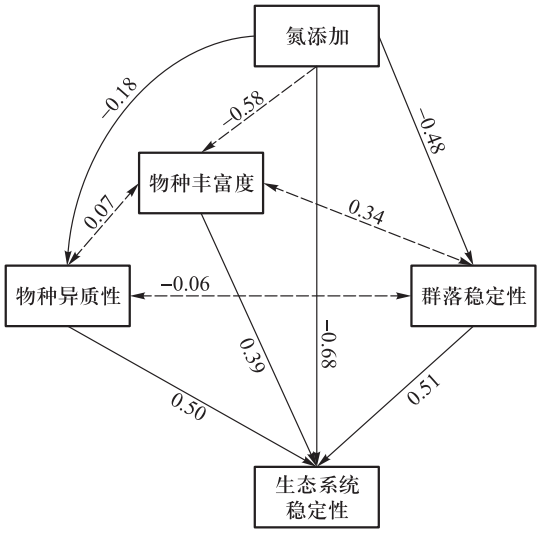
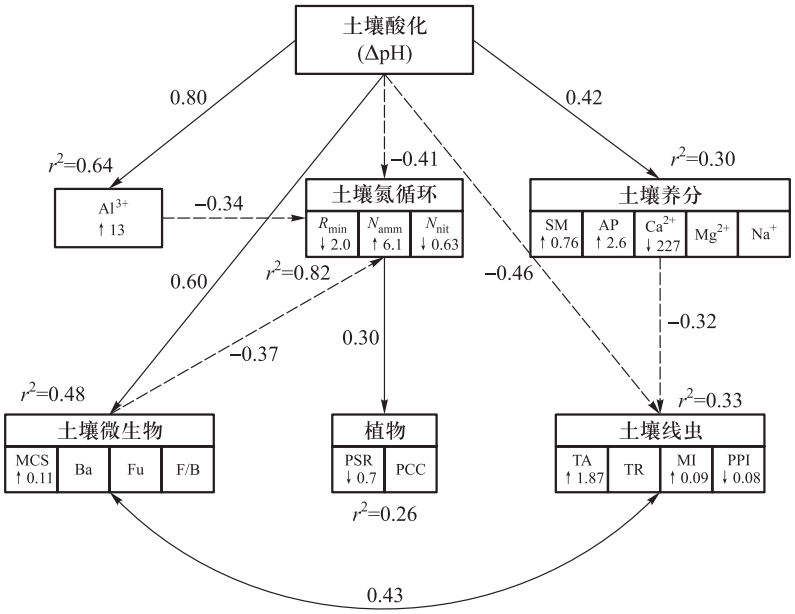


图 1.7　氮添加对内蒙古站羊草草原物种丰富度、物种异质性、群落和生态系统稳定性的影响

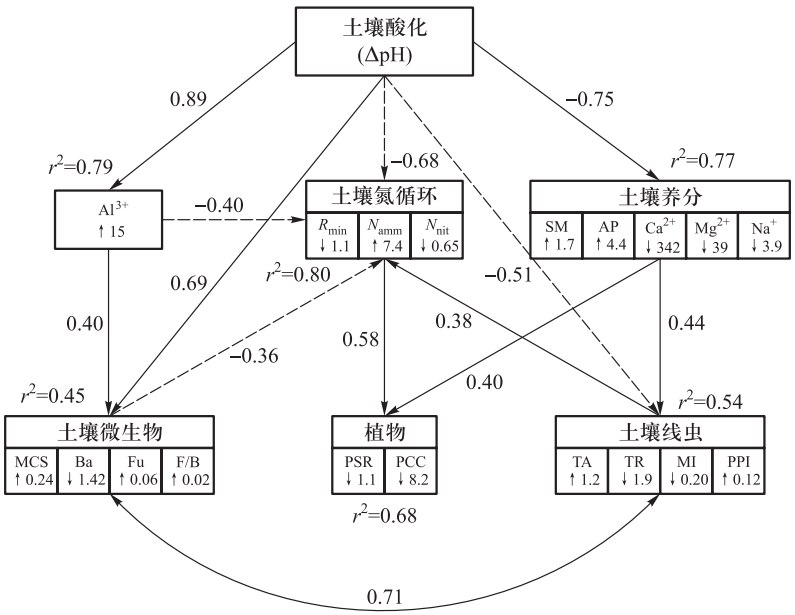
（改自 Zhang et al.，2016）

图中的数字表示相关系数。实线表示统计显著相关（$p<0.05$），虚线表示统计不显著相关（$p>0.05$）

大量研究证实外源氮素输入能影响群落生产力、植物和土壤生物结构组成、土壤碳氮循环等多个陆地生态系统过程和功能。这种影响主要来源于两个重要机制，其中之一是氮素添加直接增加土壤氮有效性，为植物和土壤生物提供生长所需的养分，从而刺激植物地上、地下部分的生长，而生物量的增加能为地下土壤食物网提供更多的碳输入；另外一个机制是长期氮添加会导致土壤酸化，酸化过程能降低植物生物量和多样性，也能改变土壤生物群落组成和土壤食物网。然而这两种机制在调节生态系统功能对氮素添加响应中的相对重要性还不明确。依托内蒙古站的长期氮素添加实验，结合土壤酸化实验，中国科学院植物研究所的陈迪马等研究人员发现：长期氮素添加和土壤酸化都降低土壤呼吸和土壤有机质分解呼吸但增加根系呼吸，其中有机质分解呼吸的降低主要是由于酸化降低了微生物生物量和真菌细菌比，而根系呼吸的增加是由于酸化增加了根系生物量和物种水平根系呼吸（Chen et al.，2015c）；另外，氮添加对土壤微食物网的影响主要来源于土壤氮添加所导致的土壤酸化过程，而并非由于土壤氮素增加所引起的土壤氮输入增加（Wei et al.，2013；Chen et al.，2016b；Ying et al.，2017），而氮素积累引起的微生物限制因素的转换改变了土壤有效态资源的化学计量比，弱化了植物和微生物间的互利关系，导致了土壤碳氮循环的解耦合（Wei et al.，2013）；此外，土壤酸化实验证实土壤酸化导致的植物多样性和生产力的降低受土壤氮循环直接调控，土壤生物主要起间接调节作用，而土壤毒害离子的增加也并不是导致植物多样性和生产力降低的直接因素（Chen et al.，2013a）（图 1.8）。这些研究成果首次系统评价了土壤生物群落和生态系统功能对氮素添加的响应中“土壤氮有效性”和“土壤酸化”两个机制的相对作用；证实了长期氮素添加导致土壤食物网、土壤呼吸、生态系统生产力和养分循环的变化主要来源于土壤氮添加导致的土壤酸化过程，而土壤氮素增加导致的土壤碳输入并不是主要途径。



(a)



(b)

图 1.8 长期氮素添加对草地生态系统土壤食物网生物组分（微生物和线虫）和植物群落的影响：（a）2010 年；（b）2011 年

R_{min}，氮矿化速率；N_{amm}，土壤铵态氮；N_{nit}，土壤硝态氮；SM，土壤含水量；AP，土壤有效磷；MCS，微生物群落结构；Ba，细菌；Fu，真菌；F/B，真菌细菌比；PSR，植物物种丰富度；PCC，群落盖度；TA，线虫丰富度；TR，分类群多样性；MI，成熟度指数；PPI，植物寄生线虫成熟度指数（改自 Chen et al.，2013a）

（3）氮素对磷素有效性的影响

与氮（N）的生物地球化学循环不同，磷（P）循环属于沉积型循环，其可再生性远低于N，因此P越来越成为植物生产力的限制因子（Elser et al.，2000）。特别是在全球变化的大环境下，人类活动加剧了N沉降使得自然生态系统中N的有效性加倍（Vitousek et al.，1997），而N有效性的增加会改变生态计量化学平衡，导致P的相对限制增加（Elser et al.，2009）。目前对生态系统N作用的研究远远多于P（Marklein and Houlton，2012），且始终未形成统一的N、P关系理论体系。由于生态学研究对象在时间、空间上差异很大，对于部分研究，例如，N、P限制，N、P添加对生物多样性的影响等均有较大争议；而在养分和水分条件发生显著改变的背景下，生态系统优势物种和生态系统功能对P限制的响应是急需了解的。内蒙古站自2009年开展N、P添加实验，主要研究了在N沉降背景下P的限制性对物种、群落及生态系统的影响。在自然环境下，单纯的P添加处理并不能显著提高植物叶片的N及P含量（或浓度），也不改变N/P；但在N和P同时添加的情况下，植物的P含量却显著提高了，说明P有效性的增加高度依赖于土壤的N含量，这可能与N添加造成土壤pH降低，从而引起P的有效性增加有关（Long et al.，2016）。进一步对N、P共同添加在不同组织水平上影响的详细分析表明：在物种水平上，N添加虽然提高了植物叶片的N/P，但也加剧了P的相对限制；在群落水平上，由于土壤有效N、P含量的年际间变异，正常降雨年份群落处于N限制，而相对湿润的年份则受到N和P的共同限制，表明P的限制性会受到水分、氮素等因子的调节；此外，从植物叶片、根系到微生物，其N/P的稳定性逐渐增加（Zhan et al.，2017）。随着N沉降的日益加剧，未来生态计量化学比的平衡会被逐渐打破，而P将会成为草地生态系统的主要限制因子。

1.4　区域生态系统重要生态学问题及其过程机制

1.4.1　内蒙古草原区生物多样性和生态系统功能的维持机制

（1）生物多样性与生产力的关系

过去几十年中，人类活动对生态系统影响的速度和广度均超过了历史上任何一个可比时期，引起了全球范围内生物多样性丧失和生态系统服务功能退化，进而对人类福祉产生了深刻的影响。生物多样性与生态系统生产力的关系以及生产力的稳定性维持机制是当前生态学理论研究的核心问题，对生物多样性保护和生态系统管理具有重要意义（Tilman，1999；Chapin et al.，2000；Loreau et al.，2001；Hooper et al.，2005，2012）。当前的主流观点认为生物多样性与生产力的关系（productivity-diversity relationship，PDR）属于驼峰型（hump-shaped）关系，即生物多样性在中等大小时生产力最高，生物多样性最高时，生产力反而处于中等水平（Grime，1973；Huston，1979；Waide et al.，1999；Mittelbach et al.，2001；Fraser et al.，2015）。然而有关PDR的关系是驼峰型还是单调的线性相关，以及影响PDR关系的生物学机制等仍存在较大争议。中国科学院植物研究所的白永飞研究员等人基于内蒙古锡林郭勒盟地区854个野外样点的调查数据，首次从不同组织层次（群丛、植被亚型和植被型）和不同空间尺度（样地尺度、景

观尺度和区域尺度）证实了内蒙古草原的 PDR 存在普遍的线性正相关，而非驼峰型；在区域尺度，PDR 受年平均降水量的影响，降水量越大，PDR 的斜率越小；此外，放牧虽然能够降低草地的生产力和生物多样性，但不会改变 PDR 的线性相关关系（Bai et al.，2007）。研究结果不仅对退化草原的恢复与管理提供了依据，还有助于人们了解未来气候变化对欧亚草原植被的影响。

生物多样性不仅关系到生态系统的生产力，还会影响生态系统的碳固持（Midgley，2012；Lange et al.，2015）。然而环境因子和人类活动如何在大尺度上影响陆地生态系统多样性－生产力－土壤碳储量之间的关系，目前学术界仍存在较大争议。内蒙古站依托中科院战略性先导科技专项（碳专项）不同生态系统（草地、森林和灌丛）下 6000 多个野外调查点的调查数据，首次在国家尺度证实了自然生态系统中多样性与生产力和土壤碳储量之间普遍存在正相关关系。其中，土壤碳储量的空间分布格局不仅受气候因子的直接控制，气候因子还能通过影响多样性和生产力对土壤碳储量进行间接调控；适宜气候条件（尤其是高降水量）下生物多样性对固碳的促进作用，有利于抵消氮沉降等人为活动对固碳的负效应（Chen et al.，2018）。该研究表明，通过适当的保护和管理措施，维持高的生物多样性有利于增加土壤碳储量，改善生态系统服务功能。

（2）蒙古高原土壤生物的分布格局和驱动因子

土壤生物在陆地生态系统元素循环、多样性维持、植物群落构建等过程中扮演重要角色。中国科学院植物研究所的陈迪马研究员等基于中国－蒙古样带调查和内蒙古站控制实验平台的研究揭示了蒙古高原土壤微生物和土壤线虫群落的分布格局和驱动因子，其中土壤线虫群落主要受降水影响，而土壤微生物群落主要受降水和土壤环境共同调控；另外，土壤食物网内不同的土壤生物组分对环境因子存在不同适应策略（Chen et al.，2015a，2015b）。相比土壤微生物，土壤线虫群落对降水有更高的敏感性，从荒漠到草甸草原，降水对土壤线虫群落的影响越来越强，而对微生物的影响逐渐减弱（Chen et al.，2015a）。

目前多样性与生产力关系的理论研究主要用植物作为模式群落，有关土壤生物是否也和植物群落一样，存在类似的多样性与生产力关系或机制还不清楚。基于蒙古高原 220 个样方调查的数据发现，土壤生物的 PDR 与植物群落的 PDR 存在较大差异（Chen et al.，2016a）。其中，土壤线虫生物量与线虫多样性（α 和 γ）存在与植物群落相似的线性正相关关系，但线虫 β 多样性与土壤线虫生物量之间呈负相关关系。另外，土壤线虫多样性－生物量之间的关系强于植物群落，当考虑环境因子（气候、土壤环境、土壤养分）对多样性和生物量的共同作用后，植物的多样性－生物量关系消失，而土壤线虫的多样性－生物量的正相互关系依然存在（图 1.9）。这些结果表明，多样性与生产力的关系在不同生物类群间存在差异，要得到普适性的多样性－生物量的关系需要考虑更多的生物类群。

（3）内蒙古草原区生态系统功能稳定性的维持机制——补偿效应

生物多样性与生态系统功能的关系已成全球范围内倍受关注的重要领域。内蒙古站的研究团队，针对多样性与稳定性的关系这一生态学热点问题，从自然生态系统的不同组织层次入手，系统地分析了羊草草原群落和大针茅草原群落连续 24 年的长期定位监测数据，揭示了不同物种和功能群之间的补偿作用是生态系统稳定性维持的重要机制，生态系统稳定性从植物种、功能群到群落水平逐渐增加（白永飞和陈佐忠，2000；Bai et al.，2004）。

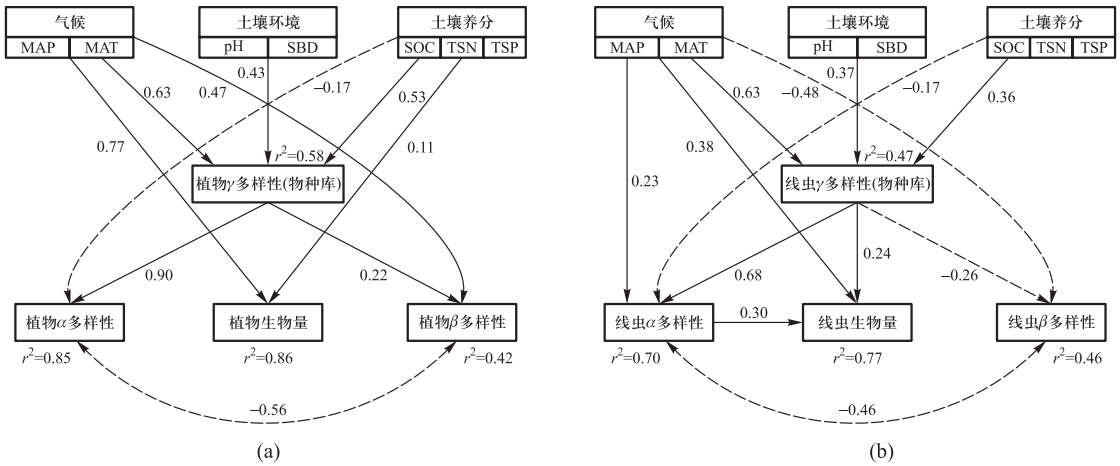


图 1.9　草地生态系统环境因子对植物（a）和土壤线虫（b）多样性组分的影响以及环境因子和多样性组分对生产力的影响：MAP，年平均降水量；MAT，年均温；SBD，土壤容重；SOC，土壤有机碳；TSN，总氮；TSP，总磷（改自 Chen et al.，2016a）

补偿效应源自不同功能群物种间的互补作用，但不同功能群的补偿作用存在差异，因此物种多样性丧失引起的补偿效应对生态系统功能的改变存在较大的不确定性。基于多年人工剔除的生物多样性实验（图 1.10），内蒙古站进一步从自然群落的角度证明了补偿效应能够缓解多样性丧失对生态系统功能的不利影响，但对于没有发育出完好补偿机制的群落来说，多样性的丧失，尤其是建群种的丧失，会对生态系统功能产生较大的影响（Pan et al.，2016）。对于受人为干扰的自然生态系统，补偿作用的表现受利用方式的影响。基于内蒙古站放牧实验平台的多年研究发现（Ren et al.，2018），无论是传统放牧区，还是混合放牧区，生态系统地上生物量在时间尺度上的稳定性相似，但起作用的原因不同，补偿作用仅在传统利用方式下起作用。

植物多样性的丧失不仅会影响植被生态系统的稳定性，还会影响土壤食物网及其调控功能。依托内蒙古站的生物多样性与生态系统功能实验平台，中国科学院植物研究所的陈迪马等研究人员探讨了植物群落调控土壤生物群落食物网及其生态系统功能的影响机制，研究发现：植物功能群丧失之所以改变土壤微生物群落，主要是由于植物群落的功能群组成和生物量发生明显的变化，而土壤线虫群落的响应主要受植物功能群组成、生物量，以及线虫食物资源的调控（上行效应）（图 1.11）（Chen et al.，2013b）；相对于次要植物功能群，草地优势植物功能群丧失对土壤食物网的影响更强烈；植物功能群丧失导致土壤食物网由真菌食物网向细菌食物网转变（图 1.12）（Chen et al.，2016c）。研究结果证实草地生物多样性－功能群的丧失能导致草地碳储存降低和养分流失，因此在草地生态系统的管理和恢复过程中，人们不仅要关注植物多样性的恢复，同时还要加强土壤生物群落的恢复。

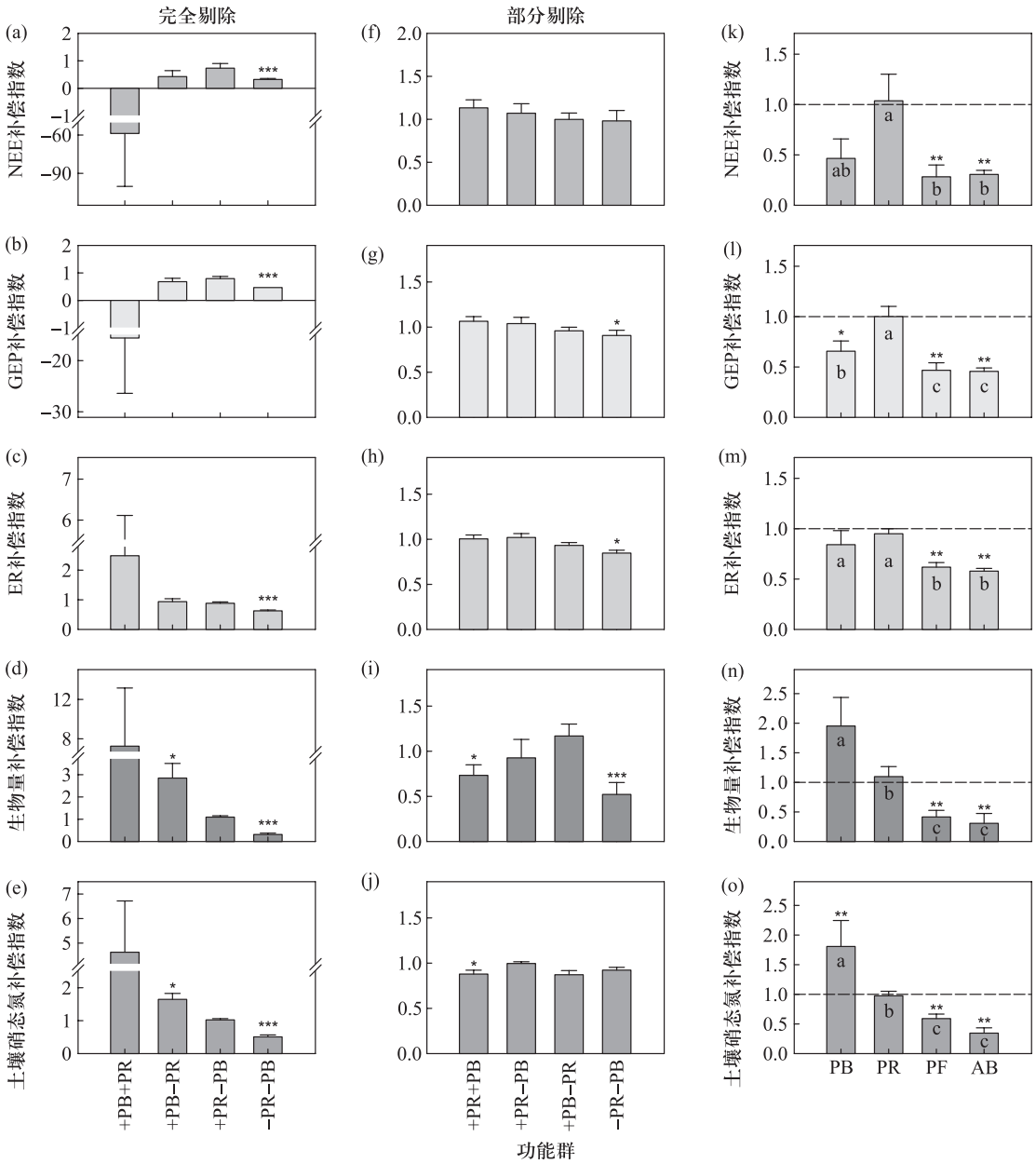


图 1.10　内蒙古站生物多样性与生态系统功能实验平台中完全剔除（a—e）和部分剔除（f—j）单个功能群对净生态系统碳交换（NEE）、总生态系统生产力（GEP）、生态系统呼吸（ER）、生物量（biomass）和土壤硝态氮（NO_3^--N）利用率的补偿指数以及不同功能群对各生态系统功能的补偿效应（k–o）。

注：+ 表示只保留单个功能群，– 表示剔除单个功能群。（改自 Pan et al., 2016）

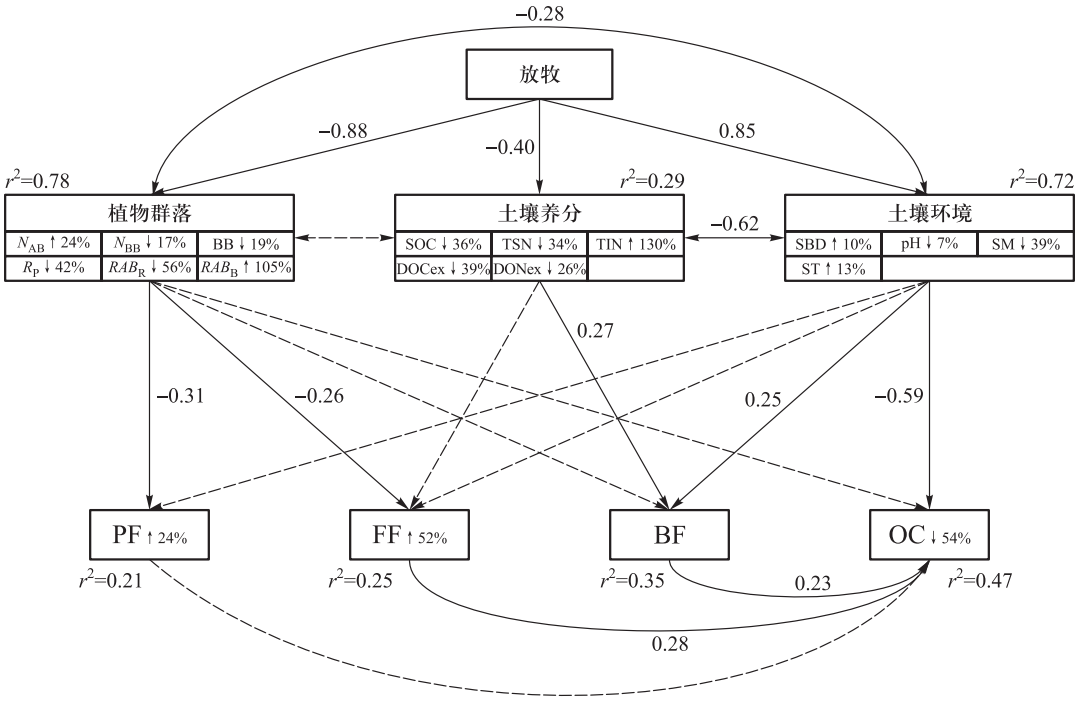


图 1.11　放牧引起的下行效应（top-down effect）导致土壤线虫群落营养级内存在上行效应（bottom-up effect）。

N_{AB}，地上植物氮浓度；N_{BB}，地下根系氮浓度；BB，地下根系生物；R_P，植物物种丰富度；RAB_R，根茎禾草；RAB_B，丛生禾草；TIN，土壤无机氮；DOCex，可溶性有机碳；DONex，可溶性有机氮；SBD，土壤容重；SM，土壤含水量；PF，植食性线虫；FF，食真菌线虫；BF，食细菌线虫；OC，杂食 + 捕食性线虫（改自 Chen et al.，2013b）

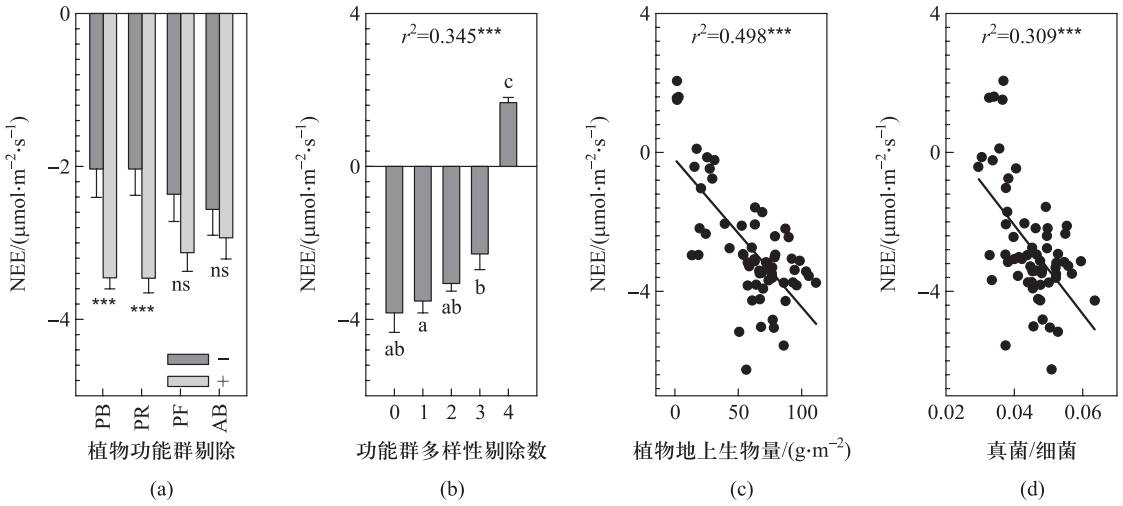


图 1.12　植物功能群丧失对净生态系统碳交换（NEE）的影响及其变化原因：（a）单个功能群丧失；（b）功能群丧失数量；（c）植物生物量；（d）真菌 / 细菌

PB，多年生丛生禾草；PR，多年生根茎禾草；PF，多年生杂类草；AB，一年生或二年生植物（改自 Chen et al.，2016c）

（4）内蒙古草原区生态系统功能稳定性的维持机制——化学计量内稳性

化学计量内稳性（环境或者食物中的养分组成发生变化而生物体维持元素相对不变的一种能力）是生物在长期进化过程中，适应环境变化的结果，是生理和生化调节的反映。因此，从化学计量内稳性的角度探讨生态系统结构、功能和稳定性成为近年研究焦点之一。韩兴国研究团队在内蒙古站基于氮磷添加实验，结合 1200 km 的样带调查和内蒙古站 27 年的长期监测数据，首次从时间和空间尺度研究了内稳性与生态系统结构、功能和稳定性的关系，证实了内稳性高的物种具有较高的优势度和稳定性（图 1.13），内稳性高的生态系统具有较高的生产力和稳定性（图 1.14）（Yu et al.，2010）。该研究成果拓展了生态化学计量学研究的范畴和生态系统稳定性的维持机制，同时，也为研究生物多样性与生态系统功能的关系，以及预测植物对全球变化的响应提供了重要的理论基础（Yu et al.，2015）。

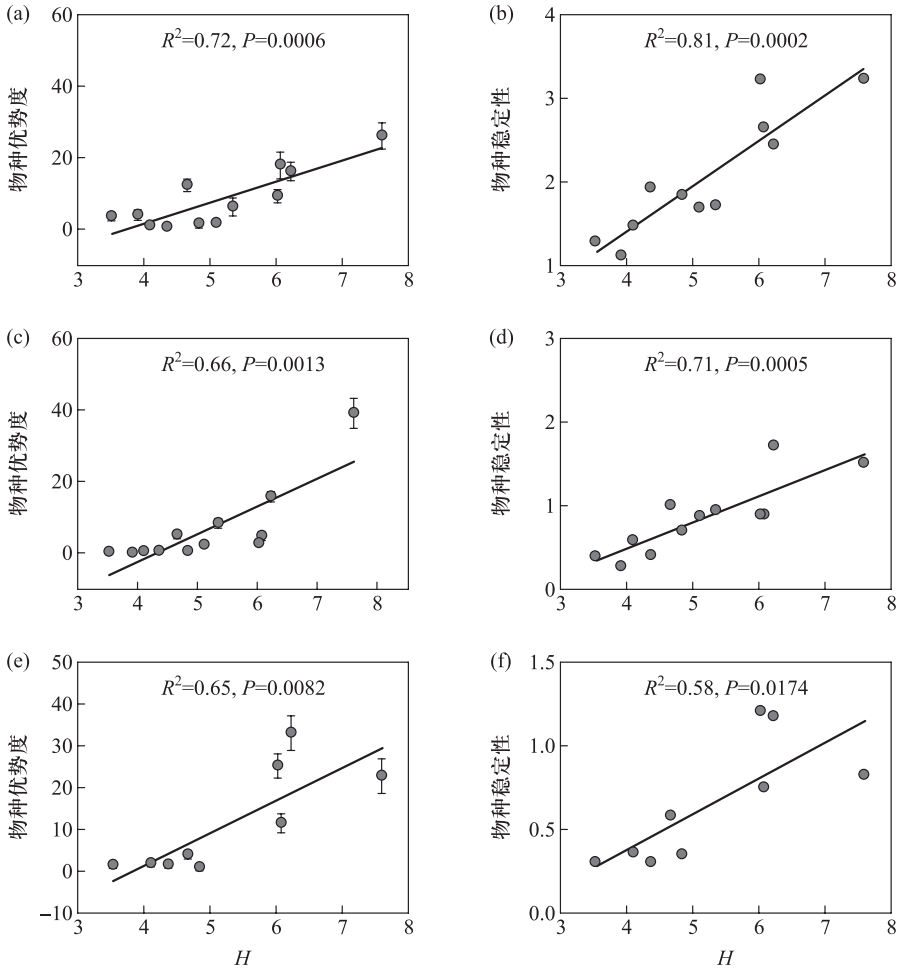


图 1.13　物种的内稳性（H）与物种优势度和物种稳定性的关系：
（a）（b）施肥试验；（c）（d）27 年监测；（e）（f）样带调查

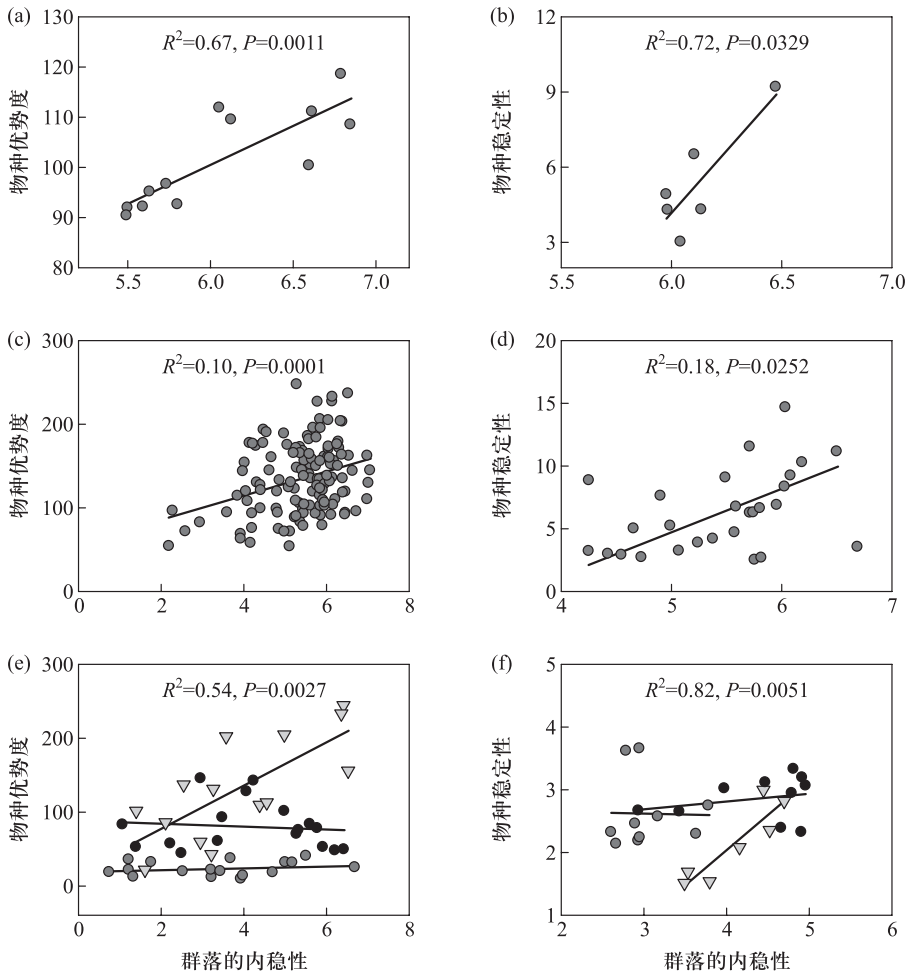


图 1.14　群落的内稳性与物种优势度和物种稳定性的关系：
（a）（b）施肥试验；（c）（d）27 年监测；（e）（f）样带调查

1.4.2　草地生态系统的适应性管理

放牧和打草是天然草原主要的利用方式，能从多个方面影响草地生态系统的结构和功能。内蒙古站自建站以来一直关注该问题，开展了大量有关不同放牧率、放牧方式和放牧季节对生态系统影响的研究。基于传统利用方式（只打草或只放牧）和混合利用方式（打草和放牧隔年轮换）的比较研究发现，混合利用方式下的草地生态系统在中度到重度利用条件下，生产力及其弹性更高，而且在混合利用方式下，放牧强度对草地生产力的影响要远小于传统利用方式，表明混合利用有助于减轻放牧对地上生物量的负效应（图 1.15）（Schönbach et al., 2011; Wan et al., 2011）。另外，与传统放牧（每年持续放牧）相比，混合利用的管理方式有助于减轻选择性采食引起的群落组成的变化（Hoffmann et al., 2016），同时，打草有助于土壤种子库的补充和群落多样性的维持（Wan et al., 2011）。

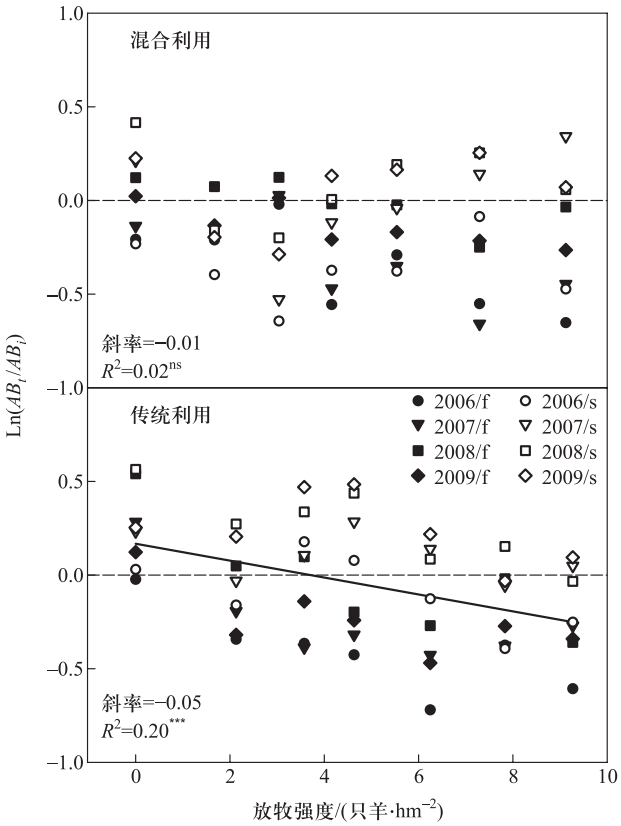


图 1.15　混合利用和传统利用下，群落地上生物量（*AB*）与不同放牧强度之间的关系

注：RI=ln（AB_t/AB_i），t 代表 2006 年、2007 年、2008 年和 2009 年，i 表示 2005 年；f 表示平地放牧系统，s 表示坡地放牧系统（改自 Wan et al.，2011）

基于不同放牧强度下绵羊生产性能的研究发现，增加放牧强度并没有明显提高绵羊的消化率和采食量，表明绵羊能够补偿逐渐减少的牧草可食量（Dickhoefer et al.，2014；Muller et al.，2014；Dickhoefer et al.，2016）。每只羊的增重效果仅在部分降水量较低的年份随利用强度的增加而降低，而其余年份则几乎没有差异（Lin et al.，2012）。因此，绵羊产量作为牧民从牲畜生产中获得潜在收入的表征，在大部分年份均随着放牧强度的增加而显著提高。但由于过度放牧容易造成草地生态系统的退化，不利于长期利用，故开展混合利用和适度舍饲喂养是确保典型草原作为畜牧业生产可持续利用的重要途径（Wang et al.，2007；Bösing et al.，2014）。

1.5　退化草地生态系统修复与生态系统管理

1.5.1　草地生产与生态功能的合理配置

针对我国畜牧业正经历着由传统利用管理模式向现代集约化发展模式转型的现状，基于长期定位研究和试验示范，内蒙古站提出了草地生产和生态功能合理配置的概念。在当前的

转型过程中，退化草地恢复和天然草地的合理利用是基础，人工草地建设是关键，而草地生产功能和生态功能的合理配置是转型成功与否的标志（白永飞等，2016）。所谓生产功能与生态功能的合理配置，就是在一定的地理区域或行政管理单元内，通过在优质土地上种植一定比例（1/20～1/10）的高产高效人工草地，在优质天然草地上建设基本草牧场，把传统畜牧业对天然草地的依赖转移到人工草地和基本草牧场，由人工草地和基本草牧场承担起主要的生产功能，使大部分天然草地的功能回归到其本来的自然生态属性，恢复和提升其生态功能，从而实现我国草牧业的可持续发展。因此，高效人工草地和基本草牧场建设是实现生产功能与生态功能合理配置的关键，建设人工草地和基本草牧场可以大大提高草地的产草量，并改善牧草品质。例如，苜蓿人工草地的产量可达 22.5 $t \cdot hm^{-2}$，是天然草地的 11 倍左右，羊草人工草地的产量可达 24 $t \cdot hm^{-2}$，是天然草地的 12 倍，青贮玉米的干物质产量可达 45 $t \cdot hm^{-2}$，是天然草地的 23 倍（杜青林，2006）。由此可见，建设优质高效人工草地和基本草牧场可以使饲草产量提高 10～20 倍，有望解决草地的饲草生产问题，并从根本上遏制过度放牧引起的草地大面积退化、生态功能严重衰退等生态安全问题（白永飞等，2016）。

实现天然草地的合理利用，使天然草地发挥其生态功能，是实现生产功能与生态功能合理配置的基础。天然草地的合理利用技术包括：① 退化草地封育技术，即针对退化草地，通过建设围栏或禁止放牧等措施，避免草地继续受到家畜的干扰，依靠其自我修复能力，逐步提高草地生产力、多样性和稳定性。迄今，草地封育是最有效的退化草地恢复技术之一，也是其他恢复技术实施的前提；② 划区轮牧技术，该技术是保护与利用相结合的有计划的放牧利用技术，该技术使得牧场有一个休息恢复的时期，是天然草地合理利用的中心环节（Wan et al.，2011）；③ 季节性休牧技术，该技术包括春季休牧和秋季休牧。其中春季休牧是指每年牧草返青期（4 月下旬—6 月中旬）禁止放牧，使退化草地得以休养生息。秋季休牧是指每年秋季牧草进入结实期，停止放牧，使牧草的种子得以成熟入土，以维持草地土壤种子库具有充足的种源；④ 割草地轮刈技术，该技术有利于保存草地土壤种子库的密度，减缓连续刈割引起的草原群落退化，促进草地的长期利用；⑤ 沙化草地治理的“三分模式”，针对占 1/3 面积的风蚀坑、流动沙丘（光头顶）、半流动沙丘等，采取工程措施（生物网格 + 固沙先锋植物）进行治理；对于占 2/3 面积的植被覆盖度较低的沙化退化草地通过围封禁牧，依靠其自我修复能力，加速植被的自然恢复，提升草地的生态功能。

1.5.2 沙化草地生态系统修复技术与示范

内蒙古站背靠浑善达克沙地，在对浑善达克沙地及严重退化沙化草地大量野外调查的基础上，发现该地区流动沙丘、半固定沙丘和风蚀坑的面积约占沙地总面积的 1/3，这类退化沙化草地需要采取人为措施进行治理；其余部分为固定沙丘、丘间平地和丘间低地，约占沙地总面积的 2/3，草地尚有一定量的植被覆盖，土壤中仍保存着一定数量的植物种子库，可以通过围封和休牧的方式，充分利用自然的力量使植被逐渐得以恢复。经过长期的试验研究，我们提出了浑善达克沙地及严重沙化草地生态恢复的“三分模式”，即对该类草地采取“三分之一治理，三分之二封育恢复”的技术。对于风蚀坑、流动沙丘（光头顶）等采用工程措施进行治理，补播固沙先锋植物，增加土壤种子库；对于固定沙丘、丘间平地和丘间低地只进行围封和休牧，依靠土壤种子库中的植物种子和现存植被的自我繁殖和更新能力，逐步实现植被的恢复。为了实施治理风蚀坑和流

动沙丘的工程措施，我们研究出了“生物网格治沙技术”。即通过播种小麦，扦插黄柳等措施，建立小麦和黄柳生物网格，再在网格内播种柠条、羊柴、沙蒿、沙生冰草、扁蓿豆等固沙先锋植物种。在生物网格的保护下，网格内的先锋植物实现定居，进而促进植被的恢复。实践证明，三年即可使风蚀坑和流动沙丘得到固定。该技术成果提出了依靠植物的自然繁殖策略、自我更新和恢复力实现植被恢复的新思路，不仅大大降低了沙地和严重沙化草地生态治理过程中的人力、物力和财力，同时显著提升了植被的恢复效果和生态效益。该项技术成果于 2007 年获得国家发明专利（专利号：ZL 200310117057.1），并在内蒙古锡林郭勒盟大面积推广。

1.5.3 人工草地种植技术与示范

人工草地建植是我国草原牧区实现草畜平衡，恢复退化草地，发展集约化草产业的基础。在我国干旱、半干旱地区，人工草地生产力低、稳定性差、利用年限短是制约草业发展的瓶颈。内蒙古站基于长期定位研究的科研成果，根据生态位理论、物种补偿作用和植物群落演替理论，在牧草品种选择上实现了四个组合：即长寿命牧草与短寿命牧草的组合，深根系牧草与浅根系牧草的组合，豆科与禾本科牧草的组合，耐旱品种与喜湿品种的组合。在生产管理上实现了旱作条件下的全程机械化。不仅提高了播种质量，通过机械化中耕和雨季施肥，显著提高了对大气降水的利用效率，确保了“肥跟水走”，为人工草地高产稳产提供了保障。本项技术不仅显著提高了多年生人工草地的生产力水平和稳定性，而且显著延长了草地的利用年限，同时改善了饲草的营养价值，提高了牧草品质。干草产量在旱作条件下，由 200 kg·亩$^{-1}$提高到 450 kg·亩$^{-1}$以上，利用年限由 3 年延长到 15 年左右。本项技术于 2007 年和 2008 年获得两项国家发明专利（专利号：ZL 200310117056.7 和 ZL 200310117067.5）。

本项技术的创新之处主要体现在以下几方面：

（1）通过长寿命牧草与短寿命牧草组合，以及根茎禾草与丛生禾草组合，充分利用了人工草地群落不同演替阶段各牧草品种的产量优势，解决了目前人工草地在种植早期产草量低和后期衰退现象严重的关键问题，实现了人工草地的长期利用；

（2）通过深根型牧草与浅根系牧草组合，以及非固氮的禾本科牧草与固氮的豆科牧草组合，发挥了不同牧草品种在水分和养分利用方面的互补性和互惠性，实现了对水分和土壤养分资源的高效利用；

（3）通过一年生牧草的保护播种，有效抑制了多年生人工草地在种植当年杂草对多年生牧草幼苗的危害，并确保播种当年有一定产草量，提高了经济效益；

（4）通过耐旱品种与喜湿品种间在不同年份的产草量补偿，发挥了各品种的产量优势，降低干旱年份与湿润年份的产草量差异，实现了人工草地的高产和稳产；

（5）在牧草品种选择上，根据不同地区的生态环境条件，选择适应性较强的国产优良牧草品种，解决了进口牧草品种抗旱性差，越冬率低等方面的问题，将牧草的越冬率提高到 95%以上，大大降低了人工草地种植的风险，同时也避免了由于盲目引进外来种可能带来的严重生态灾难。

（6）通过豆科牧草（紫苜蓿、野苜蓿）与禾本科牧草（羊草、无芒雀麦、披碱草、冰草等）的组合，显著提高了牧草的营养价值和品质。

（7）在人工草地建植过程中，实现了精量播种、杂草防除、中耕、雨季施肥、收获与加工的全程机械化，提高了播种质量和田间管理质量。特别是通过机械化中耕和雨季施肥，提高了大气降

水的利用效率，确保了“肥跟水走”，为人工草地实现高产和稳产提供了保障。

我们的试验数据表明，本项技术应用后，牧草产量是天然草地的 5～10 倍，是退化草地的 10～20 倍，是严重沙化草地的 50 倍左右。种植 1 亩高产混播人工草地可以使 10 亩的退化草地得以恢复，使 50 亩的严重沙化草地得以封育。该项技术从 2000 年开始在内蒙古锡林郭勒盟推广，显著的示范效果受到当地牧民和地方政府的热烈欢迎。

1.5.4 天然草原的放牧适应性管理

我国北方的天然草原总面积达 3.1 亿 hm^2，构成了我国草地的主体部分，是欧亚大陆连片分布面积最大的天然草原，是我国重要的畜牧业基地，同时也是我国北方重要的生态屏障和战略资源接续地。我国北方天然草原按其利用方式，主要分为放牧场和打草场两类。根据各类天然草地的利用现状，在试验研究的基础上，我们提出了“围封休牧、延迟放牧与划区轮牧相结合”的技术集成方案，即对生产力和生物多样性严重下降的退化草地，先实行“围封休牧”，使牧草得以休养生息，待草地生产力和生物多样性逐步恢复后采取“划区轮牧”的利用方式，使天然草场的使用进入良性循环，恢复和提升草地的生态功能。

根据我们的试验研究和国际畜牧业发达国家的经验，“围封休牧”可以在植物生长的两个关键阶段进行，即“春季休牧”和“秋季休牧”。春季休牧（延迟放牧）期一般为 45～60 天，从每年的 4 月中旬（牧草返青期）开始至 6 月上旬（饱青期）结束。返青期是牧草生长关键时期，对家畜放牧和践踏十分敏感。返青期延迟放牧不仅有利于牧草的返青和生长，使其增加养分贮备，增强放牧后牧草的再生和繁殖能力，大大提高当年的产草量，同时也可以避免畜群跑青，减少能量损失和对草地的践踏，进而有利于家畜生产。秋季休牧（结实期休牧），一般为 30 天左右，从每年的 8 月中旬开始至 9 月中旬结束，其主要目的是保证牧草种子成熟并进入土壤，保持草地土壤种子库有足量的新种子补充，使草地的种子更新能力得以恢复，进而有利于草地生物多样性的维持，提升草地的生态功能和生产功能。对于严重退化的放牧场和连年刈割的打草场，需要采用春季延迟放牧与秋季休牧相结合的技术手段，加速退化草地的恢复。2001 年以来，该技术成果在内蒙古自治区各盟 / 市累计推广 3000 余万亩，对于遏制草地的大面积退化，转变草地的生产和管理方式起了关键作用，产生了巨大的生态效益，受到了国家和地区有关部门的高度评价。

对保护较好或轻度退化的天然草原也可以直接进行“划区轮牧”。我们在典型草原的试验结果表明，轮牧区草地平均可食草产量比自由放牧区提高了 31%。同时，由于畜群减少了游走，降低了消耗，增加了休息和采食时间，每只羊在放牧期结束时的平均体重比自由放牧区增加了 5～8 kg。目前，该技术体系以“大区轮牧”、“小区轮牧”和“放牧场轮换利用”等多种方式在不同类型草地上得到广泛的推广应用。

1.6 展　望

过去 50 年来，我国在畜牧业生产中过度利用草地的生产功能，忽视其生态功能，导致草地大面积退化，生态功能衰退，土壤养分和水分保持能力下降，水土流失加剧，虫鼠害和沙尘暴等灾害频繁发生。据统计，目前我国约 90% 的天然草地发生了不同程度的退化，中度和重度退

化草地面积达 23 亿亩，其中内蒙古、西藏、新疆、青海、四川和甘肃等牧区省的退化草地比例高达 80%～97%。国务院在 2011 年发布的《关于促进牧区又好又快发展的若干意见》中指出，我国草原生态总体恶化趋势尚未根本遏制，草原畜牧业粗放型增长方式难以为继。针对这些严重制约国家生态安全和牧区社会经济发展的核心问题，内蒙古站将从以下几个方面加强科研监测工作：

（1）以大型联网控制实验为研究平台，突出实验生态学和联网研究特色，验证和发展生态学的相关理论。加强现有的野外受控实验平台的管理与维护（长期放牧实验、草地施肥、草原火生态、生物多样性与生态系统功能等实验平台）；积极推动野外站点和代表性生态系统类型的联网实验平台建设（极端干旱 / 降水对生态系统结构、过程和服务功能的影响机制多站联网研究、中国草地生物多样性联网监测与研究），研究极端气候对草地生态系统结构、过程和功能的影响及其机制，并采用天、空、地一体化的监测和研究手段，构建多尺度、多营养级、多组织水平的草地生物多样性监测体系，为我国生物多样性监测和研究提供强大的支撑平台，建立系统的、空间尺度清晰的国家草地生物多样性监测数据库，为我国草地生物多样性保护服务。

（2）依据可持续发展的基本原理，探索自然和社会因素对生态系统的综合作用，为我国北方草原生态系统管理和生态草牧业发展提供理论依据和技术支撑。研发提高人工草地生产力和稳定性、延长草地利用年限的措施与途径；基于长期试验研究，定量确定不同草地类型的合理利用强度、放牧场休牧与轮牧、割草地轮刈与休闲等技术方案；加强针对不同退化草地植被修复与重建技术的研究；建立草地的生产功能和生态功能的合理配置的技术研究与示范体系。

（3）深化实质性国际国内合作，加强人才培养，形成具有国际重要影响力的研究团队。依托现有的长期大型实验平台，吸引国内外优秀科学家参与，形成几个具有重要国际影响力的合作研究团队，力争在生物多样性与生态系统功能、化学计量学、草原生态系统管理等领域有重大突破，促进相关学科的发展。同时，提升科研队伍和人才培养水平，造就一批具有一定国际影响力和竞争力的高素质年轻科研人才，提升中国在草地研究领域的国际地位。

参 考 文 献

白永飞，陈佐忠 . 2000. 锡林河流域羊草草原植物种群和功能群的长期变异性及其对群落稳定性的影响 . 植物生态学报，24（6）：641–647.

白永飞，潘庆民，邢旗 . 2016. 草地生产与生态功能合理配置的理论基础与关键技术 . 科学通报，61（2）：201–212.

陈世苹，白永飞，韩兴国，等 . 2004. 沿土壤水分梯度黄囊苔草碳同位素组成及其适应策略的变化 . 植物生态学报，28（4）：515–522.

杜青林 . 2006. 中国草业可持续发展战略 . 北京：中国农业出版社 .

杜占池，杨宗贵 . 1988. 土壤干旱条件下羊草和大针茅光合作用午间降低内因的探讨 . 草原生态系统研究 . 中国科学院内蒙古草原生态系统定位站 . 北京：科学出版社，2：76–82.

杜占池，杨宗贵 . 1992. 羊草光合能力的研究 . 草原生态系统研究 . 中国科学院内蒙古草原生态系统定位站 . 北京：科学出版社，4：10–15.

杜占池，杨宗贵 . 1997. 温度对不同生育期冷蒿枝条净光合和暗呼吸速率的影响 . 草原生态系统研究 . 中国科学院内蒙古草原生态系统定位站 . 北京：科学出版社，5：131–139.

姜恕,戚秋慧,孔德珍 . 1985. 羊草草原群落和大针茅草原群落生物量的初步比较研究 . 草地生态系统研究（第 1 集）. 北京：科学出版社，1：12–23.

李永宏,汪诗平 . 1999. 放牧对草原植物的影响 . 中国草地，3：11–19.

李永宏 . 1993. 放牧影响下羊草草原和大针茅草原植物多样性的变化 . 植物学报，35（11）：877–884.

戚秋慧,盛修武,姜恕,等 . 1989. 羊草和大针茅群落光合速率的比较研究 . 植物生态学与地植物学学报，13（4）：332–340.

王炜,梁存柱,刘钟龄,等 . 2000. 草原群落退化与恢复演替中的植物个体行为分析 . 植物生态学报，24（3）：268–274.

王鑫厅,王炜,梁存柱,等 . 2015. 从正相互作用角度诠释过度放牧引起的草原退化 . 科学通报，Z2：2794–2799.

杨婧,褚鹏飞,陈迪马,等 . 2014. 放牧对内蒙古典型草原 α、β 和 γ 多样性的影响机制 . 植物生态学报，38（2）：188–200.

Bai Y F, Wu J G, Clark C M, et al. 2010. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: Evidence from inner Mongolia Grasslands. Global Change Biology, 16（1）: 358–372.

Bai Y F, Wu J G, Pan Q M, et al. 2007. Positive linear relationship between productivity and diversity: Evidence from the Eurasian Steppe. Journal of Applied Ecology, 44（5）: 1023–1034.

Bai Y F, Wu J G, Xing Q, et al. 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecology, 89（8）: 2140–2153.

Bai Y, Han X, Wu J, et al. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature, 431（7005）: 181–184.

Bai Y, Wu J, Clark C M, et al. 2012. Grazing alters ecosystem functioning and C: N: P stoichiometry of grasslands along a regional precipitation gradient. Journal of Applied Ecology, 49（6）: 1204–1215.

Bösing B M, Susenbeth A, Hao J, et al. 2014. Effect of concentrate supplementation on herbage intake and live weight gain of sheep grazing a semi–arid grassland steppe of North–Eastern Asia in response to different grazing management systems and intensities. Livestock Science, 165: 157–166.

Cease A J, Elser J J, Ford C F, et al. 2012. Heavy livestock grazing promotes locust outbreaks by lowering plant nitrogen content. Science, 335（6067）: 467–469.

Chapin F S, Zavaleta E S, Eviner V T, et al. 2000. Consequences of changing biodiversity. Nature, 405（6783）: 234–242.

Chen D, Cheng J, Chu P, et al. 2015a. Regional - scale patterns of soil microbes and nematodes across grasslands on the Mongolian plateau: Relationships with climate, soil, and plants. Ecography, 38（6）: 622–631.

Chen D, Cheng J, Chu P, et al. 2016a. Effect of diversity on biomass across grasslands on the Mongolian Plateau: Contrasting effects between plants and soil nematodes. Journal of Biogeography, 43（5）: 955–966.

Chen D, Lan Z, Bai X, et al. 2013a. Evidence that acidification–induced declines in plant diversity and productivity are mediated by changes in below–ground communities and soil properties in a semi–arid steppe. Journal of Ecology, 101（5）: 1322–1334.

Chen D, Li J, Lan Z, et al. 2016b. Soil acidification exerts a greater control on soil respiration than soil nitrogen availability in grasslands subjected to long–term nitrogen enrichment. Functional Ecology, 30（4）: 658–669.

Chen D, Mi J, Chu P, et al. 2015b. Patterns and drivers of soil microbial communities along a precipitation gradient on the Mongolian Plateau. Landscape Ecology, 30（9）: 1669–1682.

Chen D, Pan Q, Bai Y, et al. 2016c. Effects of plant functional group loss on soil biota and net ecosystem exchange: A plant removal experiment in the Mongolian grassland. Journal of Ecology, 104: 734–743.

Chen D, Wang Y, Lan Z, et al. 2015c. Biotic community shifts explain the contrasting responses of microbial and root

respiration to experimental soil acidification. Soil Biology and Biochemistry, 90: 139–147.

Chen D, Zheng S, Shan Y, et al. 2013b. Vertebrate herbivore–induced changes in plants and soils: Linkages to ecosystem functioning in a semi–arid steppe. Functional Ecology, 27(1): 273–281.

Chen S P, Bai Y F, Han X G. 2002. Variation of water–use efficiency of *Leymus chinensis* and *Cleistogenes squarrosa* in different plant communities in Xilin River Basin, Nei Mongol. Acta Botanica Sinica, 44(12): 1484–1490.

Chen S P, Bai Y F, Han X G. 2003. Variations in composition and water use efficiency of plant functional groups based on their water ecological groups in the Xilin River Basin. Acta Botanica Sinica, 45(10): 1251–1260.

Chen S P, Bai Y F, Lin G H, et al. 2005a. Variations in life–form composition and foliar carbon isotope discrimination among eight plant communities under different soil moisture conditions in the Xilin River Basin, Inner Mongolia, China. Ecological Research, 20(2): 167–176.

Chen S P, Bai Y F, Lin G H, et al. 2005b. Effects of grazing on photosynthetic characteristics of major steppe species in the Xilin River Basin, Inner Mongolia, China. Photosynthetica, 43(4): 559–565.

Chen S, Wang W, Xu W, et al. 2018. Plant diversity enhances productivity and soil carbon storage. Proceedings of the National Academy of Sciences, 115(16): 4027–4032.

Chen W, Wolf B, Brüggemann N, et al. 2011. Annual emissions of greenhouse gases from sheepfolds in Inner Mongolia. Plant and Soil, 340(1): 291–301.

Cheng J, Chu P, Chen D et al. 2016. Functional correlations between specific leaf area and specific root length along a regional environmental gradient in Inner Mongolia grasslands. Functional Ecology, 30(6): 985–997.

Clark C M, Tilman D. 2008. Loss of plant species after chronic low–level nitrogen deposition to prairie grasslands. Nature, 451(7179): 712–715.

Diaz S, Cabido M. 2001. Vive la difference: Plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution, 16(11): 646–655.

Diaz S, Lavorel S, McIntyre S, et al. 2007. Plant trait responses to grazing—a global synthesis. Global Change Biology, 13(2): 313–341.

Dickhoefer U, Bösing B, Hasler M, et al. 2016. Animal responses to herbage allowance: Forage intake and body weight gain of sheep grazing the Inner Mongolian steppe—Results of a six–year study. Journal of Animal Science, 94(5): 2059–2071.

Dickhoefer U, Hao J, Bosing B M, et al. 2014. Feed intake and performance of sheep grazing semiarid grassland in response to different grazing systems. Rangeland Ecology & Management, 67(2): 145–153.

Elser J J, Andersen T, Baron J S, et al. 2009. Shifts in lake N: P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science, 326(5954): 835–837.

Elser J J, Sterner R W, Gorokhova E, et al. 2000. Biological stoichiometry from genes to ecosystems. Ecology Letters, 3(6): 540–550.

Fraser L H, Pither J, Jentsch A, et al. 2015. Worldwide evidence of a unimodal relationship between productivity and plant species richness. Science, 349(6245): 302–305.

Gao Y Z, Chen Q, Lin S, et al. 2011. Resource manipulation effects on net primary production, biomass allocation and rain–use efficiency of two semiarid grassland sites in Inner Mongolia, China. Oecologia, 165(4): 855–864.

Gao Y Z, Giese M, Lin S, et al. 2008. Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. Plant and Soil, 307(1–2): 41–50.

Geng Y, Ma W, Wang L, et al. 2017. Linking above - and belowground traits to soil and climate variables: An integrated database on China's grassland species. Ecology, 98(5): 1471–1471.

Giese M, Brueck H, Gao Y Z, et al. 2013. N balance and cycling of Inner Mongolia typical steppe: A comprehensive case

study of grazing effects. Ecological Monographs, 83(2): 195–219.

Grime J P. 1973. Competitive exclusion in herbaceous vegetation. Nature, 242(5396): 344–347.

Hautier Y, Seabloom E W, Borer E T, et al. 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. Nature, 508: 521.

Hillebrand H, Gruner D S, Borer E T, et al. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. Proceedings of the National Academy of Sciences of the United States of America, 104(26): 10904–10909.

Hoffmann C, Giese M, Dickhoefer U, et al. 2016. Effects of grazing and climate variability on grassland ecosystem functions in Inner Mongolia: Synthesis of a 6-year grazing experiment. Journal of Arid Environments, 135: 50–63.

Holst J, Liu C Y, Bruggemann N, et al. 2007. Microbial N turnover and N-oxide(N_2O / NO / NO_2)fluxes in semi-arid grassland of Inner Mongolia. Ecosystems, 10(4): 623–634.

Holst J, Liu C, Yao Z, et al. 2008. Fluxes of nitrous oxide, methane and carbon dioxide during freezing-thawing cycles in an Inner Mongolian steppe. Plant and Soil, 308(1–2): 105–117.

Hooper D U, Adair E C, Cardinale B J, et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature advance online publication.

Hooper D U, Chapin F S, III, Ewel J J, et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs, 75(1): 3–35.

Huston M. 1979. A general hypothesis of species diversity. American Naturalist, 113(1): 81–101.

IPCC, 2007. Summary for policymakers. In Climate Change 2007: The physical science basis contribution of working group i to the fourth assessment report of the Intergovernmental Panel on Climate Change(Solomon, S. et al., eds), Cambridge University Press.

Kraft N J B, Godoy O, Levine J M. 2015. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences, 112(3): 797–802.

Lan Z, Bai Y 2012. Testing mechanisms of N-enrichment-induced species loss in a semiarid Inner Mongolia grassland: Critical thresholds and implications for long-term ecosystem responses. Philosophical Transactions of the Royal Society B: Biological Sciences, 367(1606): 3125–3134.

Lan Z, Jenerette G D, Zhan S, et al. 2015. Testing the scaling effects and mechanisms of N-induced biodiversity loss: Evidence from a decade-long grassland experiment. Journal of Ecology, 103(3): 750–760.

Lange M, Eisenhauer N, Sierra C A, et al. 2015. Plant diversity increases soil microbial activity and soil carbon storage. Nature Communications, 6: 6707.

Li W, Xu F, Zheng S, et al. 2017. Patterns and thresholds of grazing-induced changes in community structure and ecosystem functioning: Species-level responses and the critical role of species traits. Journal of Applied Ecology, 54(3): 963–975.

Li W, Zhan S, Lan Z, et al. 2015. Scale-dependent patterns and mechanisms of grazing-induced biodiversity loss: Evidence from a field manipulation experiment in semiarid steppe. Landscape Ecology, 30(9): 1–15.

Li Y H, Wang W, Liu Z L, et al 2008. Grazing gradient versus restoration succession of *Leymus chinensis*(Trin.)Tzvel. Grassland in Inner Mongolia. Restoration Ecology, 16(4): 572–583.

Li Z, Ma W, Liang C, et al. 2015. Long-term vegetation dynamics driven by climatic variations in the Inner Mongolia grassland: Findings from 30-year monitoring. Landscape Ecology, 30(9): 1701–1711.

Lin L J, Dickhoefer U, Muller K, et al. 2012. Growth of sheep as affected by grazing system and grazing intensity in the steppe of Inner Mongolia, China. Livestock Science, 144(1–2): 140–147.

Liu C Y, Holst J, Yao Z S, et al. 2009. Sheepfolds as "hotspots" of nitric oxide(NO)emission in an Inner Mongolian

steppe. Agriculture Ecosystems & Environment, 134(1–2): 136–142.

Liu J, Feng C, Wang D L, et al. 2015. Impacts of grazing by different large herbivores in grassland depend on plant species diversity. Journal of Applied Ecology, 52(4): 1053–1062.

Long M, Wu H, Smith M D, et al. 2016. Nitrogen deposition promotes phosphorus uptake of plants in a semi–arid temperate grassland. Plant and Soil, 408(1–2): 475–484.

Loreau M, Naeem S, Inchausti P, et al. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science, 294(5543): 804–808.

Lü X T, Freschet G T, Flynn D F B, et al. 2012. Plasticity in leaf and stem nutrient resorption proficiency potentially reinforces plant–soil feedbacks and microscale heterogeneity in a semi - arid grassland. Journal of Ecology, 100(1): 144–150.

Lü X T, Reed S, Yu Q, et al. 2013. Convergent responses of nitrogen and phosphorus resorption to nitrogen inputs in a semiarid grassland. Global Change Biology, 19(9): 2775–2784.

Ma Z, Guo D, Xu X, et al. 2018. Evolutionary history resolves global organization of root functional traits. Nature, 555: 94–97.

Marklein A R and Houlton B Z. 2012. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. New Phytologist, 193(3): 696–704.

McGill B J, Enquist B J, Weiher E, et al. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution, 21(4): 178–185.

Midgley G F. 2012. Biodiversity and ecosystem function. Science, 335(6065): 174–175.

Milchunas D G, Sala O E and Lauenroth W K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist, 132(1): 87–106.

Mittelbach G G, Steiner C F, Scheiner S M, et al. 2001. What is the observed relationship between species richness and productivity? Ecology, 82(9): 2381–2396.

Muller K, Dickhoefer U, Lin L, et al. 2014. Impact of grazing intensity on herbage quality, feed intake and live weight gain of sheep grazing on the steppe of Inner Mongolia. Journal of Agricultural Science, 152(1): 153–165.

Olff H and Ritchie M E. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology & Evolution, 13(7): 261–265.

Pan Q, Tian D, Naeem S, et al. 2016. Effects of functional diversity loss on ecosystem functions are influenced by compensation. Ecology, 97(9): 2293–2302.

Ren H, Han G, Lan Z, et al. 2016a. Grazing effects on herbage nutritive values depend on precipitation and growing season in Inner Mongolian grassland. Journal of Plant Ecology, 9(6): 712–723.

Ren H, Han G, Ohm M, et al. 2015. Do sheep grazing patterns affect ecosystem functioning in steppe grassland ecosystems in Inner Mongolia? Agriculture Ecosystems & Environment, 213(213): 1–10.

Ren H, Han G, Schönbach P, et al. 2016b. Forage nutritional characteristics and yield dynamics in a grazed semiarid steppe ecosystem of Inner Mongolia, China. Ecological Indicators, 60: 460–469.

Ren H, Taube F, Stein C, et al. 2018. Grazing weakens temporal stabilizing effects of diversity in the Eurasian steppe. Ecology and Evolution.

Schönbach P, Wan H, Gierus M, et al. 2011. Grassland responses to grazing: Effects of grazing intensity and management system in an Inner Mongolian steppe ecosystem. Plant and Soil, 340(1–2): 103–115.

Schönbach P, Wan H, Gierus M, et al. 2012. Effects of grazing and precipitation on herbage production, herbage nutritive value and performance of sheep in continental steppe. Grass and Forage Science, 67(4): 535–545.

Schönbach P, Wan H, Schiborra A, et al. 2009. Short–term management and stocking rate effects of grazing sheep on

herbage quality and productivity of Inner Mongolia steppe. Crop & Pasture Science, 60(10): 963–974.

Sterck F, Markesteijn L, Schieving F et al. 2011. Functional traits determine trade–offs and niches in a tropical forest community. Proceedings of the National Academy of Sciences, 108(51): 20627–20632.

Suding K N, Collins S L, Gough L, et al. 2005. Functional–and abundance–based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences of the United States of America, 102(12): 4387–4392.

Tian D, Niu S, Pan Q, et al. 2016. Nonlinear responses of ecosystem carbon fluxes and water–use efficiency to nitrogen addition in Inner Mongolia grassland. Functional Ecology, 30(3): 490–499.

Tilman D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. Ecology, 80(5): 1455–1474.

Vitousek P M, Aber J D, Howarth R W, et al. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications, 7(3): 737–750.

Waide R B, Willig M R, Steiner C F, et al 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics, 30: 257–300.

Wan H, Bai Y, Schönbach P, et al. 2011. Effects of grazing management system on plant community structure and functioning in a semiarid steppe: Scaling from species to community. Plant and Soil, 340(1): 215–226.

Wang C J, Wang S P, Zhou H, et al. 2007. Effects of forage composition and growing season on methane emission from sheep in the Inner Mongolia steppe of China. Ecological Research, 22(1): 41–48.

Wang Z P, Han X G, Wang G G, et al. 2008. Aerobic methane emission from plants in the Inner Mongolia steppe. Environmental Science & Technology, 42(1): 62–68.

Wang Z P, Song Y, Gulledge J, et al. 2009. China's grazed temperate grasslands are a net source of atmospheric methane. Atmospheric Environment, 43(13): 2148–2153.

Wei C, Yu Q, Bai E, et al. 2013. Nitrogen deposition weakens plant–microbe interactions in grassland ecosystems. Global Change Biology, 19(12): 3688–3697.

William J, Mattson Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics, 11(1): 119–161.

Wolf B, Zheng X H, Brueggemann N, et al. 2010. Grazing–induced reduction of natural nitrous oxide release from continental steppe. Nature, 464(7290): 881–884.

Yang H, Auerswald K, Bai Y, et al. 2011. Variation in carbon isotope discrimination in *Cleistogenes squarrosa* (Trin.) Keng: Patterns and drivers at tiller, local, catchment, and regional scales. Journal of Experimental Botany, 62(12): 4143–4152.

Yang Y, Ji C, Ma W, et al. 2012. Significant soil acidification across northern China's grasslands during 1980s–2000s. Global Change Biology, 18(7): 2292–2300.

Ying J, Li X, Wang N, et al. 2017. Contrasting effects of nitrogen forms and soil pH on ammonia oxidizing microorganisms and their responses to long–term nitrogen fertilization in a typical steppe ecosystem. Soil Biology and Biochemistry, 107: 10–18.

Yu Q, Chen Q S, Elser J J, et al. 2010. Linking stoichiometric homoeostasis with ecosystem structure, functioning and stability. Ecology Letters, 13(11): 1390–1399.

Yu Q, Wilcox K, Pierre K L, et al. 2015. Stoichiometric homeostasis predicts plant species dominance, temporal stability, and responses to global change. Ecology, 96(9): 2328–2335.

Zhan S, Wang Y, Zhu Z, et al. 2017. Nitrogen enrichment alters plant N: P stoichiometry and intensifies phosphorus limitation in a steppe ecosystem. Environmental and Experimental Botany, 134: 21–32.

Zhang B, Tan X, Wang S, et al. 2017. Asymmetric sensitivity of ecosystem carbon and water processes in response to precipitation change in a semiarid steppe. Functional Ecology, 31(6): 1301–1311.

Zhang X, Tan Y, Li A, et al. 2015. Water and nitrogen availability co–control ecosystem CO_2 exchange in a semiarid temperate steppe. Scientific Reports, 5: 15549.

Zhang Y, Loreau M, He N, et al. 2017. Mowing exacerbates the loss of ecosystem stability under nitrogen enrichment in a temperate grassland. Functional Ecology, 31(8): 1637–1646.

Zheng S X, Ren H Y, Lan Z C, et al. 2010. Effects of grazing on leaf traits and ecosystem functioning in Inner Mongolia grasslands: Scaling from species to community. Biogeosciences, 7(3): 1117–1132.

ICS 65.020.01
CCS B 40

LY

中华人民共和国林业行业标准

LY/T 3323—2022

草原生态修复技术规程

Technical regulation of grassland ecological restoration

2022-11-30 发布　　2023-04-01 实施

国家林业和草原局　发布
中国标准出版社　出版

前　言

本文件按照 GB/T 1.1—2020《标准化工作导则　第 1 部分：标准化文件的结构和起草规则》的规定起草。

请注意本文件的某些内容可能涉及专利。本文件的发布机构不承担识别专利的责任。

本文件由国家林业和草原局草原管理司提出。

本文件由国家林业和草原局草原标准化技术委员会(NFGA/TC 2)归口。

本文件起草单位：蒙草生态环境(集团)股份有限公司、中国科学院植物研究所。

本文件主要起草人：白永飞、王召明、邢旗、陈翔、张健、闫晓红、刘亚玲、王扬、张跃华、郑淑霞、赵玉金、李西良、杨红艳、王堃、刘克思、张晓严、阿穆拉。

中国标准出版社

草原生态修复技术规程

1 范围

本文件规定了退化草原生态修复原则，草原退化类型、程度及原因诊断，退化草原生态修复技术，不同退化程度草原生态修复技术模式，退化草原修复后健康评价指标，退化草原生态修复后的利用等的基本要求。

本文件适用于我国各类草原的生态修复。

2 规范性引用文件

下列文件中的内容通过文中的规范性引用而构成本文件必不可少的条款。其中，注日期的引用文件，仅该日期对应的版本适用于本文件；不注日期的引用文件，其最新版本（包括所有的修改单）适用于本文件。

GB 19377 天然草地退化、沙化、盐渍化的分级指标

GB/T 21141 防沙治沙技术规范

GB/T 21439 草原健康状况评价

GB/T 27515 天然割草地轮刈技术规程

GB/T 37067 退化草地修复技术规范

NY/T 635 天然草地合理载畜量的计算

NY/T 1176 休牧和禁牧技术规程

NY/T 1343 草原划区轮牧技术规程

NY/T 1905 草原鼠害安全防治技术规程

NY/T 2275 草原田鼠防治技术规程

NY/T 2736 蝗虫防治技术规范

NY/T 2997 草地分类

3 术语和定义

下列术语和定义适用于本文件。

3.1

草原生态修复 grassland ecological restoration

在不破坏或尽量少破坏草原自然植被的前提下，采用一定的生物、生态及工程技术措施，遵循生态学原理和生态系统内在机制，使受损的草原生态系统实现近自然恢复。

3.2

自然修复 natural restoration

自然恢复 natural recovery

利用草原生态系统自我修复能力，对植被和土壤不采用人工补播、施肥、切根等干预措施的恢复。

注：采用措施包括封育、休牧、禁牧等。

3.3

人工干预修复　manual intervention restoration

采用生境改善和生物等措施的退化草原修复。

注：采用的生物措施包括补播、补植等，生境改善措施包括切根、施肥及构建固沙网格、铺设覆盖物等措施。

3.4

参照系统　reference ecosystem；baseline ecosystem

在草原生态系统退化程度诊断中，与退化草原区相近类型的未受破坏或破坏程度很轻的自然生态系统，即地带性植被的顶级群落及其所着生的生态系统。

3.5

乡土植物　indigenous plantspecies；native plantspecies

原产当地并经长期的自然选择与进化，适应当地气候、土壤等环境条件的地带性植被顶级群落中的建群种、优势种和伴生种。

3.6

植被建植阶段　vegetation establishment stage

根据当地水分、土壤、气象和生物条件资源，因地制宜地对退化草原进行修复，从开始修复至草原植被以先锋植物为主，退化趋势得以初步控制的阶段。

3.7

结构优化阶段　structural optimization stage

随着环境的变化和群落的演替，退化草原原生群落优势种所占比例显著增加，土壤理化性质和生物群落明显改善，从植被建植阶段至草原健康状况达到 GB/T 21439 规定的三级水平的阶段。

3.8

功能提升阶段　functional improvement stage

草原结构优化后，草原植被、土壤各项指标逐步接近未退化水平，生物多样性和生态系统稳定性全面提升的阶段。

4　退化草原生态修复原则

4.1　符合修复的生态原则

草原生态修复以自然恢复为主，如需人工干预修复，需考虑自然环境条件，以近自然修复的原则，进行技术措施及物种的选择与配置，以恢复该区域为地带性植被的顶级群落及其所着生的生态系统为目标。

4.2　充分利用自然降水

草原生态修复以利用自然降水为主，年降水小于 300 mm 的地区或干旱年份进行草原补播时，可利用浅层水资源或机械补水等节水措施对修复初期的植被补水，不宜开采深层地下水。

4.3　用种首选乡土植物

草原生态修复用种以乡土植物为主，选择引进品种时，需充分考虑当地环境条件，避免生态风险。

4.4　尽量减少对原生植被和土壤的破坏

轻度退化草原生态修复以自然修复为主，中度及中度以上退化草原可因地制宜采取人工干预修复措施，尽量不破坏草原原生植被。

4.5 修复材料选择应坚持生态环保

草原生态修复选用的肥料、工程网格材料等需符合国家生态环保的相关要求，避免对环境造成二次污染等。

4.6 根据不同恢复阶段进行科学利用

植被建植阶段不利用，结构优化阶段可轻度利用，功能提升阶段合理利用。

5 草原退化类型、程度及原因诊断

5.1 植被调查

利用遥感和地面调查技术，调查样地植物群落的物种组成、覆盖度、地上生物量，优势种盖度和生物量，群落凋落物生物量，可食、不可食牧草及有毒有害植物的比例，不同退化阶段的指示植物数量等指标，并分析各指标相对参照系统的变化程度。

5.2 土壤调查

利用遥感和地面调查技术，调查修复区的地表特征（水蚀、风蚀痕迹，覆沙、裸地、盐碱斑面积等）及土壤理化性质指标（土壤容重、有机质、土壤养分、质地、含盐量、pH 值等），土样采集深度根据不同草原类型的土层深度确定。土壤退化诊断方法参照 GB/T 37067 执行，草原分类按照 NY/T 2997 的规定执行。

5.3 草原退化程度分级及成因

根据 5.1 和 5.2 调查分析结果，将草原退化程度划分为 3 级：轻度退化、中度退化和重度退化，分级方法按照 GB 19377 的规定。根据草原利用历史、利用方式与强度，以及取沙、取土、开垦、滥挖滥采等情况，诊断草原退化的主要压力和成因。

6 退化草原生态修复技术

6.1 自然修复措施

6.1.1 封育

将退化草原封闭，禁止割草、放牧、采集牧草种子等人为干扰，使草原以自我的恢复能力进行修复。根据草原退化程度可采取季节性封育、短期封育（小于 10 年）和长期封育（大于 10 年）。

6.1.2 禁牧

对过度放牧利用的草原或打草场等特殊利用的草原，以年为单位，采取政策性、政令性及制度性等措施，实行 1 年以上禁止放牧利用。以草原初级生产力、植被盖度、当地草原的理论载畜量作为解除禁牧的主要参考指标，具体按照 NY/T 1176 的规定执行。

6.1.3 休牧

对轻、中度退化草原，在春季植物返青期或夏末秋初，通过设置围栏或其他方式管理家畜进入，以当地植物物候期确定开始和结束休牧的时间或采取轮牧的方式进行，休牧期一般不少于 45 d，具体按照 NY/T 1176 的规定执行。

6.2 人工干预修复措施

6.2.1 划破草皮或切根

宜在早春或晚秋进行。深度 10 cm～20 cm，行距 30 cm～60 cm 为宜。宜采用拖拉机牵引的机具进行，在有坡度的地块沿等高线作业。适用于以根茎型或根茎-疏丛型为主的中轻度退化草原。

6.2.2 松耙

宜在春季进行。耙深 6 cm～8 cm，松土后立即用镇压器镇压地面。可采用机引圆盘耙、缺口重耙和松土补播机等。适用于以根茎型禾草或根茎-疏丛型禾草为主的中度退化草原，也与补播、施肥等技术结合用于重度沙化的草原修复。

6.2.3 浅耕翻

宜在雨季进行。干旱年份或雨量过大不宜翻耕。耕翻深度以 15 cm～20 cm 为宜，对于有土壤侵蚀风险的地区宜采用带状浅耕翻方式，带宽 30 m，带间距 5 m。适用于重度退化的根茎型禾草草原。

6.2.4 施肥

宜在融雪水浸灌和土壤解冻时或雨季进行。采用沟施、撒施、免耕施用有机肥料或无机肥料等方法进行草原养分补充，施肥量视土壤肥力、植物需肥量确定。适用于土壤贫瘠的各类退化草原。

6.2.5 灌溉

草原灌溉应充分利用自然降水，不宜开采地下水；灌溉方法应根据牧草种类、草原类型、产量、土壤和气候条件制定节水灌溉制度；对于干旱、半干旱草原可采用微地形、保水结构层和径流集水处理等技术增加土壤含水量。适用于有条件贮存雨水的草原地段。

6.2.6 补播移植

在春季墒情较好或夏季雨季来临前等适宜时期进行。草原修复可因地制宜采用松土补播、免耕补播或飞播等措施，种子选择以不同草原类型的乡土物种为主，慎用外来种和跨气候带引种，播种深度应根据种子的千粒重、土壤含水量、土壤质地等因素确定，或移植其他繁殖体（种苗或草皮）。适用于有一定土层、灌溉条件或年降水量不少于 250 mm 的中度和重度退化草原或退耕地。

6.3 工程措施

6.3.1 整地

对严重受损、不易进行人工或机械作业的退化草原，可先进行石块等异物清除，并采用圆盘耙或钉齿耙等机具进行地面平整处理，以利于补播即可。对于表土部分和完全丧失的严重退化的小面积草原可进行客土。适用于严重退化草原。

6.3.2 固沙网格构建

根据草原沙化程度、立地条件，固沙可采用物理、化学、生物固沙技术或结合补播、铺设覆盖物等综合措施。物理治沙措施、化学治沙措施及生物治沙措施参照 GB/T 21141 执行。适用于中度和重度沙化草原。

6.3.3 铺上覆盖物

覆盖物可选择枯草、秸秆、草帘或苇帘等材料。轻度沙化、盐渍化草原，可直接铺设覆盖物，中度和重度退化(含沙化、盐渍化)草原可结合松耙、施肥、补播乡土植物等技术进行综合修复。适用于各类型退化(含沙化、盐渍化)草原。

6.3.4 其他措施

对一些特殊情况的草原退化类型，可根据实际情况选择其他工程措施。

6.4 鼠虫害防治

6.4.1 鼠害防治

鼠害防治按照 NY/T 2275 和 NY/T 1905 的规定执行。

6.4.2 虫害防治

依据具体虫害类型，结合相关标准规定，采用化学、物理或生物方法防治虫害，蝗虫防治可参照 NY/T 2736。

7 不同退化程度草原生态修复技术模式

7.1 轻度退化草原

生态系统结构和功能基本完整，以自然修复为主，修复过程包括结构优化和功能提升两个阶段，采取的主要措施包括封育、休牧、禁牧等。

7.2 中度退化草原

生态系统结构发生中度退化，生态功能部分丧失，采用人工干预的措施进行修复，修复过程包括结构优化和功能提升两个阶段，采取的主要措施包括施肥、补播、切根等。

7.3 重度退化草原

生态系统结构严重退化，生态功能严重丧失，宜采用工程措施和生物措施进行修复或生态重建，修复过程包括植被建植、结构优化和功能提升三个阶段，采取的主要措施包括整地、构建固沙网格、铺设覆盖物、施肥、补播、补植等。

8 退化草原修复后健康评价指标

基于草原健康属性，土壤/样地稳定性、水文功能和生物完整性，退化草原修复后的健康评价指标可参考表 1 确定。评价指标需客观准确地反映修复后草原健康状况的变化，具体指标的选择根据不同地区不同退化类型的实际情况，也可参照相关标准和规范的具体要求确定。

中国标准出版社

表 1　退化草原修复后草原健康状况评价指标

序号	植被分类	指标	主要测定内容	备注
1	地表属性	面蚀(细流)	面蚀间距变化及面蚀深度和宽度变化	—
2		水流模式	土壤坡面发生漫流时，土壤表面的水流路径	—
3		固着物和/或阶地	固着物的多少，有无等情况；阶地数量、面积及高度等	固着物指岩石或植物；阶地是水运动与障碍物后土壤沉积形成
4		裸地面积	比例、数量和分布	—
5		集水沟	数量及特征(包括四周特征、底部和侧面的)植被生长、深度等	—
6		风蚀穴、风蚀窝和/或沉积区	数量、分布及面积	—
7		枯枝落叶的移动	程度和数量	—
8		土壤表层对侵蚀的抗性	土壤团聚体或未分解的有机质及生物结皮情况	生物结皮指生长在土壤表层以上或土壤表层以下的微生物(如苔藓、藻类、藻青菌、微真菌)和非维管束植物(如苔、苔藓)
9	土壤属性	土壤表层流失及退化	土壤有机质含量、养分、pH 和结构	—
10		紧实层	土壤硬度、紧实土壤结构、土壤容重等	—
11		土壤物理属性	入渗方式：垂直入渗、侧渗	—
12	植被属性	植被群落组成及分布	植被数量、类型、物种组成及分布等	—
13		指示植物	退化草原指示植物数量、种类等变化情况	—
14		功能/结构群	种类及物种情况	—
15		植物死亡率或衰退	群落中死亡或衰退(例半死、将死状态)植物相对于幼苗或成年植物的比例	—
16		凋落物数量	数量	凋落物是同植物基部分开的死植物体
17		生物量	地上部分植物净生物量总和	—
18		盖度	植被总盖度	
19		优势种占比	优势种牧草地上部的相对百分数	
20		入侵植物	数量、种类及占比等	
21		多年生植物的繁殖能力	与参照系统相比的种子数、植物分蘖及根茎的数量分布	
22	指示动物	生态系统健康重要指示动物	有无	如鸟类、蝴蝶、蜻蜓、蜥蜴、蚂蚁、顶级捕食者(鹰、狼、狐狸)

9 退化草原生态修复后的利用

9.1 植被建植阶段

轻度退化、沙化、盐渍化草原，放牧场应采取草畜平衡、轮牧等利用措施，方法按照 NY/T 635、NY/T 1343 的规定执行，不同草原类型载畜量可根据近期草原普查数据和多年草原生产力监测数据；打草场可采取轮刈、留草带等措施，方法按照 GB/T 27515 的规定执行；中重度退化、沙化、盐渍化草原不进行放牧、打草等形式的利用。

9.2 结构优化阶段

轻度退化、沙化、盐渍化草原的利用按 9.1 要求执行，中重度退化、沙化、盐渍化草原可采用轮刈、留草带等措施进行轻度利用。

9.3 功能提升阶段

修复后草原处于本阶段，按 9.1 规定的轻度退化、沙化、盐渍化草原进行合理利用。

中国标准出版社

ICS 65.020.01
CCS B 04

DB15

内 蒙 古 自 治 区 地 方 标 准

DB15/T 3761—2024

草地固碳潜力核算技术指南

Technical guidelines for grassland carbon sequestration potential accounting

2024－12－18 发布　　2025－01－18 实施

内蒙古自治区市场监督管理局　　发 布

前　　言

本文件按照GB/T 1.1—2020《标准化工作导则　第1部分：标准化文件的结构和起草规则》的规定起草。

本文件由内蒙古自治区林业和草原局提出并归口。

本文件起草单位：内蒙古自治区林业和草原监测规划院、中国科学院植物研究所、河北大学、内蒙古自治区林业科学研究院。

本文件主要起草人：白永飞、杨勇、王扬、苏纪帅、刘爱军、常书娟、刘羽。

草地固碳潜力核算技术指南

1 范围

本文件规定了草地生态系统固碳潜力核算的两种方法，即库差法和固碳速率法。

本文件适用于自治区开展退化草地修复和优化管理措施情景下的生态系统固碳潜力核算。

2 规范性引用文件

下列文件中的内容通过文中的规范性引用而构成本文件必不可少的条款。其中，注日期的引用文件，仅该日期对应的版本适用于本文件；不注日期的引用文件，其最新版本（包括所有的修改单）适用于本文件。

DB15/T 3683 草地碳汇计量与监测术语

3 术语和定义

DB15/T 3683界定的以及下列术语和定义适用于本文件。

3.1

生态系统固碳量 ecosystem carbon sequestration capacity

草地生态系统植被和土壤的碳储量或固碳速率。

3.2

退化草地修复 degraded grassland restoration

利用近自然修复、人工修复的措施（如围栏封育、灌溉、施肥、松耙、补播、防除毒害草等），使退化草地恢复或接近原有草地生态功能和生产功能的过程。

[来源：DB15/T 3683-2024，3.2.2.4]

3.3

优化管理措施 improved grassland management

草畜平衡、禁牧、休牧轮牧、轮刈、施肥等草地管理措施。

3.4

基准情景 baseline for carbon sequestration

基准时间或基准状况下草地生态系统的固碳量。

3.5

参照系 reference

未退化或优化管理措施实施下的草地生态系统，及其对应的生态系统固碳量。

4 生态系统固碳潜力核算方法

4.1 库差法

参照系和基准情景下的生态系统碳储量差值即为固碳潜力。计算按照公式（1）如下：

$$CSP = (CD_0 - CD_d) \times Area \quad (1)$$

式中：

CSP ——固碳潜力，单位为吨碳(t C)；

CD_0 ——参照系的生态系统碳密度，单位为吨碳每公顷(t C/hm²)；

CD_d ——基准情景的生态系统碳密度，单位为吨碳每公顷(t C/hm²)；

Area ——需要核算固碳潜力的草地面积，单位为公顷(hm²)。

退化草地修复的固碳潜力：选取同区域和相同草地类型的未退化草地作为参照系，计算其与基准情景（生态修复前的退化草地）的生态系统碳密度差值，即为固碳潜力。

优化管理措施的固碳潜力：选取开展了优化管理措施下的草地作为参照系，计算其与基准情景（未采取优化措施、或采取优化措施之前）生态系统碳密度的差值，即为固碳潜力。

库差法要求作为参照系的优化管理措施有一定的实施年限（3年以上）。当没有长期监测数据时，可以选择邻近未采取措施的地块作参照系，以其与实施了优化措施地块的生态系统碳密度差值核算固碳潜力。

由于草地修复措施或优化管理措施对生态系统，尤其是土壤的影响主要集中在表层，因此使用库差法进行固碳潜力核算时，土壤的野外调查取样可以仅选择表层（0 cm～30 cm）。

4.2 固碳速率法

以参照系和基准情景下的生态系统固碳速率差值计算固碳潜力。计算按照公式（2）如下：

$$CSP = \left(\overline{CSR_R} - \overline{CSR_{ck}}\right) \times Area \quad (2)$$

式中：

CSP ——固碳潜力，单位为吨碳(t C)；

$\overline{CSR_R}$ ——实施优化管理措施下，单位面积草地生态系统固碳速率的平均值，单位为吨碳每公顷(t C/hm²)；

$\overline{CSR_{ck}}$ ——未实施优化管理措施下，单位面积草地生态系统固碳速率的平均值，单位为吨碳每公顷(t C/hm²)；

Area ——需要核算固碳潜力的草地面积，单位为公顷(hm²)。

该方法需要基于涡度相关和箱式法等等测量仪器获取参照系和基准情景下的生态系统固碳速率。该方法通常需要3年以上的监测数据，以获取具有代表性的生态系统固碳速率。

5 报告编制

报告编制内容包括：核算区域概述、核算方法、参照系选择、核算结果、附表等。

ICS 65.020.01
CCS B 04

DB15

内 蒙 古 自 治 区 地 方 标 准

DB15/T 3769—2024

草地固碳速率监测技术规程

Code of practice for monitoring of grassland carbon sequestration rate

2024-12-18 发布 2025-01-18 实施

内蒙古自治区市场监督管理局 发 布

前　　言

本文件按照GB/T 1.1—2020《标准化工作导则　第1部分：标准化文件的结构和起草规则》的规定起草。

本文件由内蒙古自治区林业和草原局提出并归口。

本文件起草单位：中国科学院植物研究所、内蒙古自治区林业和草原监测规划院、内蒙古自治区林业科学研究院、河北大学。

本文件主要起草人：白永飞、王扬、杨勇、刘爱军、鲁小名、赵玉金、苏纪帅、常书娟、郑淑华。

草地固碳速率监测技术规程

1 范围

本文件规定了草地样地和区域尺度的固碳速率监测。

本文件适用于草地生态系统的固碳速率监测。

2 规范性引用文件

下列文件中的内容通过文中的规范性引用而构成本文件必不可少的条款。其中，注日期的引用文件，仅该日期对应的版本适用于本文件；不注日期的引用文件，其最新版本（包括所有的修改单）适用于本文件。

DB15/T 3683 草地碳汇计量与监测术语

DB15/T 3763 草地碳汇遥感监测技术指南

DB15/T 3764 草地碳储量调查与核算技术规程

3 术语和定义

下列术语和定义适用于本文件。

3.1

草地固碳速率 carbon sequestration rate of grassland

单位时间单位面积内草地生态系统通过光合作用将大气中的二氧化碳转化为有机碳并储存在植物或土壤中的量。常用单位为g C $m^{-2}s^{-1}$（g CO_2 m^{-2} s^{-1}）或t C $hm^{-2}a^{-1}$（t CO_2 hm^{-2} a^{-1}）。

[来源：DB15/T 3683-2024，3.2.2.2，有修改]

3.2

净生态系统碳交换 net ecosystem carbon exchange,（NEE）

单位时间单位面积草地生态系统从大气中吸收的碳通量与向大气释放的碳通量的净平衡值，是总生态系统生产力与生态系统呼吸的差值。常用单位为g C/m^2/s或g C/hm^2/a。

[来源：DB15/T 3683-2024，3.2.1.16]

3.3

生态系统碳密度 ecosystem carbon density

单位面积和一定深度土体下草地生态系统的有机碳总质量。包括：植被和土壤有机碳密度。常用单位为g C/m^2、kg C/m^2或t C/hm^2。

[来源：DB15/T 3683-2024，3.1.6，有修改]

3.4

涡度相关法　eddy covariance method

基于微气象原理估算垂直风速与物质或能量脉动的协方差估算草地生态系统碳汇的方法。
[来源：DB15/T 3683-2024，3.2.3.9，有修改]

3.5

箱式法　automated chamber method

通过测量特定环境中（密闭箱体）碳浓度的变化来确定碳通量。
[来源：DB15/T 3683-2024，3.2.3.8]

4　样地尺度的固碳速率监测

4.1　直接测量法

4.1.1　适用范围

该方法适用于日、月、季节和年等不同时间尺度的固碳速率监测。
常用观测仪器包括涡度相关测定系统和箱式法测定系统。
涡度相关测定系统测定的空间尺度是100 m^2～10 km^2。
箱式法测定系统适于样方尺度(1 m^2～10 m^2)的监测。

4.1.2　样地设置

选择代表监测区主要植被类型和利用方式的地块设置监测样地。

对于有放牧和打草利用的监测区，应设置围栏避免监测仪器被牲畜或打草机械损坏。围栏大小为20 m×20 m。

采用涡度相关法的监测样地，围栏内应定期对下垫面植被进行刈割，以保持与围栏外一致的植被高度，避免围栏内外植被差异对测定结果的影响。采用箱式法的监测样地，还需要对仪器底座中的植被进行刈割。对于无放牧和打草利用的样地，不需要进行刈割。

4.1.3　监测频次

全年连续监测。涡度相关法的监测频次不低于0.5 h～1 h。自动箱式法的监测频次不低于1 h～2 h。

4.1.4　设备维护

涡度相关法：定期清洁红外分析仪、净辐射仪镜面和光合有效辐射探头，去除三维超声风速仪的灰尘、蛛网等异物，检查雨量桶是否堵塞等。建议生长季为1～2周一次，非生长季每4周一次。

箱式法：定期清理箱体底座和基座周边的植被、箱体外立面灰尘，以及箱体内的蛛网等异物，冬季需清理底座周边的积雪。

红外分析仪需每年标定一次。

4.1.5　固碳速率计算

涡度相关和箱式测定系统的测定值为小时（0.5 h～2 h不等）的净生态系统碳交换（NEE）。不同时间尺度的固碳速率为NEE累加值的负值。不同时间尺度下的草地生态系统固碳速率计算公式见表1。

表1　不同时间尺度下草地固碳速率的计算公式

时间尺度	固碳速率 csr	净生态系统碳交换 NEE	单位
日	$csr_{day} = -NEE_{day}$	$NEE_{day} = (\sum_{i=1}^{24} NEE_h)/1000$	g C m^{-2} d^{-1}
月	$csr_{mon} = -NEE_{mon}$	$NEE_{mon} = \sum_{i=1}^{31} NEE_{day}$	g C m^{-2} mon^{-1}
年	$csr_a = -NEE_a$	$NEE_{yr} = \sum_{i=1}^{12} NEE_{mon}$	g C m^{-2} a^{-1}
注1：NEE_h表示小时的固碳速率。 注2：当单位用二氧化碳（CO_2）表示时，上述csr和NEE的值通常须乘以换算系数（换算系数=44/12）。			

4.2　库差法

4.2.1　适用范围

通过计算监测样地碳密度的年变化率估算固碳速率。

适用于年尺度的固碳速率监测。

4.2.2　样地设置

选择代表监测区主要草地类型和利用方式的地块设置监测样地，并记录样地的经纬度、海拔等信息。样地面积不小于100 m×100 m。沿样地对角线布设5～10个样方，样方间隔不小于10 m。

4.2.3　监测时间与频次

植被监测时间在地上生物量达到最大时（7～8月）进行，土壤监测可在6～9月进行。

植被监测每年一次，土壤监测每3～5年一次。

4.2.4　碳储量监测

碳储量的调查按照DB15/T 3764的规定执行。

4.2.5　固碳速率计算

样地尺度的固碳速率为两个测定年之间监测样地碳储量的年变化率。计算公式如下：

$$csr = （CD_{t2} - CD_{t1}）/（t_2 - t_1）\quad\text{.....}(1)$$

式中：

csr——监测样地的固碳速率，单位为吨碳每公顷每年（t C/hm^2/a）；

CD_{t2}——监测样地在第二个测定年的生态系统碳储量，单位为吨碳每公顷（t C/hm^2）；

CD_{t1}——监测样地在第一个测定年的生态系统碳储量，单位为吨碳每公顷（t C/hm^2）；

t_2——第二个测定年；

t_1——第一个测定年。

5　区域尺度的固碳速率核算

5.1 基于面积加权的固碳速率核算

用样地尺度的固碳速率与其所代表的草地面积乘积的加权平均值表示区域尺度的固碳速率。区域尺度包括但不限于行政区、生态功能区、地理单元、草地类型等尺度。计算公式如下：

$$CSR = \frac{\sum(csr_i \times Area_i)}{\sum Area_i} \quad \cdots\cdots (2)$$

式中：

CSR——监测区域的固碳速率，单位为吨碳每公顷每年（t C/hm^2/a）；

csr_i——监测样地i的固碳速率，单位为吨碳每公顷每年（t C/hm^2/a）；

$Area_i$——监测样地i代表的监测区草地面积，单位为公顷（hm^2）。

5.2 基于遥感反演的固碳速率核算

基于直接测量法和库差法获取的草地固碳速率数据，结合监测区域的遥感影像以及各类生态因子数据，依据不同草地类型，建立草地固碳速率的遥感反演模型，反演获得监测区域的固碳速率。

具体方法按照DB15/T 3763的规定执行。

参 考 文 献

[1] 于贵瑞, 孙晓敏等著. 陆地生态系统通量观测的原理与方法(第二版) [M]. 北京：高等教育出版社，2018

ICS 65.020.01
CCS B 04

DB15

内 蒙 古 自 治 区 地 方 标 准

DB15/T 3765—2024

草地碳汇监测与核算技术规程

Code of practice for grassland carbon sink monitoring and accounting

2024－12－18 发布　　2025－01－18 实施

内蒙古自治区市场监督管理局　　发 布

前　　言

本文件按照GB/T 1.1—2020《标准化工作导则　第1部分：标准化文件的结构和起草规则》的规定起草。

请注意本文件的某些内容可能涉及专利。本文件的发布机构不承担识别专利的责任。

本文件由内蒙古自治区林业和草原局提出并归口。

本文件起草单位：中国科学院植物研究所、内蒙古自治区林业和草原监测规划院、内蒙古农业大学、内蒙古自治区林业科学研究院、河北大学。

本文件主要起草人：白永飞、王扬、杨勇、常书娟、苏纪帅、赵玉金、刘爱军、王小亮、王成杰。

草地碳汇监测与核算技术规程

1 范围

本文件规定了基于库差法和涡度相关法的草地碳汇监测与核算技术方法。

本文件适用于草地生态系统的碳汇监测与核算工作。

2 规范性引用文件

下列文件中的内容通过文中的规范性引用而构成本文件必不可少的条款。其中，注日期的引用文件，仅该日期对应的版本适用于本文件；不注日期的引用文件，其最新版本（包括所有的修改单）适用于本文件。

DB15/T 3683 草地碳汇计量与监测术语

DB15/T 3763 草地碳汇遥感监测技术指南

DB15/T 3764 草地碳储量调查与核算技术规程

3 术语和定义

DB15/T 3683界定的以及下列术语和定义适用于本文件。

3.1

草地碳汇 grassland carbon sink

草地生态系统中，植物群落通过光合作用吸收大气中CO_2并将其固定在草地植被和土壤中的过程和功能。

[来源：DB15/T 3683-2024，3.1.2，有修改]

3.2

草地碳储量 grassland carbon storage

特定面积和土层深度下草地生态系统中植被和土壤的碳元素总质量。包括植被碳储量和土壤碳储量。常用单位为吨碳（t C）。

注：监测实践中，通常关注有机碳。若需评估包括无机碳在内的碳储量，应明确说明。

3.3

碳通量 carbon flux

生态系统在单位时间单位面积上的碳循环总量，包括碳的输入和输出。

3.4

净生态系统碳交换 net ecosystem carbon exchange,（NEE）

单位时间单位面积草地生态系统从大气中吸收的碳通量与向大气释放的碳通量的净平衡值，是总生态系统生产力与生态系统呼吸的差值。常用单位为g C/m^2/s或g C/hm^2/a。

[来源：DB15/T 3683-2024，3.2.1.16]

3.5

净生态系统生产力 net ecosystem productivity,（NEP）

草地生态系统中，净初级生产力中减去异养生物呼吸消耗光合产物之后的部分。常用单位为kg C/hm^2/a。

［来源：DB15/T 3683-2024，3.2.1.13，有修改］

3.6

库差法 stock-difference approach

通过计算两个时间点之间碳库的储量变化来估算碳的净吸收或释放量，即生态系统碳汇的方法。

［来源：DB15/T 3683-2024，3.2.3.7，有修改］

3.7

涡度相关法 eddy covariance method

基于微气象原理估算垂直风速与物质或能量脉动的协方差估算草地生态系统碳汇的方法。

［来源：DB15/T 3683-2024，3.2.3.9，有修改］

4 碳汇监测

4.1 库差法

4.1.1 样地设置

4.1.1.1 区域样地布设

以监测区域的草地类型为基本单元布设区域样地,选择代表性草地类型和利用方式的地块布设监测样地。

为保证区域样地的代表性，各类型草地所选区域样地的代表面积分别为：典型草原、草甸草原、草甸大于10000 hm^2，荒漠草原大于15000 hm^2，草原化荒漠大于20000 hm^2。

4.1.1.2 典型样地设置

选择有较好代表性和一致性的地块设置监测样地，记录经纬度、海拔等样地信息。

样地面积不小于100 m×100 m。沿样地对角线布设5～10个样方，样方间隔不小于10 m。

4.1.1.3 监测时间与频次

植被监测时间在地上生物量达到最大时（7～8月）进行，土壤监测可在6~9月进行。

植被监测每年一次，土壤监测每3～5年一次。

4.1.2 碳储量调查

包括植被碳储量和土壤碳储量：

--植被碳储量：地上生物量、枯落物生物量和地下生物量；

--土壤碳储量：有机碳含量、砾石含量和土壤容重。一般建议土壤深度为50 cm～100 cm。

碳储量的调查按照DB15/T 3764 的规定执行。

4.2 涡度相关法

4.2.1 样地设置

4.2.1.1 区域样地布设

参见4.1.1.1。

4.2.1.2 典型样地设置

选择代表监测区域植被类型和利用方式的地块设置监测样地。要求下垫面地势平坦（坡度<10°）、植被均一。样地大小一般要求保证以通量塔为中心，半径为仪器安装高度的50～100倍。

对于有放牧和打草利用的监测区，应设置围栏避免监测仪器被牲畜或打草机械损坏。围栏大小为20 m×20 m。围栏内应定期对下垫面植被进行刈割，以保持与围栏外一致的植被高度，避免围栏内外植被差异对测定结果的影响。

4.2.2 监测仪器

涡度相关监测仪器包括通量观测系统和微气象观测系统两部分。根据下垫面的均一性，仪器安装高度通常为2 m～5 m。

4.2.3 监测时间与频度

全年自动连续监测，监测频度通常为半小时。

4.2.4 监测指标

通量观测指标包括通量数据和气象数据。

4.2.4.1 通量数据

高频数据：三维风速、CO_2浓度、水汽浓度、温度等，监测频度10 Hz。

半小时数据：CO_2通量、显热通量、感热通量、辐射通量、土壤热通量等，监测频度半小时。

4.2.4.2 气象数据

太阳总辐射、净辐射、光合有效辐射、大气温湿度、降水量、土壤温湿度等，监测频度半小时。

4.2.5 数据处理

4.2.5.1 处理流程

数据处理流程包括：数据校正和质控、数据插补和通量数据拆分三个步骤。

计算原理和详细方法参见《陆地生态系统通量观测的原理与方法(第二版)》（于贵瑞，孙晓敏等，2018）。

4.2.5.2 数据校正和质控

将原始高频数据用数据处理软件进行校正，得到半小时数据，再进行质控、插补和拆分。

数据校正流程包括：数据趋势去除、延迟时间校正、野点剔除、坐标旋转、WPL（Webb-Pearman-Leuning）校正、频率响应校正等。

根据监测样地的地形、气候和植被条件，使用适合监测区域的临界摩擦风速，剔除夜间低湍流期间的异常数据。

上述处理流程可在配套商业软件中进行。

4.2.5.3 数据插补

气象数据：缺失数据小于2 h，使用相邻数据进行线性内插获得。大于2 h的缺失数据使用滑动平均法进行插补。长时段（大于10天）缺失的数据，利用不同气象变量之间的关系或临近气象站数据进行插补。

通量数据：缺失数据小于2 h，使用线性内插法。缺失大于2 h的白天数据，使用光响应方程插补。缺失大于2 h的夜间数据采用温度响应方程插补。

4.2.5.4 通量数据拆分

通量系统直接测量数据为净生态系统碳交换（NEE），如需进一步获取生态系统总初级生产力（gross primary productivity，GPP）和生态系统呼吸（ecosystem respiration，ER），需通过模型拆分。

通量数据拆分方法：

——呼吸方程法，利用夜间碳通量测量值与环境因子之间的关系建立生态系统呼吸方程，推导白天生态系统呼吸，并计算生态系统GPP。

——光响应方程法，利用白天碳通量测量值与光合有效辐射之间的关系，建立生态系统水平的光响应方程，并进一步计算ER和GPP。

5 碳汇核算

5.1 基于面积累积的碳汇核算

5.1.1 库差法

5.1.1.1 样地尺度的碳汇

样地尺度的碳汇大小为两个测定时间点之间监测样地碳储量的变化量。变化量为正值，表示监测样地为碳汇，结果为负值，表示碳源。计算公式见公式（1）。

$$cs = CD_2 - CD_1 \quad (1)$$

式中：

cs——监测样地的碳汇，单位为吨碳每公顷（t C/hm^2）；

CD_2——监测样地i在第二个测定时间点的生态系统碳储量，单位为吨碳每公顷（t C/hm^2）；

CD_1——监测样地i在第一个测定时间点的生态系统碳储量，单位为吨碳每公顷（t C/hm^2）；

监测样地的碳储量计算方法参见 DB15/T 3764 。

5.1.1.2 监测区域的碳汇

监测区域的碳汇大小为两个测定时间点之间监测样地碳储量的变化量与相应面积乘积的累加值。计算结果为正值时，监测区域为碳汇，结果为负值，监测区域为碳源。计算公式见公式（2）。

$$CS = \sum_{i=1}^{n}(cs_i \times Area_i) \quad (2)$$

式中：

CS——监测区域的碳汇，单位为吨碳（t C）；

cs_i——监测样地i的碳汇，单位为吨碳（t C）；

$Area_i$——监测样地i所代表的监测区草地面积，单位为公顷（hm^2）。

5.1.2 涡度相关法

涡度相关法直接测定的是净生态系统碳交换（Net Ecosystem Exchange，NEE）。监测样地的碳汇为一定时期净生态系统碳交换（NEE）累加值的负值，即净生态系统生产力（NEP）。当NEP为正值时，表示监测区域为碳汇；当NEP为负值时，表示监测区域为碳源。

区域尺度的碳汇为样地尺度的NEP与监测样地所代表区域草地面积的乘积。计算公式见公式（3）。

$$CS = \sum_{i=1}^{n}(NEP_i \times Area_i) \quad (3)$$

式中：

CS——监测区域的碳汇，单位为吨碳（t C）；

NEP_i——监测样地i的碳汇，单位为吨碳每公顷（t C/hm^2）；

$Area_i$——监测样地i所代表的监测区草地面积，单位为公顷（hm^2）。

5.2 基于遥感反演的碳汇核算

基于库差法和涡度相关法获取的草地碳汇数据，结合监测区域的遥感影像以及各类生态因子数据，依据不同草地类型，建立草地碳汇的遥感反演模型，反演获得监测区域的碳汇数据。

具体方法按照DB15/T 3763 的规定执行。

参 考 文 献

[1] 于贵瑞，孙晓敏等著. 陆地生态系统通量观测的原理与方法(第二版) [M]. 北京：高等教育出版社，2018

内蒙古自治区科学技术进步奖

证　书

为表彰内蒙古自治区科学技术进步奖获得者，特颁发此证书。

项目名称：退化草原生态修复技术体系创建与理论创新及修复模式示范推广

奖励等级：一等奖

获 奖 者：白永飞

内蒙古自治区人民政府

2023 年 9 月 4 日

证书号：2022-J-1-08-R02

中国科学院大学

University of Chinese Academy of Sciences

荣誉证书

白永飞 老师：

您讲授的《生态系统生态学 A》课程，荣获中国科学院大学2020年校级“研究生优秀课程”。

特发此证，以资鼓励！

中国科学院大学

二〇二一年六月

中国科学院大学

University of Chinese Academy of Sciences

荣誉证书

白永飞 老师：

您讲授的《生态系统生态学 A》课程，荣获中国科学院大学2020年学院级“研究生优秀课程”。

特发此证，以资鼓励！

中国科学院大学

二〇二一年 月

中国科学院
CHINESE ACADEMY OF SCIENCES

证书

白永飞 老师：

您在研究生培养工作中，成绩突出，荣获2017年度中国科学院“朱李月华优秀教师”奖。特发此证，以资鼓励。

中国科学院前沿科学与教育局

二〇一七年八月

中国科学院
CHINESE ACADEMY OF SCIENCES

证书

白永飞老师：

您在研究生培养工作中，成绩卓著，荣获2016年度中国科学院“优秀研究生指导教师”奖。特发此证，以资鼓励。

中国科学院

二〇一六年九月

中国科学院大学

2013年度中国科学院大学—BHPB奖学金和导师科研奖获得者名单公示通知

各研究所:

经中国科学院大学—BHPB奖学金评审委员会评议，范克龙等25位在学研究生获2013年度中国科学院大学—BHPB奖学金，其导师相应获得导师科研奖。

根据评选工作相关规定，现将奖学金获得者名单予以公示，公示期限为12月12日—12月19日，共7天。在此期间，对公示名单有异议者，请以书面形式或电子邮件向中国科学院大学国际合作处实名反映。

中国科学院大学根据获奖名单将相应经费划拨至有关单位(见附件)。请相关单位收到奖学金拨款后，造册签字发放并进行管理。

附件: 2013年度中国科学院大学—BHPB奖学金和导师科研奖获得者名单

联系地址: 北京市石景山区玉泉路19号（甲）中国科学院大学国际合作处
联 系 人: 李文宣
联系电话: 010-88256107
E-mail: liwenxuan@ucas.ac.cn

中国科学院大学
国际合作处
二〇一三年十二月十二日

附件：2013年度中国科学院大学—BHPB奖学金和导师科研奖获得者名单

序号	姓名	学生类型	性别	地区	导师	单位名称
1	范克龙	博士	男	北京	阎锡蕴	生物物理研究所
2	兰志春	博士	男	北京	白永飞	植物研究所
3	施小山	博士	男	上海	许琛琦	上海生科院生物化学与细胞生物学研究所
4	闫 卫	博士	女	上海	王恩多	上海生命科学院生物化学与细胞研究所
5	胡 政	博士	男	北京	吴仲义	北京基因组研究所
6	夏婷婷	博士	女	上海	郭非凡	上海生命科学研究院营养科学研究所
7	周光敏	博士	男	辽宁	成会明	金属研究所
8	张 磊	博士	男	上海	冯 衍	上海光学精密机械研究所
9	潘黎敏	博士	女	上海	施剑林	上海硅酸盐研究所
10	周夕淋	博士	男	上海	宋志棠	上海微系统与信息技术研究所
11	唐红杰	博士	男	北京	王 丹	过程工程研究所
12	李慧珍	博士	女	广州	游 静	广州地球化学研究所
13	吴文芳	博士	女	北京	潘永信	地质与地球物理研究所
14	王远东	博士	男	山东	侯西勇	烟台海岸带研究所
15	王国栋	博士	男	吉林	吕宪国	东北地理与农业生态研究所
16	逯一中	博士	男	吉林	陈 卫	长春应用化学研究所
17	李 蒙	博士	女	吉林	曲晓刚	长春应用化学研究所
18	李 轮	博士	男	江苏	王强斌	苏州纳米技术与纳米仿生研究所
19	李 斌	博士	男	甘肃	周 峰	兰州化学物理研究所
20	张凤娇	博士	女	北京	朱道本	化学研究所
21	康 俊	博士	男	北京	李京波	半导体研究所
22	喻 颖	博士	女	北京	牛智川	半导体研究所
23	袁敬华	博士	男	北京	李金增	国家天文台
24	刘灰礼	博士	男	上海	陈立东	上海硅酸盐研究所
25	林禹泽	博士	男	北京	占肖卫	化学研究所

注:根据中国科学院大学与BHP Billiton公司协议，本奖学金分为学生奖学金8000元/年（800元/月，共发 10个月，2013年9月—2014年6月），学生科研津贴4000元/年，导师科研奖4000元/年。

白永飞站长接受中国国际电视台（CGTN）采访

背景意义：2020 年 9 月，我国提出二氧化碳排放力争 2030 年前达到峰值，力争 2060 年前实现碳中和。“十四五”时期是实现碳达峰目标和碳中和愿景的关键时期，草原碳汇增量也是助力碳中和愿景的重要力量。锡林郭勒站在草原生态系统碳储量分布，固碳速率和潜力研究等方面积累了大量的监测数据，具备扎实的理论基础，同时开展了多种退化草原修复的试验示范，这为进一步在新时期开展草原碳汇研究奠定了重要的工作基础。

主要内容：2021 年 10 月 15 日，联合国《生物多样性公约》第十五次缔约方大会（COP15）期间，白永飞站长接受中国国际电视台（CGTN）采访，基于锡林郭勒站的长期监测研究工作，就我国的天然草原保护与修复在助力国家碳中和目标与国家生态文明建设中的重要作用进行了介绍。

工作成效：近年来，锡林郭勒站围绕草原碳汇工作，从基础研究、技术研发、标准制定和试验示范等角度，布局了多项工作。（1）2021 年，本站获得国家自然科学基金重大项目 1 项，主要研究不同管理措施下草原生产力和碳汇功能的协同与调控机制；（2）2021 年，本站申请了“草原生态系统碳汇自动测定系统”的实用新型专利。目前已经通过与公司合作，研发了基于该系统的样机，正在进行有关测定和调试中。该系统克服了传统方法人工测定频率低的问题，同时相较于涡度相关系统，能够实现净生态系统碳交换和生态系统呼吸两个碳循环组分的分别观测；（3）2021 年，与中国绿化基金会、内蒙古自治区和相关企业，联合开展草原碳汇方法学、草原碳汇系列标准的制定工作，为我国北方草原退化生态系统保护与修复提供标准体系支撑；（4）针对近年来开展的退化草原修复示范工作，在示范区进行了有关示范区内外植被与土壤碳库差异的调查研究；并与企业合作，参与了两项基于碳汇方法学的退化草原碳汇修复公益项目。

图 1　2021 年 10 月 15 日，白永飞站长接受中国国际电视台（CGTN）采访

中国科学院大学课程讲义

生态系统生态学

中国科学院大学资源与环境学院

2022 年 9 月

目　录

第一章 生态系统生态学及其前沿科学问题 1
第一节　生态系统和生态系统生态学的基本概念 1
第二节　生态系统的重要特征 2
第三节　生态系统输入过程 3
第四节　生态系统生产过程 4
第五节　生态系统分解过程 5
第六节　生态系统养分循环 7
第七节　生物多样性与生态系统功能 8
第八节　人类活动与全球变化对生态系统的影响 10
第九节　生态系统服务与生态安全 10
第十节　生态学研究中的尺度问题 12
第十一节　新技术和新方法在生态系统生态学研究中的应用 13

第二章 全球气候系统 22
第一节　基本概念 22
第二节　地球能量平衡 24
第三节　大气层系统 24
第四节　地形对气候的影响 27
第五节　植被对气候的影响 27
第六节　气候的时间变异性 28
第七节　生态系统分布与结构和气候的关系 28

第三章 地质、土壤和沉积物 30
第一节　影响土壤形成的因素 30
第二节　控制水土流失 31
第三节　土壤特性的形成 31
第四节　土壤层和土壤分类 32
第五节　土壤特性和生态系统功能 33

第四章 陆地水和能量平衡 34
第一节　地表能量平衡 34
第二节　生态系统水平衡的基本原理 39
第三节　生态系统的水分流失 42

第五章 陆地生态系统碳输入 44
第一节　生态系统碳输入 44
第二节　光合作用途径 44

第三节　陆地植物光合作用 48
第四节　总初级生产 51

第六章 植物的碳概算 54
引言 54
第一节　核心问题 55
第二节　植物呼吸 55
第三节　什么是 NPP？ 58
第四节　陆地 NPP 62
第五节　分配 66
第六节　组织周转 69
本章小结 71

第七章 分解和生态系统的碳概算 72
引言 72
第一节　核心问题 72
第二节　分解和生态系统碳平衡概要 72
第三节　分解的时空异质性 79
第四节　控制分解的因素 82
第五节　净生态系统生产 85
第六节　净生态系统碳平衡 91

第八章 植物的养分利用 94
引言 94
第一节　核心问题 94
第二节　概要 94
第三节　陆地生态系统养分向根的运动 96
第四节　养分的吸收（NUTRIENT ABSORPTION） 99
第五节　养分利用（NUTRIENT USE） 105
第六节　植物的养分丢失（NUTRIENT LOSS FROM PLANTS） 107
本章小结 110

第九章 养分循环 111
引言 111
第一节　核心要点 111
第二节　概要 111
第三节　陆地生态系统氮输入 112
第四节　氮的内循环 116
第五节　氮损失途径（PATHWAYS OF NITROGEN LOSS） 123
第六节　其他元素的循环 126

第十章 营养级动态 133
引言 133
第一节 核心要点 134
第二节 营养级动态概要 134
第三节 生态系统能量流动的控制 136
第四节 养分循环的营养级效应 140
第五节 生态效率 141
第六节 食物链长度 141
第七节 季节性和年际格局 141
第八节 养分的传输 142
第九节 基于碎屑的营养级系统 144
第十节 整合的食物网 145
本章小结 146

第十一章 物种对生态系统过程的作用 147
第一节 物种对生态系统过程的作用 147
第二节 作用类型 153
第三节 响应类型 158
第四节 植物性状对生态系统的作用 159
第五节 研究案例 162
本章小结 173

第十二章 时间动态 176
第一节 生态系统过程的波动 176
第二节 生态系统的弹性和变化 181
第三节 干扰 182
第四节 演替 187
第五节 生态系统过程的时间尺度推绎 195
第六节 研究案例 196

第十三章 景观异质性与生态系统动态 209
第一节 景观异质性的概念 209
第二节 空间异质性的起因 212
第三节 景观中斑块间的相互作用 215
第四节 土地利用变化和景观异质性 222
第五节 空间异质性与尺度推绎 226
第六节 研究案例 228
本章小结 239

第十四章 地球系统的变化 241

第一节　全球水循环.....241
第二节　全球碳循环.....245
第三节　全球氮循环.....251
第四节　全球磷循环.....254
第五节　全球硫循环.....257
第六节　研究案例.....259
本章小结.....263

第十五章 生态系统的管理和维持.....266
第一节　可持续的社会生态体系.....266
第二节　生态系统管理的概念框架.....269
第三节　生态系统原理在管理中的应用.....272
第四节　生态系统管理的社会经济范畴.....275
第五节　研究案例.....276
本章小结.....287

生态系统生态学综合作业要求.....289

生态系统生态学的前沿科学问题.....290

第一章 生态系统生态学及其前沿科学问题

第一节　生态系统和生态系统生态学的基本概念

生态系统生态学为我们理解地球系统提供了一个机理基础，生态系统作为地球的生命支持系统，为人类社会提供了多种产品和服务。然而，近 50 年来人类活动以前所未有的速度和广度改变着人类社会赖以生存和发展的生态系统，导致了全球范围内生物多样性的丧失和生态系统结构与功能的退化。同时，全球气候变化和人类活动干扰对生态系统结构与功能，格局、过程与服务的影响具有交互作用。

深刻认识生态系统内在规律和机理，对于坚持人与自然是生命共同体，人类必须尊重自然、顺应自然、保护自然的生态文明思想，树立和践行绿水青山就是金山银山理念，统筹山水林田湖草系统治理，建设美丽中国具有理论和现实意义。

1.1 生态系统的概念

生态系统（ecosystem）是由所有生物有机体和与其相互作用的非生物环境构成的一个整体系统(Chapin et al. 2011)。生态系统过程（ecosystem process）则是指能量和物质从一个库向另一个库的转移。

1.2 生态系统过程

图 1.1-1 表示的就是一个简单的生态系统模型(Jorgensen 2009)。当光能通过植物光合作用过程使 CO_2 被还原形成糖时，能量就进入了生态系统(Chapin et al. 2011)。能量和物质在生态系统中进行相互交换，所以两者是紧密相连的。当有机物通过燃烧或动植物和微生物呼吸而被氧化时，能量就会从生态系统中丧失(Chapin et al. 2011)，如图中指向生态系统边界外方的白色箭头（图 1.1-1）。物质通过一系列的过程在生态系统的非生物组分间进行交换，这些过程包括岩石的风化、水分的蒸发以及物质在水中的溶解(Chapin et al. 2011)。与生态系统中生物组分相关的过程有：植物对矿质营养的吸收，动、植物的死亡，死有机质通过微生物的分解，草食者对植物的消耗以及捕食者对草食者的消耗。这些过程大多对环境因子如温度和湿度极为敏感(Chapin et al. 2011)。以上这些过程可以归结于两个方面：能量流动和物质循环，二者也是生态系统生态学研究的重点(Jorgensen 2009)。

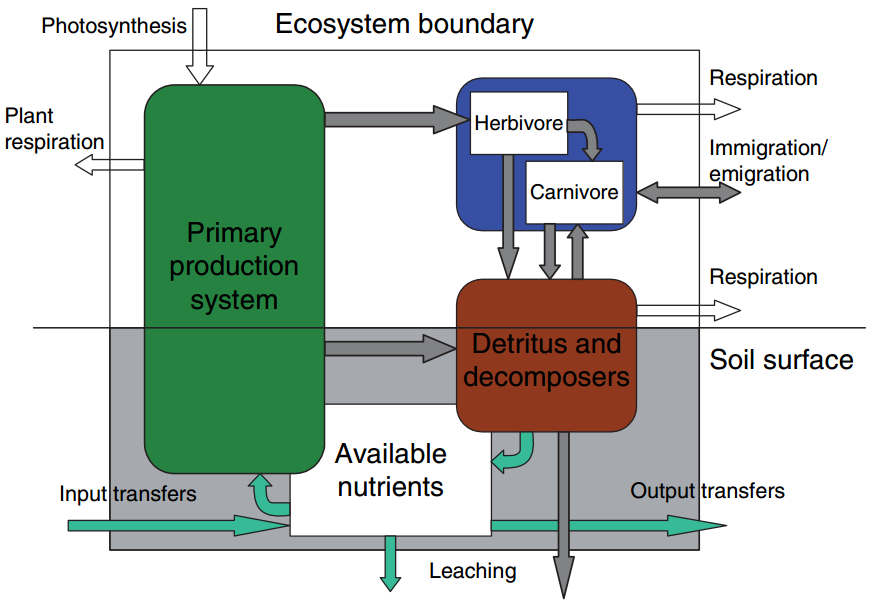


Figure1.1-1 Conceptual diagram of a simplified ecosystem. Clear arrows, energy; dark arrows, biomass; blue arrows, water (from Jorgensen, 2009).

图 1.1-1 简化的生态系统概念模型。基于以上的概念模型，我们将内容分为以下几个部分：（1）生态系统特征；（2）生态系统输入过程；（3）生态系统生产过程；（4）生态系统分解过程；（5）生态系统养分循环；（6）生物多样性与生态系统功能；（7）人类活动与全球变化；（8）生态系统服务。（引自 Jorgensen, 2009）

第二节　生态系统的重要特征

生态系统是当今生态学中最重要的概念之一。生态系统包括生物群落及其无机环境，它强调的是系统中各个成员的相互作用，所以几乎是无所不包的生态网络。生态系统生态学主要研究调节生态系统内物质和能量库与通量的因子(Chapin et al. 2011)。一般来说，一个生态系统包括以下四个部分：非生物环境、生产者、消费者和分解者。正是由于这些成分使得生态系统能够达到一种稳定状况，它包括结构和功能上的稳定。在过去二十年中，我们对生物和非生物因素如何推动生态系统功能的理解取得了很大进步，这在一定程度上是由于群落和生态系统生态学日益一体化的结果 (Sutherland et al. 2013)。因此，我们现在对群落多样性和组成如何影响生态系统过程、生态系统对环境扰动的抵抗力和恢复力、以及生态系统的生产者和分解者之间的反馈有了更好的理解(Sutherland et al. 2013)。人们也逐渐认识到生态系统如何对全球环境变化做出响应，它们调节碳和营养物质流动的能力，以及它们与地球气候系统的相互作用，但仍然存在一些挑战 (Sutherland et al. 2013)。例如：

1) 在控制群落多样性和组成方面，随机过程和确定过程的相对重要性是什么？在不同的生态系统类型中，它们是如何变化的 (Chase 2007, Chase and Myers 2011, Sutherland et al. 2013, Wang et al. 2013)? What is the relative importance of stochastic

vs. deterministic processes in controlling diversity and composition of communities, and how does this vary across ecosystem types?

2) 生态系统哪些属性对群落组成的变化最敏感?What properties of ecosystem are most sensitive to changes in community composition?

3) 我们能否基于物种的性状来预测生态系统对环境变化的响应? Can we predict the responses of ecosystems to environmental change based on the traits of species?

4) 物种性状如何影响生态网络结构(Crea et al. 2016, Tylianakis and Morris 2017)？How do species traits influence ecological network structure?

5) 生态学相互作用的网络结构如何影响生态系统的功能和稳定性 (Murphy et al. 2016)? How does the structure of ecological interaction networks affect ecosystem functioning and stability?

6) 哪些因素和机制决定了生态系统对外部扰动的弹性和恢复力？如何测度(Seddon et al. 2016)? Which factors and mechanisms determine the resilience of ecosystems to external perturbations and how do we measure resilience?

7) 我们如何知道一个生态系统何时接近临界点(Laurance 2013)？How can we tell when an ecosystem is near a tipping point? 哪些生态系统对临界点更敏感 (Sutherland et al. 2013)？为什么？Which ecosystems are susceptible to showing tipping points and why?

8) 在生态系统中，滞后现象是特例还是常态(Fauchald 2010, Sternberg 2010)？Is hysteresis the exception or the norm in ecological systems?

第三节　生态系统输入过程

进入生态系统中的有机碳最主要的来源是植物的光合作用(Paterson et al. 2009)。生态系统中的生产者（如植物）利用太阳能将无机碳转化为有机碳的形式进入到生态系统，从而进入到生态系统的物质循环和能量流动（图 1.3-1）。

9) 初级生产者多样性在多大程度驱动了更广泛的群落多样性(Otto et al. 2008, Castagneyrol et al. 2014)? To what extent is primary producer diversity a driver of wider community diversity?

10) 如何利用诸如个体大小和叶面积等简单性状的分布来预测群落属性及其对环境变的响应 (Wardle et al. 1998)？How well can community properties and responses to environmental change be predicted from the distribution of simple synoptic traits, e.g. body size, leaf area?

11) 植物如何对气候变化，如干旱等，做出响应 (Anderegg et al. 2019, Chardon et al. 2019,

Miller and McGill 2019)？How do plants respond to climate change, e.g. drought, etc.?

12) 我们如何利用物种性状作为一个指标来预测营养级相互作用的强度(Otto et al. 2008)？How can we use species' traits as proxies to predict trophic interaction strength?

13) 干扰如何影响营养级之间的相互作用(Grabowski 2004, Sentis et al. 2015)？How do disturbances affect trophic interaction?

14) 营养级之间相互作用的变化对生态系统功能有多大影响(Schuldt et al. 2018)？How much do changes in trophic interactions affect ecosystem functioning?

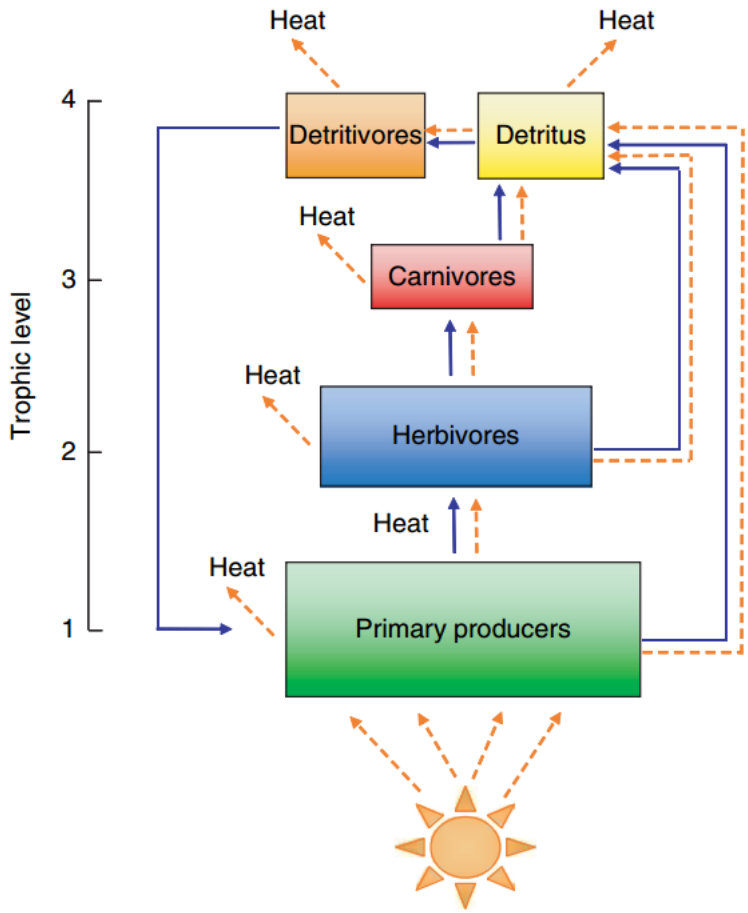


Figure 1.3-1 Energy flows and material cycles in an ecosystem (from Jorgensen, 2009).

图 1.3-1 生态系统能量流动与物质循环（引自 Jorgensen, 2009）

第四节　生态系统生产过程

生态系统中的能量流动开始于植物的光合作用对于太阳能的固定。在初级生产过程中，植物固定的能量有一部分被植物自身呼吸消耗掉，剩下的部分称为净初级生产力（net primary

production，NPP）。包括呼吸在内的全部生产量称为总初级生产力（gross primary production, GPP）。植物生产力在所有生态系统过程中都起着关键作用(Chapin et al. 2011)。

15) 植物固定的 C 在生长和呼吸之间的分配受什么机制控制(Atkin et al. 2000, Poorter 2002)？What mechanisms control the allocation of plant-fixed C between growth and respiration?

16) 净初级生产力和总初级生产力变化的机制是什么(Goulden et al. 2011)？What are the mechanisms for the changes in NPP and GPP?

17) C 分配的改变如何影响资源限制、资源获取和 NPP(Rennenberg 2015)？How do changes in allocation affect resource limitation, resource acquisition and NPP?

18) 生态系统中，除氮和磷（以及海洋中的铁）以外的营养物质如何影响生产力(Sutherland et al. 2013)? How do nutrients other than nitrogen and phosphorus (and iron in the sea) affect productivity in ecosystems?

第五节　生态系统分解过程

生态系统的分解（decomposition）是死有机质逐步降解的过程，使无机元素从有机质中释放出来。如果没有分解作用，生态系统将迅速积累大量腐烂的动、植物尸体，导致营养物质以植物不能利用的形式积累，而且大气中的 CO_2 将最终耗尽。全球土壤 C 库大概为大气 C 库的三倍，因此土壤有机质分解（CO_2）在决定未来气候变化轨迹中扮演着非常重要的作用。

19) 分解作用对生态系统系统功能的意义是什么(Hattenschwiler et al. 2005)？What are the implications of decomposition for ecosystem functioning?

20) 全球变化引起的生物多样性丧失如何影响分解作用(Ball et al. 2008, Miki et al. 2014)？How does the loss of biodiversity due to global change affect decomposition?

21) 细菌和真菌在分解过程中的作用有何差异，为什么？What is the difference between the roles of bacteria and fungi during decomposition and why?

22) 由外界干扰引起的不同微生物类群（如细菌和真菌）相对比例的改变如何影响分解过程 (Peter et al. 2011)？How do the changes in the relative proportions of different microbial groups (e.g. bacteria and fungi) caused by external perturbations affect the decomposition processes?

23) 植物与微生物之间的相互作用如何影响生态系统分解过程(McCully 1999, Andrews and Harris 2000, Bais et al. 2004, Hinsinger et al. 2005)？How do plant-microbial interactions affect decomposition processes?

24) 除土壤微生物外，土壤动物对生态系统分解有什么影响(Gonzalez and Seastedt 2001)？In addition to soil microbes, what is the effect of soil animals on ecosystem decomposition?

25) 凋落物质量、环境因子和土壤微生物是影响分解过程中三个最重要的因子，其相对重要性如何(Cornwell et al. 2008, Wickings et al. 2012, Garcia-Palacios et al. 2016)？Litter quality, environmental factors and soil microorganisms are the three most important factors affecting the decomposition process, what is their relative importance？

26) 微生物对分解作用的影响是通过分泌与分解有关的酶，而不是在体内分解死有机质，为什么？Microorganisms influence decomposition by secreting extracellular enzymes rather than by breaking down dead organic matter in their body, why?

27) 作为生态系统中一种重要的共生体，菌根对分解过程有何影响？不同菌根类型（如丛植菌根和外生菌根）有什么差异？As an important symbiont in the ecosystem, how does mycorrhizae affect the decomposition processes? What are the differences between different mycorrhizal types (e.g. arbuscular mycorrhizal and ectomycorrhizal)?

半个世纪以前，Went 和 Stark 在亚马逊雨林中发现内生菌菌丝伸长至叶片中，将菌根与落叶联系起来。他们推测这一类真菌趋近并转运凋落物中的矿质营养至宿主植物中，并把这一现象称之为“direct mineral cycling”。这一假设与我们认为的森林生态系统中，真菌是分解者，菌根真菌通过共生传输矿质营养到宿主植物体内相一致。这些作者所说的内生真菌后来被命名为丛枝菌根真菌（AMF），隶属于球囊菌门中一类不同的真菌。AMF 在有机质中定殖，研究者推测他们具有腐生功能。然而，随后的实验发现，AMF 不可独立培养，是专性共生，只能依赖于宿主植物提供碳源。事实上，AMF 不能分泌分解有机分子的裂解酶，大量研究表明 AMF 缺少同化氮、磷等矿质营养元素的能力。因此，正如 Went 和 Strak 最开始预测的那样，AMF 在趋近凋落物的营养过程中不能独立生存，“direct mineral cycling”随之被认为是不成立的假设。

最开始时，“direct mineral cycling”假说因其在热带森林的与众不同而具有吸引力。基于外生菌根真菌（EMF）可以直接分解有机质，AMF 不具备此功能，AMF 的丰富度与土壤有机质成反比，并且土壤肥力可以描述 AMF 共生植物物种的存在。如果这一框架正确，那么 AMF 共生植物应该在中纬度到低纬度和低海拔地区占优势，这些地方降解速率快，落叶层浅薄，土壤有机质含量低。但是，AMF 宿主植物在欧洲北部和中纬度地区比较盛行，并且全球调查也没有发现 AMF 丰富度和土壤有机质之间的相关性。AMF 共生植物在富有机质地区广泛分布，包括山地草甸、热带云雾林和北极等。

Bunn 等人（2019）最新研究结果表明，AMF 都能够在落叶中定殖（图 1.5-1a, b）。此外，发现落叶和土壤中由不同 AMF 占优势，导致生态位分化（图 1.5-1c）。如果上述研究得到的结果是一种普遍现象(Bunn et al. 2019)，那么：

28) AMF 可以定殖在落叶中（换言之 AMF 不完全依赖于植物提供碳源）(Bunn et al.

2019)，这一现象对分解作用以及其他生态系统功能有什么影响？AMF can colonize leaf litter (that is, not solely dependent on plant carbon sources) (Bunn et al. 2019). What is the implication of this phenomenon for decomposition and other ecosystem functions?

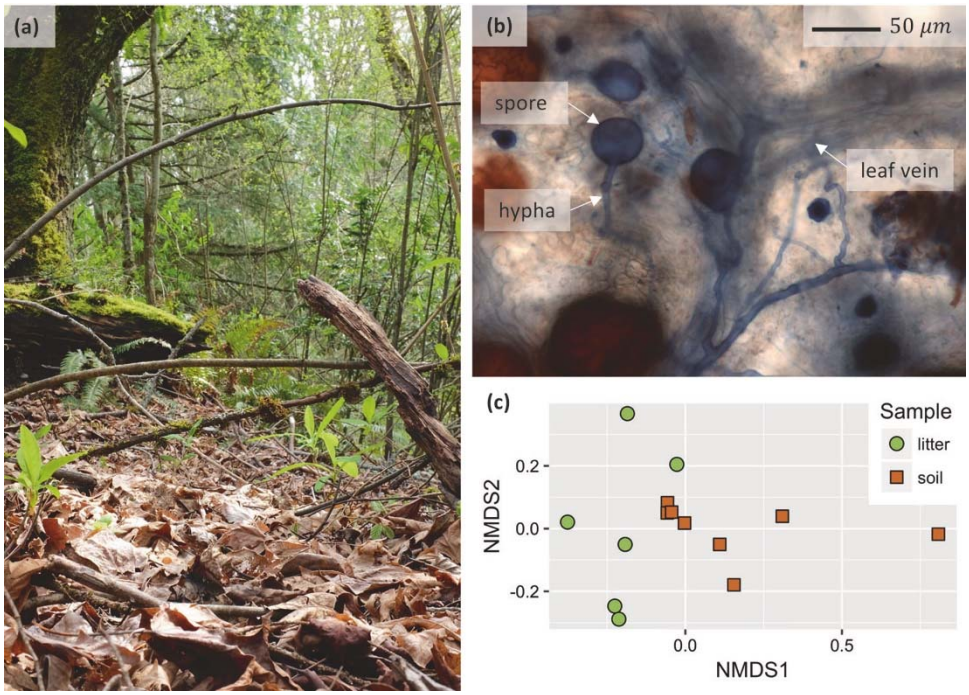


Figure 1.5-1 (a) Bigleaf maple (*Acer macrophyllum*) litter (foreground) on the floor of a temperate, North American, Pacific Northwest forest. Indian plum (*Oemleria cerasiformis*) and sword fern (*Polystichum munitum*) grow up through the litter. These leaves may have fallen from the mature bigleaf maple tree (seen here as a moss-covered, large trunk on the left). (b) Arbuscular mycorrhizal (AM) fungus-like spore with associated hyphae as well as other fungus hyphae in bigleaf maple litter. Leaf veins also are visible. Litter was cleared and stained with Trypan blue and then viewed with light microscopy at 400×. (c) Nonmetric multidimensional ordination of predominant arbuscular mycorrhizal fungi amplified from leaf litter and adjacent soil samples (from Bunn et al. 2019).

图 1.5-1 （a）北美太平洋西北部温带森林大叶枫 (*Acer macrophyllum*) 落叶层(前景)。在凋落物中生长着印度李子（*Oemleria cerasiformis*）和剑蕨（*Polystichum munitum*）。这些叶子可能是从成熟的大叶枫树上掉落下来的（图中左边是被苔藓覆盖的大树干）。（b）大叶枫凋落物中丛枝菌根(AM)真菌孢子与伴生菌丝以及其他真菌菌丝。叶脉清晰可见。将清洗过的凋落物进行台盼蓝染色，并在 400 倍显微镜下观察。（c）从落叶层和邻近土壤样本中扩增出的优势丛枝菌根真菌的非度量多维尺度排序(from Bunn et al. 2019)。

第六节　生态系统养分循环

养分循环包括营养物质进入到生态系统内部，植物和土壤之间的内部转移以及从生态系统中丧失。

29) 大气中的氮是如何进入到陆地生态系统的？How does atmospheric nitrogen enters terrestrial ecosystems?

30) 凋落物中的氮通过什么途径才能成为植物可利用氮？By what pathways can nitrogen in litters become available to plants?

31) 氮素在陆地生态系统中的转化过程有哪些(Kuypers et al. 2018)？What are the processes of nitrogen conversion in terrestrial ecosystems (Kuypers et al. 2018)?

32) 磷进入生态系统的机制是什么？What are the mechanisms by which phosphorus enters ecosystem?

33) 全球变化引起的生物多样性丧失对养分循环有什么影响(Hobbie 1992, Hooper and Vitousek 1998, Niklaus et al. 2007)？What is the impact of biodiversity loss due to global change on nutrient cycling (Hobbie 1992, Hooper and Vitousek 1998, Niklaus et al. 2007)?

34) 不同养分在循环过程中的耦合关系如何(Gusewell 2004, Vitousek et al. 2010, Penuelas et al. 2012, Rivas-Ubach et al. 2012, Penuelas et al. 2013)？全球变化如何影响这些耦合关系 (Delgado-Baquerizo et al. 2013, Yuan and Chen 2015)？What is the coupling between different nutrients in the cycling process (Gusewell 2004, Vitousek et al. 2010, Penuelas et al. 2012, Rivas-Ubach et al. 2012, Penuelas et al. 2013)? How does global change affect these coupling relationships (Delgado-Baquerizo et al. 2013, Yuan and Chen 2015)?

第七节　生物多样性与生态系统功能

生态系统科学未来的挑战就包括预测生态系统现在所经历的这些灾难性转变(Scheffer et al. 2009)，更好地理解空间尺度在推动生态系统进程中的作用，并将迅速增长的生态网络知识(Bascompte 2009)扩展到生态系统功能的研究(Sutherland et al. 2013)。另一个主要挑战是更好地理解生物多样性变化的现实情景如何对生态系统同时发生的灭绝(Cardinale et al. 2012)和入侵(Daniel et al. 2013) 做出响应。

35) 物种丢失如何影响剩余物种的灭绝风险? How does species loss affect the extinction risk of the remaining species?

36) 局地尺度的物种组成和多样性在多大程度上受区域尺度物种库和传播限制控制(Sutherland et al. 2013)？To what extent is local species composition and diversity controlled by dispersal limitation and the regional species pool?

37) 一些我们知之甚少的生态系统，例如，深海、地下水，是否在全球具有重要的生态系统功能(Sutherland et al. 2013)? Are there globally significant ecosystem functions provided by poorly known ecosystems (e.g. deep oceans, ground water)?

38) 不同组织层次的生物多样性（基因、物种丰富度、物种属性、功能属性、功能多样性）对生态系统功能的相对贡献是什么？What is the relative contribution of biodiversity at different levels of organization (genes, species richness, species identity, functional identity, functional diversity) to ecosystem functioning?

39) 在生物多样性变化的现实情景下，生态系统功能是如何变化的(Tilman et al. 1996, Tilman et al. 2014)？How is ecosystem function altered under realistic scenarios of biodiversity change?

40) 地下生物多样性如何影响地上生物多样性，反之亦然(Sutherland et al. 2013)？How does below-ground biodiversity affect aboveground biodiversity, and vice versa?

41) 地下生物多样如何影响生态系统功能(Bardgett and van der Putten 2014, van der Heijden 2016)？How does belowground biodiversity affect ecosystem functioning?

42) 微生物多样性（功能型、物种、遗传多样性）与群落和生态系统功能之间的关系是怎样的(Sutherland et al. 2013)？What is the relationship between microbial diversity (functional type, species, genotype) and community and ecosystem functioning?

43) 生物入侵和本土物种的丧失在多大程度上造成了生态系统属性的改变？To what extent is biotic invasion and native species loss creating ecosystems with altered properties?

44) 不同时空尺度下，环境异质性如何影响生物多样性(Sutherland et al. 2013)？How do spatial and temporal environmental heterogeneity influence diversity at different scales?

45) 空间结构如何影响生态系统功能，我们如何在空间尺度内和空间尺度之间进行整合评估生态系统功能? How does spatial structure influence ecosystem function and how do we integrate within and between spatial scales to assess function?

46) 在随机或定向环境变化的背景下，哪些物种在功能上是冗余的?Which species are functionally redundant in the context of stochastic or directional environmental changes?

47) 跨越多个生态系统类型，禾草与木本植物长期共存的机制是什么(Sutherland et al. 2013)？Which mechanisms allow the long-term coexistence of grasses and woody plants over a wide range of ecosystems?

48) 稀有种对生态系统功能具有哪些重要影响(Sutherland et al. 2013)？How important are rare species in the functioning of ecological communities?

49) 顶级捕食者数量下降对生态系统有什么影响? What is the impact of a decline in the number of top predators on the ecosystem?

第八节　人类活动与全球变化对生态系统的影响

人们逐渐认识到，当前的生态系统动态和生态系统功能都发生在一个以人类活动为主导的背景下，自史前以来，许多生态系统已经被人类改变和影响 (Gill et al. 2009, Doughty et al. 2010)。人类对生态系统的影响包括直接对栖息地的影响，如土地利用变化和火烧、生境改变（破碎化）、连接度变化(changes in connectivity)，以及通过去除引起的物种组成变化（由于收获或害虫控制）或引进（偶然的或其他原因）物种(Sutherland et al. 2013)。

50) 自然栖息地破碎化与消失对生物多样性的影响是什么(Aguilar et al. 2006)？What are the impacts of fragmentation and loss of natural habitats on biodiversity (Aguilar et al. 2006)?

51) 采收会对生态系统结构和动态产生什么样间接影响(Sutherland et al. 2013)？What are the indirect effects of harvesting on ecosystem structure and dynamics (Sutherland et al. 2013)?

52) 全球变化（如大气 CO_2 浓度升高、全球气温升高、土地利用变化等）将如何影响生态系统初级生产力(Cao and Woodward 1998)？How will global change affect primary productivity of terrestrial ecosystems?

53) 在多大程度上气候变化能够通过改变物候导致生态系统营养级联系解体(Edwards and Richardson 2004, Thackeray et al. 2016, Burgess et al. 2018, Renner and Zohner 2018)？To what extent will climate change uncouple trophic links due to phenological change?

54) 在全球变化下，是什么决定了物种是适应环境、改变生存范围还是走向灭绝(Onstein et al. 2018)？In the face of global change, what determines whether species adapt, shift their ranges or go extinct?

55) 种间相互作用如何影响物种对全球变化的响应(Singer et al. 2013, Mason et al. 2015) How do interspecific interactions affect the response of species to global change?

56) 什么是灭绝债务(extinction debt)?其机制是什么？自然栖息地的破碎化和丧失对灭绝债务的影响有多大？什么时候支付？What is the magnitude of the ‘extinction debt’ following the loss and fragmentation of natural habitats, and when will it be paid (Kuussaari et al. 2009, Hylander and Ehrlén 2013)?

第九节　生态系统服务与生态安全

生态系统服务（ecosystem services）是指对人类生存和生活质量有贡献的生态系统产品和服务，即人类从生态系统中获得的惠益，包括支持服务、供给服务、调节服务和文化服务(Millennium Ecosystem Assessment 2005)。产品是指在市场上用货币表现的商品，服务是不能

在市场上买卖，但具有重要价值的生态系统的性能，如净化环境、保持水土、减轻灾害等。关于生态系统服务功能的评估已有较完善的方法，同时在研究生态系统服务功能中也存在需要我们注意的问题。

众所周知，生态系统结构的空间异质性是普遍存在的，这将会引起生态系统功能或生态学特性上的空间异质性，最终使得生态系统服务出现空间异质性。即便是在一些植被类型较单一的生态系统中，由于栖息地中土壤和地形等的空间异质性而出现服务的异质性。 但是大多数关于生态系统服务方面的研究都没有考虑生态因子空间异质性的影响，通常都是将生态系统作为一个均质的整体来研究。

57) 充分考虑生态系统结构异质性导致的态系统服务异质性对于我们准确评价生态系统服务的意义是什么(Meyer 2005, Levine et al. 2016)？What is the implication of considering the heterogeneity of ecosystem services caused by heterogeneity of ecosystem structure for our accurate evaluation of ecosystem services?

一些生态系统服务可能会通过某些途径在空间上转移到系统之外的具备适当外部条件的地区并产生效能。按照“系统结构—系统功能—系统服务”的关系(Costanza et al. 1997)，一定生态系统结构能形成一定的生态系统功能，这一过程在同一空间上实现；但是从生态系统功能到生态系统服务却可能发生在不同的空间上，如从栖息地内部到外部。生态系统服务的形成往往要有一个积累过程，空间转移就常常是其积累的过程。生态系统服务功能在空间上的转移使得生态系统服务能够在远离栖息地的地方产生效益。

58) 生态系统服务功能空间转移的机理、载体、过程、途径、方向和强度如何(Plummer 2009, Newton and Cordingley 2012, Ferrini et al. 2015, Khan et al. 2018)？What are the mechanisms, carriers, processes, approaches, directions and strengths of the spatial transfer of ecosystem services?

59) 生态系统服务功能在转移过程中会发生何种转化？其影响是什么？What transformation will take place in the transfer process of ecosystem service? What is the impact?

“生态安全”通常是指一个生态系统的结构是否受到破坏，其生态功能是否受到损害。生态安全包含着两层含义：其一是生态系统自身是否安全，即自身结构是否受到破坏；其二是生态系统对于人类是否安全，即能否提供足以维持人类生存的可靠生态保障。因此，在全球变化背景下，研究生态安全具有重要意义。

60) 哪些生态系统服务会影响到生态安全？What ecosystem services will affect ecological security?

61) 生态系统服务的空间格局对生态安全格局有什么影响？What impact does the spatial pattern of ecosystem services have on the ecological security pattern?

62) 生态系统服务的状况与生态安全阈值有何关系？What is the relationship between the state of ecosystem services and ecological security thresholds?

63) 如何建立一个生态安全评价体系和预警系统（如态系统服务受损害模拟、评估和预测）？ How to establish an ecological security assessment system and an early warning system (e.g. simulation, assessment and prediction of damage to ecosystem services)?

研究生态系统服务一个重要目的就是建立一个可行的可持续利用机制。生态系统服务经济价值的评估一直是生态系统服务研究的一个热点(Peters et al. 1989, Tobias and Mendelsohn 1991, Munasinghe et al. 1994)。以往的评价都比较笼统，因此：

64) 如何建立一种更精确的评价方法来评价生态系统服务(Alexander et al. 1998, Dunford et al. 2018, Harrison et al. 2018, Rincon-Ruiz et al. 2019)？How to establish a more accurate evaluation method to assess ecosystem services?

65) 全球变化对不同类型生态系统服务的影响什么？哪些生态系统服务服务对全球变化最为敏感(Schroter et al. 2005, Tallis et al. 2012, Boone et al. 2017)？What are the impacts of global change on different types of ecosystem services? Which ecosystem services are most sensitive to global change?

第十节　生态学研究中的尺度问题

生态系统属性、格局和过程均依赖于时空尺度，生态系统格局、过程与尺度的关系是现代生态学研究的热点领域。

66) 环境的时空异质性是如何在不同尺度上影响生物多样性？How does spatiotemporal heterogeneity of environment affect biodiversity at different scales?

67) 空间结构如何影响生态系统功能？如何在不同空间尺度之内或之间整合来评估功能？How does spatial structure affect ecosystem function? How to evaluate functionality within or between different spatial scales?

68) 如何整合多尺度和类型的监测（从区域到全球的观测）来产生稳健的生态学推断？How do we combine multiple scales and types of monitoring (from field to earth observation) to make robust ecological inferences?

69) 广泛研究的生态学格局（物种多度分布、种-面积关系）在多大程度上反映了统计结果而不是生态学过程？To what extent are widely studied ecological patterns (species-abundance distribution, species-area relationship, etc.) the outcomes of statistical rather than ecological processes?

70) 决定生态系统变化大小和方向的最适基准是什么？What are the most appropriate baselines for determining the magnitude and direction of ecological changes?

第十一节　新技术和新方法在生态系统生态学研究中的应用

新技术和新方法的应用为生态系统生态学研究注入了新的活力，也为我们深刻理解生态系统的内在规律和机理提供了强大的技术支持。这些技术手段包括：高通量测序

72) 基因组学(Swenson and Jones 2017)

73) 转录组学(Swenson et al. 2017)

74) 核磁共振技术

75) 生物标记物

76) 稳定性同位素

77) 生态系统天-空-地一体化监测与研究

78) 大数据和人工智能

79) Meta-Analysis

80) 微生物网络分析

主要参考文献

Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecology letters **9**:968–980.

Alexander, A. M., J. A. List, M. Margolis, and R. C. d'Arge. 1998. A method for valuing global ecosystem services. Ecological Economics **27**:161-170.

Anderegg, W. R. L., A. T. Trugman, D. R. Bowling, G. Salvucci, and S. E. Tuttle. 2019. Plant functional traits and climate influence drought intensification and land-atmosphere feedbacks. Proceedings of the National Academy of Sciences of the United States of America **116**:14071-14076.

Andrews, J. H., and R. F. Harris. 2000. The ecology and biogeography of microorganisms of plant surfaces. Annual Review of Phytopathology **38**:145-180.

Atkin, O. K., A. H. Millar, P. Gardeström, and D. A. Day. 2000. Photosynthesis, carbohydrate metabolism and respiration in leaves of higher plants. Pages 153-175 *in* R. C. Leegood, T. D. Sharkey, and S. von Caemmerer, editors. Photosynthesis: Physiology and Metabolism. Kluwer Academic Publishers, New York.

Bais, H. P., S. W. Park, T. L. Weir, R. M. Callaway, and J. M. Vivanco. 2004. How plants

communicate using the underground information superhighway. Trends in Plant Science **9**:26-32.

Ball, B. A., M. D. Hunter, J. S. Kominoski, C. M. Swan, and M. A. Bradford. 2008. Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. Journal of Ecology **96**:303-313.

Bardgett, R. D., and W. H. van der Putten. 2014. Belowground biodiversity and ecosystem functioning. Nature **515**:505-511.

Bascompte, J. 2009. Mutualistic networks. Frontiers in Ecology and the Environment **7**:429-436.

Boone, R. B., R. T. Conant, J. Sircely, P. K. Thornton, and M. Herrero. 2017. Climate change impacts on selected global rangeland ecosystem services. Global Change Biology **24**:1382-1393.

Bunn, R. A., D. T. Simpson, L. S. Bullington, Y. Lekberg, and D. P. Janos. 2019. Revisiting the 'direct mineral cycling' hypothesis: arbuscular mycorrhizal fungi colonize leaf litter, but why? The ISME journal **13**:1891-1898.

Burgess, M. D., K. W. Smith, K. L. Evans, D. Leech, J. W. Pearcehiggins, C. J. Branston, K. Briggs, J. R. Clark, C. R. D. Feu, and K. Lewthwaite. 2018. Tritrophic phenological match–mismatch in space and time. Nature Ecology & Evolution **2**:970-975.

Cao, M., and F. I. Woodward. 1998. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. Global Change Biology **4**:185–198.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature **486**:59-67.

Castagneyrol, B., H. Jactel, C. Vacher, E. G. Brockerhoff, and J. Koricheva. 2014. Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. Journal of Applied Ecology **51**:134-141.

Chapin, F. S., III, P. A. Matson, and P. M. Vitousek. 2011. Principles of Terrestrial Ecosystem Ecology. Second edition. Springer, New York.

Chardon, N. I., C. Rixen, S. Wipf, and D. F. Doak. 2019. Human trampling disturbance exerts different ecological effects at contrasting elevational range limits. Journal of Applied Ecology **56**:1389-1399.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly.

Proceedings of the National Academy of Sciences of the United States of America **104**:17430-17434.

Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society B-Biological Sciences **366**:2351-2363.

Cornwell, W., J. Cornelissen, K. Amatangelo, E. Dorrepaal, V. Eviner, O. Godoy, S. Hobbie, B. Hoorens, H. Kurokawa, and N. Perez-Harguindeguy. 2008. Plant traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology letters **11**:1065–1071.

Costanza, R., R. dArge, R. deGroot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. Oneill, J. Paruelo, R. G. Raskin, P. Sutton, and M. vandenBelt. 1997. The value of the world's ecosystem services and natural capital. Nature **387**:253-260.

Crea, C., R. A. Ali, and R. Rader. 2016. A new model for ecological networks using species-level traits. Methods in Ecology and Evolution **7**:232-241.

Daniel, S., M. Jean-Louis, G. Piero, M. Virginie, D. A. Wardle, A. James, C. Franck, G. Bella, G. B. Emili, and P. Michel. 2013. Impacts of biological invasions: what's what and the way forward. Trends in Ecology & Evolution **28**:58-66.

Delgado-Baquerizo, M., F. T. Maestre, A. Gallardol, M. A. Bowker, M. D. Wallenstein, J. Luis Quero, V. Ochoa, B. Gozalo, M. Garcia-Gomez, S. Soliveres, P. Garcia-Palacios, M. Berdugo, E. Valencia, C. Escolar, T. Arredondo, C. Barraza-Zepeda, D. Bran, J. Antonio Carreiral, M. Chaieb, A. A. Conceicao, M. Derak, D. J. Eldridge, A. Escudero, C. I. Espinosa, J. Gaitan, M. G. Gatica, S. Gomez-Gonzalez, E. Guzman, J. R. Gutierrez, A. Florentino, E. Hepper, R. M. Hernandez, E. Huber-Sannwald, M. Jankju, J. Liu, R. L. Mau, M. Miriti, J. Monerris, K. Naseri, Z. Noumi, V. Polo, A. Prina, E. Pucheta, E. Ramirez, D. A. Ramirez-Collantes, R. Romao, M. Tighe, D. Torres, C. Torres-Diaz, E. D. Ungar, J. Val, W. Wamiti, D. Wang, and E. Zaady. 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature **502**:672-+.

Doughty, C. E., A. Wolf, and C. B. Field. 2010. Biophysical feedbacks between the Pleistocene megafauna extinction and climate: the first human-induced global warming? Geophysical Research Letters **37**:L15703.

Dunford, R., P. Harrison, A. Smith, J. Dick, D. N. Barton, B. Martin-Lopez, E. Kelemen, S. Jacobs, H. Saarikoski, F. Turkelboom, W. Verheyden, J. Hauck, P. Antunes, R. Aszalos, O. Badea, F. Baro, P. Berry, L. Carvalho, G. Conte, B. Czucz, G. G. Blanco, D. Howard, R. Giuca, E.

Gomez-Baggethun, B. Grizetti, Z. Izakovicova, L. Kopperoinen, J. Langemeyer, S. Luque, D. M. Lapola, G. Martinez-Pastur, R. Mukhopadhyay, S. B. Roy, J. Niemela, L. Norton, J. Ochieng, D. Odee, I. Palomo, P. Pinho, J. Priess, G. Rusch, S. R. Saarela, R. Santos, J. T. van der Wal, A. Vadineanu, A. Vari, H. Woods, and V. Yli-Pelkonen. 2018. Integrating methods for ecosystem service assessment: experiences from real world situations. Ecosystem Services **29**:499-514.

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature **430**:881-884.

Fauchald, P. 2010. Predator-prey reversal: a possible mechanism for ecosystem hysteresis in the North Sea? Ecology **91**:2191-2197.

Ferrini, S., M. Schaafsma, and I. J. Bateman. 2015. Ecosystem Services Assessment and Benefit Transfer.

Garcia-Palacios, P., E. A. Shaw, D. H. Wall, and S. Hattenschwiler. 2016. Temporal dynamics of biotic and abiotic drivers of litter decomposition. Ecology letters **19**:554-563.

Gill, J. L., J. W. Williams, S. T. Jackson, K. B. Lininger, and G. S. Robinson. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. Science **326**:1100-1103.

Gonzalez, G., and T. R. Seastedt. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology **82**:955-964.

Goulden, M. L., A. M. S. McMillan, G. C. Winston, A. V. Rocha, K. L. Manies, J. W. Harden, and B. P. Bond-Lamberty. 2011. Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Global Change Biology **17**:855-871.

Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. Ecology **85**:995-1004.

Gusewell, S. 2004. N : P ratios in terrestrial plants: variation and functional significance. New Phytologist **164**:243-266.

Harrison, P. A., R. Dunford, D. N. Barton, E. Kelemen, B. Martin-Lopez, L. Norton, M. Termansen, H. Saarikoski, K. Hendriks, E. Gomez-Baggethun, B. Czucz, M. Garcia-Llorente, D. Howard, S. Jacobs, M. Karlsen, L. Kopperoinen, A. Madsen, G. Rusch, M. van Eupen, P. Verweij, R. Smith, D. Tuomasjukka, and G. Zulian. 2018. Selecting methods for ecosystem service assessment: a decision tree approach. Ecosystem Services **29**:481-498.

Hattenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in

terrestrial ecosystems. Annual Review of Ecology Evolution and Systematics **36**:191-218.

Hinsinger, P., G. R. Gobran, P. J. Gregory, and W. W. Wenzel. 2005. Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. New Phytologist **168**:293-303.

Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. Trends in Ecology & Evolution **7**:336-339.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. Ecological Monographs **68**:121-149.

Hylander, K., and J. Ehrlén. 2013. The mechanisms causing extinction debts. Trends in Ecology & Evolution **28**:341-346.

Jorgensen, S. E. 2009. Ecosystem Ecology.

Khan, I., M. J. Zhao, S. U. Khan, L. Y. Yao, A. Ullah, and T. Xu. 2018. Spatial heterogeneity of preferences for improvements in river basin ecosystem services and its validity for benefit transfer. Ecological Indicators **93**:627-637.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology & Evolution **24**:564-571.

Kuypers, M. M. M., H. K. Marchant, and B. Kartal. 2018. The microbial nitrogen-cycling network. Nature Reviews Microbiology **16**:263-276.

Laurance, W. F. 2013. Tipping points and the vulnerability of Australia's tropical ecosystems. Pages 169-180 *in* P. H. Raven, N. S. Sodhi, and L. Gibson, editors. Conservation Biology: Voices from the Tropics. John Wiley & Sons, Ltd Chichester.

Levine, N. M., K. Zhang, M. Longo, A. Baccini, O. L. Phillips, S. L. Lewis, E. Alvarez-Davila, A. C. S. de Andrade, R. J. W. Brienen, T. L. Erwin, T. R. Feldpausch, A. L. M. Mendoza, P. N. Vargas, A. Prieton, J. E. Silva-Espejo, Y. Malhi, and P. R. Moorcroft. 2016. Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. Proceedings of the National Academy of Sciences of the United States of America **113**:793-797.

Mason, T. H., P. A. Stephens, M. Apollonio, and S. G. Willis. 2015. Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. Global Change Biology **20**:3872-3882.

McCully, M. E. 1999. Roots in soil: Unearthing the complexities of roots and their rhizospheres. Annual Review of Plant Physiology and Plant Molecular Biology **50**:695-718.

Meyer, J. L. 2005. Heterogeneity and Ecosystem Function: Enhancing Ecological Understanding and Applications. Pages 451-461 *in* G. M. Lovett, M. G.Turner, C. G. Jones, and K. C. Weathers, editors. Ecosystem Function in Heterogeneous Landscapes. Springer, New York.

Miki, T., T. Yokokawa, and K. Matsui. 2014. Biodiversity and multifunctionality in a microbial community: a novel theoretical approach to quantify functional redundancy. Proceedings of the Royal Society B-Biological Sciences **281**:20132498.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC.

Miller, K. M., and B. J. McGill. 2019. Compounding human stressors cause major regeneration debt in over half of eastern US forests. Journal of Applied Ecology **56**:1355-1366.

Munasinghe, M., M. Munasinghe, and J. Mcneely. 1994. Economic and policy issues in natural habitats and protected areas. Pages 15-49 *in* M. Munasinghe and J. A. McNeely, editors. Protected Area Economics and Policy: Linking Conservation and Sustainable Development. World Bank, Washington DC.

Murphy, E. J., R. D. Cavanagh, K. F. Drinkwater, S. M. Grant, J. J. Heymans, E. E. Hofmann, G. L. Hunt, and N. M. Johnston. 2016. Understanding the structure and functioning of polar pelagic ecosystems to predict the impacts of change. Proceedings of the Royal Society B-Biological Sciences **283**:10.

Newton, A. C., and J. Cordingley. 2012. Cost-benefit analysis of ecological networks assessed through spatial analysis of ecosystem services. Journal of Applied Ecology **49**:571-580.

Niklaus, P. A., J. Alphei, C. Kampichler, E. Kandeler, C. Körner, D. Tscherko, and M. Wohlfender. 2007. Interactive effects of plant species diversity and elevated CO_2 on soil biota and nutrient cycling. Ecology **88**:3153-3163.

Onstein, R. E., W. J. Baker, C. Tlp, S. Faurby, L. Herrera-Alsina, J. C. Svenning, and W. D. Kissling. 2018. To adapt or go extinct? The fate of megafaunal palm fruits under past global change. Proceedings of the Royal Society B: Biological Sciences **285**:20180882.

Otto, S. B., E. L. Berlow, N. E. Rank, J. Smiley, and U. Brose. 2008. Predator diversity and identity drive interaction strength and trophic cascades in a food web. Ecology **89**:134-144.

Paterson, E., A. J. Midwood, and P. Millard. 2009. Through the eye of the needle: a review of isotope approaches to quantify microbial processes mediating soil carbon balance. New Phytologist

184:19-33.

Penuelas, J., B. Poulter, J. Sardans, P. Ciais, M. van der Velde, L. Bopp, O. Boucher, Y. Godderis, P. Hinsinger, J. Llusia, E. Nardin, S. Vicca, M. Obersteiner, and I. A. Janssens. 2013. Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. Nature Communications **4**:2934.

Penuelas, J., J. Sardans, A. Rivas-Ubach, and I. A. Janssens. 2012. The human-induced imbalance between C, N and P in Earth's life system. Global Change Biology **18**:3-6.

Peter, H., S. Beier, S. Bertilsson, E. S. Lindstrom, S. Langenheder, and L. J. Tranvik. 2011. Function-specific response to depletion of microbial diversity. Isme Journal **5**:351-361.

Peters, C. M., A. H. Gentry, and R. O. Mendelsohn. 1989. Valuation of an Amazonian rainforest. Nature **339**:655-656.

Plummer, M. L. 2009. Assessing benefit transfer for the valuation of ecosystem services. Frontiers in Ecology and the Environment **7**:38-45.

Poorter, H. 2002. Plant growth and carbon economy. In: eLS. John Wiley & Sons Ltd., Chichester. https://doi.org/10.1038/npg.els.0003200.

Rennenberg, H. 2015. Communities and ecosystem functioning. Pages 77-92 *in* G.-J. Krauss and D. H. Nies, editors. Ecological Biochemistry: Environmental and Interspecies Interactions. Wiley-VCH, Weinheim.

Renner, S. S., and C. M. Zohner. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annual Review of Ecology, Evolution, and Systematics **49**:165-182.

Rincon-Ruiz, A., P. Arias-Arevalo, J. M. N. Hernandez, H. Cotler, M. A. Caso, P. Meli, A. Tauro, V. D. A. Akerberg, V. S. Avila-Foucat, J. P. Cardenas, L. A. C. Hernandez, L. G. Castro, V. A. C. Hernandez, A. C. Araque, J. Deschamps-Lomeli, J. M. Galeana-Pizann, K. G. Onate, J. A. H. Aguilar, A. D. Jimenez, L. A. L. Mathamba, L. M. Perez, M. L. M. Diaz, W. M. Marin, V. Ochoa, M. A. Sarmiento, J. D. Timote, L. L. T. Cardozo, A. T. Acosta, and T. Waldron. 2019. Applying integrated valuation of ecosystem services in Latin America: Insights from 21 case studies. Ecosystem Services **36**:12.

Rivas-Ubach, A., J. Sardans, M. Perez-Trujillo, M. Estiarte, and J. Penuelas. 2012. Strong relationship between elemental stoichiometry and metabolome in plants. Proceedings of the National Academy of Sciences of the United States of America **109**:4181-4186.

Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van

Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. Nature **461**:53-59.

Schroter, D., W. Cramer, R. Leemans, I. C. Prentice, M. B. Araujo, N. W. Arnell, A. Bondeau, H. Bugmann, T. R. Carter, C. A. Gracia, A. C. de la Vega-Leinert, M. Erhard, F. Ewert, M. Glendining, J. I. House, S. Kankaanpaa, R. J. T. Klein, S. Lavorel, M. Lindner, M. J. Metzger, J. Meyer, T. D. Mitchell, I. Reginster, M. Rounsevell, S. Sabate, S. Sitch, B. Smith, J. Smith, P. Smith, M. T. Sykes, K. Thonicke, W. Thuiller, G. Tuck, S. Zaehle, and B. Zierl. 2005. Ecosystem service supply and vulnerability to global change in Europe. Science **310**:1333-1337.

Schuldt, A., T. Assmann, M. Brezzi, F. Buscot, D. Eichenberg, J. Gutknecht, W. Hardtle, J. S. He, A. M. Klein, P. Kuhn, X. J. Liu, K. P. Ma, P. A. Niklaus, K. A. Pietsch, W. Purahong, M. Scherer-Lorenzen, B. Schmid, T. Scholten, M. Staab, Z. Y. Tang, S. Trogisch, G. von Oheimb, C. Wirth, T. Wubet, C. D. Zhu, and H. Bruelheide. 2018. Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nature Communications **9**:2989.

Seddon, A. W. R., M. Macias-Fauria, P. R. Long, D. Benz, and K. J. Willis. 2016. Sensitivity of global terrestrial ecosystems to climate variability. Nature **531**:229-+.

Sentis, A., J. Morisson, and D. S. Boukal. 2015. Thermal acclimation modulates the impacts of temperature and enrichment on trophic interaction strengths and population dynamics. Global Change Biology **21**:3290-3298.

Singer, A., J. M. J. Travis, and K. Johst. 2013. Interspecific interactions affect species and community responses to climate shifts. Oikos **122**:358-366.

Sternberg, L. D. S. L. 2010. Savanna-forest hysteresis in the tropics. Global Ecology & Biogeography **10**:369-378.

Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, S. R. Beissinger, T. Benton, D. D. Cameron, Y. Carmel, D. A. Coomes, T. Coulson, M. C. Emmerson, R. S. Hails, G. C. Hays, D. J. Hodgson, M. J. Hutchings, D. Johnson, J. P. G. Jones, M. J. Keeling, H. Kokko, W. E. Kunin, X. Lambin, O. T. Lewis, Y. Malhi, N. Mieszkowska, E. J. Milner-Gulland, K. Norris, A. B. Phillimore, D. W. Purves, J. M. Reid, D. C. Reuman, K. Thompson, J. M. J. Travis, L. A. Turnbull, D. A. Wardle, and T. Wiegand. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology **101**:58-67.

Swenson, N. G., Y. Iida, R. Howe, A. Wolf, M. N. Umana, K. Petprakob, B. L. Turner, and K. P. Ma. 2017. Tree co-occurrence and transcriptomic response to drought. Nature Communications

8:1996.

Swenson, N. G., and F. A. Jones. 2017. Community transcriptomics, genomics and the problem of species co-occurrence. Journal of Ecology **105**:563-568.

Tallis, H., H. Mooney, S. Andelman, P. Balvanera, W. Cramer, D. Karp, S. Polasky, B. Reyers, T. Ricketts, and S. Running. 2012. A global system for monitoring ecosystem service change. Bioscience **62**:977–986.

Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helaouet, D. G. Johns, I. D. Jones, and D. I. Leech. 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature **535**:241-245.

Tilman, D., I. Forest, and J. M. Cowles. 2014. Biodiversity and Ecosystem Functioning. Annual Review of Ecology, Evolution, and Systematics **45**:471-493.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**:718-720.

Tobias, D., and R. Mendelsohn. 1991. Valuing ecotourism in a tropical rain-forest reserve. Ambio **20**:91-93.

Tylianakis, J. M., and R. J. Morris. 2017. Ecological Networks across Environmental Gradients. Annual Review of Ecology, Evolution, and Systematics **48**:25-48.

van der Heijden, M. G. A. 2016. Ecology underground networking. Science **352**:290-291.

Vitousek, P. M., S. Porder, B. Z. Houlton, and O. A. Chadwick. 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecological Applications **20**:5-15.

Wang, J., J. Shen, Y. Wu, C. Tu, J. Soininen, J. C. Stegen, J. He, X. Liu, L. Zhang, and E. Zhang. 2013. Phylogenetic beta diversity in bacterial assemblages across ecosystems: deterministic versus stochastic processes. Isme Journal **7**:1310-1321.

Wardle, D. A., G. M. Barker, K. I. Bonner, and K. S. Nicholson. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? Journal of Ecology **86**:405-420.

Wickings, K., A. S. Grandy, S. C. Reed, and C. C. Cleveland. 2012. The origin of litter chemical complexity during decomposition. Ecology letters **15**:1180-1188.

Yuan, Z. Y., and H. Y. H. Chen. 2015. Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. Nature Climate Change **5**:465-469.

第二章 全球气候系统

第一节 基本概念

气候是预测生态系统结构和功能的唯一最佳因子。通常，气候的地理分布是相对可预测的。气候的时间变化取决于太阳能量输入、表面特性和大气捕获热量的能力。因此，如果了解了气候空间和时间变化的原因，则可以预测许多观察到的生态系统模式。

天气和气候的差异在于时间尺度的不同。天气是某一地区在某一瞬间或某一短时间内大气状态(如 T、E、P 等)和大气现象(如风、云、雾、降水等)的综合。气候是在某一时段内大量天气过程的综合，它不仅包括该地多年来经常发生的天气状况，还包括某些年份偶尔出现的极端天气状况。气候变化是指日常天气或极端气候的长期平均值的变化。

除了长期的气候变化，还有短期的。这种所谓的气候变率（climate variability）可以表现为与厄尔尼诺、拉尼娜、火山爆发或地球系统其他变化相关的周期性或间歇性变化。

例如，卡特里娜飓风于 2005 年淹没了新奥尔良，造成约 1570 人死亡，以及 40-500 亿美元的损失。人为造成的路易斯安那州沿海生态变化导致了飓风的影响。预计气候变暖将增加卡特里娜飓风等严重热带风暴的发生频率。

净初级生产力（Net Primary Productivity，NPP）是指单位时间、单位面积上植被所积累的有机物质的总量，是光合作用所吸收的碳和呼吸作用所释放的碳之间的差值，是生产者用于生长、发育和繁殖的能量值，也是生态系统中其他生物成员生存和繁衍的物质基础。NPP 不仅可以表征生态系统的质量状况和生产能力，也是判定生态系统的碳源/汇功能和评价陆地生态系统可持续发展的重要因子。NPP 总体呈现出以赤道热带南美洲地区、赤道附近非洲地区、中南半岛和印度尼西亚一带为高值区；北半球和南半球的高纬度地区、非洲北部地区、西亚中亚干旱半干旱地区以及青藏高原地区为低值区的特征。气温、降水是导致植被 NPP 变化的重要因素，研究表明全球 NPP 与降水变化在大部分地区主要是正相关关系，NPP 的全球分布格局与全球降雨格局相似；全球总体 NPP 与气温关系为显著的正相关关系，除了非洲撒哈拉沙漠等地区。

由于气候变化，干旱在全球范围内不断增加，影响陆地生态系统的结构和功能。干旱增加会降低土壤水分可用性，从而限制光合作用和生态系统碳固存。干旱指数 (AI) 通常定义为年降水量与年潜在蒸散量的比率，干旱水平为 1-AI。Berdugo 等（2020）研究表明陆地对干旱的响应可以分为三个阶段：植被衰退阶段、土壤破坏阶段、生态系统崩溃阶段。干旱水平>0.54 时，植被生产力急剧下降，进入植被衰退阶段；随干旱持续增加，干旱水平>0.69 时，进入土壤破坏阶段，此时多个生态系统结构和功能属性发生变化；干旱水平>0.83 时，植被覆盖率急剧减少，且反照率增加（图 2.1-1）。

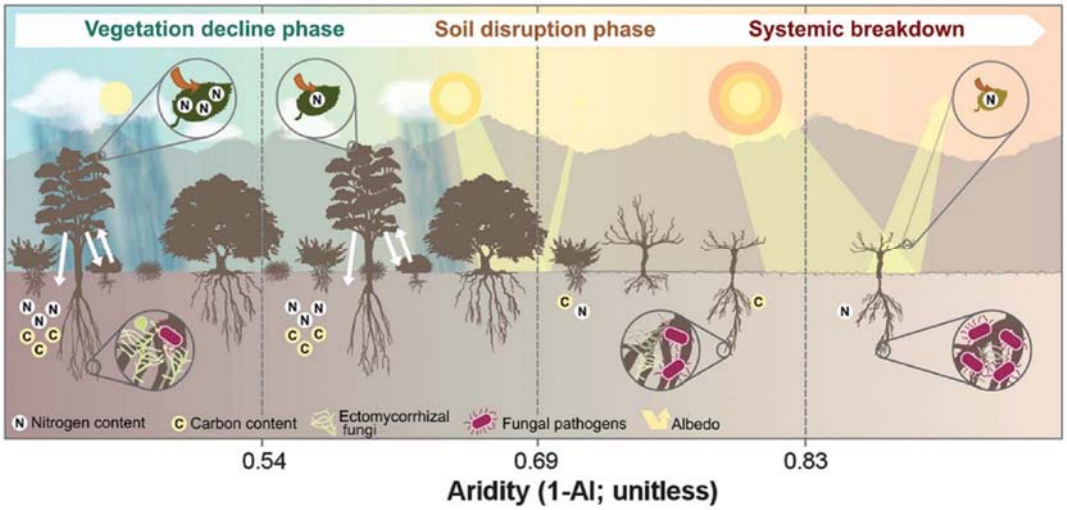


图 2.1-1 陆地对干旱响应的三个阶段：植被衰退、土壤破坏和生态系统崩溃阶段（引自 Berdugo, 2020）

环境因素对生物生长具有重要影响。条件是指影响活体生物功能的非生物环境因子，包括温度、相对湿度、pH、污染物浓度等。物种对不同条件能够做出不同的精确响应：（a）广义响应模式，如温度和 pH 等条件下，仅适宜的条件允许繁殖，极端条件是致命的；（b）适用于大多数有毒、放射性物质的释放以及化学污染条件，生物仅在高强度条件下致命；（c）适用于为生物所需，在低浓度时可作为有机体的营养物质，例如氯化钾、铜、锌、镁等（图 2.1-2）。

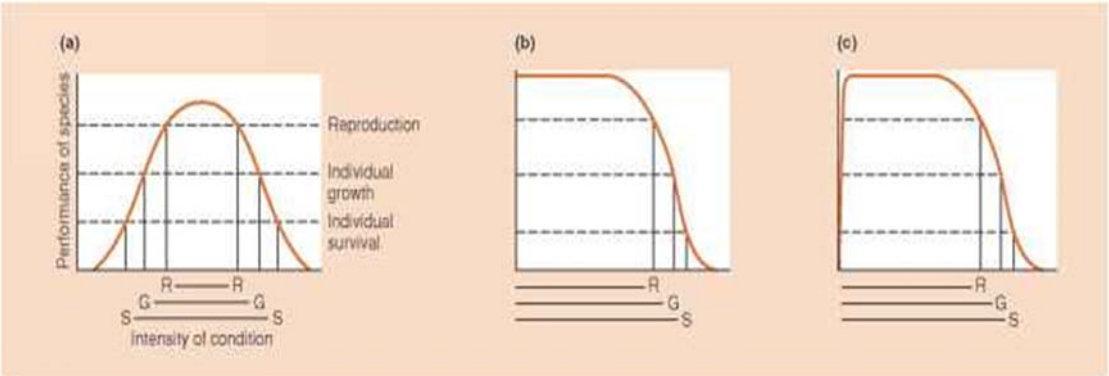


图 2.1-2 物种对不同环境条件的响应模式

生态位是指有机体对环境条件的耐受以及生境资源的需求的综合，包括其所需的物理和环境条件（如温度或地形）以及与其他物种的相互作用（如捕食或竞争）。生态位是基于环境影响因子的多维空间。基础生态位是指在没有竞争的前提下，一个物种能全部占有它的生态位，在这个基础生态位中，生物的所有环境条件都是最适宜的，而且没有竞争者和捕食者。但是基础生态位只是一种理论状态，生物的现有的环境条件即实际生态位总是不如基础生态位那么理想。

第二节　地球能量平衡

辐射的收支平衡决定了可用来驱动地球气候系统的能量多少。气候取决于太阳能输入、地表特性和大气对热量的吸收。驱动整个生态系统运转的能量主要来源于绿色植物固定的太阳能。太阳光为短波辐射，大气大部分吸收长波辐射，而只能少量吸收短波辐射，这是由大气成分所决定的，大气的主要成分氮、氧、二氧化碳、水汽并不能吸收长波辐射，但二氧化碳和水汽能够有效地吸收长波辐射，之所以还能吸收一部分短波辐射，是因为空气中含有臭氧，但臭氧含量较少，因此只能少量吸收短波辐射。大地辐射相对于太阳辐射为长波辐射，大气辐射可大量吸收大地向外发射的长波辐射。从长期来看，地球和大气吸收的太阳辐射能与其释放的长波辐射能量是平衡的。进入的太阳辐射中，大约有一半被地球吸收；通过湍流显热、潜热以及地表辐射，这些能量又被传递到大气中，一部分能量被大气层反射会地面，一部分能力逃逸到宇宙空间（图 2.2-1）。

太阳入射的短波辐射=可见光 39%+近红外线 53%+紫外线辐射 8%。

能量分配：太阳入射的短波辐射=31%反射回太空（16%云层、7%大气分子、尘、雾、8%地表）+20%被大气吸收（大气上层的臭氧+下层的云和水蒸气）+49%被地表吸收（23%直接辐射+26%漫射辐射）。

地表吸收的能量=79%长波辐射+16%潜热通量+5%显热通量。

大气层可吸收 90%的地表长波辐射。

大气层顶部：100%太阳辐射短波=31%反射的太阳短波辐射+69%释放的长波辐射（48%高层大气+9%低层大气+12%地表）。

大气层内部：20%吸收的短波+102%吸收的长波+30%潜热显热总通量=57%释放至太空+95%释放至地表。

地表：49%入射短波+95%入射长波=114%长波出射辐射+30%潜热显热总通量。

第三节　大气层系统

3.1 大气组成和化学

大气层的化学组成决定了其在地球能量平衡中所起的作用。大气组成包括氮气、氧气、氩气等惰性气体，以及二氧化碳（CO2）、甲烷、臭氧、一氧化二氮、氟利昂等活性气体。

悬浮物是指悬浮在空气中的微小颗粒。来自于火山爆发+被风扬起的灰尘和海盐+来自污染源和焚烧生物燃料的气体发生反应而产生。部分悬浮物是吸湿性的，参与气体反应，成为云凝结核，水汽在其周围凝结形成云滴。气体、云和悬浮物共同决定了大气层的反射能力（反射率），并因此控制了大气能量平衡。悬浮物，散射（反射）入射短波辐射，减少到达地表的辐射量，从而使气候趋于变凉。

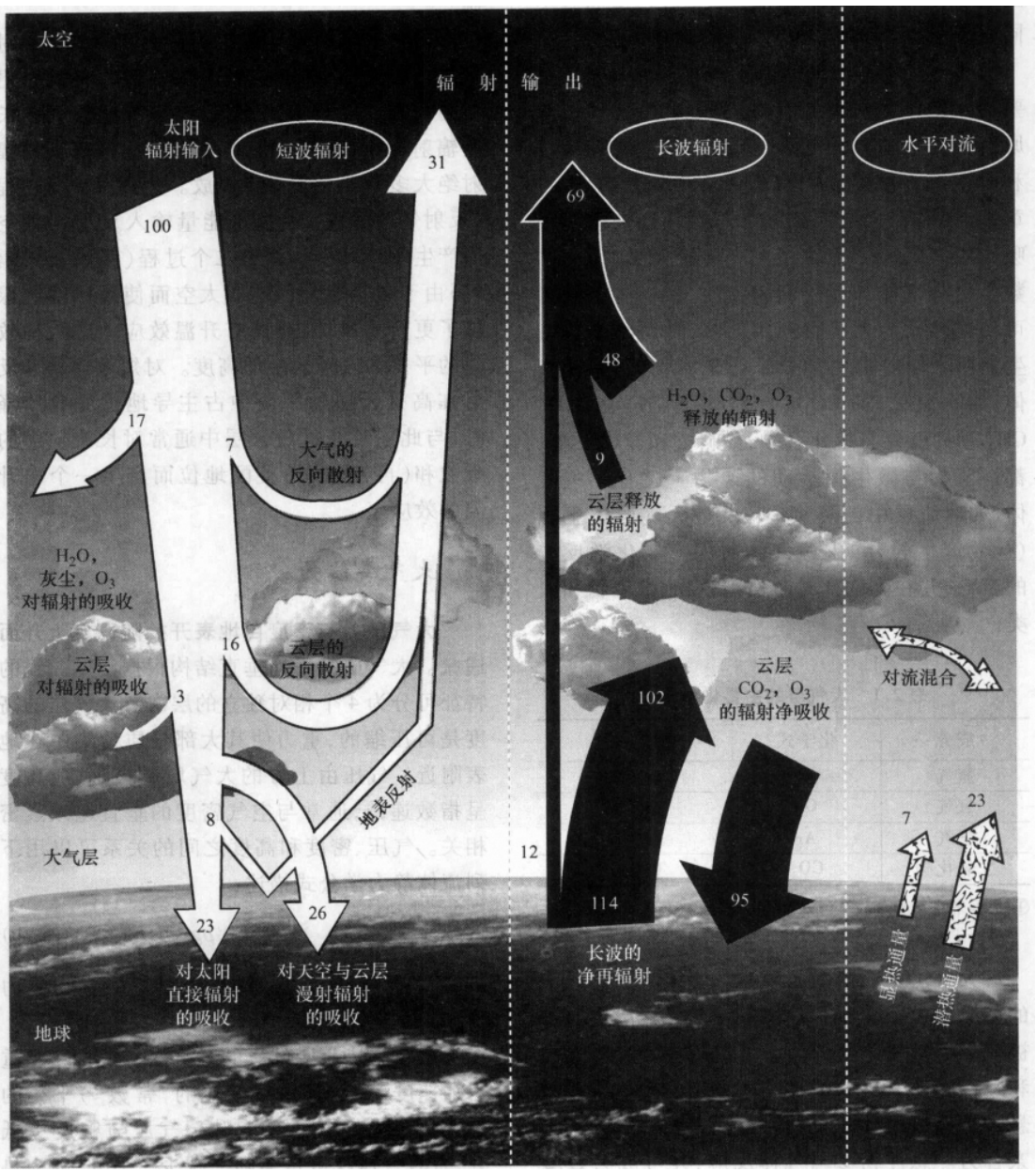


图 2.2-1 地球—大气层系统的年平均全球能量平衡。数字表示作为太阳入射辐射被吸收的能量百分比。在大气层顶部，太阳入射辐射（100%，即 342W·m^{-2}）由反射的短波辐射（31%）和释放的长波辐射（69%）来平衡。在大气层内部，被吸收的短波（20%）和长波（102%）辐射与潜热显热总通量（30%）由释放至太空（57%）和地表（95%）的长波来平衡。在地表，短波（49%）和长波（95%）的入射辐射由长波出射辐射（114%）和潜热显热总通量（30%）来平衡（Graedel＆Crutzen1995;Sturman & Tapper 1996;Baede et al.2001)。

云与地球能量平衡：与地表相比，云层的反射率较高，反射更多的入射短波辐射，将能量反射回太空而产生降温效应。云层吸收长波辐射并重新释放，阻止能量逃逸回太空而使地球系统保持了更多能量，因而具有升温效应。这两种效应的平衡取决于云层的高度：高处云

层对短波辐射的反射占主导，导致降温；低处云层对长波辐射的吸收和再释放占主导，导致净升温。

温室效应是指透射阳光的密闭空间由于与外界缺乏热对流而形成的保温效应，即太阳短波辐射可以透过大气射入地面，而地面增暖后放出的长波辐射却被大气中的二氧化碳等物质所吸收，从而产生大气变暖的效应。

阳伞效应又称微粒效应，是由大气污染物或火山喷发等对太阳辐射的削弱作用而引起的地面冷却效应。存在于大气中的颗粒物，一方面反射部分太阳光，减少阳光的入射，从而降低地表温度；另一方面也能吸收地面辐射到大气中的热量，起着保温作用。两者相比，前者大于后者，因此总的效应是使气温降低，这就是所谓的阳伞效应。

3.2 大气层结构

大气压力和密度自地表开始随高度上升而递减。整个大气层随高度不同表现出不同的特点，主要分为对流层、平流层、中间层、热成层。

对流层是大气圈中最靠近地面的一层，厚度约 9-16km，主要通过感热和潜热通量以及来自地球表面的长波辐射从底部加热。平流层位于对流层之上，延伸至 50km，平流层上部臭氧 (O_3) 吸收紫外线辐射使空气变暖，因而是地球大气层里上热下冷的一层。氟氯碳化物(CFCs)等人造化学物质被大量使用，会对臭氧层造成破坏，形成臭氧空洞。中间层是自平流层顶到约 80km 之间的大气层，热成层是大气圈最外端的大气层（>50km），这两层对生物圈的影响相对较小。

行星边界层 PBL，又称大气边界层，是对流层最低的部分，受大气层和地表的混合影响，集中了生态系统的产物（CO_2、污染物）。PBL 中的空气受到地表加热所产生的对流湍流，以及空气运动时与地表摩擦相关联的机械湍流这二者的作用而混合。PBL 中水汽、二氧化碳和其它化学组分的变化情况就可以作为地表发生的生物学生理化学过程的指示器。大气边界层是人类生命和工程活动的主要场所，是地表与大气之间物质和能量交换的通道，是空气污染和许多气象灾害的发生地。

3.3 大气环流

大气环流的根本原因是地表受热不均匀。赤道比极地接收了更多的太阳入射辐射，而地球系统的能量输入必须等于能量输出，这就促使了热量从赤道向两极移动。

对地球的主要外部影响来自辐射。由于地球-太阳系统的几何形状和地球的自转，入射的太阳短波辐射分布不均匀，而输出的长波辐射更均匀。

大气环流包括垂直和水平两部分。垂直混合驱动循环圈：空气在赤道上升，而在极点下沉，将热量从赤道输送到两极；科里奥利力驱动风向。

哈得来环流 Hadley cell：由赤道大气的膨胀上升所驱动。

极地环流 Polar cell：由极地冷缩空气的沉降所驱动。

费雷尔环流 Ferrell cell：间接地由大气动力学过程驱动。

科里奥利力（大气的旋转运动）：地球的自转导致风向在北半球向右偏移，而在南半球向左偏移，大气也会南北移动。极地空气增加其速度：西风（风从西向东移动）；赤道空气降低其速度：东风（风从东向西移动）。

地球表面的海陆不均匀分布产生了地表受热的不均匀格局，改变了气候的普遍纬度趋势。大陆和海洋的存在影响了：1.空气的升降（高低压中心）；2.风模式（风暴路径）。

第四节　地形对气候的影响

陆地、水体和山脉的空间分布改变了气候的一般纬度趋势。

水体比陆地有更高的热容量，由于热容比产生的风：哈得来环流（长期气候模式）、季风（季节性模式）、海陆风（昼夜模式）。山脉通过多种类型的地形效应来对地方性的大气环流与气候起作用：行星波、雨影（在山区或山脉的背风面，　雨量比向风面显著偏小）、气温直减率（气温在垂直方向上的变化率）、南北坡的加热差异、局部效应（逆温、下坡风）。

第五节　植被对气候的影响

植被通过作用于地表能量平衡来影响气候。土壤或植被表面吸收的能量通过长波辐射以及潜热和显热的湍流传递到大气中。地表吸收的能量分配=长波辐射+湍流通量（潜热+显热）的方式传输给大气层。显热通量和长波辐射在能量传输发生的地方直接加热大气层；潜热通量将水汽传输给大气层，水汽所贮存的能量当其冷凝成云或降水时得到释放。

通过计算机模型模拟，热带森林砍伐后可能导致气候永久性的变暖变干（森林变草地，蒸腾作用会减弱，降水减少，潜热输送会减少，地表温度会上升）。草地的根系比树木较浅，吸收的土壤水较少，导致较低的蒸腾速率。因此，草地会以显热的形式释放更多的吸收的太阳辐射，直接加热大气。

澳大利亚西部的农业开荒改变了气候：农田少 30% ppt，荒地多 10% ppt。开荒改变了能量平衡，反照率增加，吸收的能量减少；土地灌溉导致更多的蒸散，使得地表温度降低；显热减少，对流上升减少，降雨减少。

反照率决定了地面吸收的太阳辐射的能量，这些吸收的能量随后可作为长波辐射和潜热、感热的湍流通量传输给大气层。植被的反照率处于中等水平，枯叶草地、落叶林、暗针叶林的反照率依次递减。裸土的反照率一般较高。土壤的反照率决定于土壤类型和湿度，但在干燥气候下通常比植被的反照率高。反照率上升，导致地表接收的太阳入射短波辐射减少（地表降温）和地表向大气传输的能量减少（尤其是潜热，降低降水），从而导致地表降温和空气下沉，降低降水。

植被结构可以影响水分、能量的交换效率，从而影响区域性气候。在高纬度地区，与积雪覆盖的苔原相比，树木覆盖的景观在雪融化之前吸收更多的太阳辐射，因为它们的反照率（反射率）较低。反照率、潜热通量和显热通量之间的能量分配以及地表温度也会影响传输到大气的长波辐射量。长波辐射取决于地表温度，当地表吸收了大量的入射辐射（低反照率），

更少的水分蒸发，或者有光滑的表面（热传递效率低——传递给大气的潜热和感热的湍流通量效率低），地表温度倾向于升高。

目前的地球系统模型低估了这些降水和辐射反馈，主要是因为它们低估了生物圈对辐射和水压力反应的响应。

第六节　气候的时间变异性

长期（千年尺度）气候变化主要由太阳入射辐射所驱动：太阳的演化（气候系统的演化）、地球轨道的变化（冰河时代）、季节循环以及昼夜交替。由于人类活动的影响，大气表面吸热和吸热的变化现在变得越来越重要。

太阳轨道的变化导致地球太阳能输入的长期变化。偏心率：地球绕太阳公转轨道的椭圆率。地轴倾角：地球自转轴与其绕太阳轨道平面的夹角。岁差：地球自转轴相对于恒星的“摆动”，确定一年冬夏至和春秋分发生的日期。

从 1850 年到 1899 年到 2001 年到 2005 年期间的总温升为 0.76°C ± 0.19°C (IPCC，2007)。高纬度地区的气候变暖最为迅速，这种变暖趋势在西伯利亚和北美西部最为明显。

世界气象组织规定，当某个（些）气候要素达到 25 年一遇时才称之为极端气候。极端气候包括干旱、洪涝、高温热浪和低温冷害等。随着污染日渐严重，出现极端气候的现象将变得频繁，次数也将大幅增加。极端气候对自然系统、人文系统和暴露区造成严重的灾害损失，许多研究关注于极端气候的预测。

20 世纪后 50 年的气候要比过去 500 年（可能 1300 年乃至更长时间）内任何 50 年都要温暖。变暖的地点：地表，产生了巨大的生态效应。变暖的原因：小部分是因为太阳入射辐射的增加，大部分是由大气中辐射活性气体浓度的增加引起的。大气中辐射活性气体浓度增加，导致大气层捕获的地表长波辐射能量增加，使大气增温，导致大气层能容纳更多的水汽（另一种强效温室气体），进一步增强了大气对长波辐射的捕获能力。结果是地球不再辐射平衡，地球吸收的太阳辐射能量多余地球向外空间排放（损失）的能量。表现为地表增温，全球变暖。

年际气候变化：ENSO 事件。远程连接在全球范围内带来这些气候影响，例如，厄尔尼诺现象导致了 AK 和加利福尼亚州温暖的冬天。

第七节　生态系统分布与结构和气候的关系

全球植被变化既受限于气候条件，对温度和降水变化敏感响应，又对气候变化起到反馈作用，影响着地表反照率、粗糙度和陆地碳储量等地球理化属性。不同的降雨和温度形成了全球不同植被类型。在热带温度保持相对恒定的降水量梯度上，生活型优势度发生变化，随降水量的减少，植被变化依次为常绿林、常绿季节林、半常绿林、干旱落叶林、旱生灌丛、热带灌丛与半沙漠、热带沙漠。

美国著名生物学家 Clinton Hart Merriam (1855-1942)，从哥伦比亚大学获得医学博士学位，后来致力于生物学，并于 1885 年至 1910 年担任美国生物调查局局长。在此期间，他访问了美国西部的许多地方，以博物学家的眼光撰写关于哺乳动物新物种和植被类型分布的

文章，并以人类学家的眼光看待加利福尼亚的印第安人群体。他还是美国国家地理学会创始人。他相信温度，尤其是生长季节的温度，是决定性的环境因素，他开发了一些公式来总结温暖程度，就像 Crisebach 所做的那样。他将每种植被类型与温暖值相关联，将植被类型扩大到生活区（他将其命名为北方、过渡、加拿大、哈德逊、热带等）和他的生活区分布。虽然一些博物学家和生物学书籍仍然使用这个生命区术语和概念，但他的许多假设、计算和结论都受到了挑战，他的纬度推断并没有被广泛接受。尽管如此，Merriam 还是对美国植物生态学产生了强烈影响。

全球变暖导致近年来阿拉斯加出现了异常的温暖天气；导致南极冰川融化；苔原旅行季节变短（降雪较晚，融雪较早）；海洋冰川面积越来越小；永冻土层变暖。

第三章 地质、土壤和沉积物

土壤是有机物、矿物质、气体、液体和有机体的混合物，它们共同支持生命。焦点问题：风沙侵蚀区、旱地、黄土高原侵蚀。

第一节　影响土壤形成的因素

影响因素包括：土壤母质、气候、地形、时间、潜在生物群以及人类活动。

1.1 母质

成土母质是地表岩石经风化作用使岩石破碎形成的松散碎屑，物理性质改变，形成疏松的风化物，是形成土壤的基本的原始物质，是土壤形成的物质基础和植物矿物养分元素（除氮外）的最初来源，它对土壤的物理性状和化学组成均产生重要作用。

岩石是固态矿物或矿物的混合物，按其成因主要分为三大类：沉积岩、岩浆岩（也可称为火成岩）和变质岩。1.沉积岩是由沉积作用形成的岩石，指暴露在地壳表层的岩石在地球发展过程中遭受各种外力的破坏，破坏产物在原地或者经过搬运沉积下来，再经过复杂的成岩作用而形成的岩石。沉积岩的特点：具有层理构造和常含化石。2.岩浆岩是直接由岩浆形成的岩石，指由地球深处的岩浆侵入地壳内或喷出地表后冷凝而形成的岩石，可进一步分为侵入岩和喷出岩（火山岩）。分布最广的一种侵入岩：花岗岩，地表常见的一种喷出岩：玄武岩。3.变质岩是经历过变质作用形成的岩石，指地壳中原有的岩石受构造运动、岩浆活动或地壳内热流变化等内应力影响，使其矿物成分、结构构造发生不同程度的变化而形成的岩石。常见的一种变质岩：花岗片麻岩。

岩石循环：由于地质环境的改变和地质作用的进行，一种类型的岩石会在新的成岩作用条件下转变为另外一种类型的岩石。因此，不同岩石类型之间会因所处地质条件的变化而发生转变，称为岩石循环（rock cycle）。概括地说，（1）先存的变质岩（包括变沉积岩）、岩浆岩可以在高温等条件下发生熔融或部分熔融而形成岩浆，岩浆冷凝固结形成火成岩；（2）先存的火成岩、沉积岩和变质岩暴露于地表后经过风化、剥蚀、搬运和沉积而形成沉积岩；（3）先存的火成岩、沉积岩甚至变质岩在不同的温度、压力、剪切应力和活动性流体的作用下会发生化学成分、矿物成分、结构构造等的改变，就形成与原先岩石特征不同的变质岩。

1.2 气候影响

气候直接影响土壤物质迁移转化的过程，并决定母质风化、成土过程的方向和程度。气温和降水影响风化率、分解和养分循环率以及损失率。

1.3 地形

地形通过对气候的作用和对土壤微粒的差异运输来影响土壤。地形差异引起的微气候效应影响风化率、土壤质地和化学组成。侵蚀和沉积影响土壤深度和剖面发育。浅坡：摩擦力防止打滑；陡坡：下坡力促进滑移。

1.4 潜在生物群

生物可以对母质中的矿物质产生破坏和分解作用，又可以推动矿质养分进行生物小循环，并能合成有机质，因而对土壤的风化和形成均具有重大的影响。土壤生物包括植物、动物微生物，其中绿色植物在成土过程中更起着主导作用。有机质的数量和质量以及干扰效应都会对土壤形成造成影响。

1.5 时间

与其他状态因素相互作用。土壤是在上述母质、气候、生物和地形等成土因素综合作用影响下，随着时间的进展而不断运动和变化的产物，时间愈长，土壤性质和肥力的变化亦愈大。

1.6 人类活动

自 1950s 以来，人口增加了两倍以及相关的农业和工业活动对全世界的土壤发展产生了强烈影响，包括直接和间接的影响。2014 年发布的《全国土壤污染状况调查公报》，中国土壤环境状况总体不容乐观，全国土壤污染超标率达 16.1%，在工矿业废弃地土壤环境问题突出的同时，耕地土壤环境质量更加堪忧。为解决土壤污染问题，国务院印发了《土壤污染防治行动计划》（简称“土十条”）。

第二节　控制水土流失

土壤的形成取决于沉积、侵蚀和土壤发育之间的平衡。主要的侵蚀过程取决于地形、表面材料特性和水离开景观的途径。

黄土高原的土壤侵蚀现象十分严重。黄河约 60%径流来自兰州以上 30%的流域面积，约 90%的泥沙来自黄土高原。在植被恢复、水土保持工程措施以及气候变化综合作用下，黄土高原的生态水文过程发生显著变化，导致泥沙和径流都显著减少。

第三节　土壤特性的形成

土壤通过物质进入系统、物质的转化、在土壤剖面中向下和向上迁移以及物质从系统中流失而发展。

3.1 物质进入系统

来自外部生态系统的输入：降水、粉尘、沉积等大气输入；洪水、潮汐等水平输入。来自生态系统内部的物质输入：凋落物和根周转。

3.2 迁移转化

土壤风化是指地球表面或近地球表面的岩石和矿物在太阳辐射、大气圈组分、水和生物各种营力作用下所产生的物理、化学和生物学变化的总称。物理风化：岩石破碎、机械磨损；化学风化：原生矿物溶解、次生矿物形成。

物理风化是指岩石在温度变化、冻融、有机体、水、风和重力等物理机械作用下崩解、破碎成大小不一碎屑和颗粒的过程。物理风化是最简单的风化作用，在恶劣环境中占主导地位，无化学变化，发生于裂缝或磨损岩石（例如冰川），产生粗糙质地的土壤，为化学风化创造新的表面。在有化学作用和生物作用参与的情况下，风化作用进行得更快，风化的过程和产物也更丰富多彩。

化学风化是地壳表面岩石在水及水溶液的作用下发生化学分解的作用。化学风化涉及化学变化（从原生矿物到次生矿物的转化），受到水分和热量的促进，风化产物取决于母质，受酸刺激（土壤中主要的酸为碳酸）。化学风化中涉及的反应包括酸碱中和、氧化和螯合作用等。

3.3 土壤转移

垂直运动：向下淋溶、毛细上升（盐渍化）、动物混土。化学或物理状态改变：溶解（水，螯合）、沉淀（脱水）、经历反应形成新的化学环境（氧化还原、pH）。钙积层——草原；盐滩——沙漠、弃耕地；潜育土——湖泊沉积物；铁铝土——热带土壤。

3.4 土壤流失

物质主要以溶液和气体的形式从土壤剖面中流失。淋溶：阴离子易流失、单价阳离子易流失、电荷平衡。气态损失：氮微量气体、甲烷、土壤环境的影响。

第四节　土壤层和土壤分类

土壤剖面指从地面垂直向下的土壤纵剖面，也就是完整的垂直土层序列，是土壤成土过程中物质发生淋溶、淀积、迁移和转化形成的。主要土壤发生层：(1)O 层：残落物层。在通气良好而又较干燥的条件下，植物残落物堆积，有机物不能完全分解并在地表累积而形成。(2)H 层：泥炭层。在长期水分饱和的条件下，湿生性植物残体在表面累积，是泥炭形成过程中形成的发生层。(3)A 层：淋溶层。在表土层中，有机质已腐殖质化，生物活动强烈，主要进行着淋溶过程，故称为淋溶层。物质的淋溶程度随水、热条件而异。(4)E 层：灰化漂白层。在淋溶和机械淋洗的条件下，硅酸盐黏粒和铁。铝化合物淋失，使抗风化力强的石英砂粒与粉粒相对富积，以较浅淡的颜色或灰白色而区别于 A 层。通常与灰化过程有关。(5)B 层：淀积层。是淀积过程的产物，与母质层有明显的区别。黏粒、铁、铝或腐殖质在此层淀积或累积。次生黏土矿物形成，具块状或棱柱状结构，颜色变棕或棕红、红等。(6)C 层：母质层。指风化产物没有受到成土作用影响的层次，较上面土层紧实。(7)R 层：母岩层。指最下部坚硬的岩石层。

土壤发生层及其组合是土壤分类的主要依据，也是决定土壤肥力高低的重要因素。冰冻土、旱成土、灰土、黑沃土、氧化土的土壤剖面特征不同。土壤风化发育指标土壤风化发育指标土壤是由矿物质、有机质、土壤水分及土壤空气四个部分组成的。根据各个组分的含量的不同可以判断土壤的发育程度。

第五节　土壤特性和生态系统功能

5.1 土壤物理性质

土壤质地：指土壤中不同大小直径的矿物颗粒的组合状况，通常分为砂土、壤土和黏土。三种粒径颗粒的相对比例：黏土（<0.002 mm）、壤土（0.002-0.05 mm）和砂土（0.05-2.0 mm）。

土壤结构：指土壤颗粒（包括团聚体）的排列与组合形式，包括团聚体及其之间的裂缝和通道。土壤团聚体是由土壤颗粒自然形成的颗粒或小团块结构，土壤团聚体的稳定性是预测土壤水分流失和土壤侵蚀能力的重要指标。

反质地假设（Inverse-texture）预测粗质地土壤上的植物群落应比细质地土壤上的群落具有更高的地上净初级生产力 (ANPP)；预计在潮湿地区会发生相反的情况（Lane 等，1998）。在中等水平的降雨量下，出现在沙质土壤上的生态系统比质地细腻土壤上的系统具有更强的旱生（Xeric）性-以能耐受干燥条件环境的植物为特征。

堆积密度：影响化学成分、压实、土壤动物、浸润。

土壤持水量：影响可用水含量。

代表性粉砂壤土中有机质、砂土、壤土、黏土、微孔和大孔的体积分布。

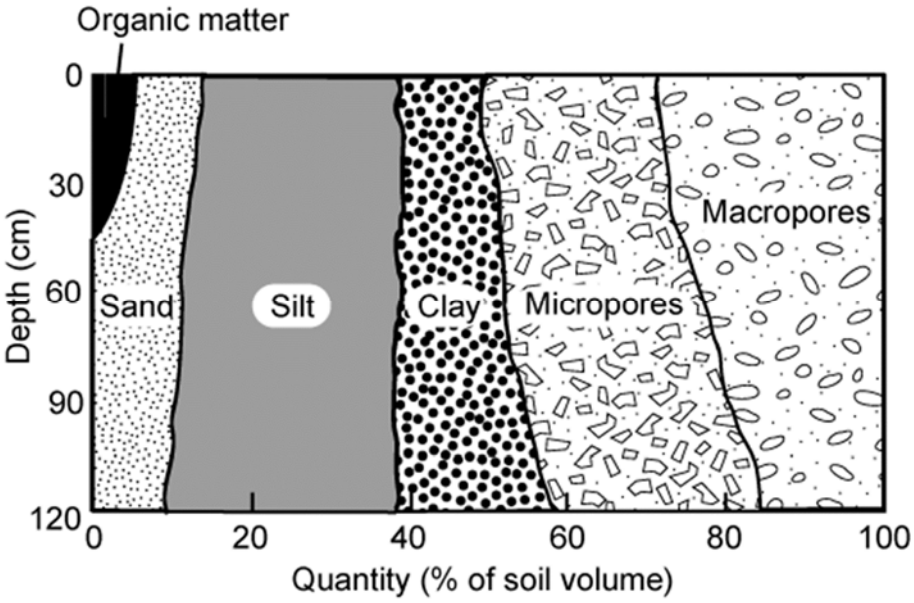


图 3.5-1 土壤物理特性

5.2 土壤化学性质

包括：氧化还原电位、酸碱度、有机含量、阳离子交换容量（碱基饱和度、缓冲能力）。碱基饱和度：总的可交换阳离子库中碱性阳离子所占的百分比。$H(Al^{3+})>H^{+}>Ca^{2+}>Mg^{2+}>K^{+}\approx NH_4^{+}> Na^{+}$。

第四章 陆地水和能量平衡

我们可以像对待地球一样看待生态系统的能量平衡。

第一节　地表能量平衡

1.1 净辐射

定义：短波和长波辐射的输入和输出之间的平衡，以瓦特每平方米为单位。

$R_{net} = (K_{in}-K_{out}) + (L_{in}-L_{out})$

短波辐射：1. 直接辐射（direct radiation），占绝大部分，90%左右。2. 漫射辐射（diffuse radiation），大气颗粒或者气体散 射形成。3. 反射（reflected radiation），云层、沙丘或雪地。

PAR（光合有效辐射）：380-710 nm，光合有效辐射占太阳直接辐射的比例随太阳高度角增加而增加，最高可达 45%。而在散射辐射中，光合有效辐射的比例可达 60~70%之多，所以多云天反而提高了 PAR 的比例。光合有效辐射平均约占太阳总辐射的 50%。

反照率：短波辐射的反射，是从表面反射的辐射能量的量。黑色物体的反照率接近 0，而白色物体的反照率接近 1.0。反照率取决于生态系统结构和吸收率。反照率因植被类型而异；存在季节变化；火灾后、施氮后都发生变化。

反照率随着叶氮的增加（高达约 2.5%）而增加，并且对叶氮的进一步增加相对不敏感。因为气体交换表面积增大，以及水和空气增加反射光谱的近红外部分。与高肥力地点的冠层相比，低氮冠层吸收的总入射辐射的比例更大。然而，叶氮和叶片反照率之间存在显著负相关的关系，这种关系仅适用于全光谱叶片反照率以及仅在 NIR 区域的叶片反照率。叶氮已被证明在广泛的植物功能类型（例如森林、草原和农田）中与盛夏冠层反照率和冠层近红外(NIR) 反射率呈正相关关系。迄今为止，驱动氮-反照率关系的机制尚未确定，影响氮可用性的因素是否也会影响反照率尚不清楚。

地面反照率的增加，会导致净辐射的减少，感热通量和潜热通量的减少，即净通量和反照率之间存在负相关关系，通量大的地方反照率小，而通量小的地方反照率大。

生态系统辐射收支：物体放射的长波取决于它本身的温度和发射率（Emissivity）。植物生态系统的发射率为 98%。短波辐射的昼夜变化要比长波辐射更大。

$R_{net} = (K_{in} - K_{out}) + (L_{in} - L_{out}) = (1 - \alpha)\, Kin + \sigma\, (\varepsilon_{sky} T^4_{surf} - \varepsilon_{surf} T^4_{surf})$

冠层结构和表面能：不规则的表面会产生机械湍流，产生涡流来传递能量，与大气紧密耦合。光滑的表面与不规则的表面相反。

1.2 能量分配

生态系统吸收的净能量（净辐射）与释放到大气或传导到土壤中的能量大致平衡。

$R_{net} = H + LE + G + \Delta S$

—R_{net} = 净辐射

—H = 感热通量，地表与大气间的湍流热通量。

—LE = 潜热通量，是当水被植物蒸腾或从叶子或土壤表面蒸发时传递到大气的能量。

—G = 地热通量，从地表传入和传出土壤的热量。

—ΔS=储能

没有雪的单位面积地平面的能量平衡：地面吸收的短波辐射+向下的长波辐射=地面反射的短波辐射+向上的长波辐射+感热通量+汽化潜热×蒸散率+地平面热容×地平面温度随时间的变化+其他（与土壤水冷冻、植物化学能等相关的能量）。

感热通量：$H=\rho c_p (T_s-T_r)/r_a$。其中，ρ 为空气密度；c_p 为空气定压比热；T_s 为地面温度；T_r 为空气温度（参考高度一般为 2m）；r_a 为空气动力学阻力。

空气动力阻力 r_a 代表热量（分子的抖动）通过近地表空气传递的难度。这种差异很大程度上取决于风速、空气动力学粗糙度和浮力，而浮力本身随温差而变化。

潜热通量：表征下垫面与大气间水分蒸发的热交换。

$e_s(T)$饱和蒸气压：在密闭条件中，在一定温度下，与固体或液体处于相平衡的蒸气所具有的压强。$e_s(T)=\exp(21.18123-5418/T)/0.622$

4 个蒸散组分：（1）蒸腾：从土壤中抽出水分然后由植物释放到大气中的通量。（2）裸露土壤蒸发：没有植物帮助的土壤水分蒸发。（3）冠层截留损失：落到叶片和凋落物上，没有进入土壤的水分蒸散。（4）雪蒸散：从积雪表面升华。

蒸气压是空气中水分子施加的分压：$e = 0.6108 \exp\left(\frac{17.27T_d}{T_d+237.3}\right)$

蒸汽压差 (VPD) 是实际蒸汽压与在相同温度和压力下被水蒸汽饱和的空气的蒸汽压之差：VPD=$e_s - e$。

能量分配的生态系统差异很大，取决于反照率、波文比 (H/LE)。

波文比（B）被定义为感热通量与潜热通量之比。不同植被类型具有不同波文比。

蒸散比（EF）被定义为潜热通量与净辐射之比。EF=1/(1+B)。当 EF→0 时，B→∞（沙漠）；当 EF→1 时，B→0（雨林）。

三个松树样地的日变化趋势比较：Rn 通常在 40 年花旗松林中最高； H 值在 20 和 40 年花旗松林中相似，G 在 12 年北美短叶松林最大，但 G 通常可以忽略不计。20 年生花旗松林的波文比通常最高，12 年生北美短叶松和 40 年生花旗松的波文比大致相似（图 4.1-1，4.1-2）。

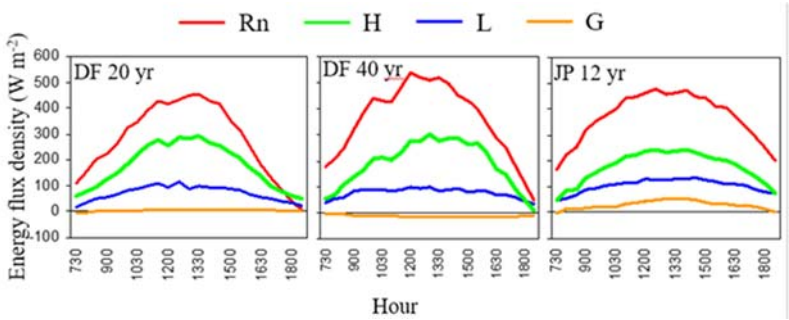


图 4.1-1 三个松树样地的净辐射（Rn）、感热通量（H）、潜热通量（L）和地热通量（G）的日变化趋势

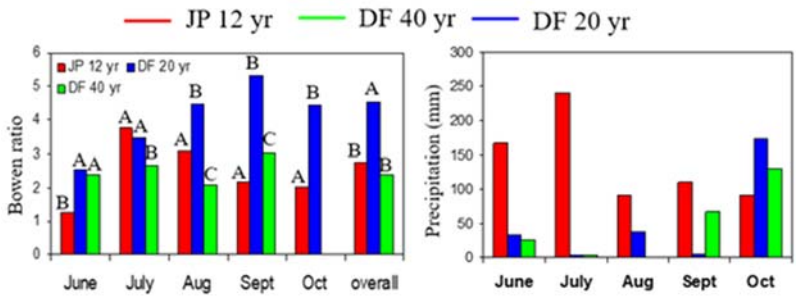


图 4.1-2 三个松树样地（12 年北美短叶松林，JP 12yr；20 年花旗松林，DF 20yr；40 年花旗松林，DF 40yr。）的波文比（左图）和年降水量（右图）。

通过涡度协方差测量的不同生态系统夏季的平均每日感热和潜热通量（图 4.1-3）。虚线表示不同的波文比（b，感热与潜热通量之比）。生态系统包括落叶林、针叶林、农作物、苔原和草原。还显示了来自地中海气候的各种生态系统，由于它们的净辐射输入量高，因此具有高通量。

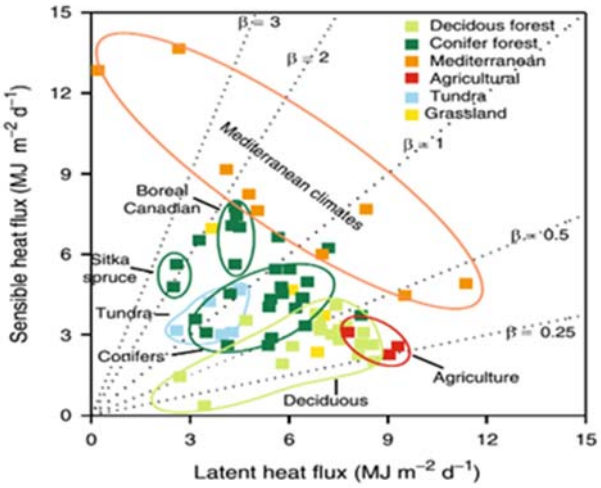


图 4.1-3 不同生态系统夏季的平均每日感热和潜热通量

传统观点：由强加气象决定的地表能量平衡。更“整体”的观点：表面能平衡、边界层结构相互交织、密不可分。

ΔF: Radiative forcing 辐射力：对流层顶净辐射通量密度的变化，一般以 1750 年的为标准，正值趋向于使系统变暖，负值趋向于变冷。

1.3 区域夏季气候的能量平衡反馈

（1）植被变化的反馈：草丛到灌木的过渡：3.4 W/m^2；苔原到森林的过渡：4.7 W/m^2。（2）太阳能输入变化 2%：4.6 W/m^2（冰期到间冰期的变化）。（3）大气 CO_2 翻倍：4.4 W/m^2。（表 4.1-1）

表 4.1-1 植被变化对区域夏季气候的影响

Fig 4.1-1 Effects of vegetation change on regional summer climate

Current vegetation	Future vegetation	Aerial extent (% of total)	ΔF (Wm-2)
Tussock tundra	Shrub tundra	53	3.4
Shrub tundra	Forest tundra	19	4.7
Wet meadow	Forest tundra	9	13.3
Mountains and lakes		19	___*
	Area-weighted average		3.9

* No measurements; we assume zero change

由于灌木扩张导致 7 月温度升高 1.0-3.5℃。

火灾对北方森林气候的影响：火灾增加落叶林比例；落叶林吸收较少的能量（高反照率）；将能量作为 ET 而不是显热传递；对气候的净冷却/湿润效应。北方森林火灾通过温室气体的正反馈循环导致气候变暖，通过反照率的负反馈通路导致气候冷却（表 4.1-2）。北方森林火灾后的净生态系统生产力 (NEP)、净初级生产力 (NPP) 和异养呼吸 (Rh) 动态变化如图 4.1-4。

表 4.1-2 强迫因子的总和在第一年产生净增温，但在 80 年中导致降温

强迫因子	辐射强度	
	Year 1	Years 0-80 (mean)
温室气体	8±3	1.5±0.7
臭氧	6±4	0.1±0.1
雪上的黑碳	3±3	0.0±0.0
海冰上的黑碳	5±4	0.1±0.1
气溶胶（直接辐射强迫）	17±30	0.2±0.4
表面冲击：-90W±40m^{-2}		
地表反照率变化	-5±2	-4.2±2.1
总计	34±31	-2.4±2.3

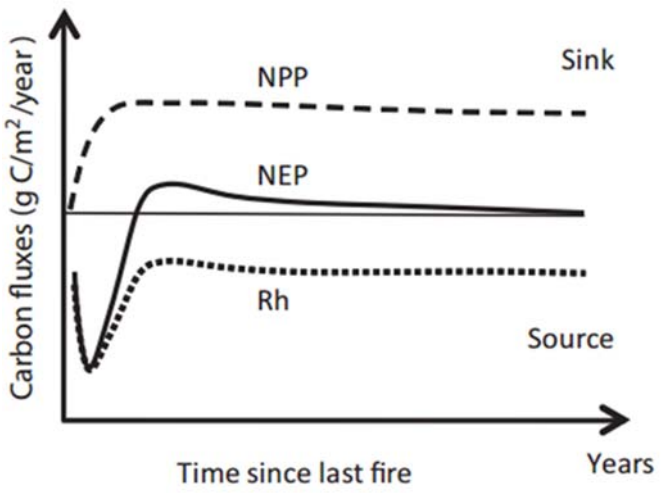


图 4.1-4 北方森林火灾后的净生态系统生产力 (NEP)、净初级生产力 (NPP) 和异养呼吸 (Rh) 动态变化

1.4 气候变暖反馈

痕量气体反馈：二氧化碳交换（北极的适度碳沉降、北方森林中的少量碳源、永久冻土融化：潜在的大型未来来源）、CH_4：大量来源。

能源平衡反馈占主导地位：（1）北极和北方地区的积雪较早融化：对变暖的积极反馈。（2）植被变化：北极灌木增加（对变暖的正反馈）、转换为北方落叶（对变暖的负面反馈）。

现有的第一个理论是基于土地利用的变化。开创性论文是 Otterman, Science, 1974；Charney et al.，Science，1975 年。最初的想法是土地利用的变化通过影响地表反照率和蒸发量而导致干旱。批评者认为，模型模拟研究规定了过度的地表变化以获得大量的降雨响应，所以他们似乎并没有完全解释干旱，但是地表反照率和蒸散反馈可能有助于潮湿或干燥状态的持续存在。

第二种现有理论基于大规模海表温度变化。Folland 等（Nature，1986）表明，萨赫勒降雨与近全球的准半球（南北）海表温度对比强烈相关（r=0.62）。Ward (J. Clim.,1998) 表明“北冷暖南”格局对长期干旱趋势很重要；年际降雨波动更多地与厄尔尼诺现象有关。

南北格局的可能原因？（自然变异？）

最近的研究集中在北印度洋变暖（Giannini et al.，Science，2003）和地中海变冷（Rowell，J. Clim.，2003）。Rowell (2003) 解释了地中海-萨赫勒连接的机制。

最近的研究试图将海表温度和地表理论结合起来。萨赫勒可能表现为具有两种稳定状态的复杂系统：“湿”和“干”（例如，Foley et al.，Ecosystems，2003）。植被反馈提供了年复一年的“记忆”，从而增加了潮湿或干燥状态的持久性（正反馈）。这些反馈可能涉及表面反照率、水分回收、灰尘。Foley 等提到 Rosenfeld 等（PNAS，2001）年的沙尘降雨假说。Nicholson（Rev. Geophys., 2000）讨论了尘埃辐射效应的一些可能影响。

1.5 干旱反馈

微量气体反馈小：非常小的净生态系统生产力。

能源平衡反馈占主导地位：加强气候干燥或湿润、生态系统反馈产生非线性响应（创造维持气候状况的记忆）、影响是区域性的、恢复生态的重要作用。

北方森林砍伐导致净降温；北方造林则导致净变暖（仅解决碳固存的措施会适得其反）。

热带森林砍伐导致净变暖；相反：热带造林导致净变暖或变冷？

1.6 热带森林砍伐反馈（净变暖）

微量气体反馈（净变暖）：碳损失（全球分散）。

能源平衡反馈（净变暖）：增加生态系统反照率（冷却），但被减少的云量抵消了；减少蒸腾作用（变暖）；降水减少，一半的降雨来自再生水，减少森林生长，可以导致改变为稀树草原/干燥条件；气候反馈稳定植被变化；社会经济影响。

蒸发蒸腾占到大气湍流能量转移的 75%。

1.7 水是主要的温室气体

水汽对升温的反馈：温暖的空气能容纳更多的水，导致更多的水蒸发，增加了大气的含水量，吸收更多的红外辐射，大气增温，等等……一个恶性循环！

为什么我们关心生态系统水资源平衡？因为降水是大多数陆地生态系统的主要水输入。许多生态过程与水的循环有关。

水平衡：1.输入和输出（垂直和横向）；2.内部迁移。

为什么植物要消耗这么多水？因为植物离不开水！植物利用的所有水几乎都来自土壤；植物蒸腾作用需要水；水分可以保持软壁细胞肿胀或坚硬；水是从土壤中吸收营养元素（溶液）的介质。

第二节　生态系统水平衡的基本原理

土壤就像一个桶。输入：以降水为主。输出：蒸发、蒸腾作用、径流。储水量取决于：桶的大小（土壤深度和质地），以及输入和输出之间的平衡。

生态系统的水输入包括：（1）降水：生态系统的主要水输入。（2）地下水：深根植物（3）雾沉降。（4）树冠拦截：通常会降低进入生态系统的降水的有效性，而不是增加水的输入。

生态系统在冠层存储方面有所不同，主要取决于 LAI 和物种种类。

2.1 生态系统中水分运动的基本原理

水沿能量梯度运动：从高能到低能

什么力使水运动？水势（ψt）：土壤表面水相对于纯水的势能 $\psi_t=\psi_p+\psi_o+\psi_m$。

ψ_p，压力势：重力，以及生物体生理过程产生的力；

ψ_o，渗透势：溶于水的物质；

ψ_m，基/衬质势：表面对水的吸附。

按照惯例，在土壤表面，没有压力的情况下纯水的水势为 0。如果水势比这一标准高的话，水势的值为正；反之为负。

水从冠层到土壤的运动：（1）透冠雨：滴落到地上。（2）茎流：向地面茎流。（3）截获：未到达地面的降水部分，对于封闭的树冠生态系统，它通常在 10%到 50%之间（Waring and Running, 1998）。

2.2 土壤中的水分运动

与重力和基质力相关的压力梯度控制着大部分水通过土壤的运动。$J_S = L_S \frac{\Delta\ \varphi_t}{l}$

J_s = 水通量率

L_s = 水力传导率

$\Delta\varphi_t$ = 水势梯度

l = 路径长度

渗透：进入土壤的水分在很大程度上取决于水力传导率（受到质地以及团聚结构的影响）、由动物和根形成的大孔、不透水层（沙漠中的钙质层；寒冷气候下的永冻土层）。

当入渗慢于降水时发生地表径流。田间持水量（$\psi_t \approx$-0.03MPa）：是土壤在田间条件下所能保持的最大含水量。永久枯萎点：大多数植物因无法从土壤中获取水分而枯萎的土壤水势（$\psi_t \approx$ -1.5MPa）。植物可用水：田间持水量与永久枯萎点之间的差异。

水分从土壤到根部的运动：通过从高水势流向低水势，水从土壤移动到蒸腾植物的根部（根毛和菌根菌丝）。生根深度反映了水分和养分有效性之间的权衡。生根深度具有重要的生态系统后果，因为它决定了植被可以利用的土壤体积。黎明前水势是土壤水分和植物经历的干旱胁迫程度的良好指标。根系获得水分降低了土壤含水量并增加了周围土壤中充满空气的孔隙空间，而残留的水分则以毛细桥和薄膜的形式紧紧附着在土壤颗粒上。

2.3 植物中的水分运动

从叶面到大气的蒸气压梯度是水分通过植物运动的驱动力(SPAC:土壤-植物-大气连续体）：$J_P = L_P \frac{\Delta\ \varphi_t}{L}$

J_p = 水通量率；L_p = 水力传导率；$\Delta\varphi_t$ = 水势梯度；L = 路径长度。

在潮湿的土壤中，水分进入根部的流动的最大阻力为细胞膜。在干燥的土壤中，根和土壤之间的接触是根的水通量的最大阻力。

水力提升：水沿着水势梯度从深层土壤到浅层土壤的垂直运动（Caldwell et al., 1998）。在低蒸腾情况下，植物处于深层湿润土壤中的根系吸收水分，并通过输导组织运至浅根系，进而释放到周围干燥的土壤中的作用。

问题：深根的沙漠植物如何通过干燥的土壤生长到地下水位？

水沿压力梯度移动：干旱环境中土壤水势的模式和植物水分运动：白天，响应强水势梯度，水从土壤（特别是深层土壤）移动到大气。夜晚，水从深层潮湿的土壤通过根系流动到干燥的表层土壤，这是水势提升的过程。

水在茎中移动：功能：水流过茎，以补充蒸腾的叶子损失的水分。驱动力：蒸腾失水产生的水势梯度。阻力：取决于路径长度和茎结构。

气穴现象：在张力下水柱的断裂。茎的水力传导率随毛细管直径的四次方变化。寒冷环境中的植物会因冻结而发生气穴。

干燥环境下的植物安全系数更大。它们在比可能导致气蚀的水势高得多的水势下运行。低水势下防止气穴产生的能力。

植物因栓塞而失去所有木质部传导性时的水势与自然界中观察到的最小水势之间的关系（图 4.2-1）。每个基准点代表一个不同的物种。1:1 线是在没有安全系数的情况下预期的线，即如果每个物种在自然界中观察到的最低水势下失去所有电导率。自然经历低水势的物种表现出更大的安全边际（即与 1:1 线的偏离更大）。

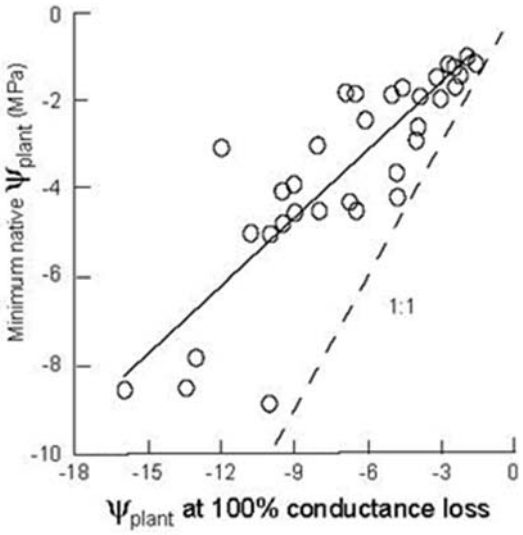


图 4.2-1 植物因栓塞而失去所有木质部传导性时的水势与自然界中观察到的最小水势之间的关系

茎的输水能力与 LAI 平衡：来自干燥环境的物种有更多的运输细胞。

植物有一定的储水能力：在大多数植物中相当有限，大部分水必须来自土壤（不是植物储存，<10%蒸腾作用）。

运输系统可能在非常干燥的条件下崩溃：可能因为茎内水柱断裂，蒸腾作用不能从根部“吸”水。

水在叶子中移动：叶片失水受空气蒸发势、土壤补水和叶片对失水调节的控制（土壤供水、空气的蒸发潜力）。空气温度和湿度的昼夜和气候差异决定了蒸腾作用的驱动力。

在干燥条件下，叶片失水率取决于供水量：影响水势梯度；植物调节气孔导度以配合供水。气孔导度是指植物气孔传导 CO_2 和水汽的能力。植物通过改变气孔的开度等方式来控制与外界的 CO_2 和水汽交换，从而调节光合速率和蒸腾速率,以适应不同的环境条件，特别是土壤供水状况和空气湿润程度。

等水植物：气孔保卫细胞内和周围的受体对这些化学和水力信号作出反应，关闭气孔，并保持叶水势。

异水植物：受体和保卫细胞不对水力信号作出反应，而是叶水势与土壤和根部水势的下降同步下降，对气孔导度的初始控制很少。

第三节　生态系统的水分流失

水的输入是生态系统水分输出的主要决定因素：

$P \pm \Delta S = E + R \quad P = E + R$

P：降水；ΔS：蓄水；E：蒸散；R :径流。

从潮湿的冠层蒸发

气候条件（蒸气压不足）以及冠层中的环境条件通过湍流与大气条件耦合的程度。气候是控制湿冠层蒸发的另一个因素。以雪或冰形式拦截降水的冠层通常储存的水量是接收液态降水时的两倍。

湿冠层蒸发取决于驱动力：（1）冠层水温，控制叶片表面的水蒸气浓度；（2）空气湿度：控制大量空气的水蒸气浓度，蒸气压不足。

蒸发在冠层潮湿的地方很大；在具有高表面粗糙度的生态系统中较大（与大气很好地结合、取决于驱动大气干燥度的条件；从光滑的冠层蒸发较少（净辐射驱动 ET）。

在大气条件高度耦合的森林里，湿润冠层的蒸发量取决于净辐射和 VPD。

干树冠的蒸散

土壤水分直接限制了干燥土壤的蒸散率。控制潮湿土壤中的 ET 比的因素：（1）边界层电导（空气动力学导度）：物理控制失水，取决于植被结构和风，土壤潮湿时的主要植被控制。（2）表面电导（表面导度）：对失水的生理控制，对植被结构不敏感（LAI），取决于气孔导度，随着土壤干燥变得越来越重要。当土壤水分充足时，植被结构和气候控制蒸散率。

边界层电导（空气动力电导）是对从生态系统到大气的水蒸气转移的物理控制的量度。$g_\beta = \left(\frac{\bar{u}}{u_*^2} + 6.2u* - 0.67\right)^{-1}$，其中 $\bar{u}$ 为平均风速（m s^{-1}）；u* 是摩擦速度（m s^{-1}）。

表面电导：衡量生态系统中叶子和土壤表面失水潜力的一种方法。

$$g_C = \frac{\gamma LE g_a}{\Delta(Rn - G) + \rho c_p VPD - LE(\Delta + \gamma)}$$

式中 Δ 为饱和水蒸气压对气温曲线的斜率(kPa K^{-1})；y 为湿度计算常数(kPa K^{-1})；LE 为潜热通量(Wm^{-2})；Rn 为净辐射(Wm^{-2});G 为土壤热通量(Wm^{-2});ρ 为空气密度(kg m^{-3});Cp 为空气的比热($Jkg^{-1}K^{-1}$)；VPD 为空气蒸气压差(kPa）。

表面电导在不同生态系统之间的差异：LAI 没有明显的趋势；在作物中往往更高；对此的生态控制在自然生态系统中没有明确定义。

气候对 ET 的影响：空气的水分含量是粗糙、混合良好的冠层的主要控制因素；净辐射是光滑、耦合不良的冠层的主要控制因素；这些环境控制在湿式和干式冠层中是相同的。

解耦系数：冠层与大气分离程度的量度。$\Omega = \frac{\Delta/\gamma+1}{\Delta/\gamma+1+g_a/g_c}$

Ω 的取值范围为 0 到 1，Ω≈0: 蒸散由 VPD 控制，Ω≈1：蒸散由净辐射控制。

水源的同位素特征：氘 (D) 与氢 (H) 的浓度比提供了不同水源的有用特征。蒸发会区分较重的同位素（氘），导致 D:H 的同位素比相对于引起蒸发的水源下降（变得更负）。通过对植物木质部中的水进行采样，可以确定植物使用的主要水源。

第五章 陆地生态系统碳输入

碳水交换是一个焦点问题。通过叶表面孔隙（气孔）进行的碳和水交换控制着日益稀缺的水资源为不断增长的人口支持粮食生产的效率。当水充足时，开放的气孔可以最大限度地增加碳获取和生产力，但代价是大量的水分流失。 在干燥条件下，部分气孔关闭会减少碳获取，但会提高水支持植物生长的效率。

什么限制了生物圈获取碳的能力？

大多数光合作用发生在什么地方和什么季节？

植物如何调节固碳和失水之间的平衡？

应用目前对固碳和失水之间权衡控制的理解，可以减少因当前粮食需求增加和支持农业生产的淡水供应减少而导致“火车失事”的可能性。

第一节　生态系统碳输入

过程：光合作用——提供驱动生态系统中大多数生物过程的碳和能量。

重要性：驱动所有生物过程的能量；占地球有机物的一半。

水和养分可用性是控制碳输入生态系统的主要因素。碳和能量在生态系统中移动时相互关联。机物质的能量因碳化合物而异，但对于整个组织，它相对恒定，大约为 $20kJ\ g^{-1}$ 的无灰干质量（Golley, 1961; Larcher 1995）。草本组织：45%；木本组织：50%。

地球系统碳循环，是指碳在岩石圈、水圈、大气圈和生物圈之间，以 CO_3^{2-}、HCO_3^-、CO_2、CH_4、$(CH_2O)_n$、有机碳等形式相互转换和运移的过程。碳的地球化学循环控制了碳在地表或近地表的沉积物和大气、生物圈、土壤圈、岩石圈和水圈之间的迁移。在碳的生物循环中，大气中的二氧化碳被植物吸收后，通过光合作用转变为有机物质，然后通过生物呼吸作用和细菌分解作用又从有机物转变为二氧化碳进入大气。

光合作用控制级别：单叶控制；通过树冠进程控制。

控制因素：（1）直接控制：光、二氧化碳；（2）间接控制：水、养分。

第二节　光合作用途径

2.1 C3 光合作用

碳输入生态系统的速率取决于光合作用的生物化学过程对环境的响应。

光合作用中有两大类反应。捕光反应：将光能转化为暂时的化学能。固碳反应：利用捕光反应的产物将 CO_2 转化为糖——一个更为永久性的化学能形式，能够储存、运输或进行代谢活动（图 5.2-1）。

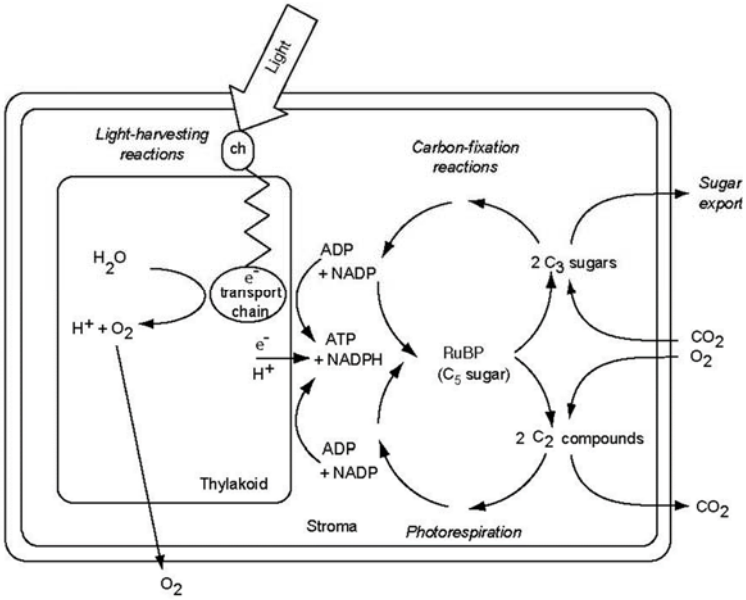


图 5.2-1 光合作用中的捕光反应和固碳反应示意图

NADP：烟酰胺腺嘌呤二核苷酸磷酸（nicotinamide adenine dinucleotide phosphate）

NADPH：还原型辅酶Ⅱ，主要起传统氢的作用

ADP：二磷酸腺苷

ATP：三磷酸腺苷

RUBP：二磷酸核酮糖

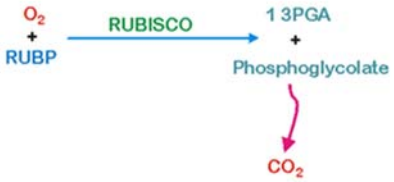
Rubisco（核酮糖-1,5-二磷酸羧化酶/加氧酶）可以增加或减少碳。羧化酶：与二氧化碳反应生成糖；导致固碳。氧化酶：与加氧酶反应将糖转化为二氧化碳；呼吸 20-40%的固定碳；光保护机制。

固碳反应的特点：(1)对 Rubisco 和其他光合酶的大量氮需求；(2)它们依赖于光捕获反应的产物（ATP 和 NADPH），而后者又依赖于辐照度（叶子接收到的光）；(3)它们经常受到向叶绿体供应的 CO_2 的限制。在毫秒至分钟尺度上，对光合 CO_2 供应变化极为敏感，在日至周时间尺度上对氮供应变化敏感。

光呼吸：植物的绿色细胞在光下吸收 O_2、放出 CO_2 的过程。光呼吸的底物为乙醇酸，经过乙醇酸代谢途径完成，整个途径涉及叶绿体、过氧化体 及线粒体三种细胞器中一系列酶的协同作用。光呼吸过程中几种主要物质如乙醇酸、乙醛酸、甘氨酸都是二碳化合物，因此光呼吸亦称 C2 循环。

“正常”反应中，CO_2 与 RUBP 结合形成 2 分子的 3PGA（三磷酸甘油酸）。

光呼吸过程中，O_2 在非生产性、浪费性反应中替代 CO_2，生成乙醇性磷酸。



暗呼吸：暗呼吸是用词不当。虽然最好在黑暗中没有光呼吸的情况下进行测量，但它始终存在于活的植物中。暗呼吸是其他生物体线粒体呼吸的功能等价物；它发生在植物线粒体本身。

表 5.2-1 光呼吸与“暗呼吸”的区别

	光呼吸	暗呼吸
底物	光合作用中形成的乙醇酸；底物一般是光下在叶绿体内新形成的	可以是碳水化合物、脂肪或蛋白质，但最常用的底物是葡萄糖。底物可以是新形成的，也可以是贮存的
代谢途径	乙醇酸代谢途径，或称“C3 途径”。只在光下进行	糖酵解，三羧酸循环，磷酸戊糖途径等。光下、暗中都可进行
发生部位	只发生在光合细胞中，在叶绿体、过氧化体及线粒体三种细胞器协同作用下进行	在所有活细胞的细胞质及线粒体中进行
对 O_2 及 CO_2 浓度的反应	在 O_2 浓度 1%~100%范围内，光呼吸随 O_2 浓度提高而增强。O2 及 CO_2 相互竞争 Rubisco 及 RuBP，如 CO_2/O_2 浓度比降低时，有利于加氧反应与光呼吸底物乙醇酸的形成，促进光呼吸；反之则有利于羧化反应，促进光合作用	O_2 及 CO_2 浓度的变化对“暗呼吸”无明显影响；O_2 及 CO_2 之间本无竞争现象

注：引自饶丽华，植物生理生化，1998

通过在叶黄素循环中加速紫黄质和玉米黄质的相互转换以及增加一个光系统 II 亚基的数量来加速适应过程。用该系统测试的烟草植株在自然野外条件下显示出大约 15%的植物生物量产量。NPQ：在光系统 II (PSII)天线复合体中，多余的激发能量可以以热量的形式无害地消散，这是一个名为叶绿素荧光非光化学猝灭的过程。当叶片从高光强到低光强时，NPQ 不能够迅速适应，因此固定的 CO2 仍然会在低光下损失，损失范围大概在 7.5-30%。

净光合作用：是指在单个叶片水平上测得的净碳增加率。它是在光下同时固定 CO_2 和叶片呼吸（光呼吸和线粒体呼吸）之间的平衡。

2.2 C4 光合作用

PEP：磷酸烯醇式丙酮酸。

C4 光合作用的三大生态学特征：（1）C4 酸移动到维管束鞘细胞中脱羧，在 Rubisco 固碳场所富集 CO_2，提高了 Rubisco 羧化效率。（2）PEP 羧化酶比 Rubisco 更有效地降低叶内 CO_2 浓度。（3）C4 途径再生碳受体分子（PEP）的净成本是每固定一个 CO_2 消耗两个 ATP（图 5.2-2）。

与 C3 光合作用的区别：

（1）C4 光合作用比 C3 增加了一套固碳反应，使得植物能够在干旱环境中提高光合作用的水分利用效率。

（2）与 C3 植物相比，C4 光合作用途径的主要优点是损失更少的水分，并且需要更少的氮来维持给定的光合作用速率。

（3）C4 植物具有同位素特征，使我们能够追踪它们在生态系统中过去和现在的作用。

（4）大多数木本植物没有 C4 光合作用。

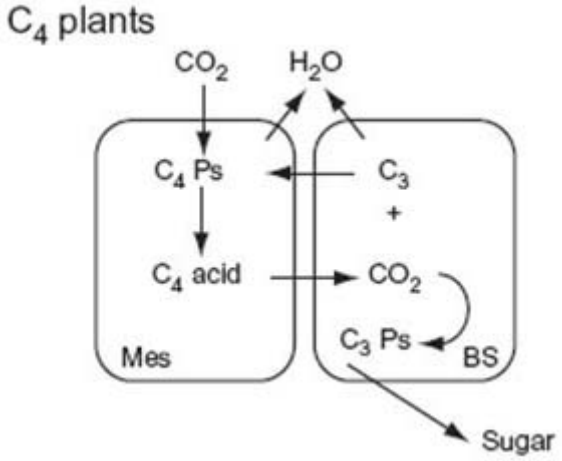


图 5.2-2 C4 光合作用的途径

2.3 景天酸代谢

景天酸代谢 (CAM) 使生态系统能够在极其干燥的条件下固定碳。

2.4 碳同位素

^{12}C、^{13}C 和 ^{14}C。较重的同位素在某些反应中反应较慢，特别是在 Rubisco 对 CO_2 的羧化作用（羧化作用）中。CAM 和 C4 植物的 ^{13}C 浓度比 C3 植物高得多。

$$\delta^{13}C(‰) = 〔 (Sam)\ ^{13}C/^{12}C\ /(std)^{13}C/^{12}C\ -1〕\times 1000$$

植物进化等级：C3 是原始的，C4 是进化的。

地域分布层次：C3 低温栖息地，C4 高温栖息地。

植物形态等级：C3 栅栏组织和海绵组织有明显差异，C4 无差异。

2.5 环境控制的基本原理

表 5.2-1 C3、C4、CAM 植物的光合和生理生态特性的比较

特性	C3 植物	C4 植物	CAM 植物
1.叶结构	BSC 不发达，内无叶绿体，无”花环”结构	BSC 不发达，内有叶绿体，有”花环”结构	BSC 不发达，叶肉细胞的液泡大, 无”花环”结构
2.CO_2 固定酶	Rubisco	PEPC、Rubisco	PEPC、Rubisco
3.最初 CO_2 受体	RuBP	PEP	光下 RuBP，暗中 PEP
4.光合初产物	PGA	OAA	光下 PGA，暗中 OAA
5.同化力需求理论值（CO_2:ATTP:NADPH）	1:3:2	1:5:2	1:6.5:2
6.最大光合速率（$C0_2$ 吸收量）（$\mu mol \cdot m^{-2} \cdot s^{-1}$）	*低（10~25）*	高（25~50）	极低（1~3）
7.CO_2 补偿点($\mu l \cdot L^{-1}$)	*高（40~70）*	低（5~10）	暗期（5），光下（0~200）
8.Warburg 效应	明显	不明显	明显
9.光呼吸	高，易测出	低，难测出	低，难测出
10.叶绿素 a/b	2.8±0.4	3.9±0.6	2.5~3.0
11.光饱和点	最大日照 1/4~1/2	最大日照以上	不定
12.光合最适温度(°C）	低（13~30）	高（30~47）	宽（~35）
13.生长最适温度	低	高	宽
14.耐旱性	弱	强	极强
15.光合产物运输速率	小	大	—
16.最大干物生长率($g \cdot m^{-2} \cdot d^{-1}$)	低（19.5±3.9）	高（30.3±13.8）	—
17.最大纯生产量（$t \cdot hm^{-2} \cdot y^{-1}$）	少（22.0±3.3）	多（38.6±16.9）	变动大
18.蒸腾系数	大（450~950）	小（250~350）	极小（50~150）
19.增施 CO_2 对干物重的促进	大	小	—

第三节　陆地植物光合作用

3.1 环境控制的基本原理

平衡光合作用物理和生化限制：（1）物理限制：将 CO2 输送到叶片；（2）生化限制：羧化作用速率；（3）光照限制；（3）酶限制（N）；（4）磷酸盐或糖磷酸盐

光合作用的 CO_2 响应曲线：在二氧化碳反应曲线线性部分，光合速率被二氧化碳向叶绿体内的扩散速率所限制，在二氧化碳浓度较高时被生化过程所限制。二氧化碳补偿点是指叶表现出净的碳获取时的最低二氧化碳浓度。

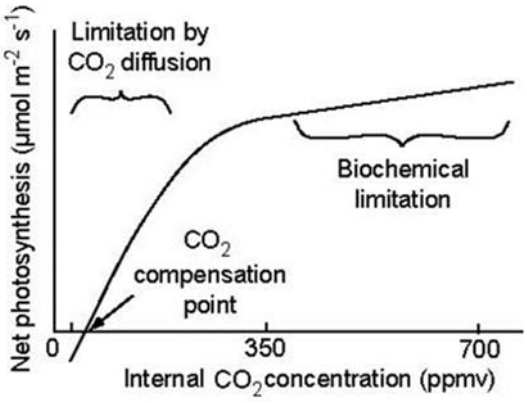


图 5.3-1 光合作用的 CO_2 响应曲线

3.2 二氧化碳限制 (CO_2 Limitation)

直接影响：净光合作用将增加；不同的植物表现出不同的反应，C3 植物是生态系统中的优势物种，C4 植物不敏感。间接影响：增加土壤水分。CO_2 升高是通过降低水分的限制而对植物生长产生更大的影响，并不是通过 CO_2 升高对光合作用的直接影响。

升高的 CO_2 会增加叶子中碳的可用性，从而导致更高的 Rubisco 活性和光合作用速率。更大的光合作用增加了叶子中非结构性碳水化合物的含量，导致更大的淀粉储备，增加生长素生物合成。长期暴露于 CO_2 中，光合作用会因碳水化合物的增加而下调。碳水化合物被运输到根部，在那里它们将刺激根部生长和基因转录。碳水化合物与激素的串扰也会改变根的生长。

一些植物会根据 CO_2 的变化改变光合能力。

3.3 光限制 (Light Limitation)

叶子调整气孔导度和光合作用能力，以在不同光环境中最大限度地获取碳。

量子产率：生成产物的数量与吸收光辐射量之比也等于产物的生成速度与吸收光辐射的速度之比。

光利用效率(LUE)是利用光固碳的效率，与光响应曲线相同。C3 植物在低光下光利用效率几乎恒定（约 6%），即光响应曲线的线性部分在所有植物中都是相同的，称为光合作用的量子产率。

生物体采取两种方法来适应变化的环境：顺应（Acclimation）或适应（Adaptation）。顺应是一种生理变化，使生物体能够应对变化的条件，是一种稳态反应。适应是进化，涉及等位基因的进化选择。顺应和适应都有遗传基础。

顺应的例子：冬天长出更厚的皮毛、在旱季产生较小的叶子、增加高海拔地区的红细胞数量、生产不同温度最适酶。

适应光线变化的机制：

（1）顺应（生理调整）：阳生叶发展出更多细胞层，以及更高的光合能力；阴生叶更多的捕光色素。

（2）适应（基因变化）：机制与顺应相同。

（3）其他改变：最大化叶面积（更多叶子、薄叶或圆柱形叶）；叶片角度；叶运动；有效利用阳光反射。

多个物种增加了光照水平的范围，在此范围内光利用效率保持不变。

叶面积决定光环境：

冠层内的光线呈指数衰减：$I = I_o e^{-KL}$

其中 I 是冠层中任何一点的辐照度（单位时间内在表面接收的辐射能量的数量），I_o 是冠层顶部的辐照度；k 是消光系数；L 是测量点上方的投影叶面积指数。

投影叶面积指数：投影到水平面上的叶面积。总叶面积指数：叶片的总表面积，包括扁平叶片的上下表面和针叶的圆柱表面。

适应在低光照强度下生长的物种被称为耐荫物种（如糖槭、铁杉、山毛榉），通常比不耐荫的物种（如白杨和许多松树）具有更低的补偿点和光饱和度。不耐荫物种在相对高水平的光子通量密度下饱和，而耐荫物种在相对低水平的光子通量密度下饱和。

3.4 氮限制与光合能力 (Nitrogen Limitation and Photosynthetic Capacity)

光合能力：在有利的光照、水分和温度条件下测得的每单位叶质量的光合速率。植物物种间光合作用能力相差 10 到 50 倍。

植被调整光合能力和叶面积以平衡土壤资源的可用性：调节土壤资源光合能力；气孔导度的调整；调整叶面积；物种组成的变化。

叶片氮决定光合能力。叶片寿命是决定光合能力的主要因素。光合作用和叶片寿命之间存在不可避免的权衡。长寿叶含有大量非光合化合物。

估计 53-76% 的这种巧合收益本身（氮沉积）在全球范围内被抵消。

影响碳增益的一系列特征：生长速率（取决于土壤资源的可用性）；叶片寿命；叶氮浓度；光合能力；叶片寿命和光合作用之间不可避免的权衡。快速生长的植物具有高的光合速率。每单位生物量的表面积，称为比叶面积 (SLA)，是光合能力的良好预测指标，比叶面积越大，光合速率更强。

3.5 水分限制 (Water Limitation)

短期响应：降低气孔导度以减少水分流失；降低叶肉电导；减少叶片内部 CO_2 扩散。

长期反应：减少叶面积；改变辐射吸收；保持高 WUE(水分利用效率）。

水分胁迫常和强光联系在一起。

水分利用效率是指每失去一单位水而得到的碳的单位数。在干燥环境中水分利用效率最高，这是效率和能力之间的权衡。机制：CO_2 的路径比水长，因此气孔导度的变化对水分流失的影响大于对二氧化碳增加的影响，比预期的气孔导度更高的光合能力。

$$WUE = \frac{\text{daily } CO_2 \text{ exchange}}{\text{water evapotranspiration}}$$

$$\text{WUE} = \frac{GPP}{ET} = \frac{GPP}{T} \times \frac{T}{ET}$$

其中 T 是植被蒸腾作用。GPP/T 是基于蒸腾作用的水分利用效率，表示植物利用水分生产干物质的效率。T/ET 是蒸腾量与蒸散量之比，反映了生态系统水汽通量如何在物理和生物过程之间分配。

3.6 温度影响 (Temperature Effects)

极端温度会限制二氧化碳的吸收。寒冷环境中光合作用能力增加；温暖潮湿环境中蒸散量高；温暖干燥环境中叶面积小。由于植物的顺应和适应，当对生态系统进行比较时，温度和野外的平均光合速率没有明显的关系。

3.7 污染物 (Pollutants)

污染物会损害光合作用体系，降低光合能力，降低植物气孔导度。

第四节　总初级生产

GPP 是生态系统尺度的净光合作用。生态系统之间年 GPP 的差异主要取决于叶面积的大小及这些叶面积光合作用的有效时间。叶面积和光合作用的季节性取决于干扰后的土壤资源（水分和养分）的可利用性、气候和时间。

4.1 冠层过程 (Canopy Processes)

冠层影响 GPP。大多数叶片尺度的影响仍然在整个冠层尺度中起作用。大部分光合作用都在冠层顶部的叶片中进行，因为冠层顶部能接收最多的光，具有最年轻、含氮量最高的叶子。冠层对环境的影响增强了冠层顶部碳获取的最大化：强光照、环境二氧化碳（树冠内下降）、高边界层电导（风）。冠层过程增加了 LUE 恒定的光强度范围。

生态系统二氧化碳净交换减少。

从卫星估计的碳获取：$NDVI = \frac{(NIR-VIS)}{NIR+VIS}$。式中，NDVI：归一化植被差异指数；NIR：近红外辐射；VIS：可见辐射。因此 NDVI 本身在 -1.0 和 +1.0 之间变化。

增强植被指数 (EVI)：$EVI = 2.5 \times \frac{(NIR-RED)}{(NIR+C1\times RED-C2\times Blue+L)}$。是一种“优化”指数，旨在增强植被信号，提高高生物量区域的灵敏度，并通过冠层背景信号的解耦和大气影响的减少来改进植被监测。

NDVI 与生态系统碳增益的关系：GPP = LUE × FPAR × PAR ≈ LUE × NDVI × PAR

VPM 模型：

基于遥感的生态模型则成为整合点位尺度通量观测和大尺度卫星遥感观测的纽带和桥梁，为区域植被生产和碳循环的研究提供了更为有效的手段(Cao and Woodward, 1998)；

一个基于遥感的植被光合模型（Vegetation Photosynthesis Model，VPM）来估算 GPP。VPM 将植被冠层分成光合有效成分(chlorophyll, 叶绿素)以及非光合有效成分(NPV)两类，并引进了新的遥感植被指数以表征物候状况对植被光能利用效率的影响；

VPM 模型已经被广泛地用于湿地、森林、草地和农田生态系统总初级生产力的模拟（Jin et al., 2013; Li et al., 2007; Liu et al., 2012; Kang et al., 2014; Xiao et al., 2004a,b）。

4.2 光合作用的要点

1. 平衡生化和物理限制
2. 将光合潜力与土壤资源相匹配
3. 调整叶面积以保持恒定的 LUE

4.3 对 GPP 的主要控制

1. 叶面积：可能会因为食草动物取食和病原体感染而减少
2. 光合季节的长度
3. 单叶片光合速率：光合能力；改变气孔导度的环境压力

由于叶面积和光合潜力的差异，吸收光能的差异可能更强烈地决定了生态系统类型之间和演替阶段之间 GPP 的差异。

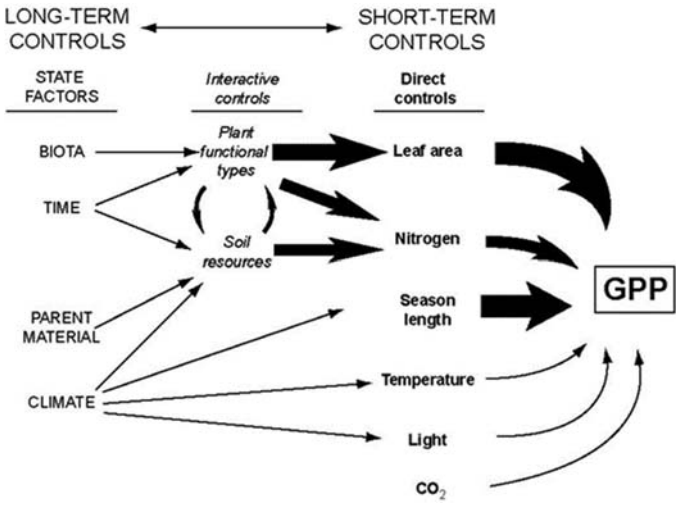


图 5.4-1 光能吸收的差异可能决定了生态系统类型之间和演替阶段之间 GPP 的差异

4.4 做好生态学研究的基本条件

1. 研究平台支撑（野外台站，重点实验室……)
2. 交叉学科背景
3. 扎实的生态学基础知识
4. 经典生态学文献
5. 严谨的实验设计
6. 记录完整的研究过程
7. 良好的文字表达
8. 长期积累

第六章 植物的碳概算

植物总初级生产（GPP）输入的碳与植物呼吸和组织更新输出的碳之间的平衡决定了植物的碳平衡。

引言

植物生产决定了可以用来供给包括人类在内所有生物的能量。我们所需要的食物和纤维都直接依赖于植物的生产，也因为植物在生态系统过程所起到的至关重要的作用而间接依赖植物的生产。大约 50%的植物总初级生产（GPP）通过植物的呼吸释放到大气中，主要用于支撑植物的生长和生命维持。净初级生产（NPP）是植物的净碳收益，等于 GPP 和植物呼吸的差。植物碳的损失主要通过以下几个途径，包括植物或者部分植物（如叶片）的死亡；植物被动物取食；向环境分泌水溶性或者挥发性有机物质；以及向共生体微生物（例如菌根真菌和固氮细菌）定向传输碳。最后，碳还可能因为火烧、人类收获或者其他干扰从植物丢失。

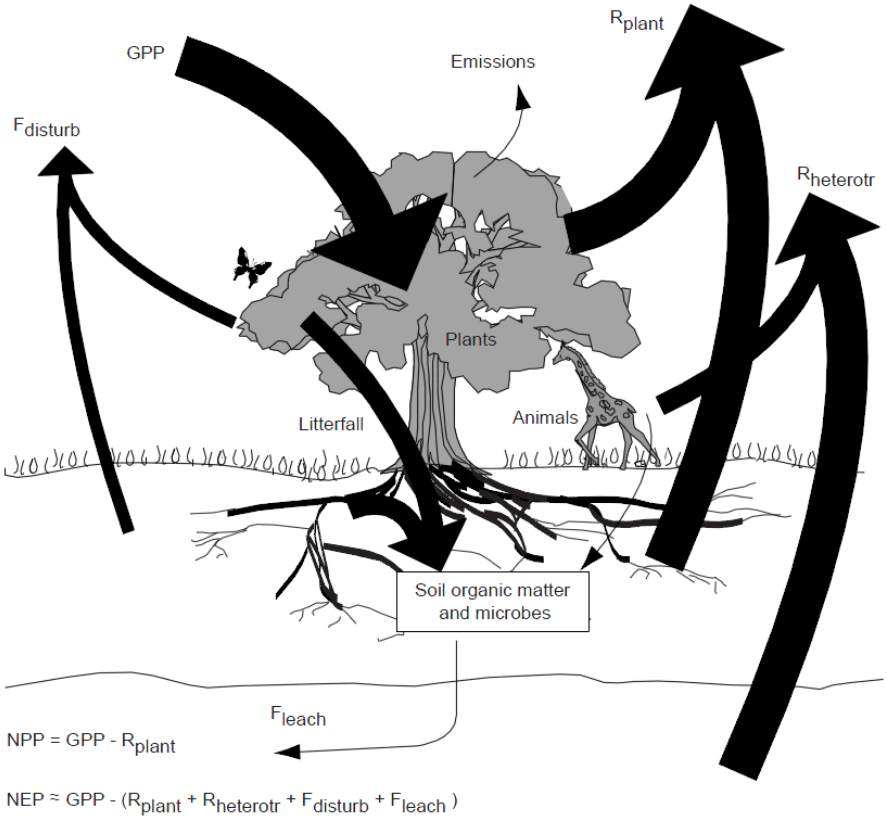


图 6.1-1 生态系统主要碳通量概图。主要通过植物光合作用，碳以总初级生产（GPP）的方式进入生态系统。根和植物地上部分以植物呼吸（R_{plant}）的方式归还大概一半从大气圈俘获的碳。净初级生产（NPP）是来自 GPP 的碳收益和通过植物呼吸（R_{plant}）的碳释放的差。大部分 NPP 通过凋落物，根的死亡，根分

泌和根向共生体的转移物转变成土壤有机质；一部分 NPP 被动物取食，有时也因为受到干扰（火烧或者收获）而从生态系统丢失。动物也可以通过分泌和死亡转移一部分碳，形成土壤有机质。大部分进入土壤的碳随即通过微生物呼吸而释放到大气中，这与动物呼吸一起被定义为异养呼吸（R_{het}）。净生态系统生产（NEP）是 GPP 和植物加异养呼吸之间的平衡。另外一些从土壤丢失的碳主要通过淋溶和扰动。净生态系统碳平衡（NECB）是指一个生态系统的净碳累积，等于来自 GPP 的碳输入减去多个不同途径的碳损失（呼吸，淋溶，干扰等）。

第一节　核心问题

生物圈（biosphere）的生产力主要集中在正经历着快速土地变化的地区。例如，热带雨林（tropical wet forests）占有 12%陆地面积，却占到陆地初级生产的 1/3。然而，这些森林正在被快速砍伐殆尽，大部分是非法的。类似的快速森林砍伐在几个世纪以前的温带地区也曾出现过，但最近正逐渐恢复森林或者正被转变成城市。土地利用变化在低生产力地区也同样重要，那些地区土地寒冷且干旱（如冻原，荒漠，草地和灌丛地），占据着一半的陆地面积，加起来只贡献了热带森林一半的生产力。哪些环境因子控制了这些不断变化的陆地景观的生产力？假如它们被其他植被类型所替代，能仍然保持相同的高产吗？等同于热带雨林的海洋海岸带同样遭受着快速变化，主要由于过度捕捞和陆地养分的径流输入。对于这些控制地球初级生产力的清晰了解是十分必要的，以在快速变化的世界里满足自然和人类生计的需求。

第二节　植物呼吸

呼吸提供了植物获取养分，制造和维持生物量的能量。植物呼吸是线粒体呼吸引起的碳释放，并不是“浪费了”的碳，起到为生长和维持提供能量的功能，就像在动物和微生物中所做的一样。我们可以将总的植物呼吸（R_{plant}）分成三个部分：生长呼吸（R_{growth}），维持呼吸（R_{maint}），以及离子吸收的呼吸消耗（R_{ion}）。

$$R_{plant} = R_{growth} + R_{maint} + R_{ion}$$

每一个呼吸组分都包含了线粒体对碳水化合物的氧化，形成 ATP，所区别的是植物将 ATP 用于什么样的功能中。将植物呼吸分成上述功能组分的优点是可以帮助我们理解植物呼吸的生态系统控制。

在将糖转变成新生物量的效率上，所有植物都是类似的。新的组织的生长离不开许多不同类别化学物质的生物合成，包括纤维素，蛋白质，核酸和脂类。合成上述每一类化合物所消耗的碳包括结合到化合物上的碳和被氧化成 CO_2，用于提供驱动该生物合成的 ATP 的那部分碳。

目前发现的植物中主要类别化合物合成的碳消耗量变化在 3 倍的范围内（图 6.2-1）。植物中能量最贵的化合物是蛋白质、丹宁，木质素（只有陆地维管植物有）和脂类。通常，代谢旺盛的组织，如叶片，具有较高含量的蛋白质，丹宁和之类。丹宁和亲脂类物质如萜类

等用于防御富含蛋白质的组织免于动物取食和寄生生物的侵袭。结构性物质具有高的木质素，较低的蛋白质，丹宁和脂类含量。具有较高蛋白质含量、快速生长物种的叶片丹宁含量通常比低蛋白质含量的叶片高。因此，大多数植物组织含有一定量较贵的组成物质，但这些组成物质的性质在不同植物部分和物种间有较大的差异。事实上，生产植物组织的碳成本在不同物种，组织类型和生态系统间惊人地相似（表 6.2-1）。这些普遍的格局在浮游植物和陆地植物上都能观察到。平均来说，大约 20%用于生长的能量消耗在生长呼吸上，其余的 80%被结合到新的生物量中。当温度和水分有利于植物的生长时，生态系统尺度上生长速率和生长呼吸速率都将增加，但生长呼吸占 NPP 相对恒定的比例，不管在什么样的环境条件下。

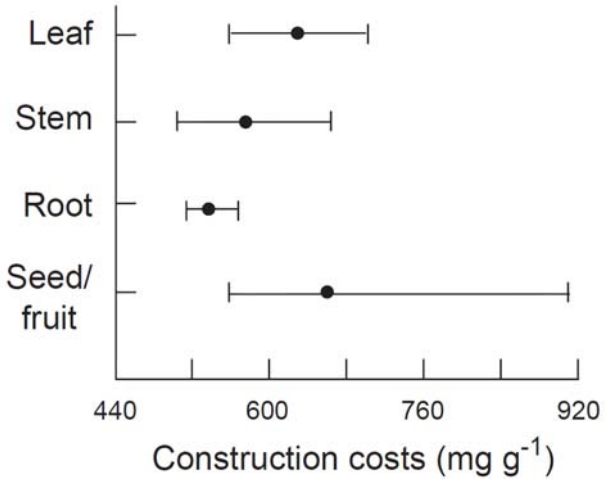


图 6.2-1 叶片（n=123）、茎（n=39）、根（n=35）和果实或者种子（n=31）生产消耗的碳量的范围。生产新的生物量引起的碳的消耗在不同植物部分间差别很小，除了果实和种子，主要用来储存脂类，从而比其他植物部分具有较高的合成消耗成本。

表 6.2-1 一种莎草科植物叶片中主要化合物组成的含量和合成的碳成本

Component	Concentration (%)	Cost (mg C g^{-1} product)	Total cost (mg C g^{-1} tissue)[b]
Sugar	11.9	438	52
Nucleic acid	1.2	409	5
Polysaccharide	9.0	467	42
Cellulose	21.6	467	101
Hemicellulose	31.0	467	145
Amino acid	0.9	468	4
Protein	9.7	649	63
Tannin	4.8	767	37
Lignin	4.2	928	39
Lipid	5.7	1212	69
Total cost			557

总的离子吸收的呼吸成本可能也与 NPP 相关。跨膜的离子运输在能量成本上是十分昂贵的，可能占到根或者浮游植物细胞呼吸的 25-50%。以下因素可以导致不同生态系统间离子吸收成本差异的主要原因。养分吸收量在高产环境下最大，虽然单位吸收养分的呼吸成本在低产环境下更高。氮吸收与利用的呼吸成本取决于吸收氮的形态，原因是硝态氮必须被还原成铵态氮（一个及其耗能的过程），然后才能组装到蛋白质或者其他有机物质上。硝态氮还原的成本也会在不同陆地植物种类和生态系统不同，取决于硝态氮是在叶片还是在根中被还原。通常，我们认为 R_{ion} 与总的离子吸收量相关，因此与 NPP 显示出正的相关性。

维持呼吸：那么维持植物生物量的成本是怎么变化的呢？所有活细胞，即使是那些不在活跃生长的细胞，需要能量来维持细胞膜内外的离子梯度，更换损毁的蛋白质、细胞膜和其他细胞组分。维持呼吸为这些维修和修复功能提供 ATP。来自实验室的实验结果表明大约 85%的维持呼吸是与蛋白质周转（大约每天替换 2-5%）有关。这就解释了为什么在蛋白质含量和非生长组织的整体组织呼吸速率之间存在强的相关性。于是，我们认为维持呼吸在具有高的组织氮含量或者大的植物生物量的生态系统最大，也意味着在高产的生态系统最大。模拟模型的结果表明维持呼吸大约占到总的植物呼吸的一半，另一半则与生长和离子吸收有关。

维持呼吸依赖于环境，同时也与组织化学特征的有关。维持呼吸随着温度升高增加，原因是蛋白质和细胞膜脂类物质降解（degrade），在高温条件下需要更加快速替换。干旱也会导致短期的与渗透性的活性有机溶质合成的代谢成本增加有关。上述环境逆境对维持呼吸的影响是主要因素，它们改变了生长与维持呼吸间的分配，从而是造成 GPP 与 NPP 转化效率产生变异的主要因素。维持呼吸在环境变化的阶段增加，但一旦适应后，维持呼吸又回到可以从生物化学组分预测的水平。因而从长期来看，只要不是在强烈波动的环境中，维持呼吸可能并不太受环境胁迫的影响。

在对不同生态系统进行比较后发现，植物呼吸通常占 GPP 相对恒定的比例。虽然任何给定植物的呼吸速率随环境温度指数式增加，适应（acclimation）和响应（adaptation）抵消温度对呼吸的直接影响。来自高温环境的植物在某温度条件下比来自低温环境下的植物具有较低的呼吸速率。上述相反的温度效应相互抵消后，使得来自不同热量环境的植物具有相似的呼吸速率，尤其是当在它们平均生境温度条件下测定时。

综上所述，与生长、离子吸收和维持等基本呼吸组分相关的研究结果表明，总的植物呼吸应该是占 GPP 相对恒定的比例。例如，综合细胞重量有 5 个数量级差异的浮游植物，呼吸产生的热量是与生物量（碳含量）成比例的。该预测也与一些植物碳平衡的机理模型的模拟结果一致，显示在一个较大范围的生态系统间进行比较时，植物总呼吸大约占 GPP 的一半（48-60%）。换句话说，植物的生长效率大约在 40-50%，即该比例的 GPP 可以转化成 NPP（图 6.2-2）。最可能导致该转化效率变化的因素就是维持呼吸。尽管在从环境获取碳和氮时采用很不相同的机制，微生物在从其基质形成生物量时具有相似的生长效率（大约 40%）。这一表面上的相似性可能反映了在合成和维持生物化学成本上存在一个共同的内在机制。然

而，在不同季节，年份，生物体，以及不同生态系统中，该转化效率是如何变化的，这方面的研究还太少。

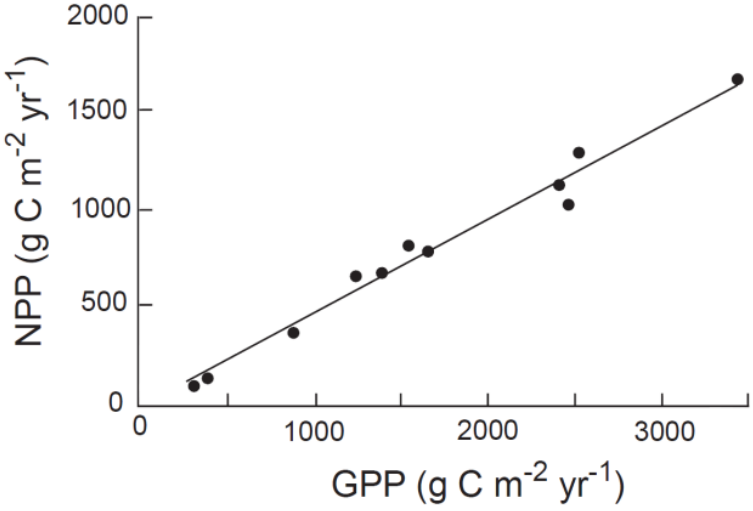


图 6.2-2 植物的生长效率大约在 40-50%之间

第三节 什么是 NPP？

净初级生产（NPP）是植物的净碳收益。它是来自 GPP 的碳收益与来自植物线粒体呼吸的碳释放之间的平衡。

$$NPP = GPP - R_{plant}$$

就像 GPP，NPP 通常在生态系统水平上测定，且总是需要一个较长的时间间隔，例如年（g 生物量或者 g C m^{-2} $year^{-1}$）。NPP 包含了植物制造的新的生物量，通过扩散或者分泌进入环境的可溶性有机物质（根或者浮游植物分泌），传输到与根共生的微生物（如菌根和固氮细菌）的碳，从叶片到大气的挥发性释放。大多数野外测定只是记录了生产的新的植物生物量，从而可能低估 NPP 至少达 30%。根系分泌物很快被根际微生物吸收，并通过呼吸释放，在野外测定时通常被当作根呼吸的一部分来测定。同样，深海浮游植物和细菌经常附着在有机颗粒表面，这样细菌可以吸收并呼吸消耗浮游植物的分泌物。挥发性释放也很难被测定，但通常只占 NPP 很小一部分（<1-5%），因而可能不是一个主要的误差来源。一些生物量在测定前就已经死亡或者被草食动物取食，因此即使野外研究中新的生物量的测定也可能低估实际的生物量生产。出于某些目的，这些误差可能并不是太重要。例如，通常测定陆地 NPP 的目的是估计生物量的增加速率。因此，根的分泌，向共生体（symbionts）的传输，草食动物的取食和气体挥发直接从植物丢失，并不直接对生物量增加产生贡献。于是，没有测定这些 NPP 组分不会对生物量累积的估计产生偏差。然而，这些从植物损失的 NPP 驱动了其他生态系统过程，例如草食动物取食，分解和养分周转，从而对整个生态系统碳动态来说是一个重要的组成部分，也是微生物的关键碳源。

一些 NPP 组分的测定特别困难，例如根的生产，有时被假定为地上生产某个恒定的比例（例如 1:1）。只有不到 10%的研究在报道陆地 NPP 时真实测定了地下生产。地上 NPP 的估计有时仅包含了大型植物（如森林中的乔木），而忽略林下灌木或者苔藓，但这一部分在一些生态系统中可能占 NPP 极其可观的比例。大多数综述 NPP 的出表物并没有很清楚地陈述哪些 NPP 组分包含在内（有时甚至没有讲清单位是 g C 还是 g 生物量）。由于这些原因，当比较这些研究中的 NPP 或者生物量数据要极其小心。总之，我们对陆地 NPP 真实范围的了解要比相关内容研究所揭示的小很多。

3.1 海洋 NPP

海洋大的面积被单位面积上低的平均生物量所抵消，因此海洋和陆地对全球 NPP 各贡献了大约 50%。虽然海洋覆盖了地球表面大约 70%的面积，单位面积平均 NPP 仅为陆地上的 20%。然而，与陆地上一样，水体中的生产力也是高度变化的。诸如珊瑚礁，海草林，以及富营养的湖泊等最高产的水体生态系统，至少与最高产的陆地生态系统相比美（图 6.3-1）。然而在广大的开放海域，这部分占大约 90%的海洋面积，其生产力与陆地上的沙漠和冻原类似。由于其面积之大，开放海域占到海洋生产的 60%，其中超微型浮游生物占到这部分生产的 90%。

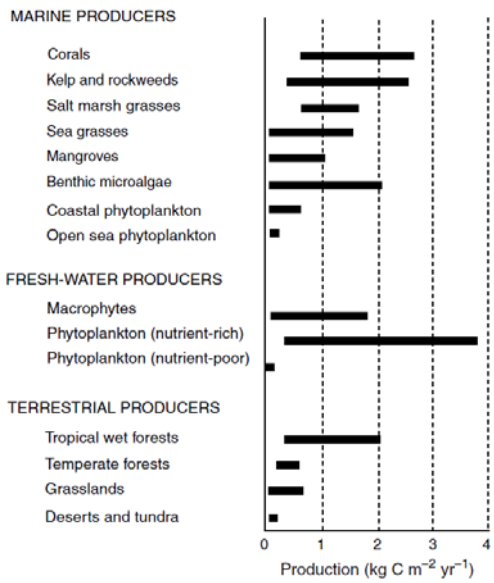


图 6.3-1 海洋、淡水和陆地生态系统 NPP 的比较。海洋和淡水生态系统表现出与陆地相似的 NPP 变化范围，但低产的海洋生态系统更加普遍。

海洋浮游生物体积小，缺少非光合作用的支撑结构，意味着海洋的初级生产者需要相对少量的生物量来支撑一定量的光合能力。例如，虽然陆地上单位面积的平均 NPP 仅是海洋中的 5 倍，陆地上单位面积的平均初级生产者生物量要比海洋中的大 660 倍（表 6.3-1）。海洋和湖泊中的浮游植物生物量每年周转 20-40 次，甚至在有利于生长的条件下可以每天周转 1 次，而陆地植物生物量通常要几年或者十几年。

表 6.3-1 海洋与陆地的特征

Fig 6.3-1 Characteristics of the ocean and continents

Unit	The ocean	Continents
Surface area (% of Earth)	71	29
Volume of life zone (%)	99.5	0.5
Living biomass (10^{12} kg C)	2	560
Living biomass (10^3 kg km^{-2})	5.6	3,700
Dead organic matter (10^6 kg km^{-2})	5.5	10
Net primary production (10^3 kg C km^{-2} $year^{-1}$)	69	330
Residence time of C in living biomass (year)	0.08	11.2
Data from Cohen (1994)		

海洋生态系统生产力最终要受来自陆地或者深海水域的养分供给速率限制。由于这个原因，海岸海域的生产力要远大于深海海洋的。沉积物中的养分通过潮汐作用进入海洋中的水柱体，并通过水柱体中的氧化作用贡献了海湾、潮间带和近海海洋生态系统的高生产力。海湾、潮间带和近海海洋生态系统也构成了海岸带区生物群区。珊瑚礁位列地球上最高产的生态系统。频繁的潮涌为生活在死亡珊瑚上的藻类生长提供了养分。由于鱼类的不停取食，这些藻类具有高的周转速率。生态系统中藻类的生物量就像远海生态系统中浮游植物的生物量都很小。人类活动海岸区大量增加的养分输入，尤其是在海湾区，河流将来自农业的地表径流、污水和侵蚀物输送到此。这样的富营养化打断了藻类、捕食者和分解者之间的正常平衡。

在深海生态系统，大陆西海岸附近的上涌提供了最高速率的养分供给。上涌支撑了秘鲁、非洲西北部、印度东部，非洲东南部以及美国西部等地球上的主要渔场生产。在这些地区，科里奥利作用导致离岸的风和表面水流。这些表面水分被来自深处的富含盐分的水分所替代。上涌也会在深海出现，那里是大的主要洋流分叉的地方。例如，上涌会出现在赤道太平洋，洋流在那里分成南北两叉，还有在南部海洋、北大西洋和北太平洋。这些地方都具有相对较高的养分供给和生产力。

水分密度的垂直梯度影响了养分从底层水域向表面水域的养分传输。在中亚热带海洋盆地的贸易风生物群区，高的太阳光输入建立了一个强的垂直温度梯度，该梯度具有极其稳定的变温层，那里低密度的温暖的水被置于高密度冷水的上面。垂直方向上的稳定性进一步收到盐跃层的支持，较高密度的含盐水分位于较低盐含量的表面水之下。水分这种稳定的成层性减少了垂直方向上由于波浪和海洋流的混合作用，使得亚热带海洋的养分可获得性和生产力极低。

随着纬度增加，海洋表面温度下降。这会减弱垂直方向上的密度梯度，风暴引起的波浪和潮流对深层富含养分水分向表层的混合作用更为强烈。与极向气流相关联的强西向风和暴雨轨迹，也影响了温带/高纬度的西风带生物群区的混合产生影响。于是，温带和极地海洋水

域养分更为丰富，生产力也比热带深海水域的的要高。养分的向上混合在冬季最盛，此时水域最冷，垂直方向上的成层性最不稳定。冬季也是自赤道向极地加热最强烈，并产生强风的季节。冬季期间，湍流混合作用驱动浮游生物在水柱体空间内向深层混合，那里通常没有足够的光照支撑生长。然而，春季太阳辐射的增加加热了表层水分，减少了混合层的深度。这会使得浮游生物在透光层区域累积，导致形成春季浮游生物水华。水华因为生长耗竭养分而结束，大部分浮游生物被浮游动物取食者所消耗。第二次水华有时出现在秋季，此时由于表面成层作用的降低增加了养分向表面水域的混合作用。

在极地生物群区，表面水域由于来自河流和溶解海洋冰的淡水输入具有较低盐度，导致水柱体空间中强烈的成层作用。随着冰雪覆盖海洋的融化，光照可获得性增加，风驱动的混合作用加强了上涌，导致夏季水华的产生。

高纬度大洋盆地高的生产力支撑了丰富的鱼群，虽然其中大部分因为过度捕捞而枯竭。海洋生产力的纬向变化也解释了几个有意思的生态学格局，例如大量鲸鱼和海鸟在南极洲和北冰洋之间的年度迁移就是充分利用了西风带生物群区极地的夏季生产力爆发和春季生产力爆发。此外，高纬度的大部分鱼群种类具有溯河性产卵（anadromous）的生活史，期间它们利用高产的海洋环境支撑成年阶段的生长，同时利用捕食者相对少的淡水环境进行繁殖。这种溯河性产卵的生活史策略随纬度增加而更受偏爱，这是因为海洋生产力随着纬度增加而增加，而陆地生产力则是随着纬度增加而下降。

总之，在海岸带 NPP 最高，养分最不缺乏。在深海海洋，养分在具有最大表面加热的区域（在热带和夏季）最为缺乏，主要是因为加热降低了表面水分的密度，从而抑制了来自海洋深处密度大，养分丰富的水分向上混合作用。凡是有利于深层混合作用的条件（强风，低温高密度的表层水分，潮汐混合作用等）可以将养分限制程度降低至使其他环境因子成为限制因素的程度。我们将在第九章讨论不同养分元素之间的相互作用对 NPP 的影响。

3.2 湖泊 NPP

未受污染影响的湖泊 NPP，就像在深海中一样，通常是受养分限制的。对湖泊浮游生物生产力的控制与在海洋中的十分相似，来自陆地的养分输入和混合作用强烈影响了生产力，正如前述海洋中的 NPP 和湖泊中的 GPP（见第五章）。在冬季，太阳辐射在较高纬度地区很低，导致较浅的透光层。此外，弱的成层作用和深层混合作用搬运浮游生物至透光层下，导致极低的生产力。光照输入在具有降雪覆盖的冰层的那些湖泊中进一步降低。在春季，太阳辐射的增加是透光带深度增加，温暖了表层水分，引起一个较浅的混合深度，并使浮游生物集中在透光层。适宜的光照和温度条件使得浮游植物利用冬天后通过混合作用进入表层水分中的养分，引起一个春季浮游植物水华。就像在海洋中一样，当浮游植物耗尽表面水分中的养分，取食者消耗浮游植物生物量后，水华就会消散。同样，与在海洋中一样，低养分条件（贫营养湖泊和仲夏季节）下小型浮游植物（微型和超微型浮游植物）占据湖泊浮游生物

生产的优势，高营养条件下大型藻类细胞的浮游植物占优势。小型浮游植物更容易被浮游动物取食者所消耗，所以“上行”（养分）效应与“下行”（捕食作用）相互作用于湖泊的 NPP。通常，养分可以解释大部分不同湖泊浮游植物生产力和生物量的变化，温度影响生物量的形成速率。大约有 13%的 GPP 被浮游植物分泌到环境中。这当然并不会对浮游植物生物量累积产生直接的贡献，但对刺激处于附近的微生物分解和养分矿化至关重要（见第七章）。

3.3 溪流和河流 NPP

对溪流和河流 NPP 的控制取决于溪流的大小和环境。通常，控制溪流 NPP 的因素与控制溪流 GPP 的因素一致（见第五章），原因是溪流和河流中光合作用和新的光合作用细胞的产生存在严格的放大（正）型反馈作用。养分、光照和温度促进 GPP 和 NPP，而底物的不稳定性、水流速度、悬浮沉积物，以及动物取食降低植物生物量，从而进一步降低 GPP 和 NPP。正如与 GPP 一样，森林地区源头溪流中的 NPP 只有大型开阔溪流中的大约一半左右。在许多河流系统中，NPP 随着从小型源头溪流到更大，更开阔的溪流和河流而增加，这也与 GPP 一样。大型河流的 NPP 也是多变的，就像所描述的 GPP 一样（见第五章）。

第四节　陆地 NPP

陆地 NPP 环境调节的特点与水体生态系统的显著不同。与浮游账务细胞直接浸泡在水和养分不同，陆地植物必须从土壤介质中获取养分和水分，而土壤中是没有光照驱动光合作用。这就使得光合作用和 NPP 之间的正反馈复杂化，原因是陆地植物新制造的生物量中很多是形成根和其他支撑结构，它们不能直接加强植物的光合能力。此外，陆生植物 NPP 通常对 CO_2 和水分的可获得性产生响应，但它们很少限制水生植物的 NPP。这就增加了控制 NPP 的环境因子数量以及环境因子间潜在的相互作用。最后，水体 NPP 只是所有细胞的简单光合作用碳收益和它们夜间呼吸间的平衡，而在陆地上，非光合组织日夜呼吸。这也使得陆生植物白天碳利用的格局复杂化。

4.1 NPP 的生理控制

光合作用，NPP，呼吸，谁在起主导作用？NPP 是来自 GPP 的碳收益和植物所有部位呼吸的碳损失间的平衡。然而，这一简单的等式关系并没有告诉我们是否控制光合作用的条件对支撑生长的碳量的可获得性起绝对支配作用，或者是否影响生长速率的条件决定光合作用的高低。换句话说，究竟是光合作用“推动”生长，还是生长“拉拽”光合作用。在较短的时间尺度上（秒到几天），环境对光合作用的控制（如光照和水分的可获得性）强烈地影响光合作用碳收益（光合作用“推动”生长）。然而，在较长的月或者年度时间尺度上，植物调节叶面积和光合作用能力，这样碳收益配得上土壤中支持生长的可利用资源（生长“拉拽”光合作用）。当环境条件有利于快速生长时，植物的碳水化合物含量通常最低（即碳水化合物被生长调低），而在干旱和养分缺乏，或者受低温限制时，植物趋于累积碳水化合物。假如光

合作用产物直接控制 NPP，我们会发现高的碳水化合物含量要么与快速生长相吻合，要么显示与生长速率没有一致的关系。

生长实验的结果也显示生长并不是简单地对光合作用碳收益的结果。陆生植物通过制造降低生长速率的激素会对低的水分、养分，或者根际区域氧气可获得性作出响应。生长速率的降低进一步引起光合速率的降低。这些实验得到的一个普遍结论是植物能够主动地探知植物环境中资源的供给，并相应地调节它们的生长速率。植物在生长速率上的变化改变了对碳水化合物和养分的**汇的强度**（sink strength）（需求）（demand），导致光合作用和养分吸收的变化。进一步引起的生长和营养上的变化决定了叶面积指数（leaf area index，LAI）和光合作用能力，这正如我们所看到的，基本上解释了生态系统在碳输入上的差异。

从汇的强度到光合作用的反馈也不是 100%有效。叶片的光合产物含量白天增加，夜间降低，使得植物能保持一个对非光合作用器官相对恒定的碳水化合物供给。同样，碳水化合物含量在晴朗天气阶段（几小时到几星期）增加，而在阴天气候下降低。在这些短的时间尺度上，影响光合作用的条件是支撑生长的碳水化合物可获得性的主要决定因素。环境对光合作用的短时间控制可能决定了 NPP 从几小时到几星期的格局，而土壤资源则决定了不同景观和生物群区植物年度尺度上碳收益和 NPP 以及 NPP 变化格局。

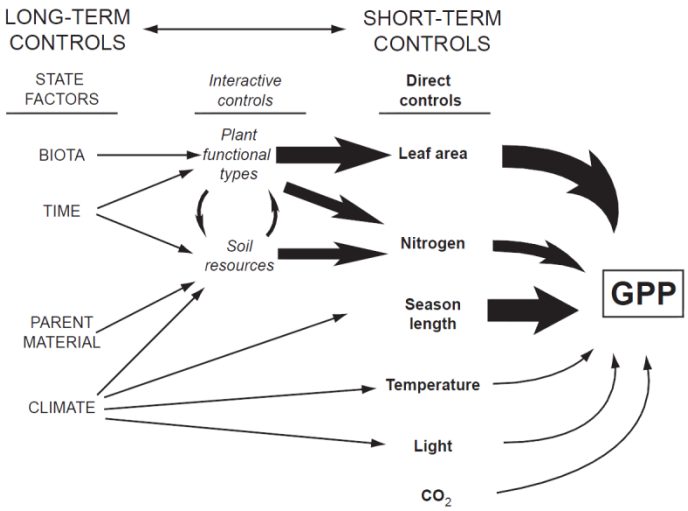


图 6.4-1 影响生态系统总初级生产（GPP）时空变化的主要因素。这些因素涵盖从近似的控制，主要决定了 GPP 的白天和季节变化，到相互控制和状态因子，它们是生态系统 GPP 差异的最终决定因素。箭头的粗细代表了该直接和间接作用的强度。可以解释大部分生态系统 GPP 变异的因子有叶面积和光合作用时间（季节）的长度，它们最终又取决于土壤资源、气候、植被和扰动节律间的相互作用

4.2 环境和物种对 NPP 的控制

气候对 NPP 的控制主要通过地下资源的可利用性实现的。在全球尺度上，生态系统在 NPP 上最大的差异是与气候的变异有关。NPP 在湿润、温暖的环境（热带雨林出现的地方）

中最大，而在干旱（例如荒漠）或者寒冷（例如冻源）的气候下最小。NPP 最强烈地与降水量相关；NPP 在 2-3 m year^{-1} 降水（典型的雨林气候）条件下最高，在极端低或者极端高的降水条件下降低。当不考虑干旱生态系统（如荒漠），NPP 也随着温度增加而呈指数式增加。NPP 最大差异反映了生物群区在气候和植被结构上的差异。当把全球生态系统组合成不同的生物群区时，NPP 平均相差 14 倍左右。那么上述 NPP 与气候（温度和水分）之间的相互关系反映了温度和水分对植物生长的直接作用吗？或者是否也包含了其他的因子？

表 6.4-1 基于生物量收获的主要生物群区类型净初级生产（NPP）

Biome	Aboveground NPP (g m^{-2} yr^{-1})	Belowground NPP (g m^{-2} yr^{-1})	Belowground NPP (% of total)	Total NPP (g m^{-2} yr^{-1})
Tropical forests	1,400	1,100	0.44	2,500
Temperate forests	950	600	0.39	1,550
Boreal forests	230	150	0.39	380
Mediterranean shrublands	500	500	0.50	1,000
Tropical savannas and grasslands	540	540	0.50	1,080
Temperate grasslands	250	500	0.67	750
Deserts	150	100	0.40	250
Arctic tundra	80	100	0.57	180
Crops	530	80	0.13	610

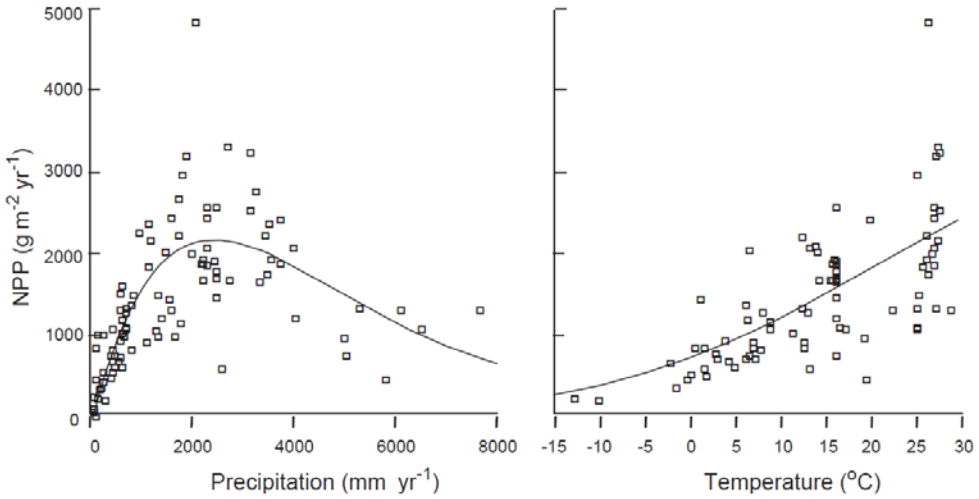


图 6.4-2 地上 NPP（生物量单位）与年平均温度和年总降水量间的关系。NPP 在诸如热带雨林的温暖、湿润的环境中最大，在诸如冻原和荒漠的寒冷和干旱的生态系统最低。在热带森林中，NPP 在极端高的降水环境（>3m year^{-1}）下降低，主要由于过多水分的间接作用，例如低的土壤氧气和淋溶引起的低的养分。

生态系统间的比较显示 NPP 在干旱的样点表现为强烈地受降水量的影响，表明 NPP 在干旱环境下是最受水分限制的。这些干旱环境也显示出 NPP 对降水年际变异和水分增加实验的最大敏感性。对任何一个给定的环境，NPP 在干旱年份对实验性增水有强烈的响应，而在湿润年份表现出对养分添加有强烈的响应。即使在荒漠生境，NPP 在湿润季节和年份也表现出对养分增加的响应。在干旱环境，NPP 更加强烈地对水分而不是养分产生响应，在湿润环境，NPP 对养分添加的响应要比对水分添加的响应更加强烈。综上所述，（1）长期来说，大多数生态系统的 NPP 受多个地下资源（水分和养分，特别湿润环境下还有氧气）的影响。（2）环境限制的特性存在年际变异，表现为干旱年份最受水分限制，湿润年份最受养分限制。（3）NPP 的水分限制最有可能出现在干旱环境，养分限制最有可能出现在湿润限制。这样，干旱环境是水分限制，湿润环境是养分限制，这种简单的归纳是一种合理的直观估计，但它忽略了所有生境经常经历的更加广泛的环境限制。

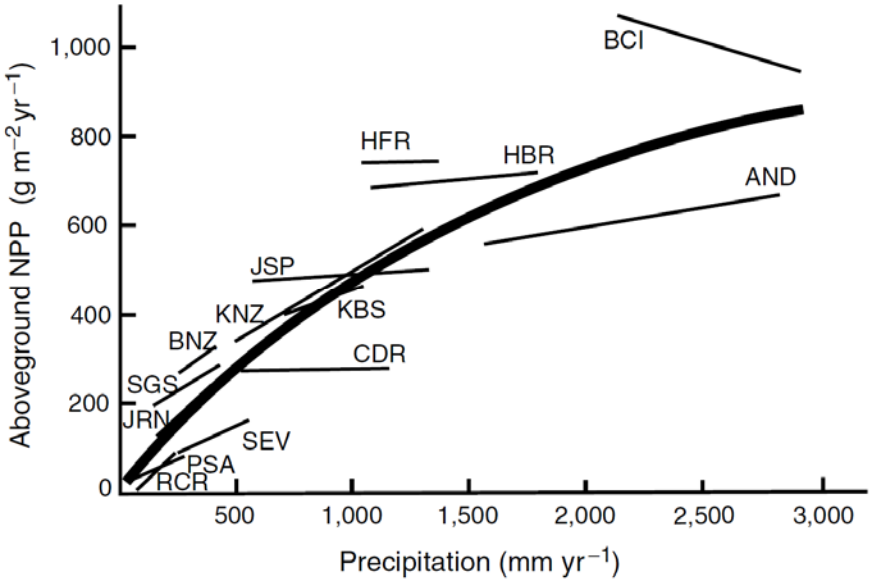


图 6.4-3 14 个生境的地上 NPP 与总的年降水量关系。粗的曲线显示在 14 个点上的平均地上 NPP 与平均降水的相关性。细的直线显示某个点上地上 NPP 年际与年降水量变异的相关性。

占据一个生态系统的植物类型也会影响生产力。任何生态系统都显示 NPP 对年际间环境变化的响应（见图 6.4-3 中的直线）范围要比所有生境点的范围里平均 NPP 的响应（见图 6.4-3 中的曲线）要窄得多。于是，一个荒漠或者草地怎么也不能比一个湿润的森林更加高产，无论它们接受到多高的养分和水分输入，因为该生境中分布的植物缺乏大型树木的生长潜势（productive potential）（生产叶面积的能力）。即使就草地而言，某个点上 NPP 从湿润到干旱年份的变化范围要比包括所有草地样点的要小，原因是占据干旱草地的植物种要比那些湿润草地的物种具有较低的生产潜势，无法充分利用湿润年份的所有水分优势。另一方面，干旱草地中的植物更加适应干旱的气候条件，不会因为严重干旱而死亡。因此，长期环境变化对 NPP 的影响至少表现在以下两个方面：（1）通过水分和养分限制之间平衡的直接影响（2）通过物种组成的变化，使得具有环境忍耐力和生产潜势的物种出现在生态系统中。

对于寒冷的生境又是怎样的，那里的气候相关性意味着 NPP 应该是温度限制的？在冻原上，对养分添加的响应比对实验性温度增加的响应使得 NPP 增加更多。因此，对于冻原，NPP 和气候的相关性可能反映了温度对氮素供给或者对生长季长度的间接影响要比温度对 NPP 的直接作用更大。同样，NPP 在北方森林中与土壤温度紧密相关，但是土壤加温实验的结果却表明温度的作用主要通过增强凋落物分解和氮素供给实现的。

综上所述，在表面上看气候和 NPP 强烈相关的生态系统，实验和相应的监测表明这主要通过气候对地下资源的作用引起的。

在温暖、湿润的气候条件下又是什么限制了 NPP，看起来温度和水分都处于植物生长的最佳条件？热带森林通常比其他森林群区具有较高的 NPP。在热带森林之间，凋落物的生产趋向于与养分供给相关，尤其是 P，表明热带森林也可能受地下资源供给的限制。NPP 在热带干性森林中受水分限制，但在极端湿润（>3m $year^{-1}$）的气候条件下，NPP 随着降水进一步增加而降低，可能是由于氧气对根和土壤微生物的限制以及养分的淋溶损失。所以热带森林的 NPP 可能也受地下资源供给的限制，包括养分，有时还有水分（相对干旱的森林）或者氧气（相对湿润的森林）。

在温带盐沼，那里水分和养分充沛，NPP 直接对 CO_2 增加产生响应，就像受到高养分供给的作物表现的那样。然而，NPP 受养分添加促进，即使在大多数肥沃的农田系统中，表明养分对生产力的限制是广泛存在的。

总之，在各种不同类型生态系统中的实验和观察逐渐得到了一个相对一致的结论。在一段很长的时间里，一个生态系统可能经历一定范围的气候条件的变化，其 NPP 可能受到多个环境因素的限制。然而相比较而言，地下资源的供给是普遍的最重要的限制因素。那些决定地下资源的供给和获取的因素以及植被的生产潜势通常是 NPP 主要的直接控制，从而影响生态系统的碳输入。

地下资源和物种特性在控制 NPP 上的重要性与我们先前得出结论是一致的，即相比受温度和 CO_2 的直接影响，GPP 更多地受叶面积和光合作用季节长度决定。实际上，模拟研究的结果表明在大的环境梯度上，NPP 占 GPP 的比例是惊人的稳定（40-52%）。这与我们关于 GPP 和 NPP 受相同因子控制的结论是一致的。

第五节　分配

5.1 NPP 的分配

生物量分配格局有利于降低资源的限制性，增加资源获取和 NPP。我们对 NPP 控制的讨论呈示了一个有趣的似是而非的问题：高的叶面积对 NPP 的极大化是必要的，但限制 NPP 的主要因素却是地下资源。植物通常要面临一个抉择，即在叶片（增加碳收益）和根（增加

地下资源的获取）之间选择分配生物量。植物展示出相对一致的分配格局（植物不同部分之间生长的分配），从而增加相应生长，以响应地上和地下资源供给速率间的平衡变化。

通常，植物将光合产物分配至相关部分，从而可以降低任何单一的资源限制。当水分和养分限制生长时，植物优先将新的生物量分配至根。当光照限制时，植物优先将新的生物量分配地上部分。植物能够通过增加某种组织的生物量，或者增加单位生物量的活性，或者保持该组织生物量较长的时间来增加某种资源的获取。例如，一个植物可以通过叶面积，或者单位叶面积的光合作用速率，或者叶片凋落前保持叶片更长的时间来增加碳的收益。同样，一个植物也能够通过改变根的形态，或者增加根的生物量，或者根的寿命，或者单位根的氮素获取速率，或者菌根真菌侵染程度等来增加氮的吸收。分配和根形态的改变对养分吸收具有特别重要的影响。正是根的这些综合活动（根的重量乘以单位根生物量的获取速率乘以时间）才能使植物地上部分和根之间达到平衡，从而使植物生长和 NPP 达到极大化。这些分配原则是所有 NPP 模拟模型以及对低水分、低养分和低光照不同分配响应的关键特征。

对不同生态系统的观测结果也展现出与分配理论的普遍一致性。例如，冻原、草地和灌丛地比森林分配更大比例的 NPP 至根。作物，由于其有利的水分和养分供给，分配到地下部分的最少。很多在地下 NPP 分配上的微妙直观差异需要谨慎解释，因为地下 NPP 测定的困难，不同方法和细根周转的假说对结果影响很大。

5.2 对多资源响应的分配

对多数生态系统来说 NPP 最强烈地受到一个单一资源的限制，但也有受该资源之外的其他资源限制。加入植物能非常完美地将生物量成功地分配到植物不同部位，以加强最限制资源的获取，那么植物就受所有资源同等程度的限制。正如我们所看到的，这样的情形很少出现。多数生态系统中 NPP 对某种特殊资源响应最强烈，例如荒漠中对水分，冻原和许多北方和温带森林中对氮素，以及热带湿润和干性森林中对磷素。因此，直观来说，荒漠是水分限制生态系统，温带森林是氮限制生态系统。然而，在许多生态系统中，NPP 对多于一种资源供给的增加作出响应。为什么会出现这样的情形？

环境限制性最简单的观点认为任何时间的任何时刻植物受单一资源供给的限制。只有在这种限制因子增加到超过了它的限制水平时，另外的一种资源才可能成为限制因子（李比锡最小因子定律）。至少有 5 个过程引起许多生态系统观察到的多资源限制性：（1）植物通过调节生物量分配增加了最受限制资源的获取（降低了该资源的限制性）。（2）环境的变化（例如暴雨或湿润年份，某种养分供给脉冲式增加）改变了资源供给的相对丰度，意味着不同时间限制 NPP 的因子不同。（3）植物具有增加获取某种最受限制资源供给的机制。（4）生物体（植物）储存了某种资源（例如养分），供其短缺时使用。（5）一个生态系统中不同物种木有不同的限制性资源，这样生态系统水平 NPP 可以对多个限制性资源的增加作出响应。上述每一个过程都对生态系统的多资源响应作出贡献。

植物调节资源获取以增加最受限制的资源吸收（从而降低该资源的限制性）。正如我们先前讨论的，植物调节新生产物质的分配到根或者地上部位，以分别减小地下或者是地上资源的限制性。植物也会改变根系统内部的分配，以增加最受限制性地下资源的获取。例如，荒漠中养分的可获得性在接近土壤表面处最大，但是水分通常较深的地方具有较为稳定的供给。一个新根的养分或者水分的获取量就取决于根形成的深度。为了获取水分，一些荒漠植物形成粗根，这样可以扎得更深，有效地传输水分，但具有低的养分获取的速率。其他植物仅形成浅层分布根，只有在土壤表面有水分供给时才活跃。

根的生物化学方面的投资对每一种营养元素来说都是特别的。例如，氮素吸收需要合成专门的吸收氮、还原硝态氮以及同化还原的氮合成氨基酸的酶，而吸收 P 时也需要各种不同的酶。这种为吸收特别养分的生物化学分配进一步微调了植物吸收某些强烈限制生长的特别养分的能力。

环境变化（例如暴雨，养分供给的脉冲式增加）改变了资源的相对丰度，因此不同时间植物限制性资源可能不同。许多生态系统经历了那些最限制 NPP 的养分限制性的时间变化，原因是那些必需资源不可能同时达到相同的可利用程度。例如，下雨时刻光照降低，而水分增加。许多生态系统在生长季开始时会经历养分供给的脉冲式增加，此时温度还没有达到植物生长的最适时刻。由于所有主要决定 NPP 的因子会在多个时间尺度上产生剧烈的变化，如果这些限制 NPP 的因子的相对重要性没有产生相应变化，那将是十分令人吃惊的。

NPP 限制性的时间变化可能受植物储存的缓冲影响。植物会在碳水化合物或者养分的可获得性高时会积累这些物质，而在供给降低时又用这些储存支持植物的生长。在季节性的尺度上，植物利用储存的碳水化合物和养分支撑植物春季的萌动生长（burst of spring growth），在其他光合作用和养分吸收超过其生长需求的时间又补充这些储存。与树木不同，大多数植物储存水分的能力很低，与它们每天对水分的需求相比，这样对水分变化要比对光照和养分变化的缓冲小。然而，一些荒漠肉质植物具有很强的水分储存能力。因此，当它们容易获得的时候，植物储存资源，当供给减少时候植物再利用这些资源，这样可以降低那些限制性资源时间上的变化。

对于养分来说，植物能增加大多数最受限制资源的供给。具有与固氮微生物形成共生性联合体的植物直接促进生态系统氮的输入。一些其他植物种类的心型和外生菌根联合体可以裂解蛋白质，并向植物传输裂解产生的氨基酸。一些植物通过形成有机螯合物溶解矿质磷或者通过形成磷酸酶分解土壤中的有机磷等增加磷的供给。植物也可以分泌碳水化合物促进根周围的矿化作用。类似地，植物利用微小的叶片截留雾水，从而增加一些云雾生态系统的水分输入。

当一些资源处于短缺时，生物体还可以保持一大部分这些养分（例如养分）。植物、动物和微生物偏爱性地固持和再循环某些生长限制养分，使得这些养分被束缚在生态系统中。正如当氮沉降使植被氮需求饱和时，那些处于有机体生物需要过量的养分很大可能被淋溶或者以痕量气体释放到大气圈中。

不同物种生长受不同的资源限制，因此生态系统尺度的 NPP 对不止一种资源的增加产生响应。一个生态系统内的许多物种具有稍微不同的环境需求，这样就可能受不同的资源组合的限制。例如在同一个冻原生态系统中，不同物种对温度、光照和养分的响应不同，有时对 N 和 P 的添加也不同。一些荒漠物种对夏季降水产生响应，而其他物种则对冬季降水产生响应。这些植物种类之间在限制或促进生长因子上的差异有利于不同物种在变化环境中共存。这在解释为什么不同物种生产力在对年际间气候变化的响应不同尤其重要，也对解释为什么生态系统生产力在年际间的变异总是要小于任何组成物种生产力的变异。限制性资源供给的空间异质性也是植物资源响应空间变异的潜在原因。

5.3 分配的日和季节循环

光合作用和生长对环境的日和季节变化是具有高度可塑性的。环境的日和季节变化是生态系统经历的两个最可预测的扰动。许多生物体基于内在的生理（24 小时）节律调节生理和行为，导致日（24 小时）循环。例如，气孔导度和碳收益即使在稳定的环境条件下都表现出一定的生理节律，原因是气孔具有 24 小时开和关的循环。植物白天将淀粉储存在叶片中，晚上将它分解，这样光合产物运送到根的速率在一个日进程中差不多是恒定的。因此，诸如根分泌和向菌根运送的碳等地下过程通过光合作用碳收益的日变化得到补充。

第六节　组织周转

NPP 和生物量损失的平衡决定了每年植物生物量的增加。每年植物只能保存一部分它们生产的生物量。植物调节了一部分这些生物量的损失，例如秋季叶片的凋萎。凋萎在整个生长季都可能出现，但在许多生态系统中作为秋季脉冲（pulses during autumn）或者旱季开始时出现。其他损失（例如动物和寄生生物取食，风倒和火烧）主要取决于环境，虽然这些组织的丢失受诸如分泌的抗菌化合物或者树皮抗火性等植物特性的影响。还有其他向土壤的生物量转移是由整株植物个体的死亡引起的。既然组织损失主要受生理控制，虽然还不完整，为什么植物会舍弃那些它们投资了许多碳、水和养分生产的生物量呢？

组织损失是植物平衡资源需求和环境的资源供给的一个重要机制。植物依赖于大量碳和水的输入，以及较小程度地依赖于养分的输入来位置重要的生命过程。例如，一旦生物量形成，植物需要持续的碳输入来支撑维持呼吸。加入植物（或者器官）不能满足这些碳的需求，植物（或者器官）就会死亡。同样，假如植物不能吸收足够的水分来置换光合作用过程中不可避免地损失的那部分水分，植物必须脱落蒸腾器官（叶片）或者死亡。所以不管什么时候资源水平下降到低于维持植物正常生长的临界值时，植物必须脱落一部分生物量。因此，凋萎在植物调节资源供给变化时与生产同样重要，也是当资源供给下降时植物减少生物量和维持成本的唯一机制。

凋萎是组织一种程序化的解体方式。凋萎的位点受生理学控制，以确定去除哪些植物最没有用的组织。例如，动物对对地上组织的取食导致根的生产的降低，于是正常的根凋萎速

率降低了根的生物量。同样，动物对地下组织的取食降低叶片寿命，进一步导致叶片生物量的降低。虽然对植物地下组织的凋萎和死亡还不完全了解，上述生产和凋萎的变化格局表现出维持了植物叶片和根系之间功能性平衡，以外界的响应环境变化。

生长和凋萎仪器使得个体植物能够扩展它们的新领地。叶片和茎杆生长通常出现在林冠顶部或者林窗，那里能够获得最高的光照。这可以平衡在不利的光环境下叶片和茎的凋萎。这个生物量生产和丢失间的平衡使得树木和灌木向光照的方向生长。同样，根也会向养分丰富或者与其他植物根的竞争最小的空间扩展，根的死亡在水分和养分枯竭的局部地方死亡可能性最高。

凋萎导致的组织丢失通常出现在维持成本大大超过资源收益的时候。在季节性变化的环境中，通常会存在较长时间可以预见的温度或者水分的不利条件。在这些生态系统中，制造能够忍受这一不利严酷时间的组织的成本以及维持对植物贡献几乎忽略的组织的成本有可能超过当环境条件有利时制造新的组织的成本。例如，极地、北方地区和温带地区生态系统可以预计将经历对植物太冷而无法获取资源和正常生长的季节。通常光周期和低温共同触发秋季叶片和根凋萎高峰（Pulses of autumn senescence）的发生。当干旱来临时，干旱生态系统同样会经历叶片和根凋萎的高峰到来。所以，凋萎和组织丢失在大多数生态系统中是高度阵发性（highly pulsed）的，且就发生在植物资源获取和生长最不利条件发生的前夕。这些季节性凋萎高峰解释了高度季节性的环境里大多数植物组织脱落的原因。

叶片寿命随不同植物种类变异很大，通常从几个星期到几年或几十年。通常，高资源供给环境中的植物形成短命、高比叶面积以及高单位面积光合速率的叶片，但它们对不利环境的抗性很小。当环境条件变得不利时（冬季或旱季），这些“可以舍弃的叶片”通常脱落，并在下一个春天被替换。来自低资源供给环境的长寿命叶片通过植物保持一定的叶面积降低对养分的需求。对根的凋萎和周转的控制，我们的了解要比对叶片的要少得多。当根受到动物或者寄生生物取食，或者遭遇不利的环境条件时看上去要死亡，通常没有凋萎和资源物质向其他植物部位再分配的程序化格局。

凋萎使植物卸掉了寄生生物、病原菌和食草动物及其影响。由于叶片和细根代表了相对大宗的养分和有机物质，它们通常不断地处于寄生生物、病原菌和食草动物的袭扰中。例如，叶际真菌（phyllosphere fungi）在发芽后不久就开始在叶片上定居生长，开始作为寄生生物，后来当叶片脱落后又成为分解者群落的一份子。这些真菌解释了许多老叶片斑驳陆离的样子。根的致病真菌是农田生态系统产量降低的主要原因，在自然生态系统中十分普遍。植物具有一系列机制察觉到天敌，并初步通过诱导化学防御的形成作出响应，在严重的情形下脱落掉受影响的组织。

许多生态系统还可能经历大的不可预见的生物量丢失。风暴，火烧，食草动物的爆发，以及流行性致病菌经常引起巨大的组织丢失，而这些丢失通常是不可预见的，并在任何程序性组织凋萎和相应的养分回收之前发生。由于凋萎过程中养分的回收，这些不可预见的生物量损失招致植物大约两倍于凋萎后发生的单位重量的养分损失。凋萎通常通过凋落物输入形

成的大量斑块，并产生在大小上从个别叶片到整个立地尺度的林窗，从而增加生态系统中光照和养分资源的空间异质性。出现在多个时间尺度上的生物量损失后，所有生态系统均处于再生长的某个阶段。

本章小结

植物呼吸为植物资源获取和制造和维持生物量提供能量。所有植物在将糖转换生物量时具有相似的转化效率。所以，生态系统在植物呼吸上的差异基本上反映了制造的生物量的量及其氮的含量上的差异，其次是不利环境，尤其是温度和水分对维持呼吸影响上的差异。大多数生态系统表现出具有相似的将光合产物（GPP）转变成 NPP 的效率，即 GPP 碳收益有一半变成 NPP，另外一半由植物呼吸释放回大气中。

NPP 是植物碳的净收益，包括新形成的植物生物量，分泌，向共生体的碳转移，以及植物挥发性有机物质的释放。海洋和湖泊生态系统间 NPP 的差异主要取决于来自水体深层的影响养分再供给的物理作用大小。NPP 在这些生态系统中具有季节性的变化，以响应光照、温度以及混合作用（mixing）的变化。光照、养分、洋流和扰动的相互作用决定了流动水域的 NPP。陆地生物群区间 NPP 的差异与地球尺度的气候相关，基本上由于温度和水分决定了支撑植物生长的土壤资源的可获得性。植物可以主动感知到这些资源的可获得性，冰调节叶片寿命，叶片面积和光合作用以匹配相应的资源供给。由于这个原因，NPP 在高地下资源可获得性的环境中最大。受干扰后，植物经常减小叶面积和 NPP 至低于环境能够潜在支撑的水平。植物通过分配新的光合产物至能获取最多限制性资源的组织使生产最大化。不断地改变分配格局可以使 NPP 受任何一种单一资源的限制性减小，使得 NPP 在大多数生态系统中可以对不止一种资源产生响应。组织的丢失对于解释植物生物量的变化与 NPP 同样重要。组织的程序化的丢失提供了植物养分供给，从而可以支持新的生物量生产。生物量和 NPP 在温暖、湿润的环境中最大，在寒冷或者干旱的生态系统中最小。光合作用季节的长度和叶面积是全球 NPP 格局的最重要的决定因素。大多数生态系统具有相似的单位叶面积的日 NPP（1-3 g 生物量 m^{-2} 叶片 day^{-1}）。

第七章 分解和生态系统的碳概算

分解是降解死亡的有机物质，最终释放碳至大气圈，同时释放养分，供植物和微生物生产利用。

引言

分解是对有机碎屑（例如死亡的植物，动物和微生物材料）的物理和化学裂解。随着有机材料的碎片化，转变成其他有机化合物，以及最后转变成无机态的营养物质和 CO_2，分解导致碎屑量的减少。如果没有分解，生态系统很快被大量有机碎屑积累，导致养分的封存无法再为植物利用，并引起大气中 CO_2 的枯竭。最终，许多生物学过程慢慢停止。虽然这从来也没有发生，也曾出现诸如石炭纪（Carboniferous period），当时分解没有跟上初级生产的步伐，导致含有碳和氮的煤和石油的大量累积。所以，初级生产和分解之间的平衡强烈地影响着生态系统和全球尺度的碳和养分的循环。

假如与人为 CO_2 排放有关的气候暖化将引起即使是很小的 NPP 和分解之间平衡的变化，都将极大地改变大气圈中的 CO_2 浓度，以及进一步的气候暖化速率。由于生物圈和地球系统中碳平衡的许多关键的作用，植物和生态系统碳循环的实质性变化已经成为一个基本的具有社会重要性的议题。

第一节　核心问题

对生物圈碳固定不适当管理加剧了人类对全球变化的影响。当人类将陆地开垦成农业用地时，自然生态系统的碳固定能力通常会逐渐退化。将热带雨林砍伐种植油料作物或者将北美草原开垦成玉米种植地后，降低这些系统的固碳能力，并且由于这些作物经营的高能量投入消耗的化石燃料往往足以抵消所生产的生物燃料。当自然植被被清除后，土壤碳将会发生怎样的变化？参与分解的生物活性主要是受环境制约，还是受植被，或者群落的组成所制约？假如温暖和湿润条件有利于植物和参与分解微生物的活性，气候变化怎样影响生态系统的净碳平衡？假如不同生态系统在碳储存和释放的能力上有差异，在什么地区人类引起的土地利用变化和气候变化会可以对生物圈的碳平衡产生最大的影响？清晰了解生物圈在生态系统乃至整个地球碳平衡上的作用对于有效阐释不断加快的气候变化速率是十分有效的。

第二节　分解和生态系统碳平衡概要

分解引起的死亡有机物质的淋溶、片段化和化学改变最终将有机碎屑转变成 CO_2 和矿质营养以及一个包含无法进一步被微生物分解的复杂有机化合物的剩余物质库。大多数有机物质的分解出现在凋落物层以及土壤的有机质和矿物质层。分解是物理和化学过程交互作用的结果，可以出现在活的土壤微生物和动物的体内和体外。分解包含了三类过程，每一个

过程特别的控制和结果。（1）水分淋溶将可溶性物质运出分解的有机物质，进入环境。这些可溶性物质或者被生物体吸收，或者土壤和沉积物的矿物质反应，或者以溶液形式从系统丢失。（2）土壤动物的碎裂将较大的有机物质片段分解成较小的有机物质片段，主要通过取食的方式，并在取食过程中产生新鲜的表面供微生物定植。土壤动物还将分解有机物质与土壤混合，并以粪便的形式将有机物质返回到土壤或者沉积物中。与取食前的有机物质相比，动物的粪便具有更高的表面积-体积比，可以提供微生物（即细菌和真菌）更加有利的分解环境。（3）虽然一些化学反应也同时出现在没有微生物介入的土壤中，死亡有机物质的化学改变主要由土壤微生物的活动引起。

死亡的植物材料（叶片，茎和根的凋落物）和动物残体逐渐被分解，直到它们原有的特征无法再被辨认，此时可以被认为是土壤有机质（soil organic matter）（SOM）。凋落物中大多数化合物都太大，不溶于水，因而难于通过微生物细胞膜。于是，微生物向环境分泌胞外酶（细胞外酶）来启动凋落物的分解。这些胞外酶将大分子物质转变成可溶的微生物可以吸收和代谢的产物。微生物也会分泌一些代谢副产品，例如 CO_2 和无机氮，并形成多聚糖类物质，可以吸附在土壤颗粒上。当微生物死亡时，微生物本身可以作物有机底物参与分解。

分解基本上是土壤动物（碎裂）和异养微生物（化学改变）取食活动的结果。塑造分解的进化作用主要是使土壤生物生长、生存和繁殖的极大化。换句话说，分解的发生是为满足分解者群体能量和养分的需求，而不是对碳循环的社会奉献。从生态系统角度来说，分解的结果是有机物质矿化成为无机成分（CO_2，矿质营养和水）和一些有机物质转换成为复杂的有机化合物，它们通常是顽拗的，也就是说难于被微生物进一步降解。

一旦土壤有机质（SOM）与矿质土壤结合后，对有机物质降解的控制就会彻底改变。矿质土壤的水分、氧气和热量变化模式（thermal regime）与凋落物层的有显著的不同。在矿质土壤中，有机质可以与粘土矿物质络合（complex）或者通过非酶催化的化学反应形成更加复杂的化合物。例如，腐殖质（humus）就是具有高度不规则结构的土壤有机化合物的混合物。土壤中有机物质的长期存留取决于化学顽拗性，有机化合物在粘土表面的吸附（sorption），以及其他对微生物活动的控制，虽然这些过程的相对重要性还不是很清楚。

微生物和动物对活的和死的有机物质的取食支撑了它们的能量和营养需求。与之相关的异养呼吸大约占一半生态系统向大气圈释放的 CO_2。碳也会通过一些含碳产物的痕量气体（例如甲烷）和野火中燃烧传输到大气圈中。最后，碳可以以溶解或者颗粒的形式通过淋溶出生态系统，也可以通过土壤侵蚀和沉降以及动物的搬运等发生侧向搬迁。这些来自陆地生态系统的碳的侧向通量是对水体生态系统的重要输入，同时也是许多生态系统碳概算的一个重要组成。

本章，我们将首先描述陆地生态系统的分解，然后是陆地和水体在分解上的显著差异，最后将碳损失途径与生态系统的碳输入整合，来评估净生态系统碳平衡。

2.1 凋落物的淋溶

淋溶是植物（组织）最初开始凋萎时决定植物凋落物质量丢失速率的步骤。淋溶是一个物理过程，在该过程中矿质离子和小的可溶性有机化合物溶解与水分中，并从凋落物碎屑中流出。当组织还存活时淋溶便已经开始，并且在凋萎过程中和凋落之后不久最为重要（见第八章）。叶片和细根的可溶性化合物要比木质茎和根中的比例更大，因而也会占更多的淋溶损失。养分在凋落物淋溶损失中所占的比例要高于碳，因而更为重要。新鲜凋落物的淋溶损失在高降水的环境中最为迅速（几分钟到几小时），但在干旱条件小几乎可以忽略。淋洗出的化合物包括那些不稳定（易降解）的或者能被土壤微生物完整吸收的糖类，氨基酸类和其他有机化合物。

2.2 凋落物的碎裂

碎裂可以产生更多的表面积供微生物定植，同时增加凋落物受微生物攻击的比例。新鲜的凋落物碎屑开始时被角质层或者植物表皮形成的保护层，或者动物表皮或者外骨架形成的保护层所包裹。这些外表的包裹层的部分作用就是为例保护组织不受微生物侵害。在植物组织内部，易降解的细胞内含物还进一步被木质素浸渍的细胞壁保护，以免受微生物侵袭。凋落物的碎裂大大促进了微生物对保护阻隔的突入，增加了单位质量凋落物的表面积，也增加土壤微生物在剩余凋落物上的生长，从而加速凋落物分解。

虽然冻融和干湿交替也会破坏凋落物的细胞结构，但动物是凋落物碎裂的主要执行者。动物对凋落物的碎裂作用其实是它们取食活动的副产品。熊、田鼠，以及其他哺乳动物可以撕裂木材或者在寻找昆虫、植物根和其他食物过程中对土壤的混合作用。土壤无脊椎动物对凋落物的碎裂能够创造更多足够小可以被吞咽的颗粒。动物肠道中的酶可以消化哪些包裹在凋落物颗粒表面的微生物“酱”，从而为动物生长和繁殖提供能量和养分。土壤无脊椎动物的存在可以对湿润温带和热带生态系统凋落物分解速率起到一个重要的作用，但对受温度和水分严重制约的凋落物分解则并没有那么重要。然而，无脊椎动物群落的种类组成对分解速率的影响只占很小一部分的比例（7%）。很明细，不太的土壤动物对凋落物的碎裂速度差不多有相似的作用。

2.3 化学改变

（1）真菌

真菌和细菌是陆地死亡植物材料最初的主要分解者，大约占所有分解者生物量和呼吸的 95%。真菌具有菌丝网（即能使真菌进入新的底物处生长和在土壤中传输物质长大几厘米到几米距离的细丝）。这些菌丝网络可以使真菌在一个地方获取碳，而在另一个地方获取氮素营养，很像植物，从大气中获取 CO_2，而从土壤获取水分和养分。例如，真菌对新鲜叶片或者木质结构凋落物的分解，可能从凋落物表面获取碳，而在凋落物深处或者更加分解的土壤层次获取氮。真菌能够分解酶，可以使它们穿透死亡叶片的角质层，或者根的栓化表皮，

以可以进入死亡植物器官的内部。真菌可以在死亡植物细胞内或者之间进行繁殖。在更小的尺度上，一些真菌通过降解细胞壁中的木质素，可以获得氮素，木质素包裹的纤维素，以及其他死亡细胞中易降解组成成分。对木质素降解酶合成投入大量能量的主要目的就是为了获取这些相对容易降解的组分。

当能量充沛时，真菌建造致密的菌丝网络，能够高效获取这些资源，将网络中的一部分资源重新进行配置，以探究新的凋落物和土壤空间。这种灵活的生长策略可以使真菌进入新的地方生长，探测更多的底物，即使在当前的底物已经消耗殆尽时。用于支撑真菌生长的一大部分（25%）碳和氮都是在菌丝网络中从其他地方运输而来，而不是直接从真菌生长的环境中吸收。

真菌具有降解所有级别植物化合物的酶系统。它们在降解低养分含量的植物组织上具有优于细菌的竞争优势，原因就是它们运输氮和磷素养分的能力。此外，真菌具有比细菌更低的单位重量生物量的养分需求（即真菌的 C/N 比常高于细菌的）。这可能解释了为什么在高的 C/N 比的土壤中真菌/细菌比较高。白腐真菌专门对木材中木质素进行降解，而褐腐真菌可以打开木质素的一些支链，但对酚类部分单元并无作用（使得木材成褐色）。当氮素营养丰富时，白腐真菌通常竞争不过更加快速生长的微生物，所以氮素添加对白腐真菌降解木质素几乎没有什么作用（或者有时还有负效应）。大多数真菌缺乏厌氧代谢能力，因此不会在厌氧土壤和水体系统沉积物中出现，或者处于休眠状态。

菌根和植物根和真菌之间的一类共生关系，通过该共生关系，植物从真菌获得养分，作为供给（真菌）碳水化合物的回报（见第九章）。虽然菌根真菌从植物根获取其大部分碳，它们也会通过将蛋白质分解成氨基酸的过程在（有机质）分解中起到重要作用。这些氨基酸支撑了真菌的生长，也会被传输到它们的寄主植物。菌根真菌也生产纤维素酶，从而进入植物根，并参与土壤有机质（SOM）的降解，但菌根纤维素酶在分解死亡有机质中的参与程度存在很大的不确定。

通过引用现代分子技术手段，对一些生态系统中的真菌多样性进行了分析，发现真菌的多样性要比植物分类群高 10 到 100 倍。真菌分类群在营养级的作用（菌根菌或腐食者—取食死亡有机质），土壤层次，活动季节，以及其他现在还不清楚的生态位维度上都有很大的不同，局域尺度来源的多样性常常高于生态系统间的变异。

（2）细菌和古菌

具有小的体积，大的表面积/体积比的细菌和古菌能够快速吸收可溶性的底物，并在底物丰富的趋于迅速生长和分化。古菌在结构上相似，但在进化上与细菌有显著区分的一类微生物。与细菌相似，它们在代谢上极具多样性。细菌和古菌（为方便起见统称为细菌）的机会主义策略可以解释它们在根际圈（受植物根直接影响的土壤区域）和死亡的动物尸体上的优势度，正是由于那些区域底物的丰富性。细菌在分解活的和死的细菌和真菌细胞上也十分重要。它们的细小个体造成的主要的功能限制是每个细菌很大程度上依赖于经过它们的底物。

其中的一些底物是细菌胞外酶的产物。这些产物沿着浓度梯度扩散到细菌表面，该浓度梯度主要下列原因形成的，（1）胞外酶的活性，这可以产生可溶性的底物；（2）细菌对底物的吸收，这可以降低细菌表面底物的浓度。其他可溶性底物主要通过土壤中流动的水分经过细菌表面。这种水分的流动则是由植物蒸腾、土壤表面的蒸发以及重力水形成的水势梯度驱动（见第四章）。水分运动（于是底物供给）在大孔隙（土壤团聚体之间相对较大的空气和水分空间）中最为迅速。于是细菌经常守候着大孔隙，吸收流经该处的底物，就像渔夫张网等待向溪流上游迁徙的大马哈鱼。植物根也偏爱利用大孔隙，原因是根在伸长过程中物理阻力降低，也为细菌提供了额外的易降解底物源。附着在大孔隙上的细菌容易受原生动物和线虫的取食，这些动物通常利用大孔隙上的水膜在土壤中快速移动。这使得暴露在颗粒表面的细菌快速周转。

大部分细菌主要出现在土壤中；其实我们通过分子手段对于它们的多度和多样性特征的认识还仅处于开始阶段，随着这些技术升级，并得到更加广泛的应用，我们预测可以获取更多的信息。生长迅速的革兰氏阴性菌专门分解植物根系分泌的易降解底物。放线菌是生长缓慢的革兰氏阳性菌，具有与真菌菌丝相似的细丝结构。就像真菌一样，放线菌合成木质素降解酶，分解相对难降解的底物。它们经常释放一些抗生素，以减少来自其他微生物的竞争。菌群成分和胞外酶活性的最佳预测指标是土壤的 pH。

包围在土壤团聚体周围的菌群具有出人预料的复杂结构。它们经常以生物膜的形式出现，微生物群落镶嵌在细菌分泌的多聚糖的基质（matrix）中。这种微生物“粘液”保护细菌免受原生动物的取食，并通过类似于海绵状物质保持水分以降低水分胁迫。这种基质也通过防止流水对它们的冲刷增加了细菌胞外酶的有效性。在生物膜中的细菌经常形成一个利益共同体（consortium）,即一组在遗传上毫不相干的细菌，每个成员仅合成某种用于降解复杂大分子的酶。将这些分子降解成可溶性产物需要多种细菌类型联合生产胞外酶。这有点类似于流水线，最终产物取决于一系列连续步骤的联合行动，除非所有步骤都在其相应位置上并生产出最终产物，否则没有一种细菌能够获益。对进化作用和种群间的相互作用在构成微生物利益共同体的组成和功能上所起的作用还了解甚少。细菌利益共同体在降解人类输入环境中的杀虫剂和其他有机残留物中起尤其重要的作用。

因为大多数细菌是不能移动的，菌落最终会耗尽其紧密相连环境中的底物，尤其是在哪些束缚水分流动的土壤团聚体中。一旦这种情况发生，它们就会转变成非活跃状态，并降低其呼吸至极低状态。细菌可以保持数年非活动状态。活的细菌可以从三百万年古老的永冻层土壤中恢复。土壤中大约 50-80%的细菌在代谢上处于非活跃状态。当有易降解的底物存在时，非活跃的细菌被激活，例如，当一条根生长经过该处土壤，并同时分泌碳水化合物时。土壤中的非活跃细菌代表了具有分解潜势的分解者库，类似于埋藏的种子库，能够提供干扰后植物定居者的一种来源。正像被埋藏的种子库，这些非活跃状态细菌的酶潜势可能有别于当前活跃菌群所生产的酶。于是，要确定土壤究竟能做什么（细菌的代谢多样性和酶潜势），DNA 探针和微生物培养技术可能是比测定当前代谢活性更好的指标。

生活在土壤中的细菌，古菌，病毒，真菌群落是高度多样的。然而，细菌和古菌要比真菌能够适应更大范围的小生境，包括厌氧、几乎没有可利用碳或氮、有毒重金属污染，或者极端温度或者紫外辐射的生境。

（3） 土壤动物

土壤动物通过碎裂、转化和运输凋落物，取食细菌和真菌种群，改变土壤结构来影响分解。小型土壤动物是最小的动物（直径<0.1mm）。它们包括线虫，原生动物，例如鞭毛虫和草履虫，以及轮虫（见图 7.2-1）。原生动物是单细胞动物，主要通过吞噬作用（phagocytosis）摄取猎物，即将它们包围在细胞内一个具有膜边界结构中。原始动物通常是可移动的，同时是贪吃的细菌和其他小型动物的捕食者。原生动物在具有快速细菌生长速率的根际圈和其他土壤其他微位点上是极其重要的捕食者。与去除原生动物的土壤相比，偏爱捕食细菌（甚至细菌的特定种类）的原始动物可能导致土壤中细菌/真菌比的降低。线虫是一个丰富，且是多营养级的类群，每个种可能专性捕食细菌、真菌、树根，或者其他土壤动物。例如，森林凋落物中捕食细菌的线虫能够消耗大概 80g m^{-2} yr^{-1} 的细菌，可以引起 2-13g m^{-2} yr^{-1} 的氮素矿化，占每年土壤中相当一部分比例氮循环的氮。原生动物和线虫是水生动物，可以在土壤颗粒间注满水分的空隙中运动，所以要比真菌和碎裂土壤颗粒的中型、大型动物对水分胁迫更加敏感。无论在空间还是在时间上，它们的种群大小由于干湿交替变化和捕食而产生剧烈的波动。原生动物一旦死亡，它们的尸体很快被土壤微生物降解，尤其是细菌。

中型动物是数量上极其丰富，分类学多样的一类动物，直径在 0.1-2mm 之间。这是一类对分解作用最大的动物。它们碎裂、摄取包裹着微生物生物量的凋落物，产生大量排泄物一类的物质，这类物质比原来的（取食前）凋落物具有巨大的表面积以及保持水分的能力。这种改变后的凋落物环境更加有利于分解。中型动物选择性地摄取那些被微生物处理过的凋落物，也选择性地取食一些土壤真菌，导致真菌群落结构的改变。弹尾目动物是一类较小的昆虫，主要取食真菌，而螨虫类是一类具有多个营养级的蜘蛛状动物，主要消耗分解中的凋落物，或者取食细菌、真菌，或者土壤动物。小型和中型动物捕食对微生物群落的生物量和活性都产生显著的改变，从而改变分解和养分周转的速率。

诸如蚯蚓和白蚁等大的土壤动物（macrofauna）是生态系统工程师，它们通过改变土壤和凋落物的物理特征来改变资源的可获得性。一些大型土壤动物就像中型土壤动物那样，也起到碎裂凋落物的作用。另外一些钻入或摄取土壤，降低土壤容重，打碎土壤团聚体，增加土壤通气和水分渗透。蚯蚓打造的通道方便水分和根穿透土壤提供了通道。它们营造了一个土壤结构格局，可以促进或者限制土壤微生物和其他土壤动物的活动。在北美牧场，蚯蚓可以处理 4kg m^{-2} yr^{-1} 的土壤，每年可以将 3-4mm 的新土搬到土壤表明。这种地表作用，经过日积月累，其数量级可以超过山崩或者地表土壤侵蚀。在温带森林，外来的蚯蚓显著地降低了土壤碳储存。蚯蚓引起的土壤混合可以逐渐破坏明显可分的土壤层次构成。一旦土壤进入一个蚯蚓的消化道，蚯蚓的混合作用和泌出过程可以刺激微生物活性，这样土壤微生物可以扮演肠道共生生物的作用。许多土壤生物在穿过肠道的过程中被消化，形成的产物也被肠道

吸收。蚯蚓在温带地区是十分丰富的，而白蚁和蚂蚁则是热带土壤中最优势的生态系统工程师。白蚁直接取食植物凋落物，在肠道共生的原生动物和细菌的帮助下消化纤维素，并将有机物质混合入土壤中。热带草地中的蜣螂（屎壳郎）执行了类似哺乳动物粪丘的作用。这种将土壤表面的有机质埋于一个湿润的环境，使分解发生更加快速。

土壤动物对于土壤碳和养分动态是至关重要的。微生物构成了 70-80%的土壤易降解碳和氮，所以从土壤中排除土壤动物，或者它们在微生物取食上的自然变化都将显著改变土壤中碳和氮的周转，虽然它们的净效应相对还不是那么大（可以达到 30%）。有时土壤动物会通过它们直接的消耗微生物生物量而抑制分解，但有时也通过降低微生物取食者的密度而促进分解。

由于它们高的呼吸速率，土壤动物将它们取食的大部分微生物生物量碳代谢成 CO_2，并即将超过它们自身生长和繁殖需要的微生物氮和磷分泌出来。这些养分可以为植物或者微生物吸收所利用（见第八章）。土壤动物只占土壤呼吸的 5%，所以它们对分解的主要作用就是通过碎裂促进微生物活动，而不是它们自身对来自碎屑的能量的处理。

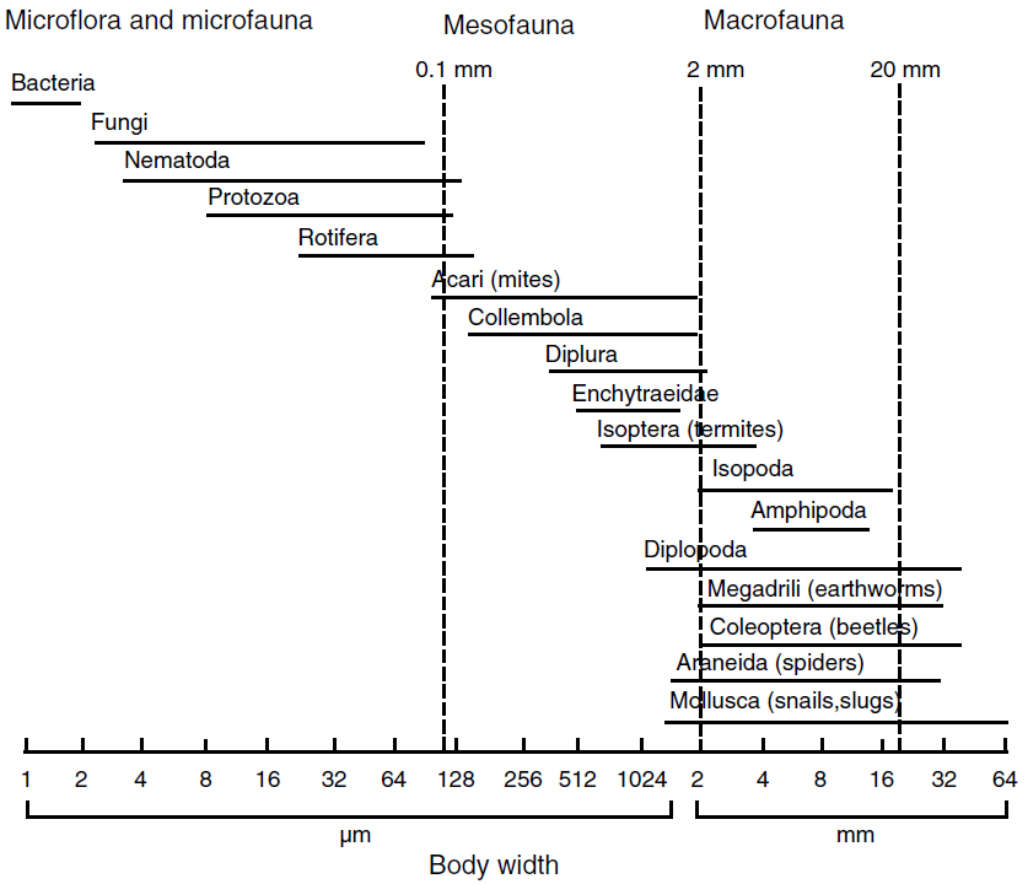


图 7.2-1 土壤动物的代表性类型和尺寸。作为捕食者，小型动物是最重要的；中型动物作为碎裂凋落物的生物体；大型动物作为生态系统工程师（改变土壤结构）

第三节　分解的时空异质性

3.1 时间格局（temporal pattern）

控制分解的主要因素随着分解时间推移而发生变化。分解是淋溶、碎裂和化学改变相互作用的结果。从叶片展开开始，就被空中产生的细菌和真菌孢子侵染，并开始降解受食草动物、病原菌或者物理碎裂的角质层和叶片表面。活叶片的叶际分解（phyllosphere decomposition）通常被忽略，原因是难以与植物控制的叶片重量和化学成分的变化区分。其他细菌和真菌生活在活的叶片内，产生可以减少食草动物取食的毒素，这样就改变了叶片的特性和功能。上述两个微生物类群都提供了一种微生物接种体，当叶片脱落到地表时，能够迅速启动易分解物质的降解过程。同样，当根的传导组织仍然在传送水分和养分时，根表皮就开始降解了，从而模糊了活根和死根的区分。

凋落物质量在分解开始时下降很快，但随着凋落物的年龄增加分解速率下降。这通常用一种指数式关系来描述，暗示了每年有一定比例的凋落物被分解。

通过库和通量计算的凋落物存留时间（residence time）通常假设某个时间的测定可以代表凋落物分解的稳定状态，当然实际情况很少是这样。气象条件的年际变异或者气候的定向变化引起的凋落物形成的变化比凋落物库的变化更快，这对（凋落物）存留时间的估计是一个挑战。分解常数随分解基质的成分变化很大。例如，糖的存留时间通常在几小时到几天，而木质素的存留时间在几个月到几十年，主要取决于生态系统类型。植物和动物组织在它们的化学成分上差别很大，从而它们的分解常数也有很大的差异。综合来说，叶片和细根的凋落物的存留时间通常在几个月到几年，木头的存留时间在几年到几个世纪，与矿质土壤络合的有机物质的存留时间在几年到千年。

所以，表示每年有一定比例的凋落物被分解的指数模型只是凋落物质量降低随时间的实际变化格局的一个近似。要更加精确地描述凋落物的分解过程，可以采用能够描述至少四个阶段的多曲线（multiple curves）（分解模型）（图 7.3-1）。细胞可溶物的淋溶在第一阶段占优势。例如，新鲜叶片和细根凋落物仅通过淋溶可以在 24 小时内降低 5%的重量。分解的第二阶段要发生得慢很多，包括土壤动物的碎裂作用，土壤微生物的化学改变，以及凋落物分解产物的淋溶等多个过程的组合。（凋落物分解的碎裂阶段会发生淋溶吗？）在分解的第二阶段，相对容易分解的基质分解凋零，留下来的是更加难于分解的物质。分解的第三阶段包含了第二阶段相似的过程，但分解更加缓慢，原因是剩余的化合物是顽拗且分解很慢的。第二和第三阶段分解的测定通常采用分解物质（死亡的叶片，根，或者枝条）的质量损失来表示，这些用于分解的凋落物通常被绑在线上，或者放在带网格的凋落物袋中，每隔一段时间称重一次。（分解第二和第三阶段的主要差别在哪里？）木头的分解可以直接放在地表。分解的指数降解模型主要用于第二和第三阶段分解的测定。分解在第四，也是最后阶段进展得很慢，包含与矿质土壤混合在一起的有机物质的化学改变以及分解产物向其他土壤层次的

淋溶。由于分解速度极其缓慢，最后阶段的分解经常采用土壤呼吸或者同位素示踪的测定来估计。分解速率和分解速率常数（k）随着这四个分解阶段逐渐降低。

在有季节性变化的环境中，微生物呼吸经常在很长的时间段都有发生，高峰出现的时间要晚于植物生长。就像植物生长，温暖、湿润的环境更加有利于微生物呼吸，所以在最大植物生长的季节微生物呼吸也最大。然而，与植物生长相比，异养呼吸通常开始的季节要早于植物生长，而结束的时间又要迟于植物的生长。这可能有以下三个方面的原因：（1）微生物呼吸发生的温度和土壤水分范围要比植物生长更宽（例如，-10-40℃）。（2）土壤对极端温度有一定的缓冲作用，但植物地上部分需要自行解决。（3）土壤温度通常滞后于大气温度，这样微生物呼吸在夏季后期和秋季仍能保持高位，而此时的植物活动能力开始降低。微生物活性也受植物活动的季节性影响。根系的周转和分泌活动经常在生长季中期最大，此时光合作用最高，导致土壤呼吸的生长季中期高峰。秋季或者干旱季节凋萎提供了额外的基质输入，支撑了生长季后期土壤呼吸。

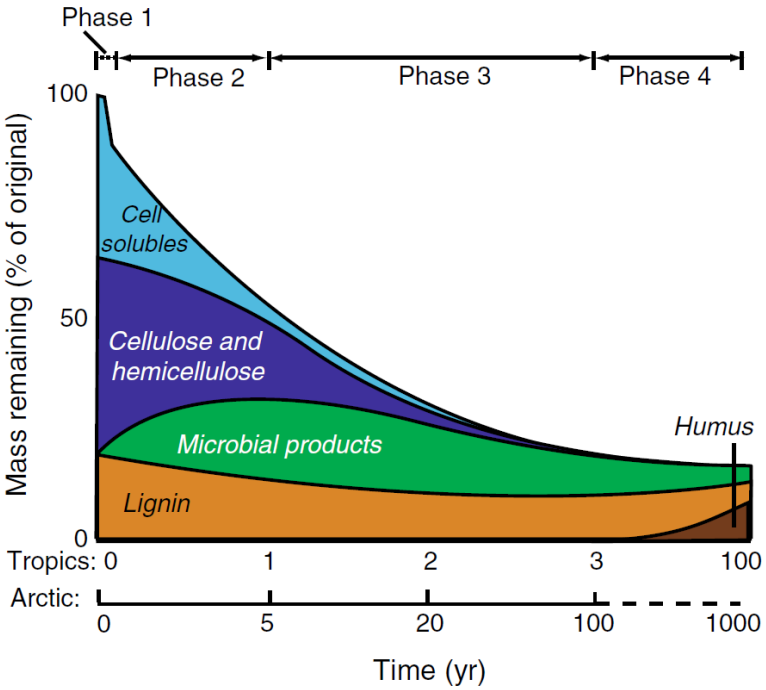


图 7.3-1 代表性叶片凋落物分解的时间进程，显示组要的化学成分（细胞可溶物，纤维素和半纤维素，木质素，微生物产物，和腐殖质），凋落物分解的四个主要阶段，以及常见的温暖（热带）和寒冷（极地）环境中凋落物分解的时间尺度。淋溶在分解的第一个阶段占优势。凋落物分解的第二和第三阶段凋落物的基质组成发生变化，因为易分解基质（例如细胞可溶物）降解比顽拗性的化合物“例如木质素和微生物细胞壁物质”要快得多。在分解的第四阶段，凋落物颗粒与矿物质表面结合，形成土壤有机质。

3.2 垂直分布（vertical distribution）

大多数分解发生在接近土壤表面，那里也是凋落物输入集中的地方。大部分地上凋落物（叶片和木头）分解与释放养分都在或者接近土壤表面。所以根也趋于生长在表层土壤中，以获取这些养分资源。这样大多数根的凋落物也是在表层土壤形成，反过来又加强了凋落物分解的土壤表层化。然而也有一些根分布到较深地方，因为通过动物对土壤的混合作用，尤其是白蚁和蚯蚓，以及淋溶也使可溶性有机物质分布到土壤的深处。大约有一半的土壤有机碳通常分布在土壤 20cm 以下的深度，即使只有 1/3 的根分布到该深度以下（见图 7.3-2）。平均来说，相比于土壤表层的碳，在土壤深处的碳是较老的，更加难于分解的，以及更加紧密地结合在土壤矿物上，但也有一部分土壤深处的碳是新的，主要来自深处根的周转。

凋落物分解在多个尺度上存在空间异质性的。表明的凋落物层存在大的温度和水文的日变化。在该层次的分解主要受真菌控制，可以通过其菌丝从下层获取氮素营养。这里的环境与下面的矿质土壤层是有根本的区别的，原因是矿质土壤层的温度和水分要更加稳定，部分有机物质已经腐殖化而难于分解，矿质土壤表面结合了死亡的有机物质微生物产生的酶。在更微笑的尺度上，围绕根的根际是一个碳含量丰富的微环境，支持了比非根际土壤高得多的微生物活动。最后，土壤团聚体内部要比在土壤孔隙表面更有可能处于厌氧状态。根、水分和土壤动物在土壤中的移动不断地改变了这些不同分解环境的配置。

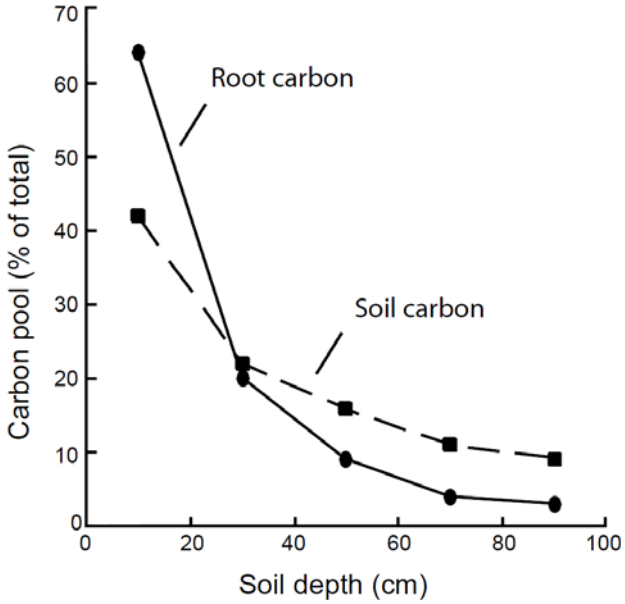


图7.3-2 全球平均的表层1m土壤剖面有机质和根的分布

在一些生态系统中，例如在热带雨林（tropical wet forests）中，大量地上凋落物被冠层中的附生植物和枝条所截留。在这些湿润的生态系统中，十分可观的分解，养分释放和附生植物根的养分吸收发生在冠层内，于是绕过了土壤介质（short-circuiting the soil phase）。一些陆生的凋落物和可溶性的有机碳（DOC）也会进入溪流和湖泊，在哪里它们成为水生食物网的重要能量来源，这部分在后面进一步描述。在营养贫乏的生态系统，很多进入溪流的

DOC 是那样难于分解以至于它们基本上保持原来的状态，导致许多热带和北方森林和温带沼泽的“黑水”河流的形成。

第四节　控制分解的因素

4.1 凋落物质量

4.2 分解的根际激励（rhizosphere stimulation of decomposition）

植物激发了根周围的凋落物分解。根际是植物根几个毫米以内区域的土壤。根际几乎占据了具有细根生长的草地中所有的土壤，根之间的平均距离在 1mm 左右；而森林根的生长要稀疏得多（根之间距离经常在 10mm 左右）。通过分泌碳水化合物和吸收养分，根系改变了根际的化学组成。上述过程在活跃生长根的根尖区最为活跃（见图 7.4-1）。在分泌区域生长的细菌得到了高的可利用碳（20-40%的 NPP）的支持，从而强烈地受到养分的限制。细菌利用易分解碳制造酶，用于“挖掘（mine）”土壤有机质（SOM）以获取养分。

微生物在根际固持养分有利于植物生长，仅当这些养分接下来被释放，并可以为根利用。两个过程可以引起根际微生物的养分释放。第一，原生动物和线虫可能取食根际微生物，利用细菌的碳来支撑它们对高能量的需求，同时分泌多余的养分。第二，当根长大且分泌速率逐渐降低时，那些侥幸躲过动物取食而幸存下来的细菌受到能量的限制，并开始降解土壤中的含氮化合物以满足它们对能量的需求，从而以铵态氮的形式向根际分泌氮。多个营养级间的食物网相互作用使得上述根际动态过程更加复杂。

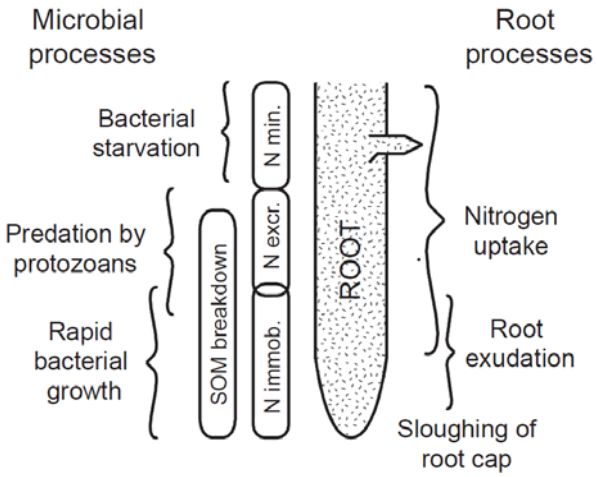


图 7.4-1 根际的根和微生物过程以及由此引起的对根际土壤有机质分解和氮素动态的影响

有关动物取食和饥饿在根际养分释放中的相对贡献并不清楚，但据估计，根际土壤中净氮矿化要比非根际土壤中的高 30%。通常，植物根的存在可以激发土壤有机质的分解达 3 倍，取决于植物种的类型和土壤条件。根际分解可能对影响植物碳水化合物状态的因素（例如光照和动物取食）要比对土壤物理环境条件更加敏感，所以对分解控制的特征（土壤环境 vs.

植物碳水化合物状态）可能在不同生态系统间差异很大，具体要取决于根际分解程度及其生态学控制的特点。

菌根真菌在功能上是根的延伸，使得根和真菌的共生体可以吸收离根很远地方的养分。围绕在菌根真菌菌丝的菌根根际（mycorrhizosphere，也作菌根际）通过菌丝周转和分泌的组合快速地将植物碳传输到非根际土壤。这也可能刺激分解，亦如在植物根的根际。

4.3 微生物群落组成和酶活性（microbial community composition and enzymatic capacity）

在决定分解速率时，土壤微生物的活性要比它们的生物量更加重要。微生物量在土壤总碳占比中相对恒定（大约 2%），所以在具有最大碳库的立地具有最高的微生物碳量，具有最大碳库的立地意味着那些具有最低的生产力和最慢的分解。（为什么？）在农田土壤中，微生物生物量也趋向于在分解较慢的极端湿润或极端干旱的土壤中要比具有分解较快的中等湿润土壤中要高。既然大多数微生物量是非活跃状态的，把它作为一个营养库要比作为分解速率的指示可能更为重要。这与对生态系统碳输入的控制是有区别的，原因是植物生物量和叶面积决定了 GPP。另一方面，就像严格地由一定数量微生物类群完成的硝化作用，其微生物过程对种群大小表现出敏感。

土壤酶活性有时也依赖于微生物群落组成。微生物群落组成对分解存在潜在重要性，原因是微生物群落组成影响酶的种类和生产速率，从而影响基质分解的速率用于普通基质（如蛋白质和纤维素）降解的酶在土壤中是普遍存在的，主要因为大多数类型微生物都可以制造这些酶。于是，组成十分不同的微生物群落经常具有相对相似的分解速率和胞外酶种类。另一方面，仅参与特殊环境中发生的过程中的酶，例如甲烷生成的厌氧过程，就表现出对微生物群落组成更加敏感。在来自其植物生长的土壤中，凋落物的分解速率要比在来自其他地方的土壤中分解的速率要快 10%。这种分解的“本地优势（home field advantage）”源于显著不同的微生物群落的发育，它们已经适应了它们频繁碰到的这种凋落物。然而，与环境效应和分解基质的质量效应，这些微生物群落组成对分解的效应是很小的。

土壤酶活性也受结合到什么样的表面的影响或者受蛋白酶降解的影响。一个酶结合到根或者微生物的外表面延长了它们在土壤中的活性，然而结合到矿物质颗粒能够改变酶的结构，或者屏蔽掉酶的活动位点，导致活性的降低。一些土壤酶系统的简短描述表明一些微生物或者土壤对胞外酶活性的控制。

大多数土壤微生物，包括心型和外生菌根真菌，能够生产一类酶（蛋白酶和肽酶），可以将蛋白质降解成氨基酸，这些物质很容易被微生物吸收，它们或者被微生物用于合成蛋白质或者微生物呼吸后提供能量。因为蛋白酶容易受到其它蛋白酶的攻击，其在土壤中的寿命是短暂的，于是土壤蛋白酶的活性正好反映了微生物的活性。然而，可以将磷酸盐从有机磷酸化合物中剥离出来的磷酸酶寿命要长得多，这样它们在土壤中的活性与有机磷酸盐的可获得性的相关性比它们与微生物活性的相关性更大。

纤维素在植物凋落物化学组成中的比例最高。它由葡萄糖为基本单元的链组成，在长度上常达到几千个单元，但在胞外酶作用之前，这些葡萄糖都不能用于微生物代谢。纤维素降解需要需要三个独立的酶系统：内纤维酶（endocellulase）降解内部的键，以打断纤维素的晶体结构（crystalline structure）。外纤维素酶负责从链条末端断开二塘单元，形成纤维二塘，可以被微生物吸收，并在细胞内部被纤维二塘酶降解成葡萄糖。一些土壤微生物，拨款大多数证据，可以生产整套的纤维酶。其他有机体，如一些细菌，仅能制造个别纤维素酶，必须与其他细菌分工协作形成微生物联合体（microbial consortia），以通过分解纤维素获得能量。

木质素的降解很慢，原因是只有一些生物体（主要是真菌）可以生产必需的酶，而这些微生物只能在无氮的情况下合成这些酶。这一过程有时是在调解快速生长细菌之间的竞争时引起的，这些快速生长的细菌降解易分解有机质，并释放氮素，这些释放的氮素抑制了生长缓慢得多的木质素真菌。木质素是通过非酶催化的一些与酚类和自由基（free radicals）的凝聚反应形成的，通常生成一种不规则结构，这种不规则结构与大多数酶要求的活性位点特异性都不匹配。由于这个原因，木质素降解酶利用过氧化氢（hydrogen peroxide）生成自由基，对基质特异性的要求较低，但氧化能力很强。氧气是生成过氧化氢必须的以及随后的自由基，所以木质素降解不会在厌氧土壤中发生。与代谢木质素的降解产物时的能量获益相比，分解者在生成木质素降解酶时通常要投资更多的能量。当能够获得木质化死细胞内部的氮时，或者能够接近被木质素包裹的纤维素时，木质素好像是被分解了。由于自由基的生成，一些参与木质素降解的酶也改变了现存的有机质，并形成更加复杂的土壤腐殖质。

4.4 环境（the environment）

（1）温度（temperature）

虽然微生物呼吸和分解短期随温度增加而增加，但一些间接效应限制了年度到十年时间尺度上的温度敏感性。微生物酶活性和呼吸在较大的温度范围内随短期温度增加而呈指数式增加（图 7.4-2），加快了有机碳矿化成 CO_2。难分解基质的降解对温度尤其敏感。例如，当温度从 10℃增加到 20℃时，可以使易分解的柠檬酸的分解增加 2 倍，但可以使难分解的单宁酸增加 3 倍，难分解的 SOM 达 5 倍。

在不同时间尺度上起作用的多个过程限制上述表现的高温敏感性。在几天到几个星期的时间尺度上，微生物可能适应了较高的温度而下调呼吸速率。基质库在较高的温度下下降较快，降低了碳的可获得性，从而限制了微生物的进一步获取能量。微生物群落组分中活性功能群的季节性转变进一步降低了分解速率的季节性变化。

（2）土壤性质（soil properties）

粘土矿物降低土壤有机质（SOM）的分解速率，从而增加土壤有机质含量。粘土通过增加持水量（water-holding capacity）改变土壤物理环境。所引起的氧气供给限制减少了湿润粘性土壤的分解。即使在中等程度土壤水分含量条件下，粘土通过束缚 SOM（使微生物酶

难于接触到它），束缚微生物酶（减少酶接触到底物的能力），束缚胞外酶活动的可溶性产物（降低这些产物的可获得性，难于为土壤微生物吸附），最终促进有机质积累。这种粘土与有机质的束缚的发生原因是粘土矿物上高密度负电荷位点对有机质（胺类物质）上正电荷的吸引或者与束缚在有机物质（例如，羧基类物质）负电荷基团上的高价阳离子（Ca^{2+}，Fe^{2+}，Al^{3+}，Mn^{2+}）形成过桥。有机质与粘土矿物结合的净效应是“保护”了有机质，降低了它的分解速率。粘土矿物对有机质（SOM）的保护在诸如草地和热带森林生态系统中最为重要，那里分解较快，土壤动物的活动使有机质与矿质土壤迅速混合。有机质的矿物质保护在针叶林或者冻原生态系统中并没有那么重要，原因是那里大部分的分解发生在矿质土壤以上的发育完好的有机土壤层次（O 层，枯枝落叶层）。

粘土的种类和数量都会影响分解。许多热带粘土矿物质具有高的铝含量，通过共价键与有机质紧密结合。具有多层晶格结构的粘土在硅酸盐层间与有机质结合，这在保护有机质中更加有效。

在其他条件相同的情况下，与中性土壤相比，土壤有机质的降解在酸性土壤中更加缓慢，主要是由于一些间接的作用。许多过程可以引起土壤酸化，包括阳离子淋洗，酸沉降，以及高度有机化的土壤中有机酸的积累。这些条件基本上与与低的养分可获得性（所以低的凋落物质量）以及导致对许多微生物（尤其是细菌）有毒害作用的铝含量有关。

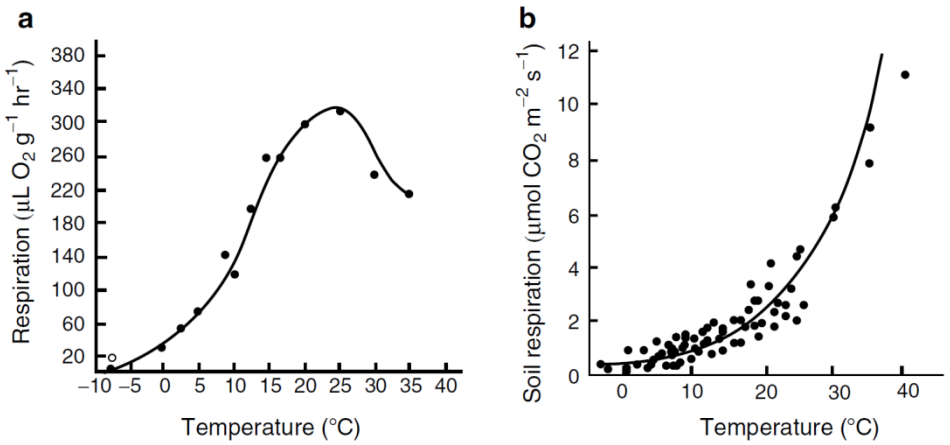


图 7.4-2 冻原土壤实验室培养过程中温度和土壤呼吸的关系（左）和 15 个全球分布的研究中野外土壤呼吸的测定，所有数据校准到 10℃时相同的呼吸速率。

第五节　净生态系统生产

在较短的时间尺度上，GPP 和呼吸基本上支配了陆地生态系统的碳平衡。它们之间的平衡定义为**净生态系统生产**（NEP）。

$$NEP = GPP - R_{ecosyst} = NPP + R_{het}$$

其中，$R_{ecosyst} = R_{plant} + R_{het}$

生态系统呼吸（$R_{ecosyst}$）是来自植物（R_{plant}）和异养生物（也即微生物和动物）（R_{het}）呼吸的和。NEP 是一个十分重要的概念，原因是它涵盖了一些主要过程，生物通过这些过程获取碳和能量（GPP），并通过呼吸利用这些能量支撑它们的生吃和维持（*Recosyst*）。这样，NEP 明确地将有机体的生理作用与生态系统的碳平衡连接在一起。NEP 有点类似植物的 NPP（GPP − R_{plant}），可以很容易地与阐述生态系统所有生物的生理过程相关的过程模型结合。

正如后面讨论，几乎不可能直接测量 NEP。然而，在陆地生态系统中，与大气圈的气体交换提供了大部分支撑 GPP 的和大多数呼吸释放的 CO_2。这个整个生态系统的净 CO_2 交换，定义为净生态系统交换，NEE，通常在短期测定时也是 NEP 比较合理的估计。NEE 目前已经在大都数的生态系统中进行了测定。NEE 可能系统性地高估了陆地生态系统的 NEP，但低估了水体生态系统的 NEP，正如后面要继续讨论的，但在那些处于近平衡状态的生态系统，NEE 可能是提供了比较合理的 NEP 地理格局的估计及其环境控制。

根据约定，NEE 被定义为从生态系统向大气圈的 CO_2 通量。NEE 对应于对一个生态系统的负的碳输入。NEE 这么定义的原因是大气科学家最早提出了这个术语，主要是试图记录进入大气圈净的 CO_2 来源（即 NEE），用来解释不断增加的大气 CO_2 浓度。于是，对生态系统的 CO_2 输入是负的 NEE。

NEP 是由导致 GPP 和 $R_{ecosyst}$ 间不平衡的因素决定的。在近期没有受到扰动的生态系统中，NEP 只是两个大的通量（fluxes）之间的微小差别：（1）光合作用碳收入和（2）呼吸碳损失（主要通过植物和微生物）。通常，GPP 在几天到几个星期的时间尺度上是与生态系统呼吸紧密相关的，因为植物呼吸和异养呼吸强烈地受通过 GPP 进入生态系统的碳量有关，这在前面已经讨论过了。当 GPP 与生态系统呼吸完全相等时，根据定义，NEP 为零。这样，不要奢望 NEP 与 GPP，NPP，或者生态系统呼吸间是一个简单的关系。然而，GPP 和呼吸很少正好平衡。在白天，光合作用固定的碳超过了呼吸作用释放的碳，但在晚上则正好相反。类似地，在生长季，NEP 是正的，因为光合作用超过呼吸作用，表现为植物累积生物量。在非生长季，当光合作用等于零，异养呼吸是主要的碳通量，NEP 就成为负的。这就给出了一个十分简单的、可以预测的 NEP 的日和季节变化格局（图 7.5-1）。

与这个季节变化格局一致（图 7.5-1），NEP 通常在有利于植物生长的季节是正的（或者 NEE 是负的）（GPP>生态系统呼吸），而在不利于植物生长的季节是负的（NEE 是正的）（图 7.5-2）。NEP 的季节变化幅度在不同生态系统有很大的差别。美国境内，落叶林具有最大的正的生长季 NEP 以及最大的负的非生长季 NEP，灌丛表现为最小的 NEP 季节变化。太平洋西北区的海岸常绿森林整年表现出较为中等的正的 NEP。所以一点也不奇怪，正的 NEP（负的 NEE）在东部美国地区的夏天最为显著，该地区落叶林分布占优势，NEP 在太平洋西北区的海岸带常绿森林地区整年比较平均分布，而在美国东南部的干旱地区夏天，NEP 是负的（正的 NEE）（图 7.5-3）。在中西部的农作物地区，夏天也有强的正的 NEP（负的 NEE）。通常，NEP 的这些季节性变化强烈地受 GPP 控制，其程度要强于受生态系统呼吸

的，因为无论是 GPP 还是生态系统呼吸都是在生长季通常最高，且与生态系统呼吸相比，GPP 在非生长季的下降更为强烈。

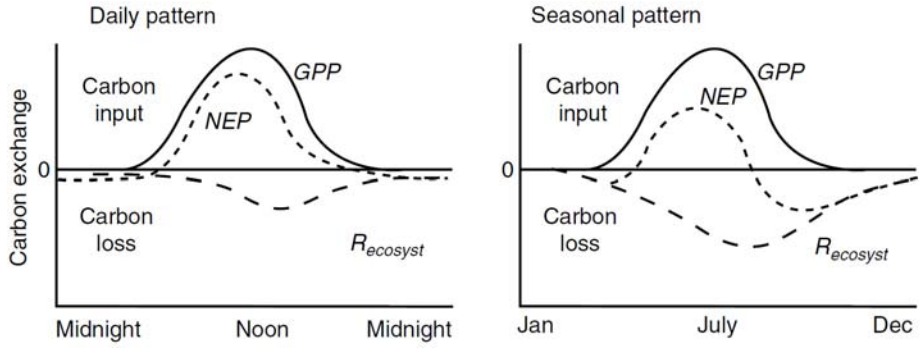


图 7.5-1 一个生态系统总初级生产（GPP），生态系统呼吸（$R_{ecosystem}$）净生态系统生产（NEP）理想的日（植物生长活跃的季节）和季节性变化格局。NEP 是两个大的通量（表现为碳输入的 GPP 和表现为碳损失的呼吸）间的差。图中，假设生态系统处于稳定状态，NEP 在白天的周期中显示为正（在植物活跃生长季 GPP>生态系统呼吸），而在年周期中接近 0。这些通量的实际变化格局取决于环境条件，演替状态和其他因素（见正文）。由于淋溶和干扰引起的碳损失在此图中被假设为 0。

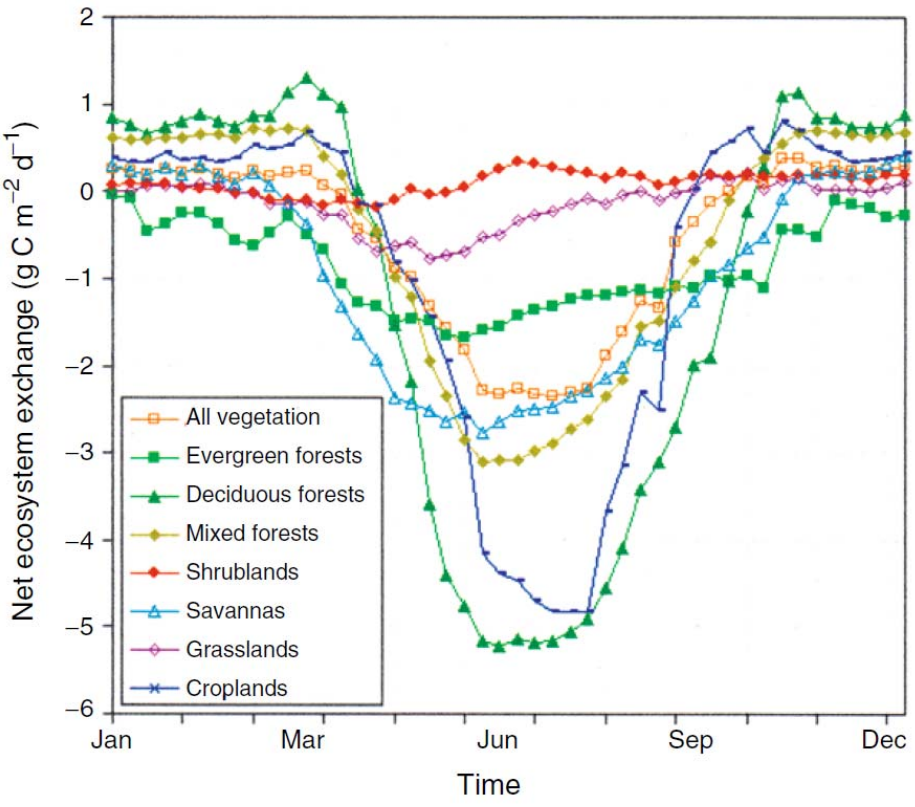


图 7.5-2 2005 年美国主要植被类型净生态系统交换（NEE）预测的季节性变化格局，主要基于美国通量网（AmeriFlux）NEE 测定的回归模型和 MODIS 卫星影像数据计算而得。

受扰动后，NEP 也会随着时间推移而发生变化。受扰动（如砍伐，飓风或者野火等）后，NEP 预料会下降，原因是扰动降低了植物生物量和 GPP。此外，由于地上生物量在扰动后向地表转移或者环境变化有利于分解，从而导致异养呼吸增加。NEP 应该会随着生物量和 GPP 的增加而逐渐恢复，而当 GPP 达到与生态系统呼吸平衡时，NEP 又逐渐接近 0。然而，令人感到惊讶的是 NEP 经常保持正的状态，即使林龄超过一个世纪后。平均来说，除了灌丛外，尽管最近并没有受到任何扰动，全美国的所有生态系统类型都显示出一个正的 NEP，这与将陆地生物圈当作一个整体的表现一样。

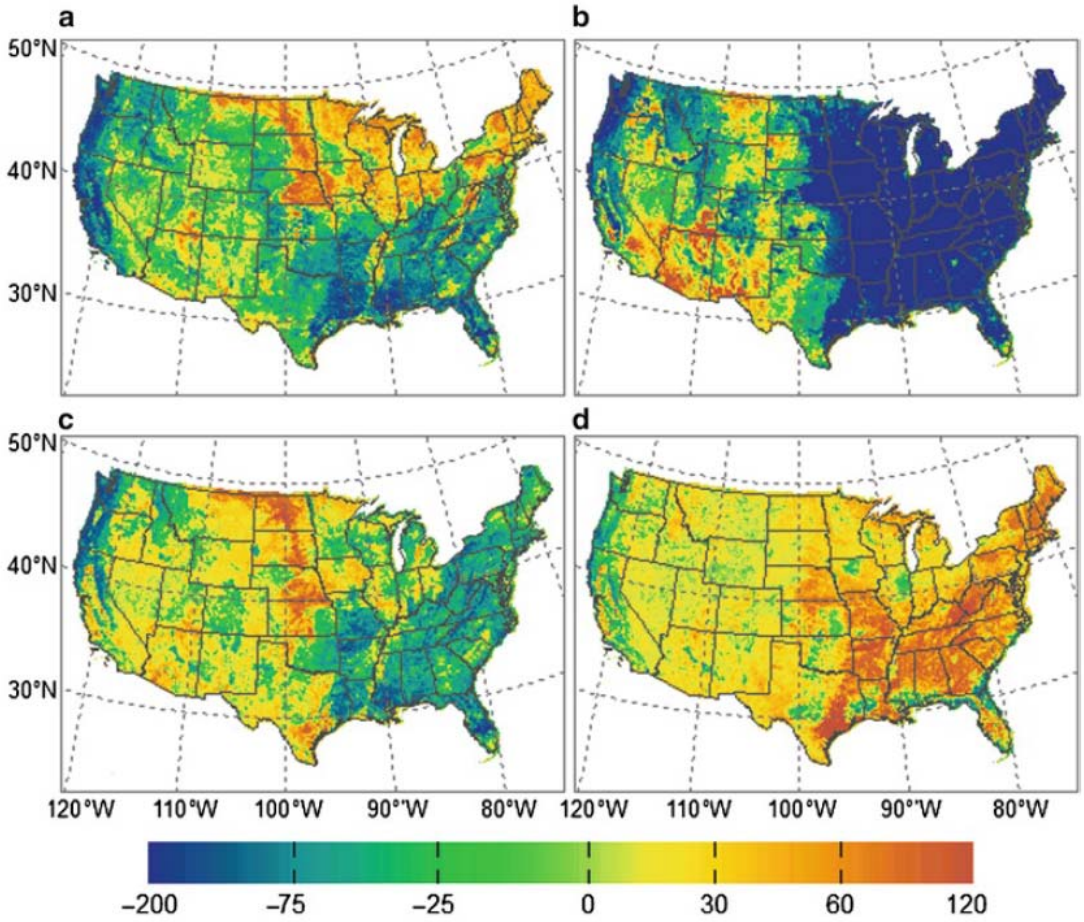


图 7.5-3 基于 AmeriFlux 通量网 NEE 观测建立的回归模型和 MODIS 卫星影像预测的不同季节净生态系统交换（NEE）图。（a）春季（3-5 月），（b）夏季（6-8 月），（c）秋季（9-11 月），和（d）冬季（12-2 月）。

针对在不同陆地生态系统普遍正的 NEP 结果，至少有 4 个可能解释：（1）这可能反映了预料中演替格局的 NEP，这些生态系统受到扰动后将经历很长时间的碳汇。换句话说，生态系统在遭受新的扰动前很少能达到一个真正平衡状态。（2）最近的环境变化，例如增加的 CO_2 浓度和氮沉降，可能刺激了光合作用，并降低了呼吸，导致更大的碳固定。（3）通过淋溶和其他转移的碳损失是陆地生态系统净碳平衡十分重要的组成成分，（但没有得到量

化），这些非气态的碳释放并没有包含在 NEE 的测定中，造成潜在地高估 NEP。（4）在样地选择、测定和模型使用时可能存在非有意的偏差。有关陆地生态系统普遍正的 NEP 测定结果，生态学家正在激烈讨论这些解释的范围和相对重要性。我们现在对这些问题展开更加详细的探讨。

NEP 通常会遵循可预计的演替格局。NEP 经受扰动后降低。例如，由于叶面积的减小（从而也降低 GPP），昆虫爆发通常降低 NEP，但增加异养呼吸。当植被恢复后，GPP 增加比呼吸更快，导致 NEP 增加。不过，大约经过 80 年后随着森林年龄的增加，NEP 开始降低。正如前面所之处的那样，NEP 很少降到 0，即使在老龄的森林中。森林中大约一半的碳累积出现在地下根和土壤中，同时在地上部分中，大约 2/3 累积在粗木质碎屑中，其他则在活的茎中。但是，即使诸如极地冻原等生态系统也很少遭受大尺度的扰动以及扰动后演替表现出具有正的 NEP，表明演替动态并不是解释陆地上普遍出现正的 NEP 的唯一解释。

全球性的大气 CO_2 对生态系统氮输入的增加增强了 NEP，原因是对 GPP 的促进要比生态系统呼吸更加强烈。例如，与酸雨有关的氮沉降促进了森林碳储存达 6%，农田碳储存达 2%，但在其他自然生态系统中变化不显著。评估 CO_2 增加对 NEP 的作用相对耿介困难，因为 CO_2 增加在整个地球都是相对均匀的。然而，实验研究显示增加的 CO_2 浓度经常促进 NEP，尤其在更加肥沃的生态系统或者为了激发氮沉降效应而添加了其他养分的生态系统。在为受干扰的陆地生态系统中，人为活动造成的环境变化通常促进 NEP。

气候条件的时空变化对 NEP 的作用是不容易被预测到的，原因是较高的温度，改善了的土壤通气情况，改善了的水分可获得性，可以促进 NEP 的所有成分：GPP，植物呼吸，以及微生物的呼吸。例如，在欧洲南部，GPP 和生态系统呼吸都强烈地受水分限制。两个通量在湿润的年份或者地区均有相同程度的增加，这样在 NEP 和水分间并没有显著的相关性（图 7.5-4）。相应地在欧洲的北部地区，那里 GPP 和生态系统呼吸主要受温度限制，两个通量在温暖的年份或者地区都有相同程度的增加，这样在温度和 NEP 之间也没有显著的相关性（图 7.5-4）。当把两者结合起来考虑时，水分要比温度对 NEP 的影响更强，主要因为干旱对 GPP 降低的影响更强。这样，气候因子的年际变异对 NEP 的影响主要通过它们对 GPP，而不是生态系统呼吸的作用实现的，正如一年内季节变异对 NEP 的影响上所观察到的一样。

尽管 NEP 对温度和水分变化的敏感性并不是那么强，但长期来看，气候驱动因素的变化可能显著改变 NEP。例如，二十世纪末期二十年的温度增加幅度可以解释很多当前森林样地间 NEP 的变异，即使这些地方 NEP 对当前年份的温度变化并不敏感。短期的温度振荡也可能产生强烈的影响。例如在欧洲 2003 年 7 月的严重干旱降低了 NEP，其程度足以抵消过去 4 年的碳固定。增温的季节性也很重要。例如，通过提前融雪日期和植物生长光合作用，春季加温增加了 GPP 和 NEP。然而在秋季，当太阳角较低时土壤温度仍较高，增温对生态系统呼吸比 GPP 的增加更加强烈，这样就降低了秋季的 NEP。由于上述这些原因，在北美，显著的春季增温导致年度 NEP 的增加，而显著的秋季增温降低了年度 NEP。

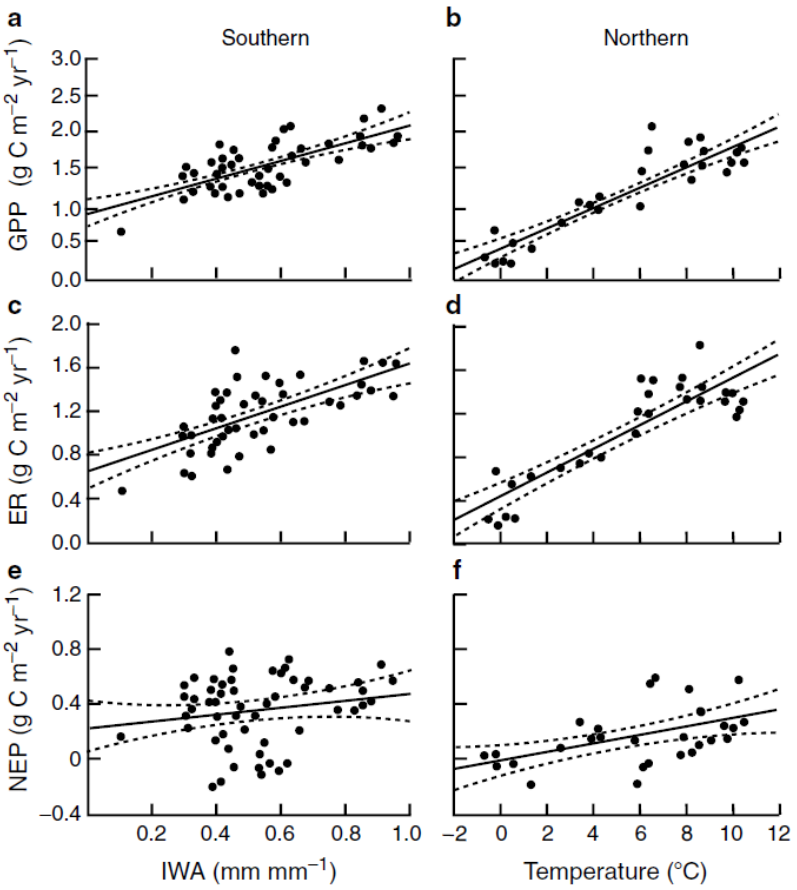


图 7.5-4 欧洲南部森林碳通量与水分可获得性指数（IWA，实际和潜在蒸散发比）的相关性和欧洲北部森林碳通量与年平均温的相关性。显示的通量包括总的初级生产（GPP，图 a 和 b），生态系统呼吸（ER，图 c 和 d）以及净生态系统生产（NEP，图 e 和 f）。实线和虚线分别表示平均和 95%置信区间。GPP 和 ER 要比 NEP 更加强烈地受环境因子的控制。

水位和土壤通气条件的变化也会引起 NEP 复杂的变化。淹水沼泽的排水最初降低了 NEP，原因是 GPP 降低了，有时还增加异养呼吸。经历较长时间后，由于更加高产的非沼泽植物种类的侵入增加了叶面积和 GPP，经常导致正的 NEP（即碳固定）。由于最近的气候暖化引起的永冻层的融化对生态系统呼吸的增加要强于 GPP，引起累积了几千年的碳发生损失。这个负的 NEP 可能转成为一个更强的气候变化放大效应（正反馈），要知道永冻层里具有两倍于大气圈的 CO_2。

总之，扰动后的自然演替过程，气候变化，以及人类对大气圈的影响都会影响 NEP，主要通过上述因素对 GPP 的作用。当前的证据表明人类活动强烈地影响了这些因素对生物圈 NEP 的控制。这些作用主要通过干扰和土地利用变化实现，它们有可能增加，也有可能降低 NEP；例如，氮沉降和大气 CO_2 浓度的增加通常增加 NEP，人为增温可能对 NEP 具有可变的效应。NEP 变化对气候系统和生物圈的净效应取决于生态系统碳储量的整体变化，这部分内容将在下一章节解释。

第六节　净生态系统碳平衡

净生态系统碳平衡（NECB）是生态系统碳累积的净速率。它是进入和离开生态系统的碳之间的平衡，即生态系统碳储量随时间的变化：

$$NECB = dC/dt$$

为便于理解 NECB，可以将生态系统看成一个具有一定体积和明确的顶、底和边的一个立方体。生态系统“箱子”的顶在陆地生态系统就是冠层上方，底是在根区下方，边则界定了要分析的面积。大多数进入生态系统的碳是以 GPP 形式，而离开生态系统则通过以下几个过程，包括植物和异养呼吸，可溶性有机碳（DOC）和可溶性无机碳（DIC），挥发性有机物质的释放，甲烷通量，以及扰动。诸如水土侵蚀/沉降，动物搬迁或者收获等侧向运输可以带来或者带出生态系统的碳（图 7.6-1）。NECB 就是这个生态系统箱子碳量的增加（正值）或者减少（负值）。

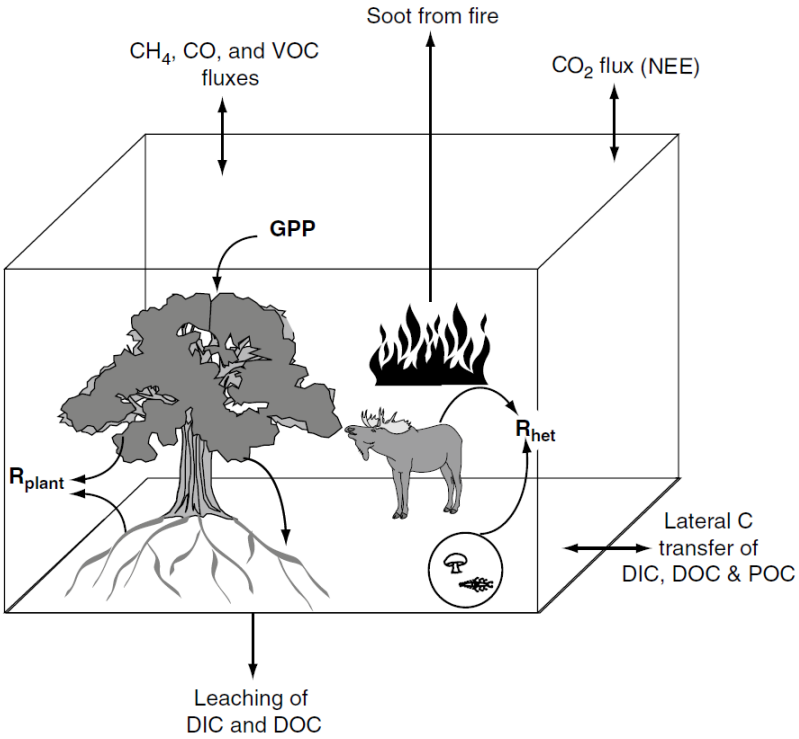


图 7.6-1 净生态系统碳平衡（NECB）的主要组成。决定净生态系统生产（NEP）的通量用粗体字表示。图中的箱子代表一个生态系统。对 NECB 和 NEP 有贡献的通量在正文中描述。

6.1 气体形式的碳通量（gaseous carbon fluxes）

大部分时间 GPP 和生态系统呼吸是主要气体形式的碳通量。然而，野火是生态系统阶段性大的额外的 CO_2 损失，CH_4 和 CO 通量是额外的对气候重要的气体释放。火烧引起的有机物质燃烧是从生态系统到大气圈的一个非呼吸性 CO_2 损失。火烧一旦发生，无疑将成为 NEE 和 NECB 的重要组成成分，尤其当在较长的时间尺度上整合 NEE 和 NECB，同时该

时间尺度又包含了扰动的发生。火烧本身不是 NEP 的一个组成成分（即 GPP 和呼吸间的平衡）。在许多情况下，火烧引起的碳损失是长期碳概算的显著组成。例如，在加拿大北方森林，火烧过程中损失的碳差不多等于平均 NPP 的 6-30%。因为对演替阶段的敏感性，NECB 和 NEE 在区域尺度上的估计取决于不同林龄森林立地的相对多度。当不断增加扰动频度时，NECB 可能是负的，正如最近北美西部野火的增加。相反，经历了上世纪大面积农田弃耕的地区，就像在欧洲或者美国北部，会产生一个正的 NECB。由于缺乏有关扰动频率区域变化的足够信息，NECB 是导致解释全球碳循环变化不确定性的重要来源。

非 CO_2 气体的通量在净 CO_2 通量较小的生态系统可能占到 NECB 很大比例。例如，在北半球永冻层和冰占主要覆盖的区域（极地和北方森林，以及北冰洋）陆地和海洋碳汇较小。大量来自湿地的甲烷排放使得该地区成为对气候具有重要的正的温室气体暖化效应。此外，由于火烧引起的 CO 释放（47 Tg C $year^{-1}$）以及从湿地和野火排放的甲烷（31 TgC yea^{r-1}）相当于净 CO_2 固定（51 Tg C $year^{-1}$），表明多个气体在区域碳平衡上的重要性。

导致生态系统内碳再分配的扰动对 NECB 的影响仅是间接的，原因是相关的碳仍都保留在生态系统内。例如，飓风或者昆虫爆发将碳从活体植物转移至土壤或立枯死植物，并没有引起碳从生态系统流失。然而，这些干扰通过减少光合能力以及增加分解者食物可获得性从而间接地影响 NECB。换句话说，这些碳平衡的变化通过它们对 NEP（=GPP-生态系统呼吸）的作用而影响 NECB。

人类对化石燃料的消耗是大气圈 CO_2 增加的一个主要来源。这在工业化农业及在许多诸如人类居住的城镇等生态系统中是一个大的碳通量。化石燃料消耗代表了从过去有机碳的惰性地质库（煤，石油和天然气）转移到了大气圈。

6.2 颗粒碳的通量（particulate carbon fluxes）

进入和流出生态系统的颗粒碳侧向运输可能对生态系统长期碳概算十分重要。碳可以通过风和水引起的侵蚀和沉降，以及动物包括人类的搬迁作用侧向流出或进入生态系统。在许多生态系统中，这些侧向运输是如此之小，以至于在大多数年份是测不到的。然而经过长时间或者经历极端事件，侧向运输可能在量上是重要的。例如，如果没有考虑来自其他国家的食品输入，欧洲 NEE 的观测结果无法解释。同样，在美国中西部的作物产品生产州，最东部的州输出大部分农作物产品，因而是一个净 CO_2 汇，而最西部的州用这些农产品饲喂动物，并将这些农产品呼吸，将碳释放到大气圈中，导致几乎没有净碳固定。在经营的森林，农业和放牧以及其他人为修饰的生态系统，这些生态系统已经占据陆地表面的很大一部分，其含碳生物量的侧向运输是 NECB 的显著组成部分。

6.3 溶解性碳的通量（dissolved carbon fluxes）

溶解的有机和无机碳（分别为 DOC 和 DIC）向地下水和河流的淋溶在一些生态系统是碳损失的一个重要途径。

总之，GPP 和生态系统以外的（碳）通量在大多数生态系统是十分重要的，尤其是在较长期的时间阶段。所以，NEP 和 NEE 的变化只能讲述部分关于陆地生态系统碳平衡的故事。

第八章 植物的养分利用

植物的养分吸收，利用和损失是生态系统矿物质循环的关键步骤。本章主要描述调节植被养分循环的因素。

引言

养分供给限制了生物圈的生产力。养分的实验性添加增加大多数生态系统的生产力，无论是水体还是陆地生态系统，表明初级生产广泛存在的养分限制性。虽然水分的可获得性是陆地生产力的主要限制，不管在哪一个气候区，通常会存在一个强烈的养分可获得性和植物生产的相关性。在湖泊和海洋，渔业产量紧密地与养分供给和初级生产相一致。集约化农业也由于持续的生产而依赖于养分的添加。鉴于广泛存在的养分限制性，对植物养分获取，利用和植物养分丢失的控制的理解是十分必要的，以归纳对植物生产以及其他生态系统过程控制的特点。

第一节　核心问题

农业和城市养分的输出增加了许多湖泊和河流的藻类生产力，降低了这些水体系统的水质和娱乐价值。养分污染使得生产力大大高于自然发生水平，导致级联效应，波及到所有生态系统组分。例如，在曾经是清水的湖泊，养分富集常引起令人可怕的藻华爆发，大大改变或者完全阻止了鱼类的生长。因此，高的生产力并不总是一件好事。为什么一些湖泊比其他湖泊对养分输入更加敏感？哪些营养元素对湖泊生产力具有最大的长期影响，如何能够在经营性的景观中降低来自陆地的这些养分输入？理解和管理这些对初级生产力的养分控制是极为重要的，无论是对一些引人关注的特殊生态系统而言，还是对全球碳动态和气候来说。

第二节　概要

植物总是对一些营养物质比其他营养物质具有更多的需求。基本的大量元素是大量需求的营养物质。大量营养元素（macronutrients）通常限制植物的生长，主要包括氮、磷和钾。植物也需要大量的钙、镁和硫，但这些营养物质对植物生长的限制并不是经常发生。微量营养元素（micronutrients）对植物生长也是必需的，但需求量较小。这些元素包括硼、氯、铜、铁、猛、钼和锌。有益营养元素（beneficial nutrients）在某些特定条件下或对某些植物而言能促进植物生长。例如，蕨类植物铝，固氮共生体需要钴，硅藻需要硅等。植物对其他元素并没有需求，或者需求量是那样的小，以至于少量的存在就可能对植物生长有害（有毒的，例如硒）。植物根基本上对这些元素有排斥作用，虽然一些植物已经进化出了对它们的忍耐机制，甚至可以累积这些元素至一定的水平，作为对病原菌和草食动物取食的防御。

通过植物循环的养分量取决于养分供给和支撑植物生长的养分需求之间的平衡。支撑植物最大生长的养分比例在大多数植物是相似的。低于最优平衡的任何养分元素都有可能限制植物生长，从而被植物偏爱吸收。任何超出植物需求而存在的养分通常被植物吸收得更加缓慢。这样，植物中的养分趋同于一个常规的比例，虽然这个比例也会产生不断的变化，主要原因是植物如何利用养分元素存在差异或者养分供给存在差异。上述趋同的结果是植物生长经常会对超过一种养分的添加产生响应（多养分限制）。其次，当一种养分元素的存在比其他必需养分元素的丰度低得多时，该限制养分元素的供给决定了大多数营养元素的循环速率。该元素的化学计量就会影响生态系统大多数必需养分元素的循环。因此，理解养分循环的关键是确定哪种（些）养分元素限制植物生长，以及控制这些元素循环的因素。在一些情况下，植物生长主要不是受养分供给的因素限制，此时，通过植物的养分通量取决于植物养分需求，而不是直接取决于养分的供给。植物可利用养分，如果没有被植物吸收，将很容易从生态系统丢失。本章我们首先讨论养分对植物生长限制的特征，然后讨论海洋和淡水生态系统，哪里养分吸收直接与它们在生长过程中的利用衔接。我们此后转向陆地生态系统的复杂养分关系，探讨植物对养分吸收的控制，养分含量与生产的关系，最后是对植物养分损失的控制。

究其本质而言，养分对植物生长的限制在具体操作上被定义为一种养分（或一些养分）添加后能够促进植物的生长。养分限制性有很多预测指标，包括植物组织的元素比例，土壤养分供给的测度，以及植物用于获取养分而对根的分配。这些指标可以为确定在一个给定的地貌单元、植物学或者环境空间中，并在这些空间可以采用养分添加实验加以验证的养分限制性提供了一个很好的证据。

尽管该定义具有直观性经验性的特点，在理解植物群落养分限制性时，一些因素可能使其应用复杂化。首先，一些植物是内在的对添加养分响应很小。例如，适应于或者生长在贫瘠立地中的植物可能对脉冲式添加养分的响应方式是将大部分养分贮藏起来，仅在生长上产生一个小的（虽然持续）的响应。相反，适应或者生长在一个肥沃立地中的植物可能吸收所有的脉冲式添加的养分，并将大部分光合产物分配至增加的生长。植物在两种情况下都是养分限制的，但肥沃立地中的植物表现为比贫瘠立地中的更加养分限制。

其次，并不是所有通过短期养分添加实验识别的养分限制是等效的。一些养分的添加可以暂时促进植物生长而不彻底改变植物群落组成，但其他一些养分的添加可能转变群落和生态系统，在短时间区分这属于哪种情形是很难的。一个在实用性上具有很强指示意义的区分的例子是上世纪70年代有关养分可以驱动湖泊生态系统富营养化（eutrophication）（过度的富集和转化）的论战。社会的不同阶层通常关注不同的元素。清洁剂是磷酸盐的主要来源，农业是硝酸盐的主要来源，而污水处理厂则是可溶解有机碳的主要来源，可溶解有机碳可能分解并释放CO_2。对营养缺乏的（oligotrophic）（低营养的）低碱性湖泊水分进行短期养分添加实验，结果表明浮游植物生长对氮、磷，或者CO_2的添加产生响应，证明湖泊水分中的浮游植物是养分限制的，但忽视了其中哪一种养分可能是导致富营养化的。然而，David

Schindler的一系列整湖实验证明了磷（也只有磷）的添加是必要的，且足够驱动湖泊的富营养化。

如何解释短期生物测定试验与整个湖泊对养分添加响应的不一致性？这里，磷的添加有利于固氮的蓝藻细菌的生长，其活动将氮带入湖泊中。在氮、磷刺激下浮游植物的生长耗竭了CO_2，引起短期更大的CO_2限制，但加大了扩散梯度以及大气圈和湖泊水分的CO_2通量。由于三种元素都得到了富集，湖泊从低营养的转变成富营养的。从清澈见底转变成了充满池塘浮渣。然而，磷的添加固然可以给湖泊带来更多的氮和碳，添加氮或者碳却不能给湖泊带来更多的磷。所有三种元素都是限制的，但只有磷的添加可以将一个低营养湖泊转变成一个富营养湖泊。我们认为一个具有转换一个群落或者生态系统能力的养分元素是一个**终极限制性营养元素**（ultimate limiting nutrient），而任何元素，其添加可以短期增强生长的，则是一个**近似限制性营养元素**（proximate limiting nutrient）。

无论是氮，还是磷，在许多生态系统中代表了近似限制性营养元素。在某个环境条件下，例如上述叙述的磷在湖泊生态系统中，任何一种都有可能成为陆地或者水体生态系统的终极限制性营养元素。陆地生态系统的动态是不同的，在于陆地生态系统是开放的系统，可以累积几十年输入（未风化岩石的抬升，降水和降尘）的养分，其中受某个特定的营养元素限制的植物和微生物善于吸收并保持该营养元素在生态系统内。近似性磷限制的发生有多个原因，包括氮或其他资源供给的增加。然而，终极性磷限制可能发生在长期风化和淋溶耗竭了古老土壤中可利用磷的供给，或者在母岩矿物风化不能提供足够的磷，使其与其他限制性资源供给匹配（或者因为母岩矿物中含有很少磷，或者因为所含的磷难于风化）。

识别和解释终极氮限制则更具挑战性，原因是潜在的生物固氮可以利用大量且可以获得的大气氮库中的氮，并转变成生物可利用氮，进入生态系统循环。要发生终极氮限制，两个条件必须满足。首先，必须存在一个氮从生态系统损失途径，且该途径不能被那些受氮供给限制的生物所阻止。有些形式的可溶性有机氮通过淋溶而丢失代表了该途径的一个例子。其次，个别因子或多个因子必然限制生物氮固定，即使在有些氮限制的地方。可能的因素包括氮固定的能量消耗（可以使那些共生固氮植物难于穿透一个已经封闭的植物冠层），固氮植物受磷或其他元素不成比例的限制，或者草食动物典型地偏爱共生氮固定生物的富含氮的组织。类似的因素也可以引起河口区域终极性的氮限制，那里由于相对较短的水分存留时间与固氮蓝藻细菌限制，这种限制是由于受铁限制和食草动物取食而保持氮限制引起的。

无论是近似养分限制还是终极养分限制对生态系统的功能过程十分重要，因而本章我们将同时考虑这两方面的（以及驱动它们的机制）内容。

第三节　陆地生态系统养分向根的运动

陆地生态系统养分循环包含了高度局域化的植物、微生物及其物理环境间的交换。与主要与充分混合的大气圈库交换的碳不同，陆地生态系统的养分被植物吸收并返回土壤通常局限在一个个体植物的根系周围。大多数陆地生态系统的植物吸收的超过90%的氮和磷是来自

前几年植被返回土壤的再循环养分。因此，对养分吸收和利用的控制，必须在一个与碳相比更加局部的尺度上探讨。个别生态系统，或者更确切地说，个别植物对氮供给具有强的局部效应。例如，深根的栎树和山茱萸能够从深层土壤吸收钙，并且形成阳离子丰富的凋落物，改变了表层土壤的化学性质，导致与众不同的地表植物区系，特别是与邻近的吸收较少阳离子，并形成更加酸性的凋落物的浅根松树相比。

根系接触到养分主要通过以下三个途径：扩散，质流和根截获。根系只能吸收到哪些可溶解的并与活的根细胞接触的养分。由于根系只占地下空间中的很小比例（小于<1%），溶解的养分必须首先从非根际土壤（即并没有与根接触的土壤）运动至根表面才能被植物吸收。

3.1 扩散（diffusion）

扩散是输送植物根系养分最多的一个过程。扩散是分子或离子沿着一个浓度梯度的运动。养分吸收和矿化通过减少根表面养分含量（吸收过程）和增加其他地方土壤中的含量（矿化过程）为向根表面扩散提供了驱动力。通过矿化和其他途径输入进入可溶性养分库是向根表面扩散养分量的主要控制。

土壤阳离子交换量（cation exchange capacity，CEC）也会影响可利用养分库向根和根系占据的土壤空间的扩散。具有高的阳离子交换量的土壤储存了更多的单位体积土壤中可交换的阳离子，也即它们具有高的缓冲能力，但由于交换反应会减慢养分向根表面的运动速率。当处于高发溶液浓度时，这些反应从土壤溶液中去除阳离子，而在土壤溶液处于低浓度时返还阳离子。于是，根在任何一个时间能够汲取比实际溶解在土壤溶液中更多的养分，尤其是在具有高的盐基饱和的土壤中，那里的交换复合体（exchange complex）具有充足的阳离子。阴离子交换量通常要比阳离子交换量小得多，所以大多数阴离子，例如硝酸根，在土壤中比阳离子扩散更加快速。然而化学上易起反应的阴离子，像磷酸根，趋向于沉淀，降低它们在溶液中的含量以及进一步向根表面的扩散速率。

由于电荷密度的差异（即单位离子水化物体积中的电荷），离子之间扩散速率差别很大。电荷密度反过来又依赖于每个离子的电荷数量和离子的水合半径。像钙和镁等二价的阳离子要比像铵和钾等单价阳离子与交换复合体结合得更紧，从而扩散得更慢。同样电荷的离子在扩散速率上也会因为半径和与该离子松散结合的水分子数量而有稍微的不同。

土壤颗粒大小和水分决定了从非根际土向根表面扩散路径的长度。离子需要扩散穿过包裹土壤颗粒表面的水膜。水分含量越高，颗粒体积越小，从非根际土到根表面的扩散路径越直接。因此，在湿润土壤中扩散要比在干旱土壤中快得多，在粘土含量高的土壤中要比在粗质地沙性土壤中快得多。

每一个吸收根都营造出一个扩散壳（diffusion shell），也即一个圆柱体土壤，其中的养分可以被根完全吸收。这个扩散壳构成了一个直接受植物根吸收影响的土壤区域。对于那些扩散快的离子，根可以接触到相对较大体积的土壤。例如，硝酸根的扩散很快，根通常可以吸收到其周围大约6-10mm半径中的养分，而只能吸收到1-2mm半径范围中的铵根离子，磷

酸盐的则不足1mm。所以，与硝酸根相比，植物需要更高的根密度才能吸收到土壤中所有磷酸根或者铵根。在许多生态系统中，根的密度是足够高的，可以利用大部分土壤空间中的硝酸根，但只能利用很小一部分土壤空间中的铵根或者磷酸根。植物加强对那些扩散慢的离子吸收的主要方法是增加根的长度，这样就可以增加植物利用到土壤的比例。

3.2 质流（mass flow）

养分向根表面的质流加强了扩散离子的供给。质流是溶解性养分在流动的土壤水中向本表面的迁移。植物蒸腾的水分损失驱动土壤溶液向根表面的质流是主要的机制。质流可能对于那些在土壤溶液中大量存在的，或者植物少量需求的养分供给是重要的。例如，钙在多数土壤中含量如此之高，所以植物对钙的需求是完全可以通过从非根际土壤向根表面的质流满足的。再例如，玉米可以通过向根表面的质流可以获得超过4倍根实际需求的钙。如果植物通过质流接受到太多的钙，植物就会主动从根向土壤溶液分泌一部分钙，就会形成离开根表面向非根际土壤的扩散梯度。其他植物需求很少量的养分（微量元素）完全可以通过质流得到满足。然而，对于那些植物大量需求，但在土壤容溶液中含量很低的养分元素，例如氮、磷和钾，依靠质流供给养分是不够的。这些大量养分元素（即植物大量需求的）主要通过扩散提供。即使在农业土壤中，那里土壤溶液含量要高得多，质流提供经常限制植物生长的那些营养元素量也不足10%。因此，是扩散，而不是质流，是提供对植物生长有潜在限制作用养分（氮、磷和钾）主要的方式。当土壤肥力下降时，扩散对养分的供给变得更加重要。

水分在土壤中的饱和性流动提供了额外的养分，并补充了扩散壳中的养分。饱和流动是水分主要在重力作用下通过土壤的运动。雨后，一旦水分含量超过土壤持水量（water-holding capacity）时，水分由于饱和性的流动从土壤自上而下排出。因为养分可获得性和矿化速率通常在最表层的土壤中很高，这种垂直方向的流动对养分再分布和根周围扩散壳养分再补充。无论是根的生长，还是土壤水分的垂直运动都在土壤裂隙中容易发生，从而很快消除围绕这些根的扩散壳。有些生态系统具有常规水平方向地下水流动，可以穿过不透水土壤层，这种饱和性流动对这些生态系统也是十分重要的。例如，冻原上根位于永冻层下的深根植物，在有快速侧向亚表层水分流动的区域要比在没有侧向地下水流动区域的，所吸收到的养分和生产力都要高10倍。河岸生态系统生长的乔木和灌木高的生产力部分是因为它们的根能经常分布到潜水面和溪流下的地下水（潜流带），那里的植物根能够吸收到通过根区的饱和流水中的养分。

3.3 根的截获（root interception）

根的截获并不是提供根养分的一个重要机制。当根伸长进入到新的土壤时，它们可以截获那些以前未被根占领的土壤中可利用养分。然而，单位土壤体积中可利用氮、磷和钾的量总是低于生长这些根所消耗的养分量，因此根的截获永远不会是植物地上部分供给养分的一种重要机制。根的生长是重要的，不是因为它截获养分，而是因为向新的土壤空间扩展，营造新的养分可以通过扩散和质流向其运动的根表面。

第四节　养分的吸收（nutrient absorption）

养分吸收，谁负责？三个因素控制植物养分吸收：土壤中养分的供给速率，根的长度和单位根的活性。正如光合作用一样，有几个因子影响生态系统尺度上的养分吸收。对这部分内容我们主要的结论是：（1）养分供给速率是主要的因素，解释了不同生态系统在平衡状态时养分吸收的差异。换句话说，土壤的养分供给，而不是植物的性状特征，才是决定植物养分吸收在生物群区间的差异。（2）诸如根的长度、根的深度或者根的活性等植物性状影响植被总的养分吸收。这主要是在以下情形下，养分供给速率超过植物养分需求（例如最近伐过木的立地或者高强度施过肥的农田），或者在植物性状可以有助于接触到其他条件下接触不到的土壤养分库（例如深层的土壤养分库）。如果有足够时间，植物会逐渐趋向于生长在其吸收养分能力与土壤养分供给相一致的地方。（3）根的长度是控制哪些植物在一个生态系统中竞争限制性养分资源最成功的主要因素。

4.1 养分供给（nutrient supply）

在一个很广的养分可获得性范围里，植被对养分的吸收主要受养分供给支配。关于养分供给决定植被吸收的最令人信服的证据是，大多数生态系统，即使是具有相对肥沃土壤的生态系统，都会对养分添加产生响应，表现为养分吸收和NPP的增加，就像在水体生态系统中所观察到的那样。

4.2 根长度的发展（development of root length）

当受扰动后的植被逐渐恢复，或者在高的土壤肥力的生态系统，根的长度强烈地影响了植物养分吸收和NPP。在这些条件下，新根长的生长可以允许植物占据新的土壤空间，使植物根的扩散壳与相邻根的不重叠，土壤中的养分还没有被现存的根系统完全利用。这种情形尤其会在受扰动后的生态系统中发生。即使有一个完全发育的“根冠”（root canopy），个别植物增加的根生长也可能是有利的，原因是增加了该植物获取的养分占总的养分供给的比例。

模拟模型定量显示了不同植物和土壤参数在决定植物养分吸收中的作用。这些模型表明养分吸收对养分供给以及根占据的土壤体积要比对养分吸收的动力学更加敏感，尤其是对那些移动差的离子如磷酸根。例如，在低养分供给时，影响扩散因素（扩散系数和缓冲能力）上的差异和根的长度（伸长速率）对养分吸收具有比动力学（最大和最小吸收能力或根对养分的亲和力）或者影响质流的因素（蒸腾速率）大得多的作用。吸收动力学在决定哪一个根得到养分时更加重要，而不是植被总的吸收。

根的长度要比根的生物量更好地预测养分吸收。在植物从土壤吸收养分的短期研究中，根的长度与养分获取存在紧密相关性。具有高的比根长（specific root length，SRL，即单位重量的根长）最大限度地扩大了单位根重量的根长度，于是最大限度地增加了给定生物量投资条件下能被植物利用的土壤体积。我们对根的形态学和生理学的了解要比植物少得多。然而，有限的可获得的数据表明草本植物要比木本植物具有更大的SRL，同时，任何生态系统中根的SRL都具有很宽的变化范围。SRL的大部分变异反映了地下器官的多重功能。根系可

能具有很高的SRL，可能是因为它们具有较小的直径，也可能因为具有很低的组织密度（单位体积的重量）。一些地下茎和粗根具有大的直径用于储存碳水化合物和养分或者运送水分和养分，从而在养分吸收上起的作用很小。也可能在SRL和细根寿命间存在权衡，即高密度根要比低密度根不容易受干燥影响和被草食动物取食。生长缓慢植物的叶片和根通常具有高的组织密度，低的资源获取（分别为碳和养分）速率，但要比生长更加迅速的植物具有更大的寿命。

根系偏爱在可利用资源高的区域生长。根在土壤中的生长并不是随机的。遇到高的养分可获得性微区的根就会大量分枝，使得植物可以优先利用这个高可利用养分的区域。这就解释了为什么根的长度在表层土壤中最大，原因是那里养分输入和矿化作用最大，即使根系是向地性的（geotropic）（即垂直向下生长）。这种对养分热点（丰富）地区的利用保证植物在一定的根投资条件下最大限度地获得养分回报。这样的根生长格局也降低了土壤养分含量在微尺度上异质性的影响。在更加微小的尺度上，作为扩展进入土壤的根表皮细胞的延伸，根毛可以增加根的长度（例如，从0.1到0.8mm），以响应硝酸根和磷酸根供给的减少。上述两者响应增加了可用于养分吸收的根的长度和表面积。然而，热点区域的利用并不是经常发生，可能在快速生长的植物要比生长缓慢的植物更加突出。植物通过根或者根毛的生长，或者与菌根真菌的结合，延长它们吸收养分的器官长度。上述每一种利用新的土壤的模式在低养分供给条件下更加突出，虽然我们这里重点集中在根的延长，因为这个过程得到了最好的记载。

4.3 菌根（mycorrhizae）

菌根可以增加植物利用的土壤体积。菌根是植物根与真菌菌丝之间的共生关系，在该共生关系中植物从真菌获取养分，并以真菌主要碳源的碳水化合物作为回报。大约80%的被子植物，所有裸子植物，许多蕨类植物是形成菌根的。这些菌根关系在十分宽广的环境和养分条件范围里是重要的，包括人工提供养分的作物。关于养分吸收，菌根的菌丝基本上作为根系统进入非根际土壤的延伸，经常为每厘米的根提供1-15m长的菌丝，也即是植物吸收长度有2-3个数量级的增加。因为养分通过菌丝传输要比沿着一个曲折的路径，穿过土壤-水分膜快得多，从而降低了植物吸收的扩散限制性。相比植物根（通常0.1-1mm），菌丝的直径（<0.01mm）较小，可以使植物在对菌根菌丝一定量的生物量投资比对根的同样生物量的投资可以利用更多的土壤空间。植物通常投资4-20%的GPP用于菌根菌丝的生长。大部分的碳用来支持菌丝的呼吸，而非菌丝的生物量，所以一定的对菌根生物量碳投资可能反映了植物一个大的碳成本。菌根对植物补充那些在土壤中扩散缓慢的养分十分重要，尤其是磷酸盐，以及硝化速率低的生态系统中的氨盐也有可能。虽然室内实验显示植物在高养分条件下一致地从根排除菌根，菌根在一个广阔的土壤肥力范围里广泛分布，包括作物生态系统，表明菌根即使在相对肥沃的土壤中也可以持续地向植物提供净的效益。

共有几个类型的菌根，最常见的是丛枝菌根（arbuscular mycorrhizae，AM；或者vescular arbuscular mycorrhizae，VAM）和外生菌根。AM真菌生长穿过根皮层细胞的壁，即涉及养分

吸收的根细胞层，很像一个根的致病真菌。与根的致病菌不同，AM形成丛枝，是高度分支的树状结构，主要由真菌形成，并有根皮层细胞的质膜围绕。丛枝是真菌和植物间交换养分和碳水化合物的结构。AM在草本植物群落中最为常见，例如草原，磷限制的热带森林，以及在早期演替的温带森林。许多AM联合体是相对非专一性的，甚至可以在受到扰动后不久与形成外生菌根植物种类形成AM菌根。当外生菌根占据这些植物根后，通常AM被排除。

对于一个确定的生态系统，丛枝菌根发育最好的是在磷缺乏的条件下，因为AM可以降低吸收的扩散限制。AM共生是植物和真菌之间的动态相互作用，表现为根和菌丝周转很快。在植物生长处于碳限制的条件下，正如在幼苗、遮荫或者高肥力条件下植物生长，菌根可能充当寄生者，并减小植物生长。在这些条件下，植物会减少新生长根中侵染点数目。随着老根的死去，这会降低侵染根的比例，从而减少植物碳的消耗。AM可能被认为是在根和真菌间的一个平衡寄生关系，受双方的严格调节。

外生菌根（ectomycorrhizae）是根和真菌间相对稳定的联合体，主要出现在温带和高纬度木本植物中。交换器官是一个围绕在根周围的真菌菌丝形成的帽或者鞘，再加上穿过皮层细胞壁的菌丝（Hartig net，海提格网）。根对外生菌根的响应是减少根的伸长，增加分支，形成短的，高度分支的小根。真菌组织占这些根尖大约40%的体积。就像AM一样，外生菌根也包含一个在真菌和根之间的养分和碳水化合物的交换。与AM不同的是，外生菌根通常延长根的寿命。外生菌根具有蛋白酶和其他可以攻击（分解？）有机氮化合物的酶，这也与AM不同。真菌可以吸收降解后的氨基酸，并将它们运输至植物。所以，外生菌根可以同时促进植物氮和磷的吸收。

其他种类菌根组合在功能上与AM和外生菌根不同。

4.4 氮的固定（nitrogen fixation）

在高光照和氮限制的环境里，固氮植物可以接近大量的氮。植物与固氮细菌形成共生关系，以消耗碳水化合物获得氮，就像在许多菌根联合体中。通过这种组合，植物能够攫取大气圈氮库中用之不竭的氮，而大气圈中的双氮是无法通过其他途径获得的。氮固定是高耗能的过程，所以最经常发生在充足光照和低可利用氮的生境中。这些生境包括许多干旱的环境，例如稀树干草原或者土壤尚未发育的区域。我们将在下一章详细讨论氮的固定。

4.5 根的吸收特征（root absorption properties）

植物在根表面从土壤溶液吸收有潜在限制作用的养分的主要途径是主动运输。植物根从土壤溶液获取养分主要通过主动运输（active transport），一种逆浓度梯度穿过细胞膜、消耗能量的离子运输。由于植物细胞内高含量的离子和代谢物，不断有养分沿着浓度梯度从根渗漏出去。例如，磷酸盐大约会以从土壤吸收它的1/3速率从根渗漏。这种被动渗漏的离子、糖和其他代谢物可能占一大部分从细根分泌的物质。进入根的离子以被动的质流和扩散方式穿过皮层的细胞壁，向根的内部运动（图8.4-1）。当养分通过皮层细胞壁向根的中心运动时，相邻皮层细胞以主动运输的方式吸收这些养分。养分可以通过细胞壁运动直到内皮层，是由

软木脂（蜡）包裹，在皮层和木质部之间的一层细胞。一旦养分被皮层细胞吸收后，它们通过一条细胞间相互连接的链运动到达内皮层，在那里被分泌进入死亡的木质部细胞。木质部细胞通过蒸腾流将水分和养分运送至植物地上部分。根大概有30-50%的碳概算是用来支持养分吸收，可见养分吸收需要消耗大量能量。植物少量需求的元素经常简单地采用质流或者扩散的方式进入根皮层细胞。

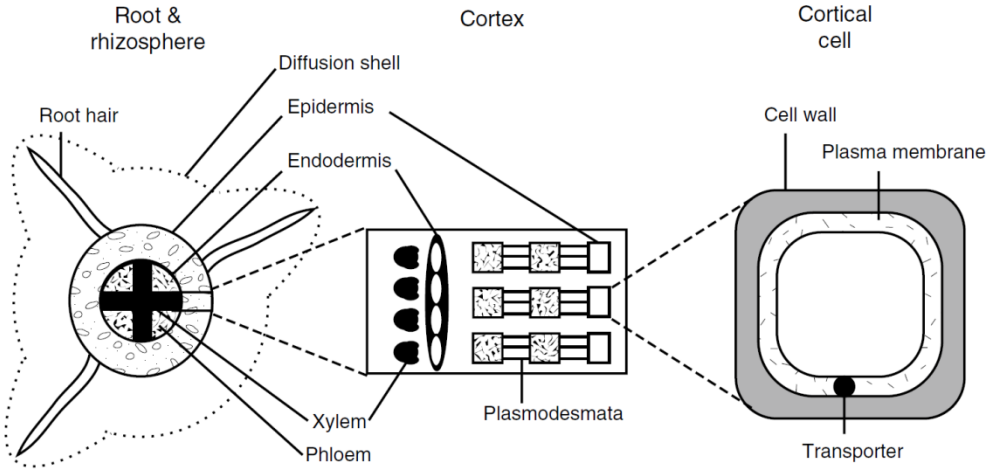


图 8.4-1 三个尺度的根的横切面。根际（或者扩散壳）是受根影响的土壤。皮层有一层外层细胞（外皮层），部分延长形成根毛。皮层通过一层蜡质细胞（内皮层）与传导组织（木质部和韧皮部）分离。每个皮层细胞吸收在细胞壁间隙里向细胞膜扩散的离子。结合在膜上的蛋白质（转运子）以主动的方式运送离子通过细胞膜。离子或者通过细胞壁，或者通过相邻皮层细胞间细胞质的连接（胞间连丝），从最外面的皮层细胞向内皮层运动。

一些植物种类可以利用其他植物无法利用的养分库。虽然所有植物需要相似比例的相同组成的养分，氮有多种可利用形式（硝酸盐、铵盐、氨基酸等），这些形式氮的可获得性在不同生态系统中存在差异。植物对这些不同氮形态的偏爱程度不同，在它们适应的生态系统中经常表现出一种强的，可以吸收最丰富形式的氮的能力。例如，虽然即使农业种植的物种也可以利用氨基酸氮，许多在冻原和北方林生态系统丰富有机质的土壤中生长的物种偏爱吸收氨基酸。群落中物种在氮吸收偏爱上差异的结果是氮素有多个植物可以竞争的显著不同的资源。在同一个群落中的物种，其组织中的氮经常具有明显不同的同位素特征，原因是它们吸收不同来源的氮，或者不同的化学形式（硝酸盐，铵盐和有机氮），或者不同的路径（不同的菌根共生体），或者不同的土壤深度（图8.4-2）。

氮的三种主要的形式被结合形成生物量时消耗的碳不同。结合氨基酸消耗的碳最小，结合铵盐时需要连接在一个碳骨架上（同化过程），才能被用来衡量植物氮吸收经济。最后，硝酸盐必须被还原成铵盐才能被同化。硝酸盐的还原是十分耗能的。大多数植物运送一些硝酸盐至叶片，在叶片里，植物利用过多的来自光反应的还原能还原硝酸盐。在这种情形下，硝酸盐还原的高能耗并不影响其他植物过程的能量利用。高的光照和硝酸盐的可获得性增加硝酸盐在叶片中还原的比例。不同植物在叶片中还原硝酸盐的能力也有差异，适应高硝酸盐

环境的植物种类通常在叶片中具有较高的硝酸盐还原能力。例如在受干扰的生境中，热带和亚热带多年生植物和许多一年生植物可以在叶片中能还原较高比例的硝酸盐，而在温带裸子植物和欧石南（杜鹃花科）植物中，大多数硝酸盐还原是在根中。氮的可获得性在温带和高纬度陆地环境中通常是十分有限的，以至于在决定植物吸收和利用氮的形式时，土壤中不同形态氮的相对可获得性要比同化消耗更加重要。植物通常吸收任何它们能吸收的氮形式。

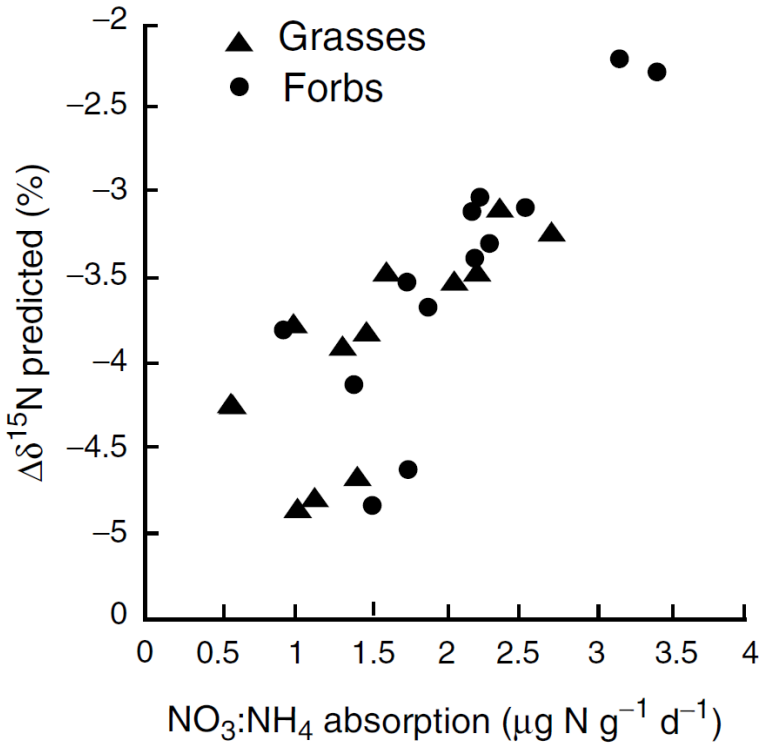


图 8.4-2 7 个杂类草和 8 个禾草预测的硝酸盐和铵盐吸收比例和预测的 δ^{15}N 含量间的相关性。在这些草地样地中硝酸盐具有高的 δ^{15}N 含量，所以物种吸收越多的硝酸盐，就会具有越高的 δ^{15}N 含量。

不同植物在它们可利用的磷库上也有区别。一些植物种类的根可能生成磷酸酶，释放植物根可以吸收的磷酸盐。例如，在以莎草科植物占优势的极地tussock冻原，通过吸收根磷酸酶作用的产物，植物可以满足它们大约75%的磷需求。其他植物，尤其是在干旱环境中的植物，分泌诸如柠檬酸或者苹果酸类的螯合剂，通过扩散从根进入非根际土壤。这些螯合剂可以从不溶于水的铁-磷酸盐复合物上螯合铁，从而溶解磷酸盐。溶解是磷酸盐此后向根扩散而被吸收。一些植物，尤其是澳大利亚和南非的山龙眼科（Proteaceae）（疑杜鹃花科？）石南类植物，可以形成致密的排根（proteoid roots），这些根在分泌螯合剂时十分有效，并溶解磷酸铁。植物可以形成许多类别的螯合剂（siderophore，铁载体），虽然这些物质的分泌对植物有什么样的帮助还不清楚。因此，不同植物在它们可利用的土壤磷库上不同，但是我们这些种间差异的生态系统的影响还只有一个初步的了解。

物种在根的深度和密度上的差异影响植被能够吸收的养分库。在相同土壤上相邻生长的草地和森林经常在养分年吸收和生产量上有很大的差别，原因是扎根更深的森林乔木要比浅

根的植物种类可以利用更大的土壤体积，从而有一个更大的水分和可利用养分库。总之，植物种类成分可以通过多个机制影响植被吸收的养分量和养分形式。

根的吸收能力会随着植物对养分需求的增加而增加。当地上环境有利于快速生长以及相应的高的养分需求，植物根就会通过在根的皮层细胞中合成更多的运输蛋白，从而增加根吸收养分的能力。物种具有高的固有的相对生长速率或者处于可以支持快速生长的条件下，通常具有高的单位根吸收养分的能力。例如，高光照和高的空气温度会增加更的吸收能力，而遮荫，干旱和处于物候上的低生长阶段通常导致低的养分吸收能力。然而，快速生长的根则具有高的吸收养分的能力。因此，植被吸收养分的速率不仅受决定养分供给的土壤因素，也受决定养分吸收的植物因素影响。在野外研究中，养分吸收与NPP紧密相关。然而，在解释这一关系时，要分清因和果却是很难的。

根在吸收动力学上的变化可以对植物吸收一些特别养分的获取有微调的作用。离子转运蛋白对个别离子的运输是专一性的。换句话说，铵盐，硝酸盐，磷酸盐，钾和硫酸盐都是由不同的个别调控的膜结合蛋白来运输。植物为这些专一限制植物生长的离子诱导额外的运输蛋白的合成。因此，受磷限制的植物根具有强的吸收磷酸根的能力，而受氮限制的植物根则具有强的吸收硝酸根和铵根的能力。将硝酸盐还原成铵盐（硝态氮形成氨基酸参与生物合成的第一步）的硝酸盐还原酶也是专门受硝酸盐存在的诱导形成。

综上所述，植物可以通过多个调节过程改善资源的平衡。这些包括：（1）改变根冠比，以改善地下和地上资源获取间的平衡；（2）根优先生长在高的养分可获得性的位置；以及（3）根吸收特别养分能力的调节，从而使植物养分的比例尽可能接近植物生长的最佳水平。

养分吸收改变了根际的化学特征。植物根的养分吸收降低了土壤中可溶性养分含量，是对诸如硝酸盐等可移动养分生态系统存留的关键控制。例如，森林皆伐或者作物移除使土壤更易于向地下水和溪流淋溶硝酸盐。

植物吸收养分的第二个主要后果是根际pH值的变化。无论什么时候根吸收额外的阳离子，都会向根际分泌氢离子（H^+），以保持电荷中性。氮可以以阳离子（NH_4^+）或者阴离子（NO_3^-）形式吸收，除了氮外，大量被植物吸收的离子是阳离子（如Ca^{2+}，K^+，Mg^{2+}），而磷酸盐和硫酸盐是主要的阴离子。当植物吸收的氮大多为NH_4^+时，植物对阳离子的吸收大大超过对阴离子的吸收，它们就会向根际分泌H^+以保持电荷平衡，结果导致根际酸化。

根也可能通过根死亡后大量碳的输入、根冠粘性碳水化合物脱落以及根分泌有机化合物等改变根际的养分动态。这些输入土壤的碳可能占植物10-30%的NPP。这些易分解碳源刺激细菌的生长，并通过矿化根际有机质获取氮。当细菌被原生动物取食或者由于根系分泌物减少而缺乏能量时，前述的氮就可能为植物根所利用（图7.4-1）植物有时在与微生物竞争土壤养分时占据优势，例如当CO_2增加促进植物碳获取时。不过，对于调节植物与微生物之间养分竞争的因素，我们知道得相对比较少。

第五节　养分利用（nutrient use）

短时间里，氮和磷共同限制大多数陆地生态系统植物生长，就像水体生态系统一样。平均来说，氮和磷在短时间内大概同等程度地限制植物生长，虽然受氮和磷限制的相对程度在生态系统内或生态系统间都有很大的差别。例如，生长在古老风化土壤上的低位热带森林趋向于对磷有最强烈的响应，而生长在新近冰川土壤上的冻原植物趋向于对氮响应更加强烈。这与来自热带植物叶片中N/P比值比来自高纬度植物高的结果一致。热带植物高的N/P比主要是叶片组织中较低的磷含量所致，就像在湖泊和海洋中的植物一样。在夏威夷山地热带森林，会有一个从年经土壤上氮作为最受限制的营养元素到古老土壤上磷作为最受限制的养分的变化，支持了有关假说，即随着土壤风化，可利用磷应该逐渐减少，生态系统应该是磷逐渐变得更加限制。然而，大多数生态系统的生产在短期都会对氮和磷产生响应，特别是两者共同增加时，说明它们的共同限制性。共限制性在长期是否同等重要，或者反过来说，是否这些养分中只有一种能够改变生态系统，就像在许多湖泊中的那样，都很难确定，因为许多陆生植物相对较长的寿命需要实施足够长时间的实验，才可能观察到物种替换的发生以及进一步（潜在的）养分输入的调节，这太具挑战性了。在一些陆地生态系统中，固氮生物的丰度和固氮速率能够对磷增加产生响应，这是一个很好例子，可以说明氮的供给随着磷而调节。相反，人类氮输入的增加在许多温带地区是普遍存在的，那里许多养分添加实验正在开展，因此许多实验的结果可能夸大了磷限制的长期重要性。

短期的共同限制格局表明，（1）植物生理上的调节尽可能减小任何一种养分的限制性，就像它们调节光合产物分配尽可能减小水分、养分或者光照的限制；（2）这些调节很少百分之百有效，所以对某个生态系统来说，经常表现为地一种养分的响应要比其他养分更加强烈，这与所看到的植物对水分、养分和光照的相对响应格局一致。那么怎么解释经常发生的植物生产对陆地生态系统多个养分的短期响应？

一些植物和生态系统过程导致NPP被多个养分的共同限制。就像光合作用产物分配的调节减少受水分、养分或者光照的单个因子的限制一样，陆地植物调节它们的养分特性以减小单个养分占优势的限制。如前所述，植物调节养分吸收使生长限制的养分吸收最大化，同时减少非限制养分吸收的能力。共生联合体也可以降低某个特别元素的养分限制。内生菌根降低了磷的限制性，外生菌根则同时降低了氮和磷的限制性。打一个比方，具有固氮细菌的共生联合体降低了寄主植物的氮限制性，也间接降低了生态系统中其他植物的氮限制性。一些在强烈受磷限制环境中生长的植物能够形成磷酸酶或者溶解磷的螯合剂，以降低磷的限制性程度。所有这些特征改变了养分获取速率，并受植物对氮和磷的相对需求调节。这些过程短期可以调节养分获取速率以满足植物的需求，这样它们不再与环境提供的养分之间的平衡成一个简单的函数关系。然而，这种适应性也有局限性，固氮可以将外面的氮输入生态系统，但没有一个生物学过程可以将新的磷输入生态系统。在有岩石和矿物不断风化的生态系统中，存在一个重要的新磷源，氮则没有相应的输入源；大多数（但不是全部）岩石含有磷，但几乎不含氮。这里，一旦固氮收到限制，氮可能成为终极性的限制资源。然而，在老的、降水

量较高，经常是热带土壤中的这些地方，风化源已经被耗尽，磷有可能成为终极限制，虽然氮和磷在两种情形下都可能短期受限制。

植物对潜在限制养分的吸收主要用来支持代谢活跃的组织生产（NPP）。来自光合作用的碳组成了大约所有植物部分干物质的一半，因而反映了生物量在不同植物部分间的分配。相反，大多数养分集中在代谢活跃的组织，虽然任何新的组织都需要一定的养分投资。例如，酶蛋白和核酸参与蛋白质合成具有较高的氮含量。能量转换（如光合作用和呼吸作用），核算，膜脂都需要磷。钾也集中在代谢活跃的组织中，因为其在渗透调节上的重要性。其他阳离子（如镁和锰）作为酶的辅助因子。只有钙作为细胞壁的组成（果胶酸钙），主要起结构支撑的作用。

作为一个重要代谢作用的结果，氮、磷和钾在植物叶片和程度稍微低一点的细根中都有较高的含量，因此这些养分对植物供给的变化对植被进一步获取碳和养分的能力具有强大的放大器作用。因此，植物对限制性养分累积增加响应，表现为室内实验中植物生长的线性增加，或者是野外实验中NPP的增加。这与整个生态系统的光响应曲线相似，生态系统碳收益（GPP）在一个较大可获得的光照范围中随光强线性增加。

当养分供给超过需求时，陆地植物在贮藏器官（如茎）和细胞器（如液泡）中积累养分。植物以这种方式利用阵发性的短期养分供给，例如在新近秋季叶片脱落受雨水淋洗的时候。这种奢侈消费（luxury consumption），有时这么称呼，改变了组织中元素的比例，因为非受限养分要比受限养分含量增加更加强烈。当生长需求超过从土壤吸收时，贮存的养分然后被利用。例如，在极地冻原，羊胡子草（cotton sedge）在没有从土壤任何养分吸收，而单纯依靠利用前几年贮存养分的条件下能够完成整个生长季的正常生长。有些时候，植物组织中养分比例的变化反映了不同元素的相对限制程度，可以用来确定诸如作物施肥的最佳养分比例。在其他一些情况，养分比与养分显著幅度几乎没有相关性。例如，一些植物种类合成生物碱一类的氮基防御物质。这些植物种类具有相对高的N/P，但并不表示与低N/P的植物相比，其氮限制性较低。最后，土壤在不同尺度上都是化学异质性的，这种尺度可以从几毫米到洲际，导致养分供给速率的差异，进一步引起植物养分比例的差异上述因子一起改变了植物养分比例，使之偏离可能被认为对生长最佳的水平，引起植物生长和生态系统NPP对多个养分的响应。

将物种按照生境进行分类可以有助于解释对养分吸收和生产力对不同生境养分供给变异的响应。乔木一类的植物具有较大的将养分用于生长的能力，在高养分输入速率的生境占优势，而贫瘠的生境主要生长具有广泛的根系统但是较低的单位根长的养分吸收能力。

养分利用效率（nutrient-use efficiency）在养分对生长缺乏的地方最大。植物间组织养分含量的差异提供了深入了解一个生态系统单位养分生产的生物量的一个途径。养分利用效率是单位获取养分的生产量。一个方便的计算养分利用效率（NUE）的指数是养分与凋落物形式丢失的生物量的比（即植物凋落物中养分含量的倒数）。该比例在生产力很低的地方最高，表明当养分供应不足时，植物在单位吸收养分生产的生物量更加高效，单位吸收养分丢

失的生物量也更多。至少有两个途径植物尽可能增加单位养分生产的生物量：（1）通过高的养分生产力（nutrient productivity）（a_n），即一个高的瞬时单位养分碳吸收速率，或者（2）一个长的存留时间（t_r），即养分保留在植物中的平均时间。

$NUE = a_n \times t_r$ [g 生物量 $(gN)^{-1}$ = g 生物量 $(gN)^{-1}$ yr^{-1} x yr]

贫瘠土壤中的物种具有长的养分存留时间但是低的养分生产力的特征，表明在生产力低的地方高的NUE主要是通过降低养分损失的特征而不是促进高的单位养分生物量收益的特征实现的。同样，与降低碳收益能力相比，遮荫更强烈地减少组织丢失。

在养分存留时间与养分生产力之间存在一个内在的生理权衡。这种现象的发生是因为允许植物保持更多养分的功能性状降低了快速生长的能力。具有高养分生产力的植物生长迅速，并具有高的光合作用速率，这与低的组织密度，高的比叶面积和高的组织氮含量是相关的。相反，长的养分存留时间主要通过低的叶片和根的替换速率实现的。为达到使植物叶片存活更长时间，它们必须具有更多的结构细胞以忍受任何不利的环境条件，以及高的木质素和其他次僧代谢物含量以阻止病原菌和草食动物的侵袭。这些性状共同导致致密的叶片，具有低的组织养分含量，因而具有低的单位重量生物量的光合作用速率。植物高的NUE也会降低凋落物分解和养分矿化速率，原因是好的防御、低养分组织一旦凋萎后导致微生物对养分的固持，从而降低分解速率。

对根的寿命和养分速率之间权衡的了解要少得多。当根的年龄增加，根毛丢失，并变得木栓化时，养分吸收下降，这样对于根来说，生理活性和寿命之间的权衡可能也会存在，而相关机制在叶片中已经很好地阐述清楚了。生长缓慢的植物在它们的根中经常有低的养分含量以及低的呼吸速率，这与它们低的养分吸收能力相对应的。

NUE和资源捕获速率间的权衡解释了沿着资源梯度的植物类型多样性。在低养分环境，通常养分保守的物种占优势，所谓养分保守是通过低的组织周转速率，高的NUE以及使组织维持很长时间必须的物理和化学性质等实现的。这些能忍受逆境的植物通常胜过那些在贫瘠养分环境中保持较低的养分的植物。高的NUE和相应的性状限制了植物捕获碳和养分的能力。在高的养分环境中，具有高的资源获取速率、快的生长速率，快的组织周转，因而低NUE的植物种胜过具有高的NUE的植物。换句话说，既不是快速生长速率，也不是高度NUE是普遍占优势的，因为这些性状间内在的生理权衡。是效率，还是快速生长对植物更为有益取决于环境。

第六节　植物的养分丢失（nutrient loss from plants）

植物，尤其是长寿命植物的养分概算像取决于养分获取一样，取决于养分丢失。植物养分损失的潜在途径包括组织凋萎和死亡，植物可溶性养分的淋洗，组织被草食动物和病原菌的消耗，养分分泌进入土壤，以及由于火烧，风暴和其他干扰的毁灭性的植被养分损失。植物养分损失是一个生态系统的内部转移（从植物转移至土壤），而不是从生态系统丢失。在

被转移至土壤后，养分可以潜在地为微生物或者植物所利用，或者从生态系统丢失。因此，植物向土壤的养分丢失具有与养分从生态系统向大气圈或者地下水的丢失完全不同的结果。

6.1 凋萎（senescence）

组织凋萎是植物养分丢失的主要途径。尤其在低资源环境中植物主要通过凋萎减少组织的周转来减少养分的损失。例如，禾草和常绿木本植物叶片在养分贫瘠或者水分不足的环境中要比在高资源环境中表现出更长的叶片寿命。同样，禾草植物根的寿命也在低养分生境中最大。物种在组织周转上的差异加强了这种低资源环境中高寿命的格局。常绿木本植物的比例随着土壤肥力的增加而降低，从而在生态系统水平上降低了叶片周转速率。其他条件相同，组织周转的降低引起相应的有关组织养分损失的降低。这种组织周转的降低可能是唯一最重要的对低养分生境中养分保持的适应。

养分再吸收是可溶性养分通过韧皮部转移出即将凋萎的组织。养分再吸收对植物养分保持起到了关键的，但对之了解甚少的作用。平均来说，大约50%的氮、磷和钾营养在植物叶片凋萎脱落前被植物再吸收，因此养分再吸收对于定量植物养分概算是重要的。具有低的初始叶片氮和磷含量（即低养分植物）的植物再吸收效率趋向于最大。然而，这些格局并不是总会出现，不同的研究观察到的养分再吸收效率有很宽的变化范围（0-90%）。这么大变化范围的原因还不是很清楚。高效的养分再吸收在有一个活跃的汇时更容易出现，例如当叶片形成与较老的叶片凋萎同时发生，如发生在禾草状（禾草和莎草）植物和许多常绿植物中。干旱可能降低养分再吸收效率，刮风经常能在非禾草状植物养分再吸收完成前抽干一个叶片。总结来说，养分再吸收效率是一个如此之重要性状，以至于大多数植物都具有一个相似的再吸收养分的能力。诸如养分脉冲、干旱和刮风之类的环境因子可能影响植物实现这个再吸收能力的程度。再吸收的养分被转移到植物其他部位（如种子，贮藏器官，或者植冠顶部的叶片），以支持植物在其他时间或者其他部位植物的生长。一些养分，例如Ca和Fe，在韧皮部并不移动，所以植物不能从凋萎组织中再吸收这些养分。由于这些养分很少限制植物生长，对它们再吸收的缺乏很少直接对植物产生不利的影响，除非酸雨大大降低它们在土壤中的可利用性。

植物似乎并没有从根的凋萎和再吸收这种物候上程序化的格局，当物理胁迫、根取食者，或病原体降低它们的生理能力至阈值以下时，根简单地停止任何运作。然而，由于还没有太多对根的凋萎进行的研究，这种看起来根缺乏凋萎和再吸收也可能反映了我们的无知。

6.2 植物的淋洗损失（leaching loss from plants）

从叶片的养分淋洗是植物养分损失的一个第二重要的途径。淋洗大约占每年从地上部分植物回收到土壤的养分的15%。降水溶解植物叶片和茎表面的养分，并以**冠流**（降水穿过冠层的部分）或**茎流**（降水沿着树干流下的部分）的方式携带这些养分到达土壤。茎流典型地由于茎表面的淋洗作用而具有高的养分含量；然而，仅有很少一部分水以这种方式流到土壤。冠流通常占从植物淋洗养分的90%。虽然具有高养分的植物单位叶片丢失更多的养分，

通过淋洗作用再循环的养分比例在各种生态系统之间出人意料的相似。淋洗损失最显著的是那些高度溶解或者不被再吸收的养分。例如，在一个苹果叶片，多达50%的钙和80%的钾在24小时之内被淋洗出来。当雨水首次接触到叶片时，淋洗率最高，然后随时间指数式降低。于是，与凋萎（再吸收）相比，具有不同降水格局的生态系统可能归还相似比例的养分至土壤。虽然淋洗损失对于定量植物的养分概算是重要的，植物没有明确的降低养分损失的适应。常绿叶片厚的角质层减少了淋洗损失，解释了为什么常绿植物可以在湿润、养分缺乏的森林中出现。然而，没有证据表明淋洗损失与角质层厚度有关。正如养分再吸收，植物淋洗损失对于植物养分概算定量是重要的一项，但对此还了解不够。生物学家对植物碳和养分获取的了解要远好于对这些资源损失的了解。植物冠层也能够吸收可溶于降水的养分。植冠从降水吸收养分在强烈养分缺乏的植物生长系统中最大。

6.3 动物取食（herbivory）

动物取食有时是一个植物养分损失主要途径。在许多陆地生态系统中草食动物只取食相对很少一部分（1-10%）植物生物量。然而，在诸如高生产力草地，草食动物通常要取食很大一部分植物生物量，并且在草食动物种群爆发之际，草食动物可能要取食大部分地生植物生物量（见第十章）。草食动物对植物养分概算影响要比对生物量损失所揭示的影响要大得多，原因是草食动物的取食要先于养分再吸收，因此动物取食所造成的养分损失可能是凋萎引起的单位生物量氮和磷损失的2倍。动物通常也偏爱取食具有丰富的氮和磷的组织，从而使草食动物对植物养分的影响达到最大。于是，植物选择了化学和形态上的防御来阻止草食动物取食和病原菌的侵袭。这些防御最大量出现在生活时间长的组织中，以及在养分供给不足于经常性地偿还因草食动物取食丢失的养分的环境中。大多数从植物转移至草食动物的养分很快以粪便和尿液的形式归还到土壤，从而很快被植物利用。草食动物通过这种方式加速了养分循环（第十章），尤其在放牧经营的生态系统中。当过度放牧降低了植物生物量至植物无法吸收草食动物归还到土壤中养分的程度，养分容易从生态系统丢失。

6.4 植物养分损失的其他途径

对养分损失的其他途径还了解很少。虽然实验室的研究表明根的分泌物中含有的氨基酸可能是植物碳概算的显著组分，植物氮通过该途径损失的幅度还未知。其他植物养分损失的途径包括槲寄生的植物寄生，以及通过菌根从一种植物向另一个植物转移的养分。虽然这些养分转移可能对群落中物种间的养分分布至关重要，但从总体上来说，对并不对植被养分固持或损失改变太多。

干扰可能引起植被偶尔的大的脉冲式养分损失。火烧，刮风，疾病传播，以及灾害性的干扰发生时引起大量养分从植被损失。火烧和人为收获是一个例外，植被养分的损失代表了养分从植被到土壤的转移，而不是从生态系统损失。伴随这种大的凋落物输入，脉冲式的分解和矿化不仅导致早期演替植被对养分的快速吸收，同时也会引起潜在的生态系统淋溶损失（见第九章）。火烧过程中植被的养分损失随养分种类和火烧强度而变化。例如，氮和硫在火烧中的挥发要大于钾和磷的，而钙和镁多半被转移至灰分中。氮的损失从造成林分替换火

灾的80%到易于起火的萨瓦纳和草地等轻度损失，萨瓦纳和草地的火烧通常发生在植物凋萎和养分再吸收后的旱季，且烧掉的主要是凋落物，而不是活的植物生物量。在火烧可能发生的期间，生态系统中大多数植物养分储存在地下。

本章小结

养分的可获得性是陆地生物圈生产力的主要限制。植物碳的获取主要取决于植物的性状特征（叶面积和光合作用能力），而养分的吸收通常更加强烈地受环境（土壤供给速率）制约甚于植物性状特征。然而，在早期演替阶段，植物性状对生态系统水平上植被养分吸收有更加显著的影响。扩散是从非根际土壤向植物根表面主要的养分输送过程。土壤水分流动过程中养分的质流主要在补充扩散壳以及提供那些在土壤中大量存在或者植物少量需求的养分时重要。

植物通过几个途径调节它们的养分获取能力。在养分限制条件下优先将光合作用产物分配至根，尽可能增加吸收养分的根的长度。根的生长集中在养分相对高可获得性的位点，尽可能多的从生产的根得到养分回报。植物进一步通过与菌根真菌形成的共生联合体增加养分获取能力。生长快的植物，或者是因为有利的环境，或者是因为高的相对生长速率，通常具有高度养分吸收能力。植物改变养分吸收动力学，吸收那些最限制生长的营养元素。就氮这种情况，它是一种在许多陆地生态系统中最强烈的限制性元素，植物通常吸收任何土壤中存在的可利用形式。当所有形式的氮都处于同等程度的丰富时，大多数植物偏爱吸收铵盐或者氨基酸，而不是硝酸盐。然而，因为硝酸盐的高度可移动性，其吸收也是十分重要的。

在将养分投资到新的生长的最大速率与养分用于生产生物量的效率之间不可避免存在着权衡。植物在养分缺乏条件下单位养分生产生物量效率最高。养分利用效率通过延长组织寿命，也即通过减少养分的丢失速率达到最大化。凋萎是植物养分丢失的主要途径。植物通过在叶片脱落前吸收其组织中大约50%的氮、磷和钾，从而减少生长限制性养分的损失。每年大约有15%从地上植物回归至土壤的养分通过淋洗过程，主要以冠流的形式从林冠滴落至地表。动物取食也可能是重要的养分损失途径，原因是它们偏爱取食养分丰富的组织，且通常在养分回收发生前取食这些组织。由于这些原因，植物由于动物取食损失的单位生物量的养分通常是通过凋萎途径损失的养分的两倍还多。其他引起偶尔植被大量养分丢失的因素包括干扰（如火烧和刮风）和疾病引起的组织或者植物的死亡。

第九章 养分循环

养分循环包含进入和输出生态系统的养分以及养分在生态系统内部的转移。本章描述这些养分动态。

引言

人类活动对养分循环的影响已经在根本上改变了生态系统过程的调节。碳和水分的循环速率最终受能量和一些化学资源的可获得性调节，所以，这些资源的可获得性的改变将从根本上该表所有生态系统过程。化石燃料的消耗向大气圈释放了大量氮和硫的氧化物，并增加了它们向生态系统的输入。化肥使用和固氮作物的耕种进一步增加了农业和下游水体生态系统的氮通量。这些人类的影响加起来使生物圈的氮背景输入速率是原来的两倍，磷的输入是原来的四倍。引起的植物生长的增加足以改变全球碳循环。人类干扰，森林转化，收获和火烧，增加了养分库可利用成分的比例，从而容易造成丢失。其中一些养分的丢失是可溶性养分元素通过淋溶发生的，引起土壤阳离子的耗竭，土壤酸性的增加，以及养分向水体生态系统输入的增加。氮的气态形式的损失影响大气圈化学和辐射特性，导致大气污染，加强温室效应。因此，养分循环的变化剧烈地影响生态系统间的相互作用，以及碳循环和地球的气候。

第一节　核心要点

养分从淡水系统向海洋的流动已经在世界 2/3 河口形成或者加剧了死亡带。来自农业地区的养分输送到河口和海岸带刺激了死亡有机质的形成，并向海洋深处沉积。这使得水中氧气耗竭，导致大面积鱼、虾和其他无脊椎动物的死亡。如何通过更加精心地管理这些农田和城市，以减少这些地方来源的养分的影响？如何使化肥施用与作物的养分需求相匹配，从而减少化肥需求，并进一步减少污染的异地影响？输送到海岸带那些过量养分的去向有哪些？理解生态系统养分通量的调节可以帮助回答上述这些重要的管理问题。

第二节　概要

养分循环包含了养分进入生态系统，它们在植物、微生物、消费者及环境之间的内部转移，以及从生态系统丢失。一些营养元素，例如氮，可能或者通过水，或者在空中运动，而其他一些元素，例如磷，明显缺乏气相物质，通常你能以水溶液向下运动或者作为粉尘在大气圈运动。营养物质通过侧向迁移，岩石的化学风化，大气氮的生物固定，以及从大气圈以降雨、风吹颗粒或者气态物质沉降的方式为生态系统所用。内部的循环过程包含有机和无机形式的内部转换，使元素从一种离子形式向另一种离子变化的化学反应，植物和微生物的生

物吸收，以及土壤内部介质表面的养分交换等。养分同淋溶、痕量气体排放、水土流失、火烧，流出，掩埋以及收获过程中物质移除等途径离开生态系统。

非经营性的生态系统中大多数植物生长所需要的氮和磷是通过过去初级生产，包括植物凋落物和陆地环境中土壤有机质（SOM）的分解，水体生态系统水柱和沉积物中有机质的矿化等途径提供的。进入或输出这些生态系统的养分量只占内部循环养分量的一小部分，形成养分循环保守的相对封闭的系统（closed systems）。相对于内部转换，人类活动趋向于增加输入和输出，并使得生态系统的养分循环更加开放。

我们已经描述了通过植物的养分循环（第八章）。在这章中，我们主要聚焦在生态系统内部的过程，可利用养分从死亡有机质的再生。

第三节　陆地生态系统氮输入

生物氮固定是未受污染的陆地生态系统新的氮输入的主要途径。只有固氮细菌具有打开N_2分子中三个键的能力，将其还原成铵（NH_4^+），从而支撑它们自身的生长。固氮植物主要通过形成富含氮的凋落物和此后的降解过程，使固定的氮为群落中其他植物所利用。

3.1 生物氮固定（biological nitrogen fixation）

固氮酶是用来催化N_2还原成NH_4^+的酶，该酶的特征基本上决定了固氮的生物学特性。受固氮酶催化的N_2还原需要消耗高的能量，因此仅出现在细菌具有丰富的碳水化合物供应以及适当的磷存在的条件下。在氧气存在的条件下，该酶就会变性，所以生物体需要保护该酶免受氧气的接触。最后，温度经常限制碳的供给固氮酶的活性，因此氮的固定在热带环境中最为显著，而在高纬度地区则受限制。

（1）氮固定者的类群（groups of nitrogen fixers）

与植物形成共生联合体的固氮细菌具有最高的氮固定速率。这种现象的发生是因为植物能够提供足够的碳水化合物，满足氮固定的高能量需求。最常见的共生氮固定者是根瘤菌（*Rhizobium*）的一些种类，它们与豆科植物（大豆，豌豆等）形成联合体，其次是放线菌（*Frankia*）的一些种类，主要与赤杨，鼠李（*Ceanothus*）和其他豆科木本植物形成联合体。这些与植物结合的共生固氮细菌通常生活在根瘤中，在那里固氮酶得到了很好的保护，不会与氧气接触。例如，豆类植物具有豆血红蛋白（leghemoglobin），一种与氧气结合的色素，类似于脊椎动物血液中输送氧气的血红蛋白。根瘤中的固氮细菌是异养的，依赖于植物提供的碳水化合物来满足氮固定的能量需求。在实验室条件下，氮的固定的能量需求可能达到大约25%的GPP，高出从土壤吸收无机氮的能量消耗达2-4倍。在野外条件下，氮固定和氮吸收的相对消耗是很难估计的，原因是难于确定菌根、硝酸盐还原和根吸收的消耗。当自然条件下无机氮很丰富，或者无机氮被人为加入土壤中，固氮植物通常降低它们固氮的能力，并吸

收土壤中的氮。磷的可获得性经常制约固氮植物的生长。而且，土壤中高的磷酸酶活性与固氮者相结合，为固氮者提供了无机磷的补充。

自由生活的异养氮固定细菌通常氮固定速率最低。这些细菌从环境获得有机碳，在具有高的有机质含量提供碳底物的土壤或者沉积物中最为活跃，这些碳底物推动（fuel）氮的还原。其他异养性的固氮者出现在根际中，依赖于根的分泌物或者根周转作为它们的碳供给。在厌氧的白蚁尾肠中生活的氮固定者提供了一种重要的氮源，可以促进热带地区木材的分解。需氧的异养生物通过各自不同的机制降低固氮酶周围氧的浓度，包括可以耗尽细菌细胞周围氧气的高的细菌呼吸速率，或者形成黏液以降低氧气向酶的扩散。

许多自由生活的氮固定光能利用菌（phototroph）能够通过光合作用生产自身需求的有机碳。例如，那些存在于水体生态系统中以及许多土壤表面的蓝藻细菌（蓝绿细菌）。许多光能自养菌具有专门的非光合作用细胞，称为异形胞（heterocyst），可以保护固氮酶不会受邻近的光合作用细胞在光合作用过程中产生的氧气影响而变性。

还有一些联合的（共生性的）氮固定光能自养菌。例如，固氮地衣由绿藻或者蓝藻细菌作为光合作用共生体，蓝藻细菌固定氮，真菌用于提供物理支撑。这些地衣在许多早期演替的生态系统中提供了一种重要的氮输入。小型氮水蕨类红萍（*Azolla*）以及诸如念珠藻类（*Nostoc*）的蓝藻细菌形成一个光自养的联合体，它们在稻田和热带水体系统中常见。

豆类植物以及其他共生氮固定者具有最高的固氮速率，经常达到5-20 g m^{-2} $year^{-1}$。光能自养共生体，例如念珠藻类与红萍的联合体在稻田可以固定10 g m^{-2} $year^{-1}$。当念珠藻类单独生活时，也就能固定2.5 g m^{-2} $year^{-1}$。相反，自由生活的异养生物能固定0.1-0.5 g m^{-2} $year^{-1}$，与未受污染的环境中氮的沉降输入量接近。

（2） 氮固定变异的原因（causes of variation in nitrogen fixation）

对氮固定的生物和非生物限制导致许多生态系统的氮限制或者氮的共同限制。在不同生态系统间氮的固定速率变异很大，部分反映了不同生态系统氮固定者类型的差异。然而，即使同一类型的氮固定系统，氮的固定速率也变化很大。是什么引起这样的变异？假如氮在许多生态系统中都限制了植物的生长，为什么氮的固定不是出现在所有地方？你可以预测氮的固定者相对于没有自身固氮能力的植物和微生物具有竞争优势。为什么氮的固定者通过继续固氮对氮的限制作出响应，直到氮不再是生态系统的限制因子？多个因素限制了氮的固定，于是维持了许多生态系统氮的限制性或者共限制性。

在封闭冠层的生态系统，能量的可获得性限制了氮的固定速率。与吸收铵盐或者硝酸盐相比，共生或者自养生物氮固定者固氮的消耗（3-6 C g^{-1} N，不包含形成根瘤的消耗）是很高的。因此，固氮基本上被限制在高光照环境，那里光照不会比氮更限制。随着演替，冠层之间封闭，能量逐渐成为那些群落建群者生长的限制性因素。这些植物当处于林冠中时可以固定氮，但固氮的消耗使得它很难穿过阴暗处到达林冠。豆科植物在热带森林和稀树干草原是常见的。在稀树干草原，火烧引起大量氮的流失，豆科植物具有很高的结瘤程度很高，固

定大量的氮。在热带森林中的豆科植物结瘤率并没有那么高，但是它们的富氮的生活方式是依靠这些生态系统中高的氮可获得性来维持的。这里，豆科植物对氮的年输入贡献一般，但对森林的长期氮经济仍是十分重要的。在水体生态系统中，固氮在浅水或者在低浑浊度从而光照能达到底栖蓝藻细菌的水域最为常见。当磷的可获得性适度，这些底栖蓝藻细菌具有高度固定速率。

非共生性的异养固氮细菌也会受可降解有机碳的可获得性限制。当可利用碳稀少时异养型固氮是没有好处的。腐烂的木头含有较低的氮和高的有机碳水平，经常具有十分可观的异养性氮固定，包括那些在热带白蚁肠道中发现的。异养性固氮也可以出现在厌氧的底栖物中，但由于反硝化（denitrification，即硝酸盐转化成气体形式的氮）引起的氮的气体损失通常会超过固定的氮。

在许多生态系统中，固氮受其他营养元素如磷的可获得性的限制。由于大气氮的易获得性，固氮植物的生长经常受其他营养元素的限制，尤其是磷，它对大多数生态系统中植物生产具有共同限制或者第二位限制性的营养元素。固氮者经常具有高含量养分的化学计量关系，它们在利用大量氮的同时也会利用大量的磷。因此，固氮者的生长经常比其他植物更早发生磷的限制。其他能够限制氮固定的营养元素包括钼，铁，硫，它们都是固氮酶必需的辅助因子。例如，钼在澳大利亚草原和低位的热带森林强烈风化的土壤上经常对氮的固定产生限制。海洋生态系统中的氮固定者可能受铁限制，这在前面已经讨论过。在这些情况下，磷、铁、硫或者钼有可能是限制生产的终极性“主控元素（master element）”，即使在短期实验里氮还是初级生产强力响应的一个因子。

固氮生物的消耗经常限制它们持续支撑高固氮速率的能力。虽然许多固氮植物可以通过形成生物碱的氮基防御（nitrogen-based defense）阻止一些普适性的取食动物（见第十章），固氮者典型的高蛋白质含量对许多草食动物来说具有很高的适口性。对许多固氮植物的高强度取食限制了它们的丰度和对生态系统的氮输入。在排除食草动物的区域，通常具有更多的固氮植物，从而对生态系统具有更大的氮输入，以及最后更高的生产力和生物量。

3.2 氮的沉降（nitrogen deposition）

氮以颗粒、溶解和气体沉降形式进入生态系统。所有生态系统都会接收到来自大气沉降的但输入。这些输入是很少量的，通常在0.1-0.5 g m^{-2} $year^{-1}$，主要发生在未受污染公海水域下风处的生态系统。海岸生态系统的氮输入主要来自有机颗粒和海洋飞沫蒸发盐中的硝酸盐（NO_3^-）以及来自海水中挥发的氨气（NH_3）。在内陆地区，氮主要来自土壤和植被挥发的NH_3以及来自沙漠风蚀、未耕作的农田和其他零星植被的生态系统产生的尘土。闪电也可以固定氮并最终贡献大气氮沉降。

人类活动现在已经是在世界上许多地方沉降氮的主要来源。施用尿素或者氨肥引起NH_3的挥发，挥发的NH_3然后在大气中转变成NH_4^+，然后通过降水沉降。驯化动物饲养也会大量增加NH_3向大气的排放。氮氧化物（NO和NO_2，合称为NO_x）通过化石燃料燃烧、生物量焚

烧，以及施肥农田系统挥发等向大气的排放在全球尺度上要比自然源的排放大得多，所有NO_x通量中80%是人为的。这些来源的氮可以被输送到下风处远离工厂或者农业地区的地方才沉降下来。例如，在极地海洋和加拿大北极岛屿上空的“极地霾”主要是由来自中国和东欧的污染物形成的。向生态系统的人为氮输入可能是很大的，例如在美国东北部1-2 g m^{-2} $year^{-1}$，或者在中国北方5-10 g m^{-2} $year^{-1}$，要比背景水平的氮沉降高10-100倍。最高的沉降量与植被每年吸收和通过凋落物循环的量相当（见第八章）。大多数生态系统具有巨大的将这些输入的氮贮存在土壤和植被中的能力。然而，一旦这些库转变成氮饱和（nitrogen saturated），向大气和地下水释放的氮也可能是十分巨大的。一些污染生态系统中的氮循环已经从90%以上封闭（见第八章）转变成像碳循环那样开放，即通过植被每年循环的碳或者氮的量与生态系统每年获得和丢失的量相当。农田系统经常是氮饱和的，并向地下畜水层和水体生态系统释放大量氮；后面我们会更加详细讨论农田系统中的养分循环。相反，大多数森林增加它们的碳固定以响应氮沉降增加，表明这些森林还没有达到氮饱和状态。然而，全球尺度上氮沉降对碳固定只是表现出适度的影响，说明人为氮输入还不太可能通过加强碳固定“解决气候问题”。

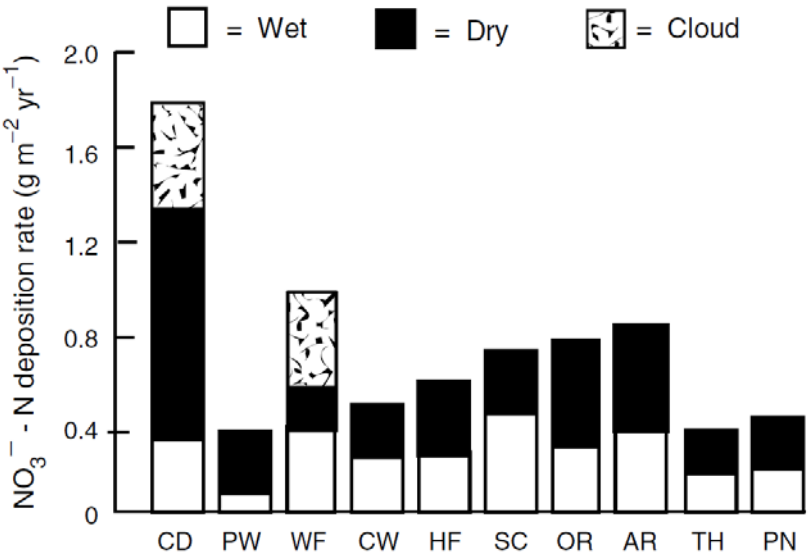


图 9.3-1 一些生态系统的氮的湿、干或者雾水沉降。

气候和生态系统结构决定了氮在生态系统沉降的过程。沉降主要通过3个过程发生。（1）湿沉降以溶解在降水的方式输送养分。（2）干沉降通过沉积（垂直沉降）或者嵌入（水平方向沉降或者像HNO_3蒸汽那样气体的直接吸收）等方式输送尘土或气溶胶等化合物。（3）云雾水沉降输送水滴中的养分至浸润在云雾中的植物表面。虽然最容易获得的数据只是湿沉降，原因是比较容易测定，湿沉降和干沉降通常是氮输入的同等重要的源（图9.3-1）。通常在湿润生态系统中要比在干旱生态系统中氮的湿沉降更大。然而，氮的干沉降表现出与气候没有明显的相关性，虽然干旱生态系统获得更大比例的氮输入是以干沉降方式。雾水沉降通常在云雾覆盖的山顶或者受海岸多雾影响的区域。氮的湿、干和雾水沉降的相对重要性也取

决于生态系统的结构。例如，针叶树冠要比落叶树冠趋向于累积较多的干沉降和雾水沉降，因为它们具有较大的叶表面积。它们相对粗糙的树冠也会导致潮湿空气穿透林冠更深，从而接触更多的叶表面。

氮沉降的形式决定了它们对生态系统的影响。NO_3^-和NH_4^+能够立即被植物和微生物吸收，而一些有机氮首先必须被矿化。一旦硝酸盐伴随碱性阳离子淋溶出生态系统，硝酸盐以硝酸的方式（以及铵盐的输入，假如输入后紧接着进行硝化作用，即铵盐转化成硝酸盐）输入会导致土壤酸化。有机氮化合物占大约1/3的总的氮沉降，但是它们的化学特性在不同生态系统有很大的差异。例如，在海岸地区，沉降的有机氮主要以海洋来源的还原性的化合物为主，如胺类物质。在受空气污染影响的内陆地区，大多数沉降的有机氮为氧化性有机氮化合物，主要来源于有机化合物在大气中与NO_x进行反应。

沉积岩的风化可能对一些生态系统的氮概算有一定的贡献。沉积岩占地球表面出露岩石的75%，有时候含有一定量的氮。在一些流域下面具有高氮含量的沉积岩，岩石风化对生态系统有显著的氮输入。然而，在大多数生态系统，岩石风化被认为是对生态系统仅贡献很少量的氮输入。

第四节　氮的内循环

4.1 矿化作用概要（overview of mineralization）

在自然生态系统中，植物吸收的大部分氮通过有机质的分解转变成可利用的形式。在大多数生态系统中，大部分（>99%）土壤氮保存在来自植物、动物和微生物的死亡有机质中。当微生物在分解过程中将这些死亡有机质降解，氮就会以可溶性的有机氮（DON）在胞外酶的作用下被释放（9.4-1）。植物和菌根吸收一些DON，利用它们支持植物生长。参与分解的微生物也会吸收DON，利用它们支持微生物生长的氮或者碳的需求。当DON不足于满足微生物对氮的需求，微生物就会从土壤溶液中吸收额外的无机氮，主要以NH_4^+的形式。固持（immobilization）是指无机氮由于微生物吸收和化学固定（chemical fixation）从可利用氮库的移出。微生物生长通常是碳限制的。在这样的情形下，微生物降解DON，利用碳骨架支持它们生长和维持的能量需求，同时向土壤分泌NH_4^+。这个过程被定义为氮的矿化或者氨化，原因是铵盐是该过程直接的产物。在一些生态系统中，一部分或者所有NH_4^+被转换成亚硝酸盐（NO_2^-），然后转换成硝酸盐（NO_3^-），即硝化过程。

4.2 可溶性有机氮的产生和去向（production and fate of dissolved organic nitrogen）

从非溶解性的有机氮向可溶性有机氮的转化使氮能为植物和微生物利用。与无机氮库的形式相比，土壤中巨大的颗粒有机氮库说明这个氮矿化的初始步骤是限制矿化速率的步骤。所有最后被矿化作用转变成NH_4^+和NO_3^-的有机氮必须被转换成可溶性的有机氮形式，这样微生物可以吸收，并将其矿化。因此，相对于其他氮通量，经过DON库的通量是很大的，即

使在DON含量很低的生态系统。颗粒有机氮的降解是在颗粒有机碳降解和利用平行进行的，所以受与分解相同的生物体和因素所控制。这些控制包括底物的数量和化学性质，调节土壤微生物和动物活性的环境因子，以及微生物群落的组成。

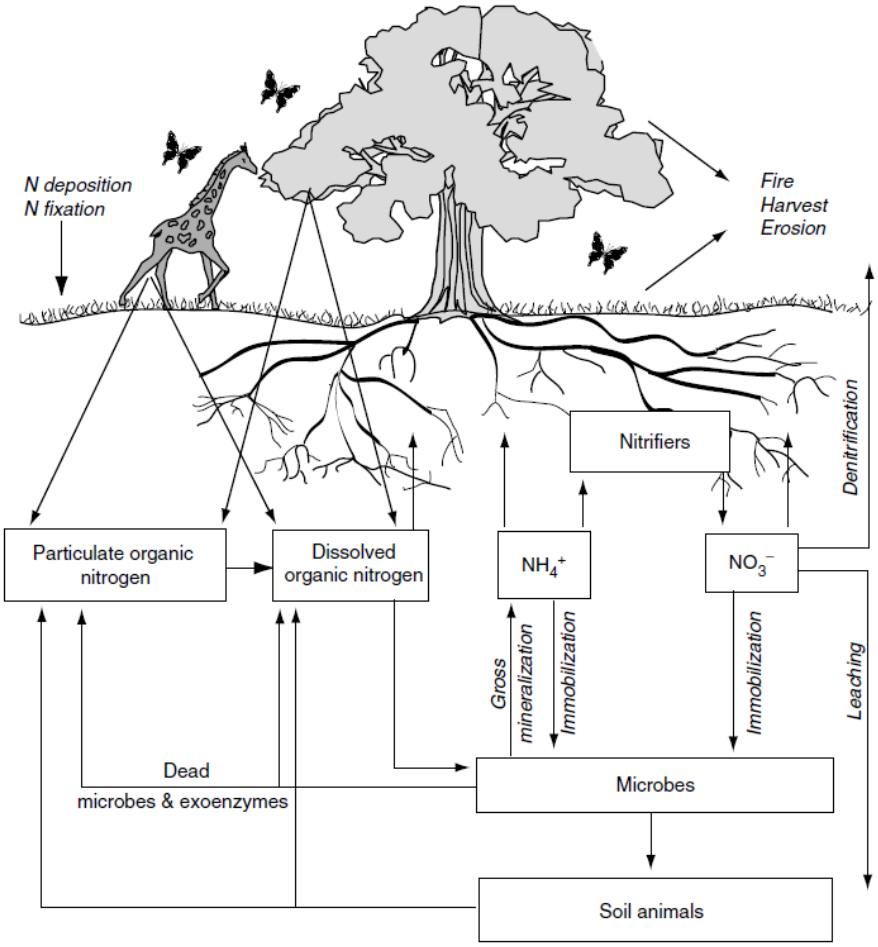


图 9.4-1 陆地氮循环的简化流程图。植物和微生物都吸收可溶性有机氮（DON），NH_4^+和 NO_3^-，并释放颗粒有机氮（以死亡有机质的形式）和 DON。当微生物吸收的多余它们生长的需求时，也会释放铵。硝化细菌是一个专性的微生物类群，或者将铵转化成亚硝酸盐或者将亚硝酸盐转化成硝酸盐。当动物取食植物或者土壤微生物时，氮被动物消耗，并以颗粒有机氮和 DON 形式返回到土壤。氮通过反硝化作用，淋溶，侵蚀，收获或者火烧从生态系统丢失。氮通过氮沉降或者氮的固定进入生态系统。

大部分死亡有机质中的氮被保持在复杂的聚合物中，例如蛋白质，核酸和几丁质（来自真菌的细胞壁和昆虫的外骨架，它们都太大而无法通过微生物的膜。微生物于是需要分泌胞外酶，例如蛋白酶，核糖核酸酶和几丁质酶将这些大型的聚合物降解成小型的水溶性的，可以被微生物细胞吸收的亚单元，例如氨基酸和核苷酸。脲酶是一种将动物尿液或者化肥中的尿素降解成CO_2和NH_3的胞外酶。微生物本身也容易受微生物蛋白酶的攻击（attack），因此，微生物必须持续地需要氮合成胞外酶，从环境中获取氮，所以这是一个潜在的十分昂贵的过程。胞外酶经常结合在土壤矿物质和有机质上。假如活跃位点的性状发生改变，就可能使酶

失去活性，也能够保护酶免受其他胞外酶的供给，从而延长酶在土壤中保持活性的时间。蛋白酶是由菌根和腐生真菌生成，也可以由细菌生成。

植物，菌根真菌，或者降解微生物都可以吸收DON。对土壤微生物来说，这既是碳，也是氮的重要来源。直接或者通过它们的菌根真菌吸收DON的植物并不需要通过矿化来获取其中的氮。这种直接由植物吸收有机氮的现象可以在大多数生态系统中发生，并能够满足很大一部分植物对氮的需求，尤其是在氮限制的生态系统。即使是作物也会吸收和利用DON。

DON是化学上十分复杂的混合物，其中仅有百分之几含有氨基酸和其他易降解形式的氮。大多数土壤都展现出类似的氨基酸平衡。微生物细胞吸收的易降解DON可以被直接结合在微生物蛋白质和核酸上。这些和其他DON化合物叶可以通过代谢提供碳或者氮，以支持微生物生长和维持。DON也能够被吸附在土壤交换复合体（soil exchange complex）上，被结合形成腐殖质，或者从生态系统淋溶进入地下水。氨基酸同时拥有正和负电荷的基团（分别为NH_2^+和COO^-）。小的中性的氨基酸，例如甘氨酸，在土壤中最具可移动性，从而最容易被植物和微生物吸收。

4.3 铵的产生和去向（production and fate of ammonium）

铵的净吸收或释放取决于碳的状态。当微生物生长处于碳限制时，微生物利用DON中的碳支持生长和呼吸，并将NH_4^+作为废物分泌到土壤溶液中。这个氨化的过程是DON被矿化成土壤中NH_4^+的一个机制。其他氮限制的微生物可能吸收，或者叫固持（immobilization），上述矿化过程形成的一部分铵，用于生长。例如，在富含氮的位点的矿化形成的氮可以扩散到邻近的氮限制的位置，在那里被植物或者其他微生物吸收。由于这种在微小尺度上土壤可利用氮异质性的存在，一定量的氮可能在微生物释放和吸收之间循环许多次，直至被植物吸收，或者转向其他去向。总矿化（gross mineralization）是从矿化释放的所有氮的量（无论紧接着被固持是否）。该速率主要取决于微生物食物（土壤有机质）的数量和土壤中的微生物生物量。净氮矿化（net mineralization）是土壤溶液中某一给定时间间隔里净的无机氮（铵盐+硝酸盐）累积。当微生物生长强烈地受碳限制而不是氮限制的时候就会发生净矿化作用，相反，当微生物生长是氮限制的时候就会发生净固持作用（net immobilization）。氮的净矿化作用是快速的，当任何一个生物学过程，例如食微生物者取食，或者非生物过程，例如冻融和干湿交替过程都会引起微生物种群的崩溃（crash of decomposer population）。在任何一种情形下，幸存的微生物都可以接触到大量的富含氮的组织。

最容易被植物利用的氮的形式取决于微生物生长究竟是氮限制的（氮的固持>矿化）还是碳限制（氮的矿化>固持）的微环境的相对丰度。在氮极其限制的土壤，例如极地或者高山冻原和北方森林，那里氮的固持占优势，由菌根和腐生微生物的胞外酶生成的DON是土壤中占优势的可利用氮形式，贡献了大部分植物吸收的氮。当氮的可获得性增加时，氮矿化微位点的比例也增加，从这些微位点扩散出来的铵可以为植物和微生物利用。此外，当铵的可获得性增加时，利用铵作为一种能源的硝化细菌，将比例不断增加的铵转变成硝酸盐。综上

所述，当氮的可获得性增加时，微生物生长从氮限制转变成碳限制，此时，不断增加比例的DON被微生物吸收用于支持生长的能量需求，并将多余的氮以铵的形式分泌，硝化细菌利用其中的大部分可利用铵作为一种能源支持它们的生长，所以硝化作用成为占优势的过程。

净氮矿化是对具有高的氮可获得性的生态系统植物氮供给的一个很好的测度，在这类生态系统中微生物生长主要是碳限制的，同时微生物利用DON作为碳源，并以铵的形式分泌出剩余的氮。在这些情形下，植物和微生物之间对氮几乎没有竞争。例如，北美东部落叶阔叶林的年净矿化量近似等于植被吸收的氮。在不这么肥沃的生态系统，例如极地冻原，植物主动吸收DON，净氮矿化速率低估了每年植物获取的氮的量。

氮的矿化速率受DON和无机氮的可获得性，土壤微生物的活性及其对碳和氮的相对需求所控制。进入土壤的有机质的数量和质量是分解和氮矿化共同的可利用底物的主要决定因素，所以对这些输入的生态学控制既调节了分解速率，也调节氮的矿化速率。

氮的矿化速率对两个方面的底物质量产生响应，（1）碳的质量，可以调节死亡有机质降解成可溶解形式的速率，以及（2）C/N，可以决定微生物生长的碳和氮限制之间的平衡。微生物生物量的C/N比大约是10：1。当微生物降解有机质，它们可能将底物中40%的碳结合在它们的生物量中，并将剩余的60%的碳通过呼吸以CO_2的形式返回到大气中。基于这40%的生长效率，微生物需要具有大约25：1的C/N比的底物就可以满足它们对氮的需求。在更高的C/N比的条件下，微生物从外面输入氮以满足它们对氮的需求；在更低的C/N比的条件下，底物中的氮超过了微生物生长的需求，这样就被分泌到凋落物和土壤。实际上，微生物的C/N比有一定的变异（细菌5-10，真菌8-15），虽然现在还不是很清楚这种变异是否也会影响任何生长效率上的系统变异。当底物中的碳或者氮限制微生物生长的时候，如在逆境的环境中（较大的维持呼吸），或者遇到更加难降解的底物时（较大的维持呼吸以及需要更多的胞外酶），所有微生物将底物转变成生物量的效率都会受到影响。但是，25:1通常被认为是C/N比的临界值，超过该值时，就不会在分解有机质时产生净的氮释放。C/N比通常在新鲜的凋落物中最高，特别是木本凋落物，随着时间推移逐渐降低，在相对未受干扰的生态系统的土壤中，C/N比接近14，而在农田生态系统土壤中C/N比接近10。因此，随着凋落物分解的进行，氮的状态存在一个转变过程，从新鲜凋落物氮的固持（或者矿化，取决于初始C/N比值）逐渐转变成氮的矿化。注意，虽然C/N比只是间接地影响凋落物分解，反映了与分解底物碳质量的相关性，但它对氮的净固持或者净矿化都具有明显的机械效应（mechanistic effect）。

在凋落物C/N比和氮的矿化或者固持之间似乎有一个普适性的关系，该关系依赖于底物的质量，但与气候无关。气候只是简单地影响氮的矿化或者固持发生的速率。有利的环境条件经常促进新形成的或者木本凋落物氮的固持，那些凋落物具有高的C/N比，但也促进分解后期或者长期研究中的矿化作用，此时C/N比可能比较低。例如，在长期实验室培养实验显示温度在有利的水分条件下对净氮矿化通常是一个正的作用。这个现象的发生是因为温度能刺激维持呼吸要比刺激微生物生长更加强烈，导致高的温度对微生物生长的碳限制影响，从而引起铵的分泌。此外，不仅高度温度，而且微生物生长都会促进土壤动物对微生物的捕食，

引起更大的微生物周转和向土壤分泌的氮。水分效应则更加复杂，氮的矿化通常随着水分增加至一个临界值，进一步增加水分就会导致氧气扩散，微生物活性和净氮矿化受限。由于更加有利的土壤温度和水分以及其他因素，新近采伐森林地区要比为采伐地区通常拥有更高速率的净氮矿化。然而，在美国中部大平原的一个水分梯度上，高的水分阻碍了分解和氮的矿化，因此在水分梯度的湿润端大的植物氮库反映了植物和生态系统对氮的更大的存留作用而不是水分对氮矿化的刺激作用。很显然，氮的矿化的环境效应的预测需要注意多重的植物和微生物的过程，包括微生物生长，呼吸，以及基质依赖的固持与矿化间的平衡。

氮的矿化作用产生的铵有几个潜在的去向。除了被植物或者微生物吸收外，铵容易被带有负电荷的土壤矿物质和有机质吸附，减少了土壤溶液中NH_4^+的含量（常低于<1ppm）。植物和微生物的吸收进一步耗竭了土壤溶液中的NH_4^+。这使得可溶解库和可交换库之间的平衡产生转移，导致被吸附的离子从交换复合体（exchange complex）再回到溶液。于是，阳离子交换复合体充当容易利用的NH_4^+和其他阳离子的贮存库。NH_4^+也可能被固定在某些铝硅酸盐粘土的夹层部分或者与稳定的土壤有机质络合，这就降低了NH_4^+对植物和微生物的可利用性，只要这些有机矿物复合体保存完好。最后，主要通过细菌，NH_4^+可以被氧化成NO_2^-和NO_3^-，或者被转化成氨气（NH_3），丢失到大气圈中，这在后面的章节描述。

4.4 硝酸盐的产生和去向（production and fate of nitrate）

硝化是NH_4^+被氧化成NO_2^-，并进一步氧化成NO_3^-的过程。与由一系列分解者参与的氨化作用不同，大部分硝化作用是严格地由硝化细菌（nitrifying bacteria）来完成。主要有两类硝化细菌。自养的硝化细菌利用NH_4^+产生的能量来固定碳，用于支撑其生长和维持，有点类似于植物利用太阳能通过光合作用固定碳。异养硝化细菌通过降解有机质获取能量。

自养硝化细菌有两个类群，一个类群将铵转化成亚硝酸盐，例如*Nitrosolobus*以及“Nitroso-”属的其他种类，另一个将亚硝酸盐转化成硝酸盐，例如*Nitrobacter*和“Nitro-”属的其他种类。这些自养型硝化菌是专性的需氧菌，它们通过利用氧化 NH_4^+或者NO_2^-所获得的能量还原CO_2驱动CO_2定来合成结构和代谢需要的碳化合物。在大多数生态系统中，两个类群的微生物出现在一起，所以NO_2^-不会在土壤中累积。当*Nitrobacter*的活动受到限制时，或者在一些施肥的生态系统中，氮的输入相对高于植物和微生物对氮的需求时，NO_2^-才有可能在旱季的旱性森林和萨瓦纳生态系统中累积

虽然自养性硝化作用在许多生态系统中占优势，异养消化作用可能在低的氮可获得性或者在酸性土壤中重要。许多异养真菌和细菌，包括放线菌，从NH_4^+生成NO_2^-或者NO_3^-。一些异养菌在上述过程中也利用有机氮。因为异养菌从有机物质获得它们需要的能量，还不太清楚它们将NH_4^+氧化生成NO_3^-所获得的好处是什么。

硝化作用对生态系统过程有多重的影响。在硝化的第一步NH_4^+氧化成NO_2^-，每消耗1摩尔NH_4^+将产生2摩尔H^+，从而趋向于酸化土壤。催化这一步的单氧酶（monooxygenase）具有很宽泛的底物专一性，也可以氧化许多氯化烃类（chlorinated hydrocarbons），表明硝化细菌

具有降解杀虫剂残留物的功能。最后，主要在硝化过程生成的一氧化氮（NO）和氧化亚氮（N_2O）气体具有重要的大气化学效应。

NH_4^+的可获得性是硝化速率的最直接决定者。至少在某些土壤微位点，NH_4^+的含量必须足够高，才能允许硝化细菌与其他土壤微生物进行竞争。这对自养硝化细菌尤其重要，因为其对NH_4^+的依赖性，将NH_4^+作为它们的唯一能源。NH_4^+的供给反过来又受底物质量和环境对氨化速率的影响调节，这一点已经在前面描述过了。化肥输入和铵的沉降对许多生态系统来说都是额外的铵源。相反，植物根降低了NH_4^+在土壤溶液中的含量，从而与硝化细菌对NH_4^+展开竞争。高产的生态系统通常具有高的硝化速率，这是因为高的矿化速率提供了足够的铵盐作为硝化作用的底物。然而，硝酸盐是相对容易移动的（见第三章），并经常很快被植物吸收或者被反硝化，所以土壤硝酸盐含量并不一定是硝化速率好的指标。

硝化细菌种群通常在贫瘠土壤中很小，难于支持显著的硝化作用。当有可利用的铵盐底物时（例如通过氮的添加，或者矿化速率的增加），硝化细菌种群和硝化速率就会增加。在一些土壤中，这样的响应是很快的，但在其他一些土壤中又表现出较长时间的延迟。次生性代谢物，如丹宁，在一些生态系统被假设可以抑制硝化作用，包括那些处于演替后期的生态系统，但是演替后期硝化速率的降低通常更好地被解释为铵的供给的降低，而不是由于酚类物质对硝化细菌的毒性。其他资源引起的硝化细菌活性的限制是另一个硝化速率慢或者延迟的可能原因。然而在大多数情况下，铵的可获得性通过其对硝化细菌种群密度和硝化细菌活性的影响最终控制硝化作用速率。

氧气是另外一个控制硝化作用的重要因素，因为大多数硝化细菌需要氧气作为NH_4^+氧化的电子受体。反过来，氧气的可获得性又受许多因素影响，包括土壤水分，土壤质地，土壤结构，以及微生物和根的呼吸（见第三章）。

硝化细菌的活性对温度敏感。然而，在低温条件下，硝化作用能够持续维持低的硝化速率，所以经过一段长的冬季后，可以发生很可观的硝化作用，尤其在富含氮的农田土壤中。氮的硝化在干旱土壤中很慢，主要因为过于薄的水膜限制了NH_4^+向硝化菌的扩散。在极端干旱条件下，低水势进一步限制了硝化细菌的活性。将农田土壤在实验室进行培养，发现最大硝化速率出现在pH6.6到8.0之间，pH小于4.5时几乎可以忽略。然而，许多具有酸性土壤的自然生态系统都具有可观的硝化速率，甚至在pH为4.0时。

矿化的氮被氧化成硝酸盐的比例在不同生态系统间变化很大。在许多未受污染的温带针叶和落叶系统中，硝化只是占净氮矿化很小一部分（例如，0-4%），原因是植物和分解者生物与硝化细菌竞争铵盐。氮的沉降可以增加矿化氮硝化的比例至23%。相反，在热带森林，净硝化作用通常接近100%的净矿化作用，即使在低的净矿化作用且没有额外氮输入的地方。在热带生态系统中，植物和微生物生长经常受氮以外的养分限制，它们对氮的需求很低，所以硝化细菌很容易获得NH_4^+。

硝酸盐可能去向有植物和微生物吸收，与阴离子交换位点交换，或者通过反硝化或淋溶从生态系统丢失。硝酸盐在土壤溶液中是相对容易移动的，原因是它带负电荷，不会受阳离子交换位点束缚。因此，它可以通过质流或者扩散容易地运动到植物根表面，或者淋溶出土壤。一些微生物也吸收硝酸盐，并通过**异化的硝酸盐还原**（dissimilatory nitrate reduction）将其还原成铵盐，也即硝酸盐还原并不需要微生物同化（氮的固持）。这个过程是极其耗能的，主要发生在当微生物在厌氧条件下接触到大量的硝酸盐及易分解碳的时候，例如在热带雨林中。既然这样的条件组合也有利于反硝化作用，这在后面会讨论，异化的硝酸盐还原可能是一个氮在湿润环境存留的重要机制。在许多酸性针叶林土壤中观察到的低硝酸盐含量反映了低的硝化速率和土壤微生物和植物低的硝酸盐吸收两者的结合。

虽然NO_3^-比多数阳离子更具移动性，它可以被吸附在具有很高阴离子交换量的土壤交换位点上（见第三章）。具有足够阴离子交换量的土壤能够阻止受干扰后硝酸盐的淋溶损失。在大多数土壤中，阴离子吸附强度是$PO_4^{3-}>SO_4^{3-}>Cl^->NO_3^-$，所以$NO_3^-$很容易地解吸附，并相对容易被淋溶。

4.5 时间和空间上的变异性（temporal and spatial variability）

微小尺度生态学控制引起氮循环大的时间和空间上变异。土壤中氮的转换速率极其多变，相邻土壤样品或采样日期的速率高低差异经常可以达到1个数量级。这样的变异性反映了微小时空尺度上控制因素的差异。例如，土壤团聚体内部有利于反硝化作用（见下文）的厌氧条件可以在毫米级厌氧土壤空隙发生。与非根际土相邻，细根形成了一个具有高的碳含量和低的可溶性氮含量的根际，在那里受碳限制的土壤微生物通过矿化有机氮来满足它们的能量需求。具有致密根分布的微区，植物耗尽了土壤中的NH_4^+，抑制了硝化作用，而在没有根分布的区域，硝化作用则是十分客观的。这种微小尺度上空间异质性对氮循环的影响是很难研究清楚的，所以我们只能从定性的角度了解它们的重要性。

在环境上的时间变异和极端事件对氮的矿化作用具有的影响。例如干湿变化和冻融变化使许多微生物细胞破裂，引起短时间养分释放。由于这个原因，长时间干旱后的第一次降雨经常引起一个脉冲式的硝化作用，以及此后的硝酸盐淋溶。在北方或者山地生态系统春季形成的径流也经常携带养分进入溪流导致脉冲式的养分丢失，原因是冻融事件及冬季缺乏植物对氮的吸收。例如，极地阿拉斯加的Toolik湖每年90%的氮素输入发生在融雪最初的10天时间里。

氮矿化的季节性常与植物氮吸收的季节性不同。在植物有一段时间休眠的生态系统，土壤微生物仍继续矿化氮。这种微生物活性和植物吸收在时间上的非同步性导致植物休眠季节可利用氮的累积，当植物活跃生长时这部分累积的氮才被利用。例如，在温带森林中，冬季的矿化（即使在积雪层下）形成一个巨大的可利用氮库，一直要到下一个春季才会被植物利用。这种非同步性在低养分环境中尤其重要，在植物最旺盛生长的季节，微生物可以固持氮，

与植物展开有效的氮竞争。在冻或者旱的土壤中，微生物细胞的死亡提供了额外的易降解基质，一旦环境条件再次适合微生物活动时，可以支持剩余微生物的净矿化作用。

第五节　氮损失途径（pathways of nitrogen loss）

5.1 氮的气体损失

氨的挥发，硝化，以及反硝化是生态系统气态氮损失的主要途径。这些过程以氨气、一氧化氮、氧化亚氮以及氮气形式释放氮。气体通量受土壤过程速率控制，也受调节土壤扩散速率的土壤和环境特征影响。一旦在大气圈，这些气体能够发生化学变化，并在下风处沉降。

（1） 生态学控制

氨气（NH_3）可以从土壤和凋萎的叶片释放。在土壤，氨气是NH_4^+和NH_3之间受pH影响的平衡产物。在pH值大于7时，很大一部分NH_4^+被转换成氨气。

$$NH_4^+ + OH^- \leftrightarrow NH_3 + H_2O$$

此后氨气从土壤扩散至大气圈。该扩散过程在具有大的气室的干燥的粗质土中最快。在致密的林冠中，一些从土壤释放的NH_3会被植物叶片吸收，并结合入氨基酸中。

对于大多数生态系统来说，NH_3通量是很低的，原因是NH_4^+受植物和微生物吸收以及与土壤交换复合体结合的影响，维持在一个较低的水平。然而，NH_3通量在NH_4^+由于大量氮输入而累积的生态系统则是巨大的。例如，在放牧生态系统，尿液斑块是空中NH_3通量的优势来源。施用铵盐化肥或者尿素的农田经常以NH_3的形式丢失20-30%施入的氮，尤其是当肥料被置于土壤表面时。富含氮的碱性土壤尤其易于NH_3挥发，原因是pH对NH_4^+和NH_3之间平衡的影响。当含氮化合物被分解并转移至贮藏器官时，凋萎期间的叶片也会释放NH_3。施肥和驯化动物的养殖大大地增加了向大气圈释放的NH_3通量。

硝化期间NO和N_2O的产生主要取决于硝化作用速率。在NH_4^+向NO_3^-的硝化转化中，作为副产品生成少量NO和N_2O，通常二者的比例在10-20之间。NO和N_2O释放的量是与硝化过程中总的通量相关，说明硝化作用有点像一个渗漏的管子，一小部分（可能在0.1-10%）的氮在硝化过程中作为痕量气体从管子中“漏了出来”。

硝酸盐或者亚硝酸盐通过反硝化作用还原成气体氮在高硝酸盐和低氧气的条件下发生。许多种类的细菌参与了生物反硝化作用。当氧气含量低时，它们利用NO_3^-或者NO_2^-作为电子受体氧化有机碳作为能量。大多数反硝化细菌都是兼性厌氧生物，但有氧气存在时，它们利用氧气而不是NO_3^-。除了生物反硝化，当NO_2^-在低pH土壤中累积时，化能反硝化可以将NO_2^-（亚硝酸盐）通过非生物途径转化成一氧化氮气体（NO）。当然，化能反硝化要比生物反硝化的作用要小得多。

NO_3^-还原的过程是：$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$，后面3种产物，特别是$N_2O$和$N_2$，以气体形式释放到大气中。大多数反硝化细菌潜在具有完整还原过程的酶，但生成不同比例的N_2O和N_2，部分取决于氧化剂（NO_3^-）和还原剂（有机碳）的相对可获得性。当NO_3^-比有机碳相对更多时，反应只能部分完成，生成的N_2O要比N_2更多。其他更有利于N_2O生成的因素还有低的pH，低的温度，以及高的氧气含量。虽然在实验室培养条件下，NO在反硝化过程中经常有释放，但在自然条件下很少有净的释放，原因是NO向大气的扩散释放在充满水分的空隙中被阻止。一些生成的NO被反硝化细菌充当底物被进一步还原成N_2O和N_2。

发生显著的反硝化作用需要满足3个条件，低的氧气，高的硝酸盐含量，以及有机碳的供给。在大多数非淹水的土壤中，氧气和硝酸盐的可获得性对反硝化施加了最强的控制。高的土壤含水量减少了氧气供给，阻止氧气扩散通过土壤空隙。反过来，土壤水分有受其他环境因素控制，如坡位，土壤质地，以及降水和蒸散发的平衡。土壤氧气含量也对土壤微生物和根的（氧气）消耗敏感。在温暖、潮湿的环境中消耗最快。

对反硝化的第二个控制是底物NO_3^-的适当供给。因为硝化主要是一个有氧过程，有利于反硝化的低的氧气条件常限制NO_3^-的供给。例如，一些湿地尽管土壤水分处于饱和，且由于大量有机质存在，却具有低的反硝化速率，原因是低的硝酸盐可获得性。只有在（1）湿地能从系统外获得接受到NO_3^-（侧向运输），（2）湿地在厌氧层上方具有一个厌氧区（垂直运输），例如在一些部分排干的湿地，或者（3）像许多水稻田那样经历淹水和排干交替的循环（时间上的分隔）。在更小的空间尺度上，反硝化可以在土壤团聚体内发生，或者在其他厌氧的微小地方发生（例如小块土壤有机质），主要由于适度排水良好的土壤存在微尺度土壤氧气含量和硝化作用的异质性。

最后，有机碳底物的可获得性限制反硝化作用，原因是反硝化作用主要由异养细菌完成。例如，农田土壤的长期耕作减少土壤有机质含量，足以限制反硝化作用。正如对全球氮平衡主要组分所估计的那样，反硝化作用在数量上是重要的，约占没有受人为干扰的（unmanaged）陆地生物圈1/3的氮损失。

火烧也会造成巨大的氮的气体损失。火烧过程中挥发氮的量和形式取决于火烧的温度。具有活跃火苗，能产生相当大湍流的火烧通常有很好的氧气供应，释放的氮主要是以NO_x形式。闷燃的火烧（smoldering fire）释放更加还原形式的氮，例如氨气。大约1/3释放的氮是以N_2的形式。严重的造成林分替换的火烧能引起大部分生态系统氮的丢失，但在火烧后的演替中逐渐归还。在较寒冷的地表火烧中，较少的有机质被燃烧，从而更少的氮损失。在一些地方火烧的抑制，而在另一些地方的生物量燃烧改变了许多生态系统中氮素循环格局。

（2） 气态氮在大气圈中的作用（atmospheric roles of nitrogen gases）

四种氮的气体在大气圈中具有不同的作用和影响。进入大气圈的NH_3可以与酸反应，从而中和大气圈中的酸性。

$$NH_3 + H_2SO_4 \leftrightarrow (NH_4)_2SO_4$$

上述反应中，NH_3被转换回NH_4^+后在下风处附着在干的颗粒表面，或者以NH_4^+形式溶解在降水中沉降下来。氨气的挥发和沉降将氮从一个生态系统转移至另一个生态系统。氨气本身也可以经由气孔被植物吸收。其实，植物通常具有一个关于氨的补偿点，有点类似于光合作用的CO_2补偿点。

在大气圈中，氮氧化物（NO和NO_2，统称为NO_x）由于其快速的互相转换通常处于动态平衡中。NO_x的反应能力极强，其含量调节了几个重要的大气化学反应。例如，高的NO_x含量可以催化一氧化碳，甲烷，以及非甲烷的碳水化合物进行反应，生成对流层的臭氧（O_3），是城市、工厂和农村地区光化学烟雾的重要成分。

$CO + 2O_2 \leftrightarrow CO_2 + O_3$

在低的NO_x浓度时，CO的氧化会消耗O_3。

$CO + O_3 \leftrightarrow CO_2 + O_2$

除了催化剂的作用可以改变大气化学并产生污染，NO_x的可以被长距离运输，并改变下风处的生态系统功能。以亚硝酸的形式，NO_x是酸沉降的主要成分，可以增加土壤中氮的可利用性和酸性。以气体的NO_2形式或者HNO_3形式，NO_x可以被植物从叶片气孔吸收，并参与代谢。NO_x也可以微粒态（particulate）形式沉降，另一种不被忽视的施肥形式。

与高度活性的NO_x不同，氧化亚氮（N_2O）在大气圈中的寿命可以达到150年，在对流层并没有强的化学反应性。N_2O低的反应性导致一个新的环境问题。N_2O是一个温室气体，在吸收红外辐射上，其效率要比CO_2高200倍。此外，N_2O在平流层紫外辐射存在的条件下与受激发的氧气反应生成NO，可以催化破坏平流层O_3。

虽然这些损失可能影响生态系统的氮库，但考虑到大气圈中的N_2已经达到了78%，通过反硝化作用向大气圈释放的N_2不会对大气圈产生显著的影响。大气圈中N_2的周转时间达数千年。

5.2 溶解氮丢失（solution losses）

氮通过淋溶以可溶性有机氮的形式可以从所有生态系统丢失，或者以硝酸盐形式从富含氮的生态系统丢失。未受干扰和未受污染的生态系统丢失的氮很少，主要以可溶性有机氮的形式。虽然硝酸盐在土壤中也是高度可移动的，植物和微生物可以在其被淋溶至生态系统根下区域前吸收大部分。然而，干扰通过营造促进氮矿化环境条件或者通过减少植被生物量从而减少对养分的吸收，经常增加硝酸盐从生态系统淋溶。例如，在美国东北部Hubbard Brook森林，实验性的去除植被导致大量硝酸盐、钙和钾进入地下水和溪流水丢失。然而，一旦植被开始再生长，不断累积的植物生物量吸收了大部分矿化产生的养分，溪流水中的养分含量逐渐回到植被去除前的水平。因此，当人为氮添加缓解了氮对植物和微生物的限制后，作为在生态系统功能上所产生的变化，硝酸盐的淋溶于是可以作为判别生态系统**氮饱和性**的

一个指标。普遍来说，氮通过淋溶和反硝化途径损失比例的增加要比保持在生态系统内氮库比例的增加更大。换句话说，氮素添加是生态系统渗漏（leaky）得更多了。

硝酸盐从地下水的丢失可能引起对人类健康和水体生态系统生态整体性方面的严重后果。在还原条件下，硝酸盐被转化成亚硝酸盐，可以降低动物运输氧气的血红蛋白能力的降低，尤其是对婴儿。集约化农业地区的地下水硝酸盐含量经常超过公共健康标准。

从陆地生态系统淋溶出来的氮经地下水运动至湖泊和河流，进一步通过反硝化作用释放到大气中，或者运输至海洋，正如前面讨论的那样。

经土壤移动的溶液必须保持电荷平衡，像带有负电荷的硝酸盐离子被阳离子或者质子平衡。因此，从土壤淋溶的每个硝酸盐离子会携带一个阳离子，如钙，钾和铵离子以维持电荷平衡。当从淋溶丢失阳离子超过风化和沉降的阳离子供给速率，净的阳离子丢失可能导致阳离子缺失。当这些阳离子被耗尽，硝酸盐会携带H^+或Al^{3+}，这将对下游生态系统造成有害的影响。硝化作用也会产生酸性：

$$2NH_4^+ + 3O_2 \leftrightarrow 2NO_2^- + H_2O + H^+$$

在上述反应中，释放的氢离子与土壤阳离子交换位点上的阳离子交换，使得这些阳离子更加容易通过淋溶丢失。

5.3 侵蚀损失（erosional losses）

侵蚀是氮丢失的一个自然途径，经常在土地利用变化后剧烈增加。正如淋溶一样，氮的侵蚀损失也包含有机的无机的形式，虽然与土壤团聚体和颗粒物相关联的有机物是最重要的侵蚀通量。

第六节　其他元素的循环

在养分元素来源（岩石或者大气圈），化学性质，植物需求上的差异决定了不同元素循环的格局和速率。由于许多植物具有相似的化学元素计量比（见第八章），在所有通过生态系统循环的必需元素循环格局上存在较大范围的相似性。正如在水体生态系统中所观察到的那样，当这些元素穿过植被循环循环时，计量化学比建立了一个功能上的连接。例如，高产的生态系统比低产的通过植被循环更多的所有必需养分元素。尽管在这些元素循环之间具有较大范围的相似性，但无论在不同营养元素之间，还是在不同生态系统之间都存在很重要的差别，这些生态系统依赖于这些植被所需要的营养元素来源（岩石或者大气圈），化学性质，以及不同的量。与由生物学过程控制的循环相比，向生态系统提供营养元素的非生物过程（尤其是风化和大气沉降）通常具有很不相同的元素比例，这种生物学与地质学元素计量化学的相互作用增加了我们对陆地生态系统元素循环分析的多样性和复杂性。

生态系统在各种岩石起源的营养元素的可获得性上有很大的不同，取决于母岩材料和研究区域的水土侵蚀和风化历史。例如，主要来自海洋沉降的石灰岩经常具有可观的磷含量，

要比较少磷含量的岩石更少发育磷限制的生态系统。相反，像氮这种大气来源的营养元素更加强烈地依赖于生命有机体之间的相互作用。生态系统内元素循环的紧密性（tightness of element cycling）也取决于元素在水中的可溶解性和植物对它们的需求量。例如，与溶解性低的必需大量元素磷相比，溶解性高、植物需求量低的氯元素，其循环趋向于更加开放。

然而，除了这些宽泛的普遍性以外，元素的特殊性质及其植物对它们的利用在不同元素循环间产生重要的差异。我们简要描述经常对生态系统生产力有限制作用的大量元素（氮，磷和钾）循环的主要特点，举例说明对生产力较少限制的大量元素（钙和硫），很少量需求的微量元素（氯），以及生物没有需求且有潜在毒害作用的元素（铅）。

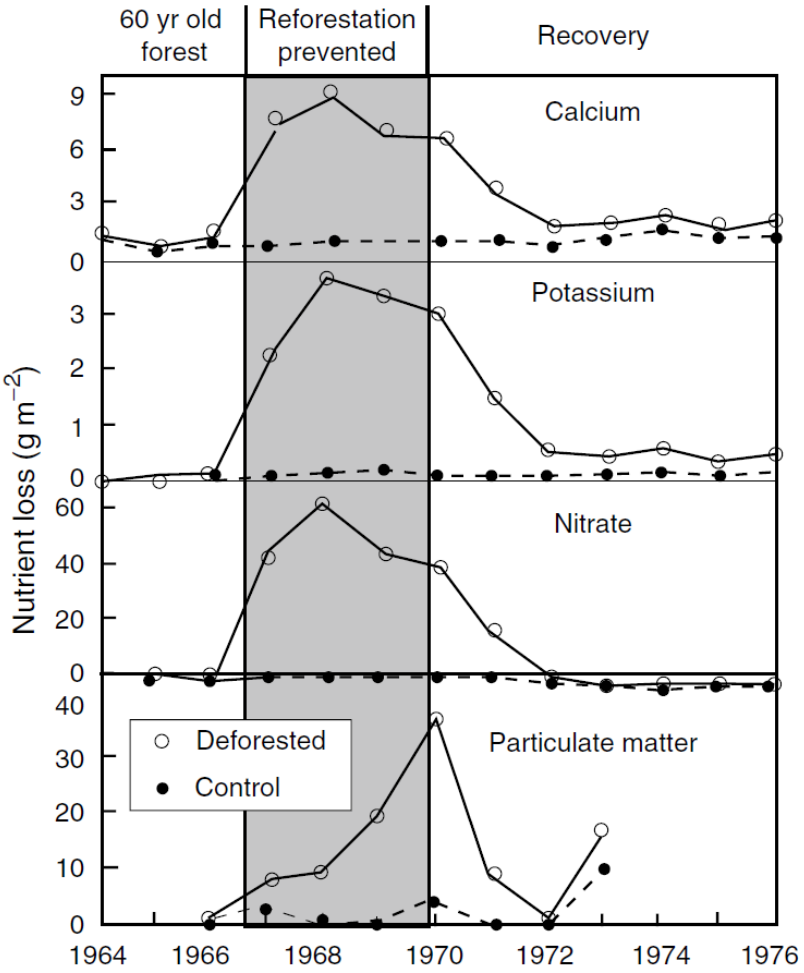


图 9.6-1 美国东北部 Hubbard Brook 森林实验小流域森林砍伐前后钙、钾和颗粒态有机质随溪流水分的丢失。阴影区域显示植被去除后以及使用除草剂的时间段。

6.1 磷

磷是通过植被循环的元素，与氮素具有十分紧密的耦合关系。与植物每年的需求量相比，这两个元素在土壤溶液中可获得性最低，于是经常限制或者共同限制植物的生产力。氮和磷

是驱动植物生产（光合作用和呼吸作用）发动机的必需成分。这样，它们在植被循环格局上具有许多相似性就不足为奇了。通过降解含有氮和磷的颗粒有机物质，以及凭借比扩散更加快速地运输养分到根表面，菌根真菌在植物对这两种元素的吸收上具有重要的作用。温带和高纬度森林中外生菌根典型地在氮素获取上，以及草地和热带森林中丛枝菌根典型地在磷素获取上具有尤其重要的作用。植物将这两种营养元素优先分配到代谢活跃，有资源需求的组织（叶片和细根），营造出一种放大作用的（正的）反馈，加强植物捕获额外资源的能力。叶片中大约一半的氮和磷在叶片凋萎过程中被再吸收。

虽然这些共同的特征将氮和磷的循环连接在一起，有些过程会对这种耦合起加强的作用，而另外一些则起破坏耦合的作用。在生物内部，这种耦合作用是通过调节个别营养元素吸收，如上调氮素限制植物硝酸盐和铵盐的吸收，上调磷素限制植物磷素的吸收。这样，植物以及它们所产生的凋落物碎屑趋向于按照一定的比例循环氮和磷，从而有利于植物的生长（N:P大约在28的时候），虽然这个比例在生态系统内和生态系统之间都有很大的变化。在几年到几十年的生态系统尺度上，氮的固定趋向于增加氮素限制生态系统中的氮，而当有超过植物和微生物需求的可利用氮累积时，生态系统中厌氧的微位点反硝化和硝酸盐淋溶趋向于减少氮。这些通量在量上是巨大的，从而强烈影响氮的含量及其在全球尺度上的同位素组成。这些过程增强了氮和磷循环之间的耦合，所形成的N:P也有利于植物和微生物的生长。

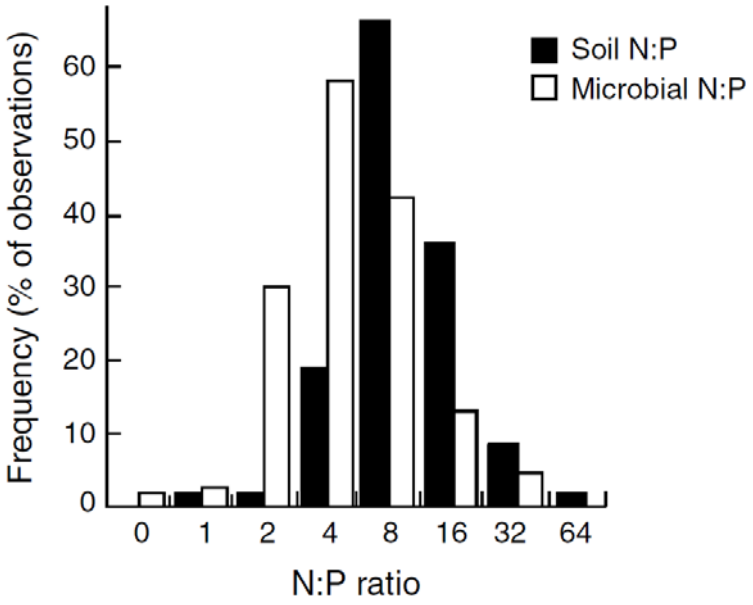


图 9.6-2 土壤和微生物生物量中 N:P 比（经过以 2 为底的对数转换）的频度分布

同样在不同生态系统土壤（13.1 ± 0.8）和微生物（6.9 ± 0.4）生物量之间也存在相对恒定的氮和磷的比例，分别为13.1 ± 0.8，6.9 ± 0.4（几何平均）（图9.6-2）。正如在海洋和淡水中的那样，磷含量的变化站、占很大一部分生态系统间N:P的差异。例如，微生物N:P比森林高于草地的，原因是森林中较低微生物磷含量。

植物比（28:1）微生物高的N:P比（7:1）可能反映了它们在生物学上的差异。微生物比植物具有更高的生长潜势，主要是微生物需要对高度可变的土壤环境中作出更加快速的响应。这样应该需要更高的磷素含量（于是低的N:P比）来支持快速的蛋白质合成。相反，植物因为光合作用（大约一半的氮在叶片中）具有高的氮需求（于是高的N:P比）。这样，所观察到的N:P比差异就可以解释通了。在相同的环境中，我们预计植物相对氮限制，而微生物相对磷限制。每一个类群的生物应该调节养分获取和释放，以满足它们对养分的需求，同时归还具有其生物量N:P比特征的死亡有机质。通过这些过程，正如所观察到的那样，我们预测土壤具有介于植物和微生物之间的N:P比。

氮和磷在化学特征上的差异弱化了二者在循环上的耦合，尤其是在一个长的时间尺度上（几十年到几百年）。两种元素进入生态系统的途径具有本质的区别，氮通过生物固定持续地从取之不尽的大气库获得，而磷来自原生矿物的风化，且可能通过几百万年风化而耗竭（图3.5-1）。例如，在发育时间较短的生态系统，含磷的磷矿石被土壤呼吸释放的碳酸风化，释放可利用形态的磷，而这个时候氮的供给经常处于缺乏的状态（9.4-1）。

然而，随着时间的推移，风化源的磷可能被耗尽，尤其是处在冰川和间冰川循环影响下的湿润地区，在那里地质抬升和侵蚀很慢。一旦矿物中的磷被耗尽，系统内部来源的磷素就很少甚至没有，磷的输入就主要依靠来自农业或者干旱地区的上升风对沙尘的运输。相应地在生态系统尺度上氮和磷供给的耦合被解除，古老土壤上的生态系统中磷比氮更有可能成为限制（因素）。

死亡有机质的微生物过程能够弱化氮和磷循环的耦合。与氮的周转相比，磷的周转与分解的连接并没有那么紧密，原因是连接磷和碳的酯键（C-O-P）可以在不降解碳骨架的情况下用酶断开。相反，氮与碳的耦合更加紧密，氮直接与碳骨架上的有机物质成键（C-N），并通常要在打开碳骨架形成氨基酸和其他可溶性的有机含氮化合物后释放出来。分解过程碎裂有机质，同时将C-O-P键暴露在酶的作用下。土壤中低的磷可获得性和高的氮可获得性诱导植物和微生物将氮素投资到用于获取磷素的酶中。植物根及其菌根对象，尤其是丛枝菌根，产生磷酸酶以打开有机质上的酯键以释放磷酸盐（PO_4^{3-}）。因此，许多生态系统中磷在有机物质和植物根之间的循环十分紧密。例如，在热带雨林中，凋落物层菌根形成的垫状物产生磷酸酶，从有机质上切下磷酸盐。菌根在磷酸盐与土壤中的矿物相（mineral phase）产生作用前直接吸收大部分磷酸盐。只要土壤中有足够的氮，低土壤磷酸盐就会诱导植物和微生物分泌具有高氮含量的磷酸酶。这与蛋白酶相反，，蛋白酶的活性更加强烈地与微生物活性相关，而不是与土壤有机质含量。

微生物生物量常占土壤中有机磷的20-30%，远高于微生物碳（大概2%）或者氮（大约4%）的比例。微生物生物量于是一个重要的潜在可利用的磷库，尤其是在高度碱性或者酸性土壤中，这些土壤中磷被强烈束缚在矿物质的表面。微生物的磷要比无机的磷酸盐更具有潜在可利用性，原因是受到了保护，免于与土壤中的矿物相发生反应，正如后面所描述到的。

虽然C:N比经常被认为对理解生态系统养分循环至关重要，但死亡有机质的C:P比在控制磷素矿化和固持的平衡，从而进一步对植物的磷素供给可能也很重要。

在控制土壤中磷素可获得性上，与土壤矿物的化学反应起到了一个关键作用。与氮不同，土壤中的磷并没有经历氧化-还原反应，也没有重要的气态相。此外，自然界中许多控制磷的可获得性的反应是地球化学的，而非生物学的。磷酸盐（PO_4^{3-}）在土壤中是主要的可利用态无机磷。磷酸盐最初通过阴离子交换被静电吸引在矿物质表面带正电荷的位点上。在那里，随着与矿物质表面的金属形成一价或者二价的共价键，磷酸盐更加紧密地被束缚（于是无法被植物利用）。磷可以被可溶性的矿物（尤其是铁氧化物）束缚形成难溶的沉淀物。这些沉淀反映帮助解释为什么高度风化的热带土壤（氧化土和老成土）具有极低的磷的可利用性，以及为什么这些土壤上的森林生长经常是磷限制的（见第三章）。与热带氧化土中的氧化物相比，温带土壤中占优势的硅酸盐粘土矿物固定磷酸盐的程度较低。

磷酸盐的可获得性对pH十分敏感。在低pH，铁，铝和锰可溶性十分高，与磷酸盐反应形成难溶解的化合物：

$$Al^{3+} + H_2PO_4^- + 2H_2O \leftrightarrow 2H^+ + Al(OH)_2H_2PO_4$$

溶解的　　不溶解的

在有高含量钙和碳酸钙（$CaCO_3$）存在的土壤中，这些土壤典型出现高pH，高磷酸钙沉淀，从而降低溶液中磷酸盐的可获得性：

$$Ca(H_2PO_4)_2 + 2Ca^{++} \leftrightarrow Ca_3(PO_4)_2 + 4H^+$$

溶解的　　不溶解的

磷酸钙的沉淀是磷酸盐化肥在富含钙的温带农业生态系统中很快成为不可利用的一个主要原因。由于在高pH和低pH时发生沉淀反应，磷在pH6.5左右的一个很窄范围里最容易被利用（图9.6-3）。

土壤中的有机化合物也可以直接或者间接调节磷的束缚和可利用性。例如，带电荷的有机化合物可以在氧化物表面与磷酸盐竞争束缚位点，或者与金属形成螯合物，以防止它们与磷酸盐发生反应。上述两个过程均可以增加矿质土壤中磷酸盐可利用性。另一方面，有机化合物与铁、铝和磷酸盐形成络合物，可以保护这些化合物免受酶的攻击。在热带水铝英石土壤中，这些络合物构成了一个磷的主要的汇。

以铁、铝和钙化合物的形式形成沉淀的大部分磷不能为植物所利用，这部分磷被称为闭蓄态磷（occluded phosphorus）。在土壤发育阶段，原生矿物因为风化和侵蚀而侵蚀流失而逐渐消失。土壤中磷酸盐的量也趋向于从矿质态，有机态，半闭蓄态到闭蓄态和有机束缚的形式发生变化，引起生态系统在长的时间尺度上从氮限制到磷限制的转变（图3.5-1）。

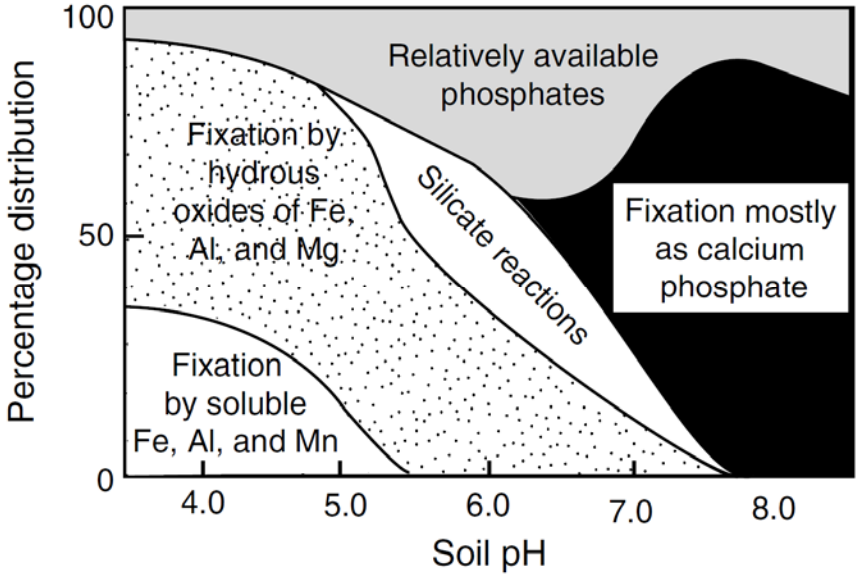


图 9.6-3 pH 对土壤中主要形态磷的影响。磷化合物在低和高 pH 两端的低可溶性导致只剩一个很窄的 pH 在 6.5 左右的磷酸盐可利用窗口。

大多数土壤中磷酸盐与有机质或者土壤矿物的紧密束缚引起90%的磷的丢失是通过表面迳流和土壤侵蚀从含磷颗粒丢失的，而不是通过可溶性磷酸盐向地下水的淋溶丢失的。进入地下水的可溶性磷的三分之二是有机的，从而与土壤矿物很少发生反应。

不论是铵态氮还是硝态氮，高等植物都是主要通过特定的转运蛋白对其进行吸收。吸收后的氮素一部分在根系中直接被同化利用，一部分在叶片中同化利用。不同氮源在植物体内的运移、存储等过程是有很大差别的，但硝态氮和铵态氮都是植物需要的良好氮源，吸收到作物体后，除硝态氮需先还原成NH_4^+（NH_3）以外，其余同化过程完全相同。

植物对硝态氮和铵态氮的吸收和同化途径不同，两种氮源的混合比例和使用环境亦会对植物生长有显著影响的，因此要根据植物对氮源的喜好以及环境要素来确定氮源的形态和配比。

6.2 硫（略）

6.3 必需的阳离子（略）

6.4 微量营养元素和非必需元素（略）

参考文献：

Marschner H（2012）Marschner’s mineral nutrition of higher plants. Academic press

Yuan L, Loque D, Kojima S, et al. The organization of high-affinity ammonium uptake in *Arabidopsis* roots depends on the spatial arrangement and biochemical properties of AMT1-type transporters. The Plant Cell, 2007, 19(8):2632-2652

第十章 营养级动态

营养级动态控制了碳、养分和能量在一个生态系统生物体之间的运动。本章描述对生态系统营养级动态的控制。

引言

虽然陆地上的动物仅消耗了相对较小的一部分净初级生产（NPP），但它们强烈地影响了大多数生态系统中的能量流动和养分循环。在前面的章节中，我们强调了植物和土壤微生物的相互作用，原因是这两个类群生物直接解释了大多数陆地生态系统中 95%的能量传递。植物利用太阳能将 CO_2 还原成有机质，它们中的大多数凋萎、死亡，并直接进入土壤，进一步被细菌和真菌分解。同样，大多数在生态系统转换的养分包含植物的吸收，并通过死亡有机质回归到土壤，此后通过微生物降解被释放。在大多数生态系统中，我们对初级生产和分解估计的不确定性超过了所有从植物到动物的能量传递。可能因为这个原因，许多陆地生态系统生态学家在经典的生产和生物地球化学循环的研究中都忽略了动物。相反，水体生态学家却无法回避动物，因为食草动物的取食占据了碳和养分传输比陆地生态系统大得多的比例（图 10.1-1）。可能是因为这个原因，水体生态系统生态学家在生态系统功能研究中普遍领导了与营养级动态作用有关的理论发展。

控制能量和养分向动物传输的因素具有重要的社会含义。许多人强烈地依赖高蛋白质动物产品作为食物。不断增加的人口和膳食转向消耗更多肉类使得世界食物供给面临越来越大的压力。找到一个向不断增加的人类有效供给食物的生态学可行的策略需要很好地了解调节植物生物量向动物生物量，包括人类，的转化效率。

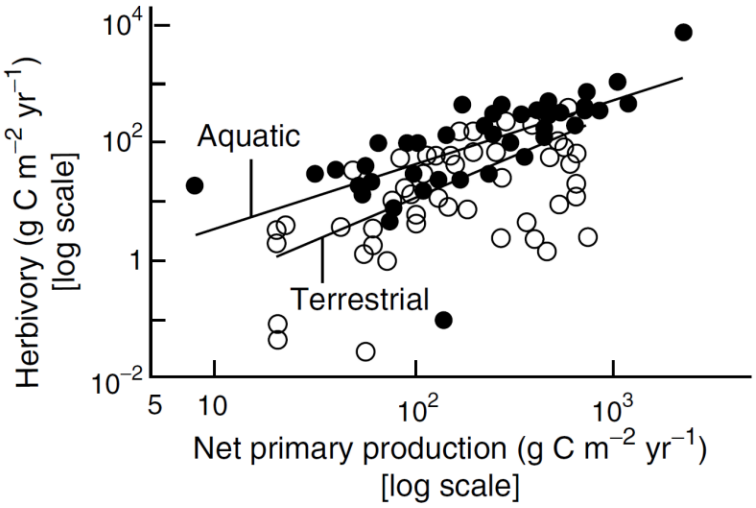


图 10.1-1 水体和陆地生态系统初级生产和草食作用速率的比较。

第一节　核心要点

强烈的草食动物取食，要么是由于驯化动物的过度载畜，要么是从并不是强烈经营的生态系统移除捕食者，降低了适口植物的多度和多样性。这是人类对地球最为广泛的影响，主要通过从大部分世界海洋中移除大型捕食性鱼类，从为人类居住和利用的强烈经营的土地，以及从广泛家畜放牧的草地和稀树草原的土地中移除捕食者。为什么一些草食动物比其他的一些草食动物取食一些植物种类更多的植物生物量？植物，草食动物及其捕食者之间的相互作用是如何影响生态系统的结构与功能的？动物取食后的能量和养分发生了什么？人类对肉和植物食物比例的选择如何影响满足陆地上不断增加人口的食物需求？对这些问题的回答可以为解决社会面临的一些最受争议的生态学问题提供一个框架。

第二节　营养级动态概要

能量和养分传输定义了生态系统的营养级结构。观察生态系统生物之间活跃的相互作用最简单的方法就是追踪一部分能量，从进入生态系统开始直至它们最后离开生态系统。**营养级传输**（trophic transfer）包含了一个生物对另一个生物或者死亡有机质的取食。植物被称为**初级生产者**（primary producers）或者**自养生物**（autotrophs），因为它们将CO_2，水和太阳能转化成生物量。异养生物（heterotrophs）是取食活的或者死亡有机质获得能量的一类生物。异养生物担任两个主要营养途径的角色，一个基于活的植物（植物营养系统，plant-based trophic system），另一个是基于死亡的有机质（碎屑营养系统，detritus-based trophic system），碎屑营养系统在一个生态系统中通常占据大部分通过动物的能量传递。**消费者**（consumers）是取食其他活生物的一类生物。这些包括草食动物（herbivores），取食微生物的食微生物者（microbivores），以及取食动物的肉食动物（carnivores）。一个食物链是一群生物通过消费（或取食）过程连接在一起。例如，禾草，蝗虫和鸟组成一个食物链。获取能量主要来自从植物或者碎屑开始传递次数相同的生物被认为属于同一营养级。这样，在一个植物营养系统中，植物组成了第一个营养级，草食动物为第二个营养级，初级肉食动物为第三级，次级肉食动物取食初级肉食动物为第四级，等等。同样，在碎屑营养系统中，细菌和真菌主要降解死亡的土壤有机质，吸收降解产物支撑它们的生长和维持。这些**初级碎屑取食者**（primary detritivores）在碎屑食物链中处于初级营养水平，在一系列营养级水平上被动物取食，这与植物营养系统类似（图10.2-1）。

虽然食物链是描述生态系统营养级动态的简便方法，它们总体上还是过于简化了，有些生物能够取食超过一种的食物。例如，人类可以取食多个营养级水平的食物，包括植物（第一个营养级），奶牛（第二个营养级），鱼类（第二以及经常更高的营养级），以及蘑菇（碎屑取食者）。许多其他哺乳动物和鸟类也取食草食动物和食碎屑昆虫和其他动物。实际发生在生态系统中的能量传递通常是复杂的食物网（图10.2-1）。我们只有了解了生态系统中一个营养级对每一个动物食物的贡献，才可以追踪沿着这些食物网的能量传递。虽然食物网结构在许多生态系统中只是部分得到了描述，定量的食物网能量流动格局还知道得很少，尤其是那些碎屑营养系统。

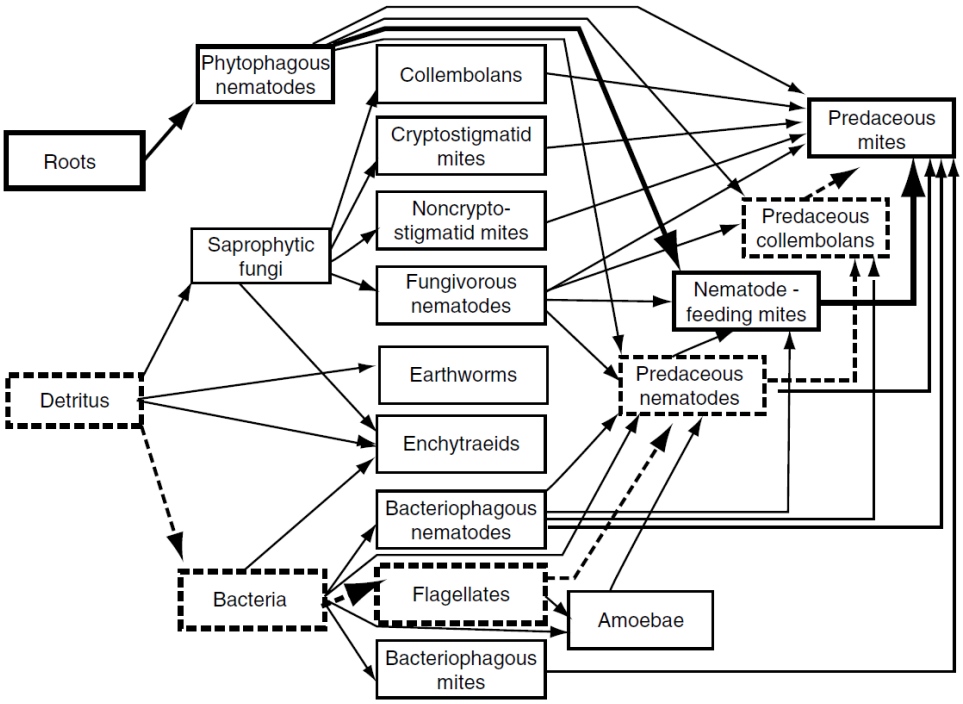


图 10.2-1 草地食物网地下部分的能量流动格局。食物网是由许多相互连接的食物链组成。一个植物营养系统（实线）和一个碎屑营养系统（虚线）用黑体显示。

食物不光是有能量组成。事实上，动物选择食物经常既基于食物的能量含量，也取决于植物中的蛋白质含量，因为动物比植物需要更多的氮（动物组织中的含量为7-14%，相对于植物组织中0.5-4%）。磷的含量通常在动物中也要普遍高于植物中的，因此或者是氮或者是磷可以限制动物生产。食物摄取也强烈地受植物防御化合物含量的影响，这些物质有毒性或降低可消化性。上述正面的和负面的食物质量决定因素强烈地影响了营养传递的时间和空间格局。

对流经食物网的能量和养分的调节是十分复杂的，且在不同生态系统中变异很大。然而，两个理论模式规定了可能控制的范围。（1）在食物链（植物或者碎屑）基础上食物的可获得性通过**上行控制**（bottom-up controls）限制了上一个营养级的生产。在这种情况下，食物的质量和数量，包括氮、磷和防御化学物质的含量，决定了被取食，并随后用来支撑动物生产的食物量。（2）或者，能够调节食物多度的捕食者对食物网施加了一个**下行控制**（top-down control）。大多数营养系统都展示出上行和下行控制一定程度的组合，二者的相对重要性随时间和空间而变。例如，在深海生态系统，养分、光照和温度解释大部分生产的地理和季节性变化格局（上行控制），但一旦浮游植物开始旺盛生长，浮游动物很快生长并繁殖，减少了浮游植物的生物量（下行控制）。

营养级能量和养分的传递对生态系统功能具有深远的意义。它们减少了植物生物量，从而改变了植物介导的生态系统过程，包括水分、能量和养分的循环。动物对植物和碎屑的消

耗也加速了养分向环境的归还，虽然，正如我们会看到的那样，草食动物取食对养分循环的影响取决于最初养分的可获得性。

第三节　生态系统能量流动的控制

3.1 上行控制（bottom-up controls）

植物生产是植物营养系统和碎屑营养系统能量流动的上限。平均来说，动物在植物营养系统消费的能量不可能超过最初通过初级生产进入生态系统的能量。这构成了一个生态系统能支持的动物生产的基本限制。当对陆地上所有生态系统进行比较时，草食动物生物量和生产趋于随着初级生产的增加而增加（图10.3-1）。当在相似类型生态系统之间比较时，初级生产和草食动物生物量的相关性尤其的强。例如，在阿根廷沿着水分可获得性梯度的自然或者经营的草地，哺乳动物的生物量随着地上生产的增加而增加（图10.3-2）。在非洲的塞伦盖蒂（Serengeti）草原，大群有蹄类动物也是在更加高产的草地获取它们的大部分食物。同样，高产的森林要比低产的森林通常具有更多的昆虫取食。当森林增加养分输入以增加生产时，这也通常增加草食动物的取食。

世界上大的渔场依赖于强烈的初级生产和动物生产的相关性，尤其是在海岸区域，那里上涌的富含养分的底部水分支撑了高的浮游植物、浮游动物和鱼类的生产。而在另一端，在热带海洋的中央环流区（the central gyres of tropical oceans），那里远离营养丰富的底部水分，以及在加拿大地盾区（the Canadian Shield）贫营养（养分含量极低）湖泊，哪里的土壤被更新世的冰川（Pleistocene glaciers）刮走，导致生产力很低。

补贴（subsidy）可以帮助一个生态系统次生生产超出NPP能支撑的水平。例如，大多数森林中拥有上游溪水流的活跃区域都有陆地凋落物的输入。这些外来的（allochthonous）输入（即溪流外生态系统的输入）提供了支撑水体食物网的能量。在更加微小的尺度上，浅滩溪流中滤食性（filter-feeding）无脊椎动物获得的大部分能量来自上游水塘中的藻类生产。靠近海洋、河流和湖泊的陆地食物网经常得到水能输入的补充，例如当鸟类或者熊取食鱼类，或者蜘蛛取食海洋碎屑的时候。高强度的农业生产强烈地得到人类输入的养分、水分和化石燃料的补贴。

生物圈之间在草食作用上的差异反映了NPP、养分平衡以及植物向结构和化学防御分配上的差别。在生态系统类型间，草食动物取食最大的差别来自植物对物理支撑分配光合产物上的差异。湖泊、海洋，以及许多河流和溪流是浮游植物占优势，它们将大部分能量分配至细胞质，而不是结构支撑。大部分浮游植物是很容易为浮游动物消化，所以动物可以取食很大比例的初级生产，并将它们转化成动物生物量。即使在浮游植物之间，绿藻（裸绿藻）通常比形成保护性外衣浮游植物，如硅藻类，鞭毛藻类以及金藻类，更加容易被取食。在另一端，森林具有很大比例的生产分配至富含纤维素，木质素的木本组织，这些物质很难被动物直接消化。然而，一些动物，如反刍动物（如奶牛），盲肠消化者（如兔子），以及一些

昆虫（如白蚁），具有共生性的肠道微生物可以降解纤维素。这些动物可以同化一部分微生物降解细胞壁释放的能量。因此，NPP被动物消费的比例在森林中要低得多，原因是森林植物将大部分它们的生物量分配至结构性物质。

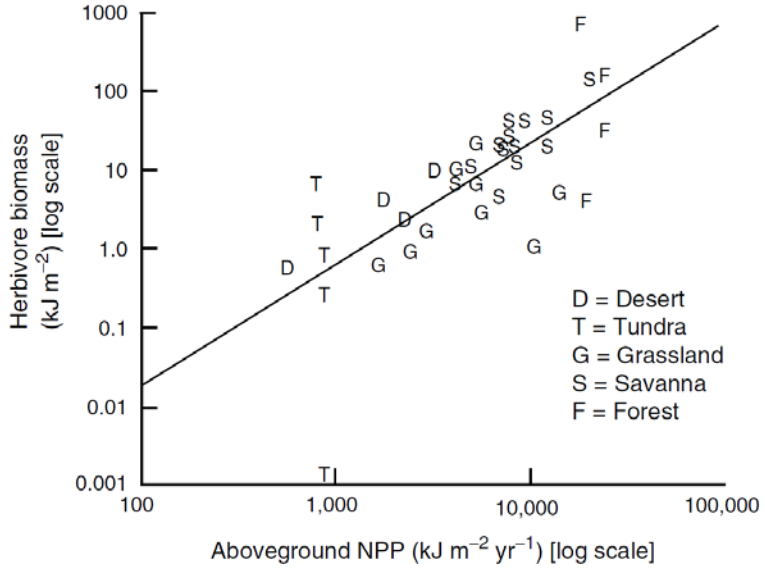


图 10.3-1 地上净初级生产（NPP）与草食动物生物量的对数转换相关性。1g 去除灰烬的生物量与 20kJ 的能量相当。不同类型生态系统地上食草动物的生产和生物量与地上 NPP 相关。

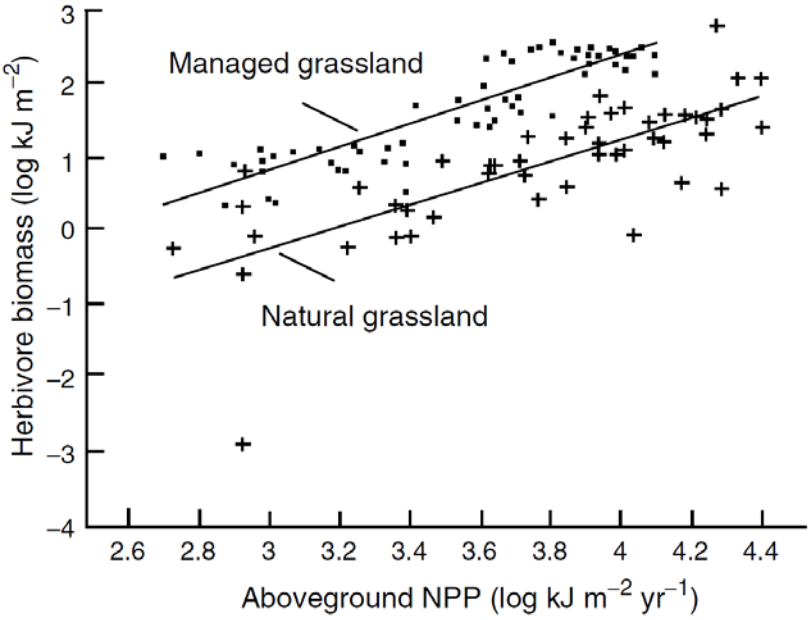


图 10.3-2 南美自然和经营的放牧生态系统哺乳草食动物生物量和地上植物生产之间对数转换后的相关性。草食动物生物量随着 NPP 增加而增加。对于给定的生产水平，经营草地的动物生物量比自然草地上的要大 10 倍，因为经营者在经营的系统中通过控制捕食，寄生以及疾病的发生，提供饮用水和矿质营养。草食动物生物量在经营和自然生态系统中的差异说明了 NPP 并不是动物生产的唯一限制。

不同陆地生态系统之间，在植物生物量被食草动物取食的量有1000倍的差异。草食动物在生产力很低的生态系统，如冻原，消费单位面积最少的生物量。然而，食草动物消费的能量在生物群区内和群区之间都有很大的变异。与总的地上NPP相比，草食动物的消费显示出与可食组织（如叶片）的生产之间存在一个更加强烈的相关性，因为许多植物生产的木本支撑结构地草食动物消费贡献很小。

植物的化学和物理防御减少了转化成草食动物能量的比例。在限制草食动物多度上，是食物的可获得性，还是捕食，存在争论，因为世界被没有动物取食的绿色生物量所覆盖。然而，不是所有的绿色生物量都是可消化从而充当食物的。例如，反刍动物和昆虫需要植物生物量至少具有1%的氮含量才能增加体重，对于繁殖期的动物来说，这个要求还会更高。在低养分生境，植物不仅具有低的氮和磷含量，还具有高的化学防御物质的含量。例如，在非洲，肥沃的草地要比不肥沃的草地可以支撑更高的食草动物多样性和生产。在热带森林也可以看到同样的格局，与肥沃土壤相比，更高水平的化学防御和更低水平的昆虫取食出现在贫瘠的土壤上。三个因素决定了植物将光合作用产物分配至防御：（1）遗传因素，（2）植物生长的环境，以及（3）季节性的分配规划。

前两个引起植物分配至防御（遗产和环境）的变异导致贫瘠土壤上高水平的植物防御。植物防御要么是直接有害的，要么是减少摄入（ingestion）和消化（digestion）过程中草食动物限制性资源的可获得性。例如，丹宁，与蛋白质结合，减少了草食动物对氮的可获得性；生物碱可以作为神经毒素；荆棘减少哺乳动物的取食速率。

氮和磷之间的平衡，以及可消化能量影响这些资源支撑动物生产的效率。非活性材料具有很广的C:N:P比例的范围。然而，活的原生质体中这些营养之间的比例要受限制得多，原因是在所有活细胞中的生化过程是基本相似的。通常，磷的含量比氮的更加多变，无论是在植物，还是在动物中。正如在植物和微生物中所观察到的那样，动物生产受食物中最低含量资源（氮、磷、可消化能量）的限制，同时动物通过偏爱最限制营养元素的获取加强氮和磷循环的耦合。例如，动物可以从低氮含量食物中更加高效地摄取氮，主要通过选择性觅食，在肠道中对氮的高速吸收，或者降低损失速率。限制性低的营养元素从食物摄取的效率也较低，并可能被优先释放到环境。这些**化学计量关系**（stoichiometric relationships）（**元素比例**）是所有生态系统中营养元素循环速率的决定因素，这在前面章节中已经讨论过，并在本章进一步讨论。

3.2 下行控制（top-down controls）

捕食者的消费经常改变食物网多个营养连接的生物多度（营养的级联效应）（trophic cascade）。例如，一个捕食者可能降低它的猎物的密度，这可以使它的猎物的猎物从消费者的控制中释放出来。**营养的级联效应引起营养级间生物体生物量的交替变化**。例如在许多溪流中，假如只有藻类存在，它们不断生长直到养分限制，形成了一个“绿色”的表面（图10.3-3）。假如有2个营养级（植物和草食动物），草食动物取食将植物维持在一个低的生物量水

平，留下一个光秃秃的表面，只有零星的快速生长的藻类。当有3个营养级存在时，次级消费者降低了草食动物的生物量及其取食压力，从而又使得藻类达到一个高的生物量。当有偶数（2，4，等）的营养级时，藻类生物量通常较低。奇数营养级水平在营养的级联效应降低食草动物生物量，并释放藻类，形成一个“绿”色世界。

营养的级联效应已经在广泛的生态系统范围中得到了证明，从公海到热带雨林，以及微生物食物网。营养的级联效应通常源自各个物种之间强的相互作用，所以最好在物种水平进行探讨，而不是在生态系统水平。因为营养级联效应的物种专一性特性，当一个单一种类在营养级水平占优势，例如一个湖泊中当水蚤（daphnia）是优势食草动物或者一种食鲦鱼的鱼成为占优势的肉食动物时，它们最有可能在生态系统尺度上突显出来。同样，美国西部狼的移除引起麋鹿和其他有蹄类的种群爆发，导致过度啃食。狼的重新引入逆转了这个效应，主要通过捕食和有蹄类动物躲避区域高的捕食风险。

淡水富营养化经常导致强烈的物种优势度，从而提供了级联效应发生的条件。营养的级联效应具有重要的实践意义；在恰当的情形下，引入食鲦鱼的鱼，可以释放浮游动物草食者种群，能够剿灭藻类过度生长引起的水华，增加水体透明度。包含无脊椎食草动物和恒温脊椎动物捕食者的营养级联效应是特别强的。不幸的是，当营养动态改变后，意料之外的物种相互作用经常变得重要，导致物种引入或者去除后意外的响应。因此，通过营养级联效应的操控来回答管理问题需要对包含物种生态学以及控制它们相互作用的因素的全面理解和精心测试。

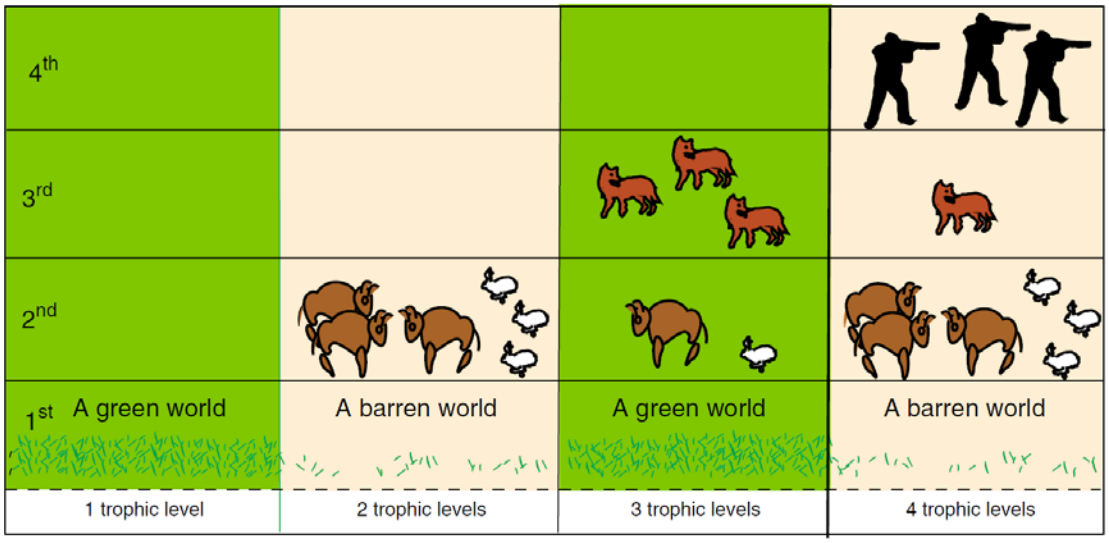


图 10.3-3 在具有营养的级联效应存在的情形下，食物链长度对初级生产生物量的影响。当具有营养级的数量奇数（1，3，5，等）时，植物生物量较丰富，因为此时草食动物的生物量较低；当营养级的数目是偶数（2，4，6，等）时，植物生物量减少，因为此时具有较多的草食动物生物量。

第四节　养分循环的营养级效应

食草动物促进了高产生态系统的生产，却减少了低产生态系统的生产。低养分环境中由具有发育完好化学防御的植物占优势，草食动物光顾这些生态系统的频率较低，因为动物避免选择适口性差的景观中的斑块。在这些环境中的草食动物（就像植物本身一样）有效地保持并再循环氮和磷等养分，同时形成养分含量很低的排泄物，加强了土壤微生物对养分的固持。食草动物通过选择性地取食低防御植物，间接地减慢了这些低养分环境中的养分循环，导致强防御植物的多度增加，这些植物产生的凋落物具有低的养分含量和高的植物防御物质的含量。许多对土壤微生物有毒性的植物引起凋落物分解速率降低，并进一步降低低营养环境中的土壤肥力（图10.4-1）。

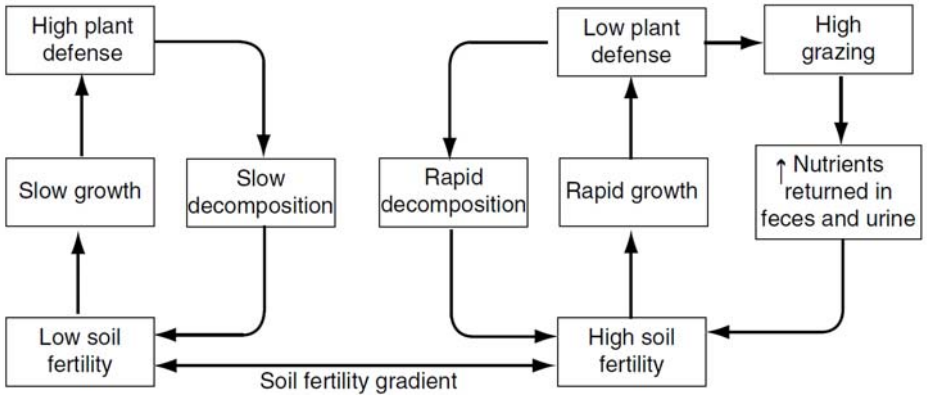


图 10.4-1 草食动物取食与植物防御之间的反馈使生态系统在土壤肥力上产生两极分化。在贫瘠土壤上，食草动物因为植物防御而选择，降低了凋落物质量，减慢了凋落物分解和养分供给的速率。在肥沃土壤上，草食动物取食加快了可利用养分回归到土壤。

草食动物在肥沃环境中更加丰富，那里植物生产力更高，也具有更高的适口性。草食动物的取食加速了植物生物量周转，并以粪便和尿液等形式返还给土壤可利用养分。这种凋落物分解和氮矿化的“捷径”（short circuits），促进了植物生产。大约1.5%的组织氮含量显示了一个分界线，可以区分贫瘠生态系统和肥沃生态系统，在前者草食作用引起养分循环速率降低，而在后者草食作用促进养分循环。

肥沃环境中的植物常对草食动物取食产生了适应。肥沃的草地经草食动物适度取食后，要比没有任何草食动物取食的生产力更高。然而，许多经营的生态系统的放牧强度常超过自然生态系统中的，原因是人们通过放牧强度和捕食者的控制来控制草食动物的密度。高的放牧强度，无论是在自然的还是经营生态系统中，能够降低生产和植物盖度，并增加土壤侵蚀，导致一个生态系统的土壤肥力和生产力的下降。

第五节　生态效率

5.1 营养级效率和能量流（trophic efficiency and energy flow）

每个营养级传输时能量的损失限制了高的营养级水平上的生产。

5.2 消费效率（consumption efficiency）

消费的效率主要取决于食物的质量，次要地取决于捕食。

5.3 同化效率（assimilation efficiency）

同化效率取决于食物的质量和消费者的生理。

5.4 生产效率（production efficiency）

生产效率主要取决于动物的代谢。

第六节　食物链长度

生产与其他因素的相互作用决定了食物链长度和群落的营养级结构。NPP和能量传输的低效性限制了下一个营养级水平可利用的能量数量，从而影响了一个生态系统能支撑的营养级数量。例如，生产力最低的生态系统可能只有植物和草食动物，而产量高一点的生境也可能支撑多个营养级的肉食动物。碎屑食物链也是在更加高产的生态系统趋向于更长。然而，在一些水体生态系统中，这种趋势可能向相反方向发展。贫营养生境能够支撑倒置的生物量金字塔（inverted biomass pyramid），其中大型长寿命鱼类要比支撑它们的浮游植物和无脊椎动物更加常见。当对一个大范围生产力梯度的生态系统进行比较时，NPP和营养级数量并没有表现出一个简单的相关性。其他诸如环境变异性和环境的物理结构要比食物链各营养级能获得的能量对营养级数量具有更大的影响。

第七节　季节性和年际格局

在陆地生态系统中，一个营养级水平的生产很少在时间上与下一个营养级的消费是同步的。捕食者和猎物在时间上的关联是高度可变的，但也显示出一些共有的格局。植物和它们的昆虫捕食者经常利用相似的温度和光周期线索启动春季的生长。然而，昆虫不可能承受食物出现前羽化，因此，春季总会有一个短暂的窗口期，植物免受无脊椎动物的取食（图10.7-1）。当昆虫羽化（insect emergence）后，经常在叶片变太硬或产生毒性前有一个短暂的窗口期。与昆虫相反，恒温草食动物在植物休眠的寒冷季节也可以持续消费食物。此外，许多草食动物可以通过季节性迁移以响应食物质量和环境的季节性变化。然而，这些仅是植物和它们的草食动物之间相互作用上高度专一的季节性格局的3个例子。更高一个营养级动物的捕食经常集中在猎物最脆弱的时刻，例如当无脊椎动物生产下一代时，当鲑鱼迁徙时，或者

当昆虫专注觅食的运动中。当然，这些专门的形式也是十分多样的，取决于捕食者和猎物的生物学特性。重要的一点是一个营养级水平上的生产和被下一个营养级的取食在任何年度周期的任何时间是相同的。

捕食者-猎物之间的相互作用也会有年际变异，部分是因为捕食者和猎物经常在它们对气候年际变异

捕食者-猎物之间的相互作用也会有年际变异，部分是因为捕食者和猎物经常在它们对气候年际变异或者对气候的长期趋势的响应有很大的差异。例如，美国西部长期增温和干旱的趋势引起了山地松甲虫广泛的爆发，原因是增加了这种昆虫的过冬成活率与干旱引起的数目抗性的下降。广泛的树木死亡事实上改变了所有生态系统过程，使得这些森林从一个区域性的碳汇变成碳源。捕食者-猎物间的相互作用也能够驱动一些小型哺乳动物的种群周转，导致它们食物供给的变化以及植被相关的生态系统过程的变化。

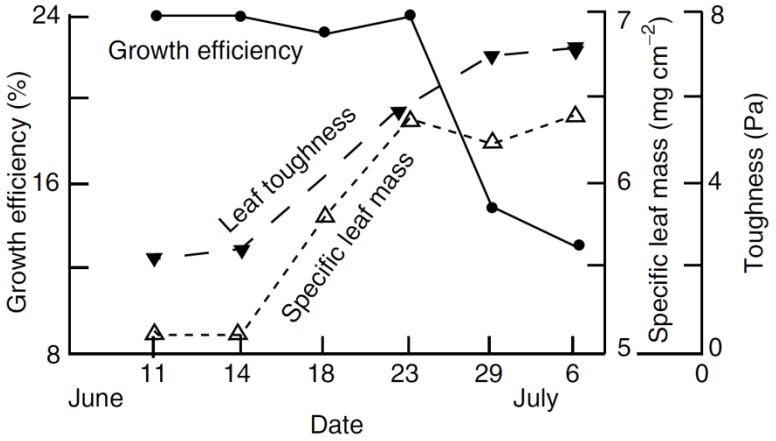


图 10.7-1 芬兰桦树叶片比叶重和叶片韧性以及桦蛾第四代幼虫生长效率的季节性变化格局。当植物叶片变硬和成熟前草食动物生长效率最高。在这个叶片发育的 2 个星期的窗口期后，草食动物生长很慢。

第八节　养分的传输

食物链的养分转移途径通常与能量的传递是相似的。植物和动物中的氮、磷和其他养分或者被有机物束缚，或者溶解在细胞内含物中。动物取食的生物量中含有的养分通常在食物链中沿着与能量传递相同的途径，从植物到草食动物到初级肉食动物到次级肉食动物，等等。在食物链每个节点上，养分被动物消化，同化，就像能量被消化和同化，虽然这些过程的效率可能有很大的不同。正如能量那样，养分的丢失也会在每一个营养级的传输时发生，通常以未被取食的食物，粪便以及尿液的形式，因此传递的养分量必然随着每个依次的营养级连接而下降。这样，养分传输的金字塔在形状上与能量流动的相似，虽然在量的动态上通常有差异。

这个规则的一个重要的例外是钠，该元素被动物用来传递神经和肌肉中的脉冲信号。与动物不同的是，大多数植物并不需要钠，并且主动地将其排除在叶片和根外，所以植物组织

中的含量要低于根据土壤溶液中的含量推算的。因此，钠可能对草食动物是限制性的。许多陆生草食动物通过摄入土壤或者富含矿物质的泉水或者出露的岩石中盐砖上的盐来补充食物中获得的钠和其他矿质元素。这样，矿物质元素可能会表现出与其他养分不同的营养级传输途径。

植物生产所包含的养分传输到陆地草食动物营养级的比例要比能量的大。大多数陆地草食动物选择性地取食嫩的植物组织，具有更多养分含量和可消化的能量，但纤维素和木质素的含量较低。因为草食动物对高含量养分组织的选择性，来自植物的养分通过植物营养系统循环的比例要比碳的比例更大。

陆地草食动物不仅选择养分丰富的组织，它们循环养分的速率也要比植物更快。叶片凋萎期间，植物会从叶片，吸收大约一半的氮和磷，所以与被动物取食的那部分活的组织相比，植物凋落物通常只有一半的氮和磷含量。由于这个原因，在陆地生态系统中，草食动物对叶片的取食对氮和磷循环的影响至少是2倍于对生物量和能量的影响。动物的养分周转速率取决于养分和能量相对重要性。陆地上的草食动物分泌超出它们需求的养分，这些养分通常以无机态形式或者像尿液和尿酸那么简单的有机物的形式，可以在土壤中很快被水解。总之，陆地上的草食动物加快了养分循环的速率，主要通过以下3种方式：（1）通过移除比常规以凋落物方式回到土壤更加富含养分的植物组织；（2）归还养分到土壤的速率要比通过植物再循环的方式速率更快；以及（3）以植物可以直接吸收的方式将养分归还到土壤（图10.8-1）。

植物和草食动物必需营养元素的比例决定了生物体的养分限制的特性和生态系统养分循环的格局。无论是淡水还是陆地植物需要氮和磷的摩尔比为30：1（图10.8-1）。食草性浮游动物和昆虫的N:P比与植物中的相似（大约26：1）。然而，N:P比无论在不同植物还是在不同动物之间变化很大，不仅反映了超出即时需求的氮或者磷的储存，也反映了生物体之间在两种营养元素的需求上的差异。例如，快速生长或者处于繁殖期的浮游动物具有高含量富含磷的核糖体以支撑蛋白质合成，所以具有较低的N:P比（较高的磷需求）。大型脊椎动物也具有低的N:P比，原因是它们向骨骼的分配比例较高需要高的磷的投资。例如，在贫养湖泊中，鱼类可能占有水柱体（water-column）中75%的磷，鹿角可能贡献了北方森林中10%的磷的周转。

鉴于植物和动物较大范围的N:P比变化，草食动物经常碰到一些食物，其营养元素比例与自身的有很大的不同。这种不平衡性通常可以通过高效地获取最强限制性的营养元素，并归还没有限制自身生长的那些营养元素至环境，通常这些营养元素的归还量与自身含量不成比例。这一点趋向于进一步支持生态系统养分限制性的格局。湖泊中不同捕食者间N:P比的差异阐述了这种作用的重要性。水蚤（daphnia）是一个快速生长的水蚤类草食动物，比生长缓慢的挠足类（copepods）有较高P的需求，以支撑它的快速生长（较低N:P比）。与挠足类是优势的食草动物相比，在水蚤占优势的条件下，草食动物累积了更多的P，并分泌更多的

N；这会导致在水蚤占优势时短时间的浮游植物生长P的限制性，而在挠足类占优势时短时间N的限制性。

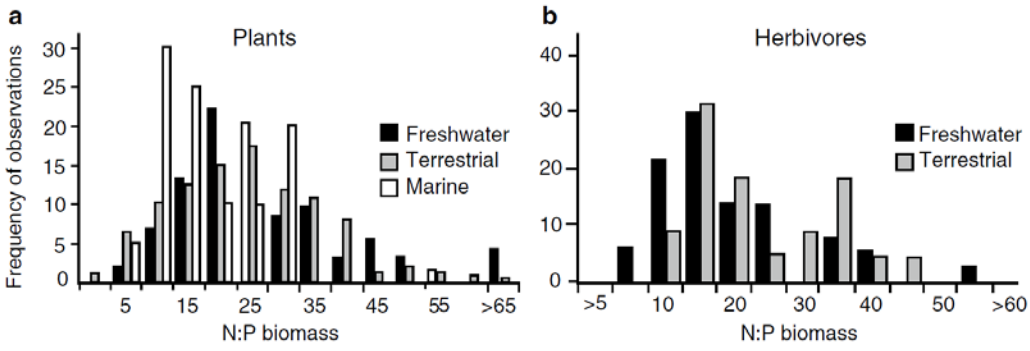


图 10.8-1 淡水、陆地和海洋植物（左）和陆地和淡水草食动物（分别为昆虫和甲壳纲动物，右）的 N:P 摩尔比的分布频度

陆地植被中养分的周转是十分多变的。与水体生态系统相比，虽然食草动物只是占陆地生态系统中所有从植物向环境归还的养分中较小一部分比例，它们仍然对土壤和植物的N:P比有重要的影响。例如，美国黄石公园的麋鹿保持了可观的P以支持骨骼和鹿角的生长，分泌N，从而提高被取食植被的N:P比。化学计量关系到分析提供了一个令人振奋的理论框架，可以将生物的养分需求与生态系统中的养分循环格局连接起来。

营养的级联效应向下传送最终影响土壤中碳和营养元素的周转。动物通过对进入土壤的有机物质的数量和质量的作用影响土壤碳和营养元素的周转。例如，黄石公园狼的再次引入降低了麋鹿的多度，将麋鹿的分布从高产的捕食者偏爱的低地生境驱赶至更高海拔的生境，导致草食作用和氮素矿化作用在低地生境的降低。草食动物的取食要比山坡的位置对景观格局土壤碳周转的控制更加重要。同样，在美国东北部长期种植田块中，蜘蛛的显著去除改变了植物种类组成，同时增加了凋落物质量和氮素矿化速率，表明营养级动态对生态系统生物地球化学的重要性。

第九节　基于碎屑的营养级系统

碎屑营养级系统要比植物营养级系统转可以向生产转化更多比例的能量。分解者有机体（主要是细菌和真菌）取食植物、动物和微生物的残体，就像草食动物取食植物一样。就像在以植物为基础的营养级系统，那里也存在一个取食分解者有机体的动物食物链。控制该食物链能量流动的原理与基于植物的食物链的一致。

死亡有机质的输入速率和质量是流过该碎屑系统能量高低的主要决定因素。碎屑食物链表现为生长和维持呼吸以及排泄物的能量丢失，这与植物食物链的一致。此外，每一个营养级的传递还要伴随无机N和P的分泌，从而为植物所利用，这也与植物营养级系统一致。

植物和碎屑营养级系统在结构上的主要区分是植物营养级系统包含的是单向的能力流动，要么是沿食物链向上传输，要么是以呼吸、为消耗的食物，或者排泄物从食物链丢失。然而在碎屑食物链中，没有被取食的食物，排泄物和死亡有机体可以再次成为食物链基部分解者的底物。于是在碎屑食物链中的能量流动具有一个很强的在循环成分。能量被保持并可用于支持以碎屑基础的生产，直到它被呼吸而释放到大气，或者转化为难于降解的腐殖质材料。由于进入食物链基部的碳的高效利用，碎屑食物网占生态系统大部分能量流动，并支撑了最大的动物多样性。

碎屑营养级系统的营养效率通常要比植物营养级系统要高。碎屑食物链的消费效率要高，原因是所有潜在的食物可以被消费好多次，直到最终被呼吸消耗。分解者（细菌和真菌）的同化效率也要高，因为它们的消化是在细胞外进行，因而根据定义，所有分解者消耗的物质都被同化了。碎屑食物链中分解者的生产效率（40-60%；见第九章）动物和动物的生产效率（35-40%）也要比食物营养级系统中的高。综合这些高的营养级效率解释了为什么碎屑营养级系统占生态系统大部分次生生产。

第十节　整合的食物网

食物网模糊了每个物种在一个生态系统中的营养级位置。在现实的世界中，许多动物可以取食来自多个营养级的食物，即有来自植物营养级系统，也有来自碎屑营养级系统以及系统内多个营养级水平。由于这个原因，要把大多数生物归置到一个营养级是很难的。例如，在深海生态系统，浮游动物选择食物基于大小和形状多过于物种的特性，取食浮游植物、碎屑颗粒和小型动物。在陆地上，食菌动物取食真菌的混合体，即有从植物获取能量的菌根真菌，也有从分解死亡有机质的腐食真菌。细菌也有从根系分泌物（一种NPP的组分）汲取能量，也有从死亡有机质获取能量。于是取食细菌和真菌的土壤动物一部分属于植物营养级系统，另一部分又属于碎屑营养级系统。以植物根为食的螨类和线虫沦为动物的猎物，而那些动物又取食碎屑食物链的动物（图10.2-1）。因此整个食物网处理着来自难于厘清的植物和碎屑能量和养分的混合物。地上动物也取食相当一部分碎屑物质，例如真菌和土壤动物。例如，知更鸟同时取食蚯蚓和草食性昆虫。熊可以取食植物根和陆地来源（分别是植物食物链和基本上碎屑食物链）的蚂蚁，和水体食物网的鱼类。许多昆虫在幼虫阶段是碎屑取食者，但到了成虫阶段则吸吮花蜜或者血液（基于植物的营养级系统）。大约75%的食物网同时包含基于植物的和基于碎屑的组分，所以混合营养级系统是规则而不是例外。

像秃鹰、鬣狗、蟹类和许多甲壳虫类等的腐食动物在技术上属于碎屑食物网的一部分，虽然它们的取食、同化和生产效率与那些肉食动物相似。腐食动物经常杀死那些柔弱的动物，许多捕食者以刚被其他动物杀死的猎物为食，进一步模糊了植物和碎屑食物链间的界线。

寄生虫，病原体和疾病在营养级上类似于捕食者。就像捕食者那样，它们主要从寄主组织获取能量，利用这些细胞的产物进行它们自身的生长和繁殖。然而，要将寄生虫、病原体

和疾病生物量从它们寄主分开实际上是很难的，所以消费和同化效率的概念很少适应于这些生物。于是，寄生虫、病原体和疾病常被处理成伤亡的媒介，而不是消费者。

共生者也会混淆营养级关系。菌根真菌能够从共生者转变成寄生者，取决于寄主植物的环境条件营养状态。在共生条件下，菌根真菌扮演草食动物从植物向真菌运送碳水化合物，然而也会出现相仿方向的养分运输（碎屑食物链）。因此，这两类生物的营养级角色取决于对组分的兴趣。虽然对营养级动态宽泛的概括具有清晰的概念基础，自然的复杂性和我们对地下过程了解的不足常造成对这些食物网进行定量描述的困难。

本章小结

在以植物为基础的营养级系统中，养分供给和其他控制NPP的因素限制了更高营养级能量的获得。这些相同的因素控制了凋落物输入到土壤的数量和质量，从而也控制了碎屑营养级系统的可利用能量。这些因素行成了对营养级系统的上行控制。从一个营养级水平向下一个营养级传递能量的营养级效率取决于取食、同化和生产效率。消费效率取决于食物数量与质量与受更高一级营养级水平捕食的相互作用。消费效率在以木本或者良好防御的植物占优势的低生产力生境中最低。肉食植物通常比草食动物具有更高的消费效率。同化效率主要取决于食物的质量。同化效率在低产生境中要比在高产生境中低，草食动物又要比肉食动物低。与营养级效率的其他组分相比，生产效率主要取决于动物的生理特征；例如，变温动物比恒温动物具有更高的生产效率。陆地生态系统大部分次生生产发生在碎屑营养级系统中。在该系统中，没有被消耗或者没有被同化的有机质回到食物链的基部，继续沿着食物链再循环，直到被呼吸释放或者转化成难降解的腐殖质。大多数食物网既含有植物营养级组分，也含有碎屑营养级组分。包括那些来自人类活动的对任何一个食物营养级的影响常波及到食物网的其他营养级。

第十一章 物种对生态系统过程的作用

第一节　物种对生态系统过程的作用

为什么要研究物种对生态系统过程的作用？物种对生态系统过程有哪些直接和间接的影响？什么是生物多样性与生态系统功能(BEF)、生物多样性与生态系统多功能性(BEF)和生物多样性与生态系统服务？

1.1 什么是生物多样性

“Biological diversity” 一词在 1980 年由保护生物学家 Thomas Lovejoy 首次使用。国际知名生态学家、哈佛大学教授 Edward O. Wilson 于 1986 年在国家研究委员会组织的全国生物多样性论坛上提出了“Biodiversity”这一新的英文名词，并于 1988 年首次作为论坛会议的标题出版(图 11.1-1)。

生物多样性是指地球上所有形形色色的生物体构成的生态综合体及其相互作用，即生命形式的多样化(基因、个体、物种、种群和生态系统)。

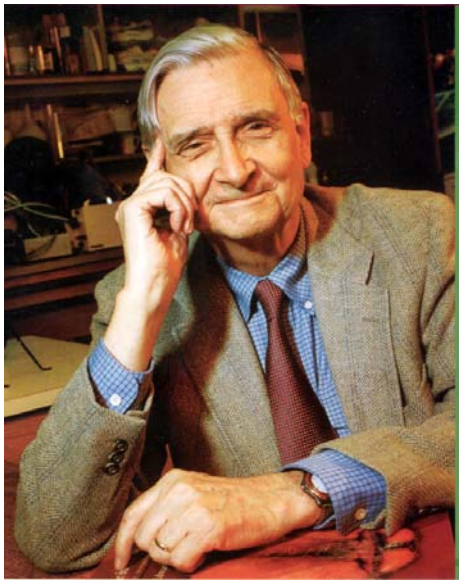


图 11.1-1 Edward O. Wilson

科学家简介：

Edward O. Wilson 被认为是社会生物学之父。他童年时对昆虫和其他生物的迷恋发展成为一种智慧的激情，这种激情点燃了现代科学最伟大的事业。威尔逊在13岁时取得了昆虫学上的第一个重大发现。当他完成研究生学业时，他已经被公认为是世界上最权威的蚂蚁研究专家。基于他在哈佛大学的基础，他周游世界，收集稀有的标本，对这些复杂生物的进化和

行为有了前所未有的了解。威尔逊率先研究了动物之间的化学交流，并提出了岛屿生物地理学理论，为今天的保护实践提供了指导。他对群居昆虫的里程碑式研究成为现代社会生物学的基石。在他1975年出版的《社会生物学: 新合成》一书中，威尔逊将这一学科应用于所有物种的行为。他对人类本性和社会的生物学起源的观察激起了一场激烈的争论。威尔逊忍受了来自批评家的人身攻击，他们中的许多人严重误解了他的工作；但在几年之内，他的观点在科学界赢得了广泛的接受。

代表性论文：

- Wilson, E.O. 1951. Variation and adaptation in the imported fire ant. Evolution 5: 68-79.
- Wilson, E.O. 1953. Origin of the variation in the imported fire ant. Evolution 7: 262-263.
- Wilson, E.O. 1959. Source and possible nature of the odor trail of fire ants. Science 129: 643-644.
- Wilson, E.O. 1965. Chemical communication in social insects-insect societies are organized principally by complex systems of chemical signals. Science 149: 1064-1065.
- Wilson, E.O. 1967. First Mesozoic ants. Science 157: 1038-1040.
- Wilson, E.O. et al. 1988. Dense heterarchies and mass-communication as the basis of organization in ant colonies. Trends in Ecology and Evolution 3: 65-68.

1.2 地球正处于由人类活动导致的生命史上第六次大灭绝事件中期

目前的灭绝速度高于有史以来的任何时期，它主要是由生物因素驱动的，尤其是人类活动，如土地利用变化，外来物种入侵、全球变暖等大气环境变化。虽然人类冲击在全球尺度上影响的过程很多，但其中物种多样性由于其不可逆性尤为引人关注。因此，理解目前物种多样性的大量丧失所引起的机能性后果，是相当紧要的任务。虽然物种的全球性灭绝是主要的保护议题，但物种的局部灭绝或多度的巨变发生得更为频繁，而且对生态系统的机能执行产生的影响最大。

1.3 物种灭绝对生态系统的影响

人类活动对物种多样性造成的显著且大多不可逆转的变化，具体表现为：第一、地球上物种的分布愈发单一化；第二、与地球历史进程中的典型背景速率相比，人类已经使物种灭绝的速度加快到高达 1,000 倍（图 11.1-2）；第三、10 - 30%的哺乳动物、鸟类和两栖物种目前濒临灭绝（图 11.1-3）。

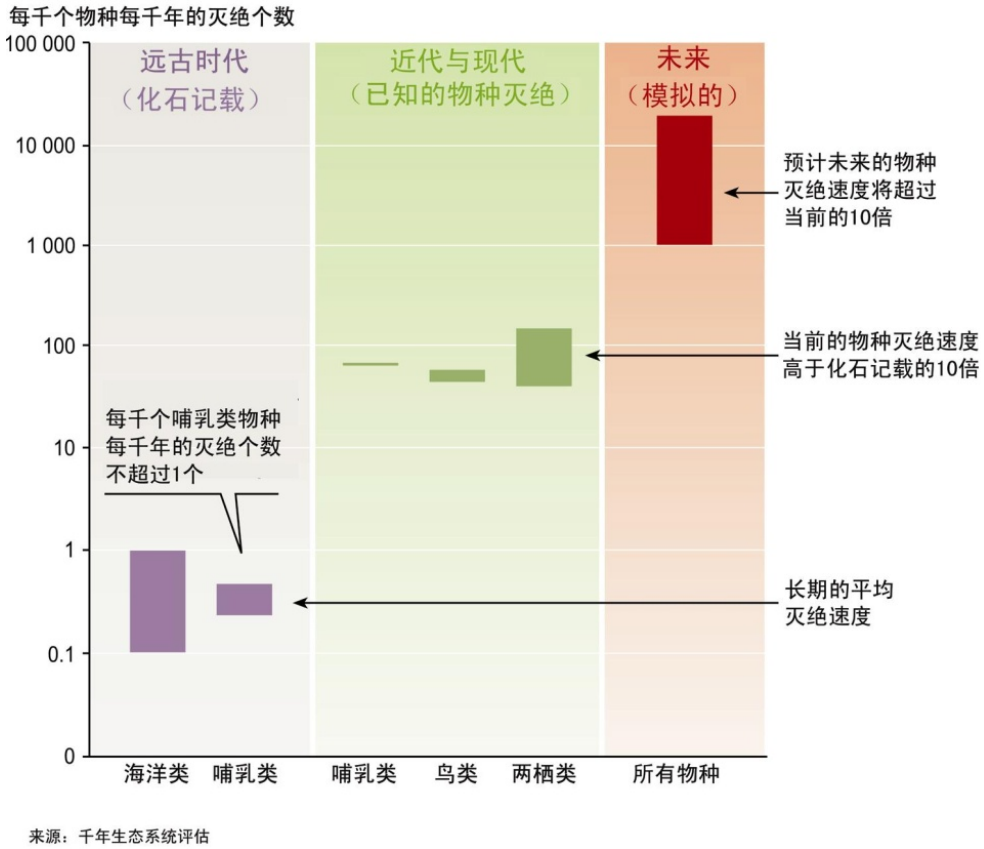


图 11.1-2 人类活动对物种灭绝速率的影响(MA 2005)

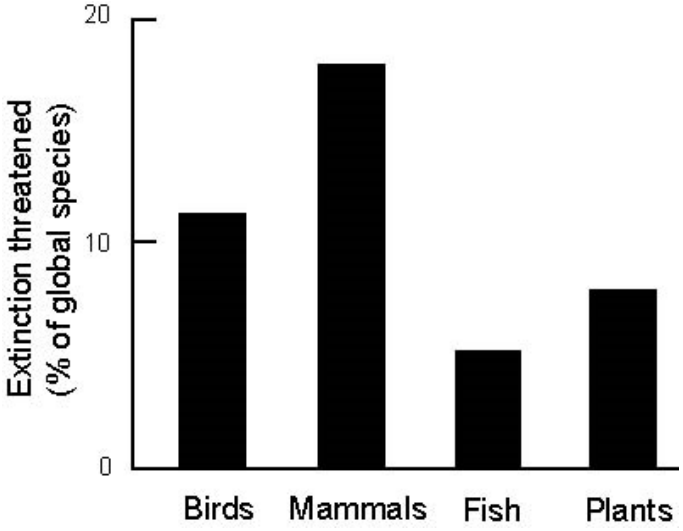


图 11.1-3 哺乳动物、鸟类和两栖物种的灭绝速率

1.4 为什么要研究物种对生态系统过程的作用

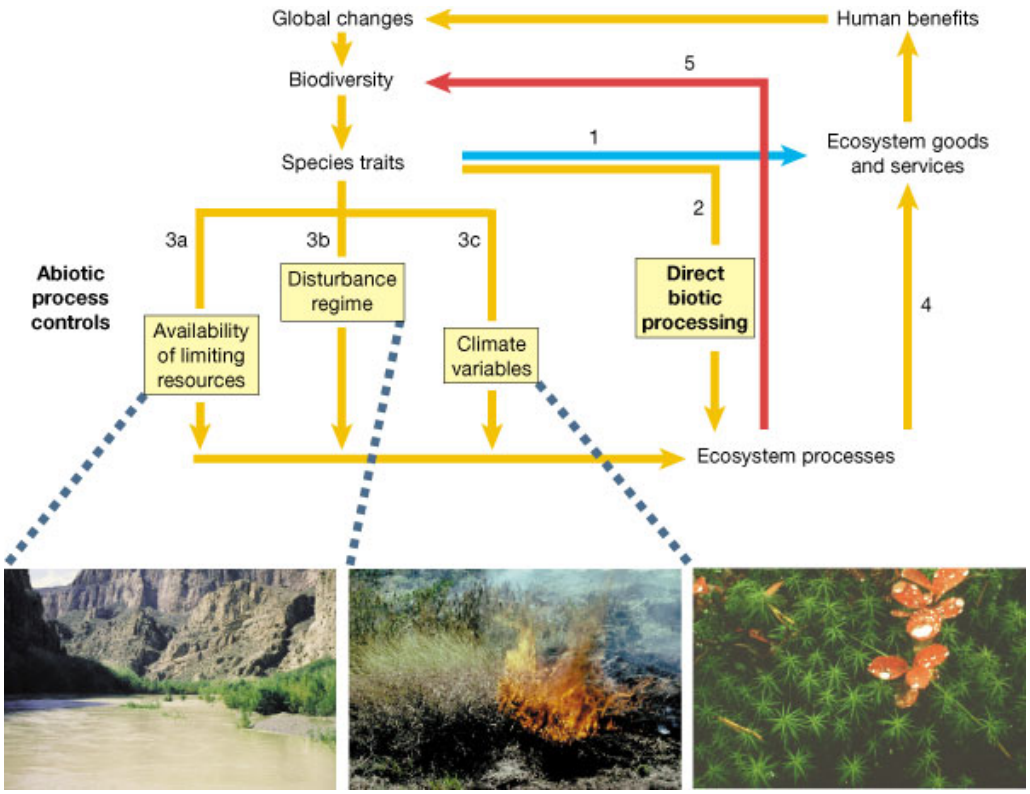


图 11.1-4 全球变化和人类活动干扰共同作用下物种对生态系统过程、服务和人类福祉影响

过去几十年中，人类活动对生态系统改变的速度和广度均超过了历史上任何一个可比时期，引起了全球范围内生物多样性丧失和生态系统服务功能退化，进而对人类福祉产生了严重的影响(图11.1-4)。生物多样性与生态系统生产力的关系以及生产力的稳定性维持机制是当前生态学理论研究的核心问题，同时对生物多样性保护和生态系统管理具有重要意义(Tilman 1999, Chapin et al. 2000, Loreau et al. 2001, Hooper et al. 2005, Hooper et al. 2012)。当前的主流观点认为生物多样性与生产力的关系（PDR, productivity-diversity relationships）是骆峰型（hump-shaped），即生物多样性在中等大小时生产力最高，生物多样性最高时，生产力反而处于中等水平(Grime 1973, Huston 1979, Waide et al. 1999, Mittelbach et al. 2001, Fraser, Pither et al. 2015)。然而有关PDR的关系是驼峰型还是单调的线性相关，以及影响PDR关系的生物学机制等存在较大争议。中国科学院植物研究所的白永飞研究员等人基于内蒙古锡林郭勒盟地区854个野外样点的调查数据，首次从不同组织层次（群丛、植被亚型和植被型）和不同空间尺度（样地尺度、景观尺度和区域尺度）证实了内蒙古草原的PDR存在普遍的线性正相关，而非驼峰型（hump-shaped）；在区域尺度，PDR受年平均降雨量的影响，降水量越大，PDR的斜率越小；此外，放牧虽然能够降低草地的生产力和生物多样性，但不会改变PDR的线性相关关系(Bai et al. 2007)。研究结果不仅对退化草原的恢复与管理提供了依据，还将有助于人们了解未来气候变化对欧亚草原植被的影响。

生物多样性不仅关系到生态系统的生产力，还会影响生态系统的碳固持(Midgley 2012, Lange et al. 2015)。然而环境因子和人类活动如何影响陆地生态系统大尺度多样性-生产力-土壤碳储量之间的关系，目前学术界仍存在较大争议。中国科学家在不同生态系统（草地、森林和灌丛）下6000多个野外调查点，首次在国家尺度证实了自然生态系统中多样性与生产力和土壤碳储量之间普遍存在正相关关系。其中，土壤碳储量的空间分布格局主要受气候因子控制，但气候因子还通过影响多样性和生产力对土壤碳储量进行调控，适宜气候条件（尤其是高降水量）下生物多样性对生态系统固碳的促进作用，有利于抵消氮沉降等人为活动对固碳的负效应(Chen et al. 2018)。该研究表明，通过保护和管理措施，维持高的生物多样性有利于增加土壤碳储量，改善生态系统服务，减缓气候变化的影响。

1.5 外来物种有时会改变物理和生物环境，这足以改变一个生态系统中本地物种的多度甚至排除本地物种

美国西南部索诺兰沙漠(Sonoran Desert)中，亚利桑那高地的主要是由多种灌木和仙人掌组成，通常被裸露的地面隔开。这些裸地正迅速被纤毛狗尾草(*Pennisetum ciliare*)侵占。纤毛狗尾草是从非洲热带稀树草原引进的一种多年生草本，用于控制风蚀，并为亚热带其他地区的牲畜提供饲料。当地的纤毛狗尾草可以在一到二十年里排除本地灌木和仙人掌，形成一个连续的，产量超过 4000 kg ha^{-1} 的重燃料区，并且能够在以前很少发生火灾的地方引发大火(图 11.1-5)。

图 11.1-5 索诺兰沙漠的亚利桑那高地主要由多种灌木和仙人掌组成，大部分裸地正迅速被纤毛狗尾草(*Pennisetum ciliare*)侵占。

1.6 性状、功能性状、关键物种和功能型

性状是指任何从个体水平上测定的形态、生理和物候特征，从细胞到整个生物体水平，而不考虑环境或任何其他水平(Violle et al. 2007)；功能性状：生物体个体的特征，通过对其生长、繁殖或生存的作用而影响其适应性；关键种：区别于生态系统中所有其他物种在生态作用上的物种，对生态系统或群落过程的影响要比通过其生物量预测的大(Power et al. 1996); 功能型：在对生态系统的影响(影响功能型)或对环境变化的响应(响应功能型)方面具有“生态相似性”的物种群。

近年来，植物功能性状的研究为功能生态学，特别是生物多样性与生态系统功能关系的机理研究注入了新的活力(Diaz and Cabido 2001, McGill, Enquist *et al*. 2006, Kraft, Godoy *et al*. 2015)。通过植物功能性状，研究植物对气候变化和人类干扰的响应与适应机制，有助于揭示物种替代和群落演替的机理，对于探明草原退化过程和机制具有重要意义(Diaz, Lavorel *et al*. 2007)。内蒙古大学的王炜教授团队通过分析 1983-1993 年内蒙古退化草原群落（退化实验样地）中 8 个主要植物种群的个体性状变化，揭示了个体小型化是过度放牧下群落生产力衰退的重要表现。个体小型化表现为植株变矮、叶片变短、节间缩短，以及植物根系分布浅层化等性状的集合。个体小型化是植物对过度放牧的负反馈机制，是从个体水平上认识退化演替机理的关键(王炜, 梁存柱 *et al*. 2000, 王鑫厅, 王炜 *et al*. 2015)。此外，植物性状是影响物种对放牧响应的关键。基于放牧实验的研究发现，植物的比叶面积和叶片氮含量能够较好地预测植物对不同放牧强度的响应(Li, Xu *et al*. 2017)。

1.7 物种对生态系统过程的作用具有差异性

一个物种对生态系统过程的影响是由许多因素决定的，如丰度，所占据的地理范围和每个个体的影响力。相比于稀有种数量变化，优势种数量变化对生态系统过程的影响更大。Sala et al. (1996) 提出了在一个生态系统中生态生态系统过程与物种数量，相对多度和物种类型之间的预期关系 (图 11.1-6)

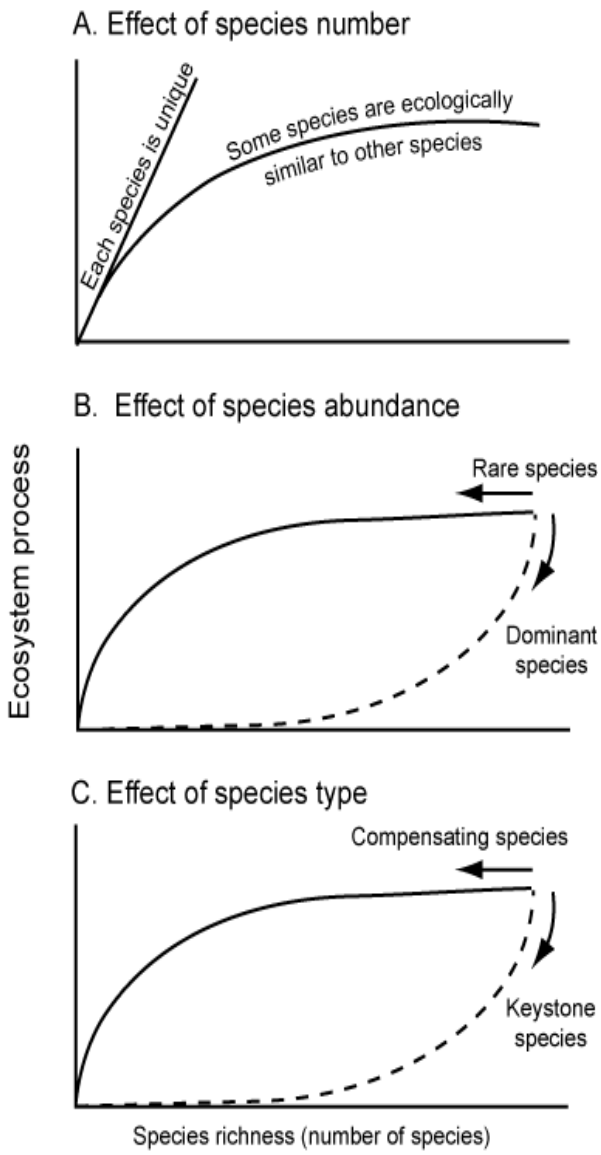


图 11.1-6 生态系统过程与生态系统中物种数量，相对多度和物种类型之间的预期关系。(A)某些过程(或可能随着物种数量的增加而增加(如图所示)；而其他过程可能呈指数增长(Vitousek and Hooper 1993)；(B)从生态系统中移除优势种比移除稀有种对生态系统过程的影响更大；(C)同样，移除关键种会对生态系统产生重大影响，而移除一个功能型中的一个物种就使得该功能型中其他物种的多度增加，这种补偿只会对生态系统过程造成中等程度的影响，除非该功能型中的大部分物种被移除。箭头表示生态系统过程对物种丢的预期变化。基于 Sala et al. (1996)。

第二节　作用类型

2.1 植物如何影响生态系统

植物能够从多方面对生态系统产生重要影响，例如植物进行光合作用将二氧化碳转化成碳水化合物，固定的碳一部分以可溶性碳形式通过根系分泌物输入到土壤中，为土壤微

生物提供碳源；另一部分以凋落物的形式返还到土壤表面，改变土壤微环境(土壤温度和水分)，从而对生态系统过程产生影响(图 11.2-1)。

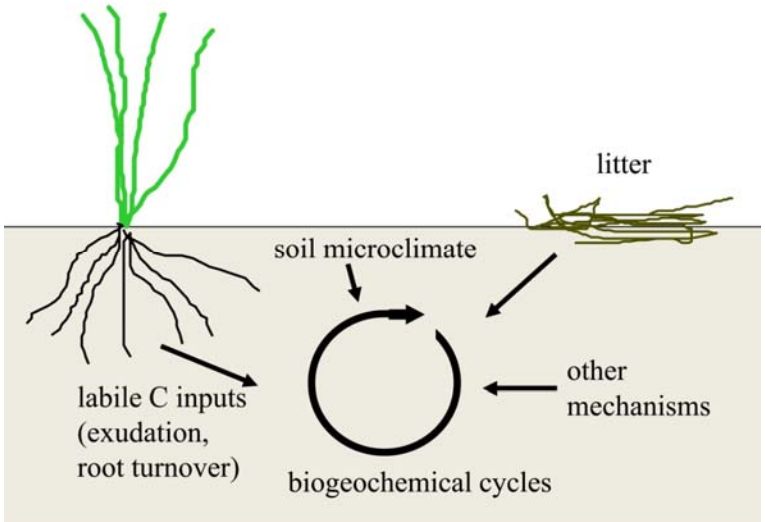


图 11.2-1 物种对生态系统过程的影响。首先植物会通过根系分泌物或根系周转将可溶性碳释放到土壤中；其次，植物凋落物会影响土壤温度和水分等土壤微环境；这些结果都会对土壤微生物等产生重要影响，并最终影响生物地球化学循环。

2.2 物种对生物地球化学的作用

物种对生物地球化学的影响主要表现在以下几个方面：第一、养分供应，影响营养物质输入和损失的物种性状对生态系统产生重要的影响。例如，夏威夷山区森林引入外来固氮树(*Morella faya*)以后，在氮输入，净氮矿化速率和凋落物氮含量方面都有了显著的增加(图 11.2-2)。加利福尼亚州的一年生草地和桉树林表现出了不同的生态特征，主要是由于组成两个群落植物的根系深度不一样(图 11.2-3)。相比于一年生草本而言，深根系的桉树能进入深度更深的土壤剖面，所以桉树能都吸收更多的水分和营养。因此在干旱和营养限制的生态系统，桉树在增强生态系统生产力和营养循环方面的作用比草本植物更大。

第二、营养物质周转，物种之间凋落物质量的差异会放大不同地方土壤肥力差异。由于植物凋落物质量的差异，强烈影响凋落物的分解速度。在低营养条件下形成的凋落物分解缓慢，因为凋落物中氮和磷浓度低，而木质素、丹宁和蜡质等难分解物质多，不利于微生物的分解作用，降低了土壤中营养物质的可利用性。相反，在资源充足的地方产生的凋落物，由于含有较高的氮和磷，以及较低浓度难降解的化合物，从而增加了该土壤中营养元素的可利用性。在相同土壤中的试验表明，凋落物质量(碳氮比，C:N)显著影响了净氮矿化速率，随着凋落物质量降低(碳氮比增大)，净氮矿化速率不短减小(图 11.2-4)。

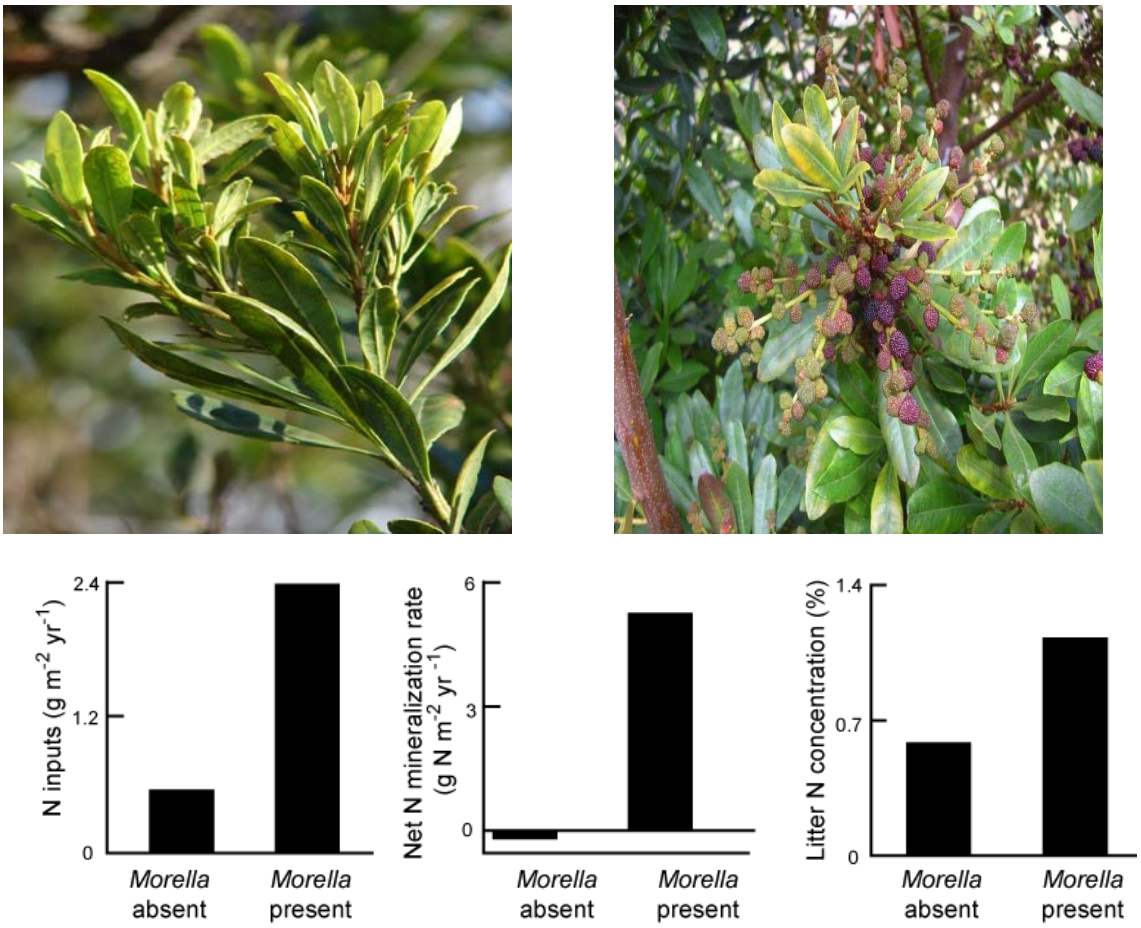


图 11.2-2 固氮树(*Morella faya*)对夏威夷山地森林氮素输入(N inputs)，净氮矿化速率(net nitrogen mineralization rate)和凋落物中氮含量(litter nitrogen concentration)。数值=平均值±标准误(Vitousek et al. 1987)。

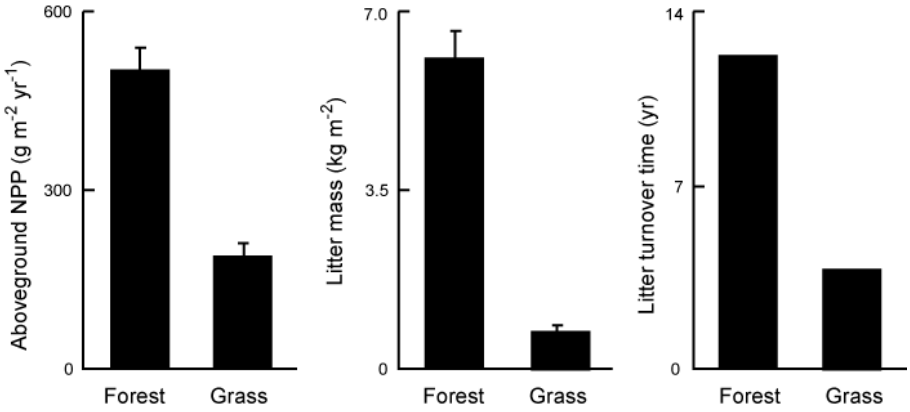


图 11.2-3 由不同根系深度组成的两个群落生态系统过程的比较：以加利福尼亚州的一年生草地和桉树林为例。数值=平均值±标准误(Robles and Chapin 1995)。

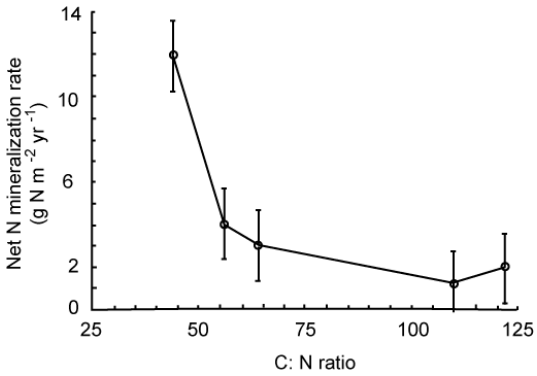


图 11.2-4 生长在土壤含氮量为 100 g N m^{-2} 的不同碳氮比的草原牧草对氮矿化的影响。数值=平均值 ± 95%置信区间(Wedin and Tilman 1990)。

2.3 物种对生物物理过程的作用

物种对微气候的作用会影响生态系统过程，这种影响在极端环境最强烈。例如，针叶林的反射率和气孔导度较低，能将大量显热传递到大气中；相反，落叶林由于它们存在较高的反射率，以潜热形式传输更多的能量进入大气，故吸收更少的能量，导致对大气的直接升温作用较小(图 11.2-5)。

物种对水分和能量的交换的作用会影响区域气候。在生态系统中，优势种的高度、根系深度以及密度决定了表面的粗糙程度，极大地影响了空气传导动力，因此，影响生态系统和大气圈之间的水分和能量交换。

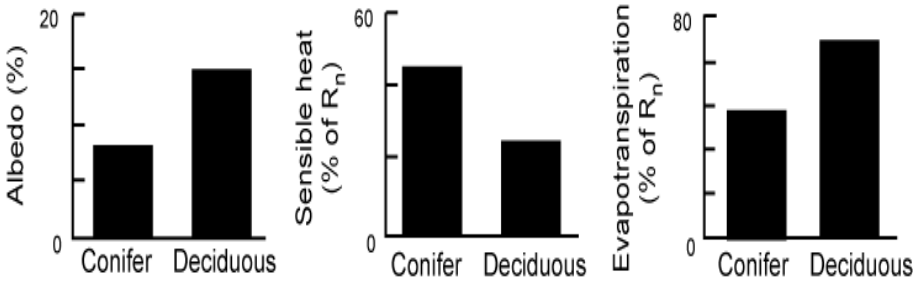


图 11.2-5 北方落叶林和针叶林的显热和潜热通量。反射率(Albedo)，显热(Sensible heat)和蒸发散(Evapotranspiration)。数据来自 Baldocchi *et al*. (2000)。

显热 (sensible heat) 是指当此热量加入或移去后，会导致物质温度的变化，而不发生相变。物质的摩尔量、摩尔热容和温差三者的乘积为显热。即物体不发生化学变化或相变化时，温度升高或降低所需要的热称为显热。

潜热 (latent heat)，相变潜热的简称，指物质在等温等压情况下，从一个相变化到另一个相吸收或放出的热量。这是物体在固、液、气三相之间以及不同的固相之间相互转变时具有的特点之一。固、液之间的潜热称为熔解热（或凝固热），液、气之间的称为汽化热（或凝结热），而固、气之间的称为升华热（或凝华热）。

2.4 物种对营养关系的作用

改变营养动态的物种会对生态系统产生重大影响。例如，当顶级捕食者被移除，猎物种群有时会爆发以至于耗尽食物资源，从而导致级联性的生态反应(图 11.2-6)。又如，添加或移除一个物种，常常会沿着食物链产生级联放大的关键种效应，俄罗斯毛皮商人为了经济利益，过度捕杀海獭，引起了海胆种群爆发(图 11.2-7)。最近在北冰洋过度捕鱼，也会引发类似的海胆爆发，因为虎鲸为了觅食迁移至离海岸更近处，而海獭成为虎鲸的替代食物。在没有高密度海胆种群的地方，大型海藻为潮下带种群提供了物理结构，削弱了波浪，否则海岸侵蚀和暴风雨造成的损失会增加。

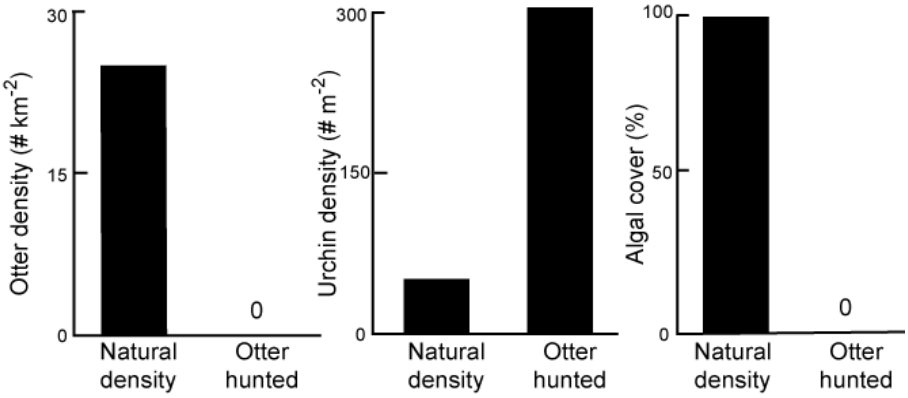


图 11.2-6 阿拉斯加 Aleutian Islands 的海獭密度、海胆密度和大型海藻覆盖度。水獭密度的差异是由于 300 年前捕捞压力不同。数据来自 Estes and Palmisano (1974)。

图 11.2-7 阿拉斯加 Aleutian Islands 中海獭占据潮下带栖息地的海带林与俄罗斯毛皮商贩消灭海獭而形成的海胆占主导地位的荒地比较。三种主要的海带分别是 *Eularia* (*Alaria*)(一种向海面延伸的一年生物种)，*Laminaria*(形成较低的冠层)和 *Agarum*(叶片上有孔)。照片由 Jim Estes 和 Mike Kenner 提供。

2.5 物种对干扰体系的作用

在控制生态系统过程中，改变干扰体系的生物体会改变物种定殖和物种相互作用的相对重要性。扰动以后，大多数生态过程都发生了明显的变化。机制之一是通过它们作为生态系统工程师的行为，创造或改变栖息地，如囊地鼠(Jones et al. 1994; Lawton and Jones 1995)。囊地鼠(产自北美的一种地鼠)可以干扰土壤物理结构，为幼苗定植创造适宜的地点，有利于演替早期的物种生长。同样，通过踩踏苔藓并促进营养物质的循环(图 11.2-8)。

物也可以通过影响可燃性来改变干扰体系，在其他情况下，植物对稳定土壤，降低干扰起着关键作用，减少了演替早期的风化和土壤侵蚀。将草本植物引入森林或灌丛中，能增加发生火灾的频率，导致热带稀树草原取代森林(Mack et al. 2001)。

图 11.2-8 地鼠对草地群落结构和演替的影响

第三节　响应类型

3.1 在表征生态系统过程速率持续范围内，对环境响应的种属差异使得环境条件范围变宽

占有任何限定的生态系统物种，通常会有不同的地理范围以及对过去气候变化存在不同的历史响应。因此，它们可能对目前气候季节和年际变化做出不同的响应，在环境中发生定向变化。

3.2 响应多样性还可以提高生态系统资源利用和固定资源效率

物种多样性高的实验样地比地多样性样地的植被覆盖率更高，而土壤硝态氮浓度更低(图 11.3-1)。这说明，物种多样性越高，利用更多资源的可能性增大，即互补的资源利用模式。例如，在荷兰，多样性更高的石南荒原生产力更强，不是因为存在单一多产的物种，而是因为几种低产物种种植在一起，导致大量生产力。这种互补性通常都是通过自然选择或利用未完全被其他物种利用的资源。

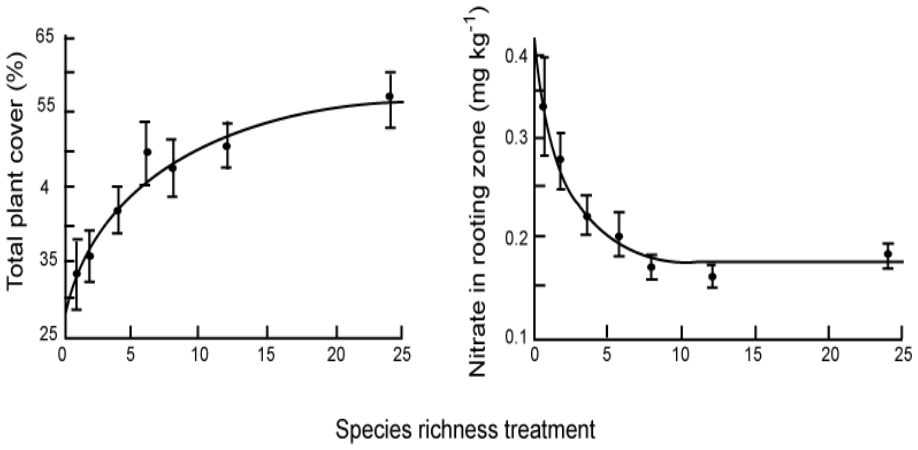


图 11.3-1 物种数量对植物总盖度和根际区硝态氮浓度的影响。播种后的第三年开始测量。数值=平均值±标准误。引用自 Tilman *et al*. (1996)。

第四节　植物性状对生态系统的作用

4.1 多性状的功能矩阵(Functional Matrix of Multiple Traits)

生物体可以通过多性状的作用以多种方式影响生态系统，如对火的忍耐性，与生长相关的性状，温度忍耐性，根系深度或扩散能力。

性状的功能矩阵，扩展了功能群类型，考虑出现在一个生态系统中的所有性状，每一个性状都可以作为生态系统中每一个物种的一个连续变量(Eviner and Chapin 2003)。

Valerie T. Eviner

科学家简介：

Valerie T. Eviner 在加州大学伯克利分校获得博士学位。她的研究重点是理解植物-土壤相互作用的机制，并将这种理解应用于生态系统管理、恢复、入侵、生态系统过程和变化环境中的牧场。她对植物群落相互作用和多种生态系统服务特别感兴趣，以及这些模式是如何随着时间和环境变化在景观中发生变化的。她的大部分工作都在加利福尼亚的草原上进行。其他研究系统包括：湿地、河岸生态系统、内蒙古退化草原、东北森林(特别是林下植被动态)、高山草甸和森林，以及加利福尼亚、伊利诺斯州和纽约的种植系统。

代表性论文：

- Eviner, V.T. and FS Chapin III. 1997. The nitrogen cycle: plant-microbial interactions. Nature 385: 26-27.
- Eviner, V.T. and FS Chapin III. 2003. Gopher-plant-fungal interactions affect establishment of an invasive grass. Ecology 84: 120-128.
- Eviner, V.T. 2004. Plant traits that influence ecosystem processes vary independently among species. Ecology 85: 2215-2229.
- Eviner, V.T. and F.S. Chapin, III. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology, Evolution, and Systematics 34: 455-485.
- Eviner, V.T., et al. 2006. Seasonal variations in plant species effects on soil N and P dynamics. Ecology 87: 974-986.

4.2 响应性状和作用性状之间的联系 (Linkages Between Response and Effect Traits)

环境变异和变化对生态系统过程的影响依赖于环境响应和物种生态作用之间的联系。比如，具有较高氮吸收、光合作用、生长能力的物种，对氮供应的响应十分敏感，产生快速分解的凋落物以及占据大量含氮量地方，然而不能及时对环境反馈做出变化的物种只能占据含氮量少的地方。这是由于响应性状和效应性状存在很强的联系，生态系统对氮素供应变化的响应十分敏感。

植物对生态系统过程的作用随着时间发生变化。在植物生长期(如生长季)，植物将光合作用固定在体内的碳通过根系分泌物分泌到土壤中，为土壤微生物提供碳源，从而影响相关土壤过程(如有机质分解)。在非生长季，植物地上部分(如草地生态系统中草本植物)会以凋落物的形式落到土壤表面，一方面凋落物会改变土壤微环境(如土壤温度和水分)；另一方面凋落物质量(如碳氮比)会影响影响土壤有机质(SOM)的形成，最终影响与分解相关的土壤过程(图 11.4-1)。

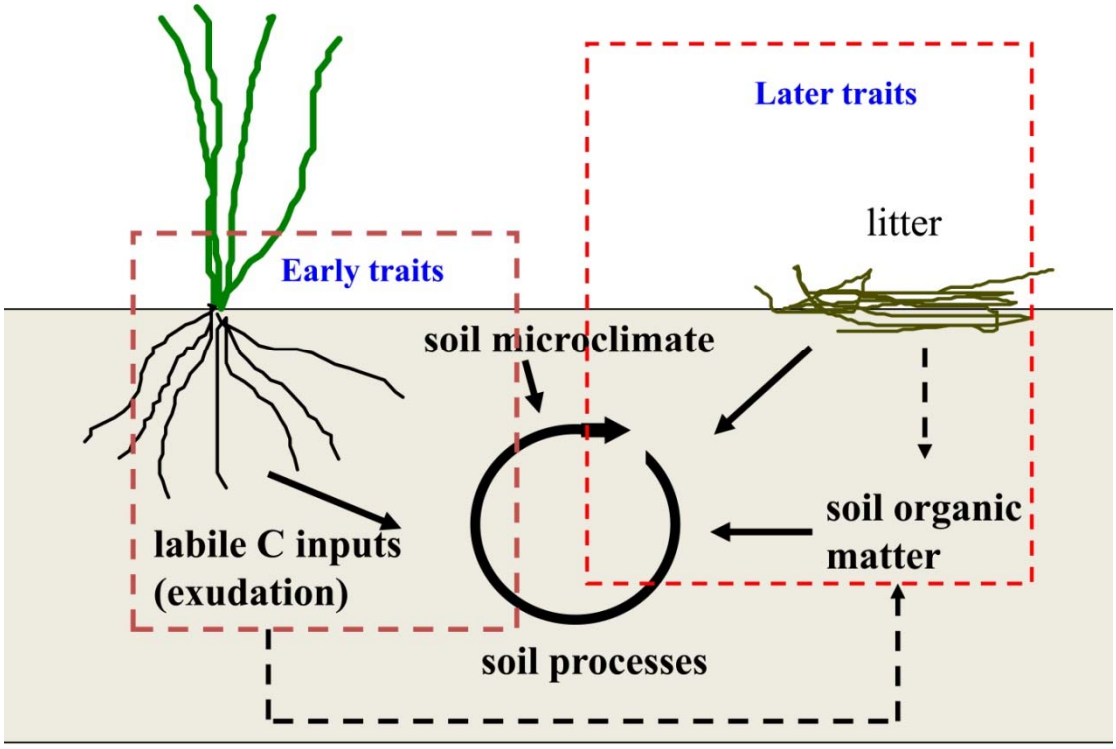


图 11.4-1 植物对生态系统过程的作用随着时间发生变化。在植物生长期(如生长季)，植物将光合作用固定在体内的碳通过根系分泌物分泌到土壤中，为土壤微生物提供碳源，从而影响相关土壤过程(如有机质分解)。在非生长季，植物地上部分(如草地生态系统中草本植物)会以凋落物的形式落到土壤表面，一方面凋落物会改变土壤微环境(如土壤温度和水分)；另一方面凋落物质量(如碳氮比)会影响影响土壤有机质(SOM)的形成，最终影响与分解相关的土壤过程。

4.3 多样性对生态系统的作用 (Diversity as Insurance)

多样性对生态系统的作用主要表现在以下几个方面，第一、在极端或新的条件下，多样性为应对功能变化提供了保障。利于某些物种的条件可能降低其他具有类似功能的竞争优势，从而稳定了总生物量或整个种群的活力。比如，在北极苔原，气候的变化至少导致二倍的产量变化。但是，在五年的研究中发现，有利于某些植物生长的年份会减少其他物种的生产力，所以在生态系统尺度上，不会造成生产量的明显变化。第二、多样性提高了生态系统资源利用效率。第三、稳定多变环境下的生态系统过程。第四、在应对生态系统发生根本变化方面提供保障，造成某些物种灭绝的任何气候变化或气候极端事件，不可能导致某一功能型中所有成员都灭绝，因为响应性状和影响性状分布在不同的物种组合中。在某一功能-响应型中的物种数量越多，越不会发生灭绝事件或一系列造成生态系统严重后果事件。

4.4 物种间相互作用与生态系统过程 (Species Interactions and Ecosystem Processes)

物种间的相互作用改变了单个物种对生态系统过程的影响。物种间的相互作用包括互惠共生、营养级间的相互作用等，这些交互作用直接改变能量流动和物质循环影响生态系统过程，或间接改变有关键作用物种的性状或多度，这些都会对生态系统过程产生重要的影响。此外，许多物种对生态系统的影响是间接的，不易预测(图 11.4-2)。例如，在草地，豆科植物和 C_4 植物组合增强了土壤碳固定，因为豆科植物可以固定大气中的氮并释放到土壤中，而 C_4 植物能充分利用氮素促进根系的生长，这会增大土壤碳的储存。

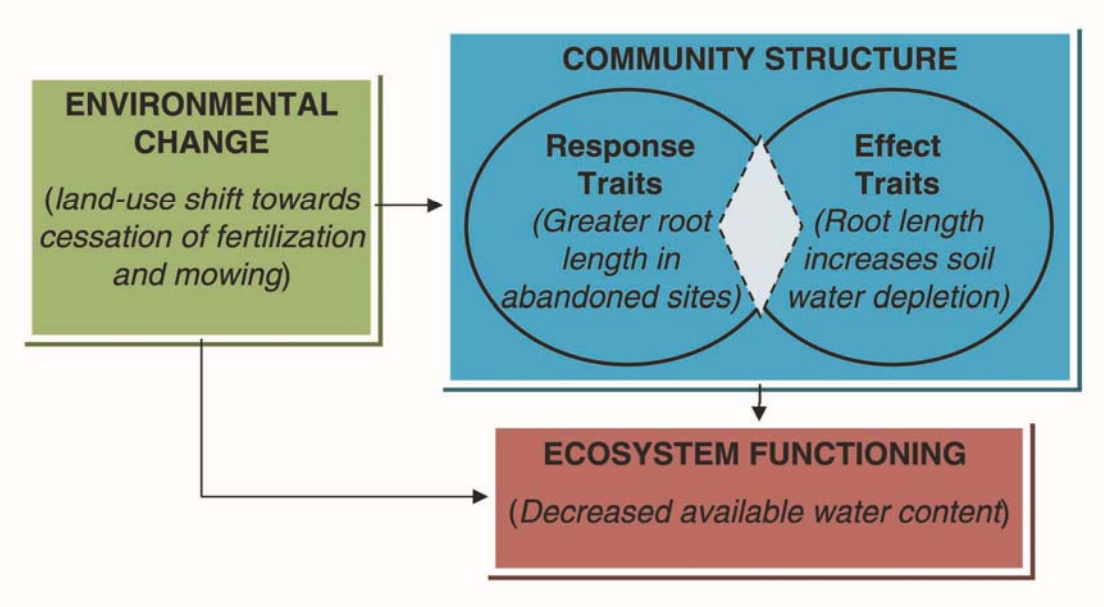


图 11.4-2 作用和响应检测框架(Suding et al. 2008)

第五节 研究案例

案例 1 生物多样与生态系统功能关系研究：以内蒙古草地生态系统为例 (Testing Biodiversity-Ecosystem Functioning Relationship in the Inner Mongolia Grassland: A Case Study)

研究背景(Background)

生物多样性既是全球变化驱动因素影响的响应变量，同时也是一个影响生态系统过程，服务和人类福祉的因子。全球气候变化和人类活动等因素导致物种大量灭绝，而物种丧失直接引起生物多样性下降(Isbell et al. 2013)。研究表明生物多样性降低直接对生态系统功能和过程产生重大影响(MacDougall et al . 2013)，主要表现在生境破坏、生物地球化学循环以及生态系统生产力等方面。生态系统功能为人类提供各种服务，与人类发展息息相关(Lavorel et al. 2013)。因此研究生物多样性与生态系统功能之间的关系对于人类自身发展，环境保护、

维持生态系统过程良性循环都有着重要意义。

草地生态系统面积为 5250 万平方公里，占世界陆地面积的 40.5%，而欧亚大草原是世界上最大的连续生物群落。作为欧亚草原的一部分，中国草地面积为 400 万平方公里，占全国陆地面积的 41.6%。

前期研究结果

生态系统稳定性模式及其根本机制(Bai et al. 2004)：一项 24 年研究的证据。研究结果表明，第一、1-7 月降雨是导致群落生物量波动的主要气候因素(图 11.5-1)；第二、生态系统稳定性沿着层次结构组织水平逐渐增加(如物种-功能群-整个群落)；第三、群落水平稳定性是由于物种和功能群中主要成分之间的相互补偿作用维持的(图 11.5-2)。

生物多样性与生态系统功能：多种研究策略(BEF: Multiple Research Strategies)

组合实验(Synthetic-assemblage experiments, SAEs)：人为的将不同物种或功能群组合，以代表不同的多样性水平。

多样性与生态系统功能之间的机制联系（如物种丰富度与生产力之间的关系）。对于真实生态系统的解释和相关性仍存在较大的争论。除了物种和功能群丰富度以外的生物多样组分却很少被提及，如功能性状和物种相对多度。

移除实验(Removal Experiments, REs)：从自然或半自然群落移除物种或功能群，如植物，无脊椎动物，大型有蹄类动物，土壤动物群落和微生物群落等。

移除实验最适合用于研究局部物种非随机灭绝对生态系统的影响。干扰效应包括资源供应的变化或对栖息地物理结构的干扰。

观测研究(Observational Studies)：基于自然聚集的群落研究生物多样性变化对生态系统过程的影响。相关研究很难揭示生物多样性影响的因果机制。

科学问题(Research Question)

植物功能多样性(FD)和群落组成的变化如何影响生态系统功能?

剩余的物种和功能群对单个和/或多个功能群的剔除有何反应?

剩余物种的性状如何影响补偿效应的大小？

假设和预测(Hypotheses and Predictions)

预测 1：随着移除功能群数量增加，生态系统功能将会下降。

预测 2：功能同一性、相对多度和功能组成都是生态系统功能的重要决定因素。

预测 3：补偿效应的强弱主要取决于剩余物种或功能群的性状。

预测 4：完全移除(把一个功能群完全移除)和部分移除(将一个功能群中的一部分移除)在功能响应方面的差异会随着时间逐渐减小。

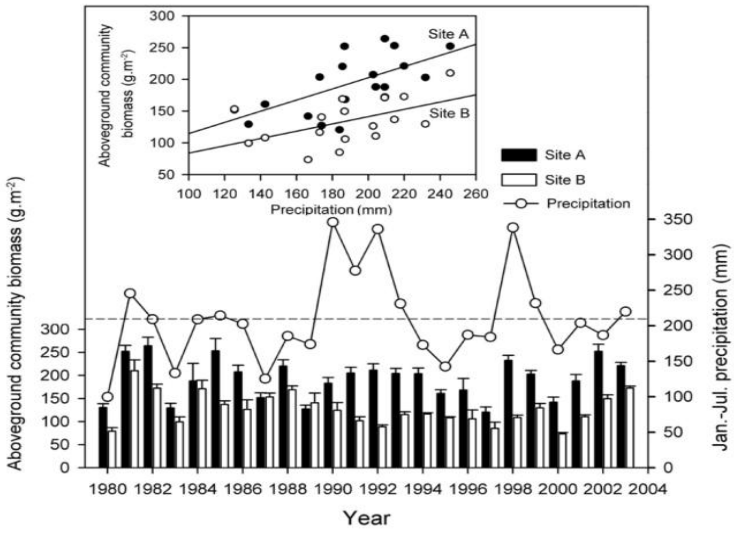


图 11.5-1 降水波动对羊草草原和大针茅草原群落初级生产力的影响

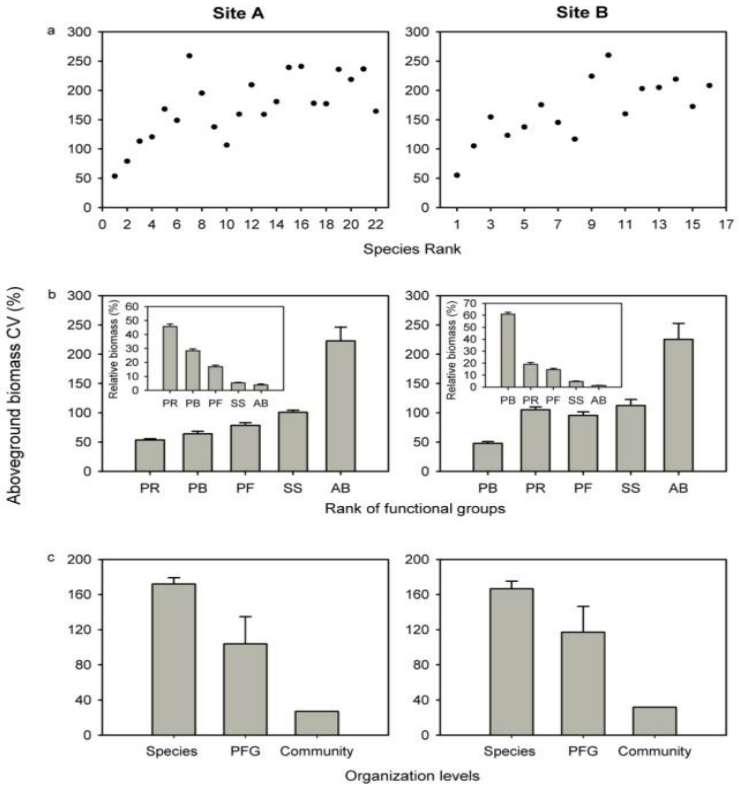


图 11.5-2 物种和功能群水平的补偿作用及其对生态系统稳定性的影响

研究方法(Methods)

研究地点，中国科学院内蒙古草原生态系统定位研究站(116°42′E, 43°38′N)；海拔为 1187 m；气候类型为温带半干旱大陆性草原气候；年平均温度为 0.3 °C；年均降雨量为 346.1mm；生长季为 5 - 8 月；土壤类型为黑钙土；建群种分别为羊草(*Leymus chinensis*)和大针茅(*Stipa grandis*) (图 11.5-3)。

实验设计(Experimental design)：我们将植物分为 5 个功能群，分别为多年生丛生禾草(PB)、多年生根茎禾草(PR)、多年生杂类草(PF), 灌木半灌木(SS)和一二年生草本(AB)；功能群剔除梯度分别为 1、 2、 3、4 和 5 个；理数为 32 个；每个处理 8 个重复；移除方法采用了完全移除和部分移除两种方法；共 512 个 6 m×6 m 小区，并按随机区组设计排布(图 11.5-4)；处理时间为 2006、2007、2008 和 2009 年。

补偿效应的测定(Measure of compensation)：利用补偿效应指数来表征补偿效应。

补偿效应指数：观测到的生物量与预期生物量之差除以功能多样性丧失后生物量的预期损失 (Adler & Bradford, 2002)。

$$C = \frac{\sum_i^n (O_i - E_i)}{\sum_i^N - \sum_i^n E_i}$$

O_i 表示移除群落中 i 物种的生物量；E_i 表示移除群落中 i 物种的期望生物量；n 表示移除群落中的物种数量；N 表示未移除群落中的物种数量

部分补偿，0＜C＜1；平等补偿，C=1；过度补偿，C＞1，表示抵消了负相互作用，从而增加了净产量；负补偿：C＜0，表示丧失了存在于整个群落中的相互作用或促进作用。

图 11.5-3 中国科学院内蒙古草原生态系统定位研究站

图 11.5-4 实验地各区组和小区分布平面图

重要发现(Major findings)

a) 随着剔除功能群数量增加，平均地上净初级生产力($ANPP_{mean}$)呈减小趋势，而地上净初级生产力变异(CV_{ANPP})线性增加。

b) 土壤水分随剔除功能群数量增加而线性增加，表明功能多样性越大，土壤水分利用率越高。

c) 补偿强度主要是由剩余物种或功能群补偿率和扩散能力的差异决定。

案例 2 草地生物多样性与生态系统功能关系研究：以蒙古高原草原生物多样性的格局与维持机制研究为例

研究背景

在全世界范围内，气候（水分）、放牧和火烧被认为是草地生物多样性和生态系统结构与功能维持的重要因子(Gibson 2009)。Tilman 和 Elhaddi (1992)研究表明，严重的干旱使草地植物群落的物种丰富度和生物量分别降低了 37%和 47%，干旱后物种丰富度的恢复显著滞后于生物量的恢复。高生物多样性群落同时具有较高的抗旱性和干旱后的恢复力(Tilman and Downing 1994)。Collins 等(1998)长期实验研究结果表明，施肥和频繁的火烧降低了高草草原的物种丰富度，但放牧使物种多样性得以恢复和维持。家畜放牧是草地生态系统最主要的土地利用方式，一些研究表明，放牧对植物多样性的影响会随着土壤肥力和降水量而发生变化，在湿润和肥沃的生境中放牧通常增加了植物多样性，在干旱和相对肥沃的生境中则降

低了植物多样性，而在干旱和贫瘠的生境中对植物多样性没有影响(Olff and Ritchie 1998)。Milchunas 和 Lauenroth(1993)对全球 263 个实验的结果进一步分析表明，放牧对物种组成的影响主要与群落生产力水平和放牧史的长短有关，放牧对物种组成的影响随生产力水平的提高和放牧史延长而增大。放牧对多年生丛生禾草的影响要大于其它多年生植物和一年生植物。多年来，草地生物多样性和生态系统功能维持机制的研究主要受两个假说的影响：(1) 中度干扰假说(intermediate disturbance hypothesis, IDH)，该假说认为在中度干扰下下生物多样性最高(Connell 1978)。(2) 放牧优化假说(grazing optimization hypothesis)，该假说认为生产力先随着放牧强度的增加而增加，在中等放牧强度下达到最高，即经过优化的放牧强度可以潜在地增加草地的初级生产力(McNaughton 1979)。这两个假说引起了学术界很大的争议，迄今为止仍然很难达成共识。近年来，一些研究表明草地物种组成对放牧的响应是否呈现出具有阈值的非线性变化，主要受气候和土壤条件的影响(Briske et al. 2005; Sasaki et al. 2008)。在环境条件较好的半干旱草原，植被组成对牧压梯度的响应呈非线性，具有明显的生态阈值，支持中度干扰假说的预测，而对于环境条件较严酷的干旱草原则不支持该假说(Sasaki et al. 2008)。

国际上通过控制实验来验证生物多样性与生态系统功能关系的相关理论和假说始于上世纪 90 年代。其中，最具代表性和影响力的两个实验研究是：1）David Tilman 等于 1994 年在美国 Cedar Creek 长期生态学研究站开展的“草地生产力、生物多样性与生态系统功能(Productivity, Biodiversity, and Ecosystem Functioning)”长期实验研究；2）Andy Hector 等几十位科学家在欧洲 8 个地点（7 个国家）联合开展的“草地生物多样性与生态系统过程(Biodiversity and Ecosystem Processes in Terrestrial Herbaceous Ecosystems, BIODEPTH)”实验研究，该项目开始于 1996 年。上述两个长期生物多样性实验取得的重要研究成果是：生物多样性对多个生态系统功能和过程（生产力、稳定性、养分保持能力、碳固持、抵御外来种入侵）均具有正效应，这种正效应会随着时间的进程而增强(Tilman et al. 2006; Hector et al. 2007; Cardinale et al. 2007)。多样性导致生态系统功能增加的主要机制是互补效应(complementarity)和选择效应(selection effect) (Hector et al. 1999; Loreau and Hector 2001)。而多样性导致生态系统的时间稳定性增加的主要机制是均衡效应(portfolio effect) 和超产效应(overyielding effect)(Tilman et al. 2006)。

国内关于生物多样性的格局与维持机制方面的研究工作开展得较晚，特别是以控制实验为平台和手段的系统性研究则刚刚起步。一些代表性的工作主要包括：北京大学方精云研究团队有关中国山地植物多样性格局与驱动机制的研究(Wang et al. 2009)；北京师范大学张大勇研究团队在生物多样性的维持机制，特别是中性理论及相关假说的验证方面(Zhou et al. 2008)；中国科学院植物研究所马克平研究团队开展的森林生态系统生物多样性大样地联网研究(Zhu et al. 2010)；中国科学院内蒙古草原生态系统定位研究站开展的草地生物多样性与生态系统功能关系的研究(Bai et al. 2004, 2007, 2008, 2010)；以及中国科学院动物研究所有关中国昆虫、鸟类、哺乳动物的多样性分布格局与编目等等。

科学问题

(1) 在多个尺度上，沿气候、土壤等环境梯度，蒙古高原的草原生物多样性具有什么样的空间格局和尺度特征？土地利用历史（放牧、火烧、开垦等）对不同尺度的生物多样性格局有何影响？植物功能性状、功能多样性与 α、β 和 γ 多样性之间有何内在联系？关键驱动因子是什么？

(2) 植物的响应性状(response traits)和影响性状(effect traits)是如何对气候、土壤、放牧、火烧等因子做出响应，并对生态系统过程进行反馈与调节的？

(3) 在生态系统水平上，植物功能性状、物种丰富度、功能多样性和生态系统多功能性之间有何内在的联系？植物功能性状、物种多样性、功能多样性和多个生态系统功过程是如何对放牧、火烧、养分添加做出响应的？功能冗余(functional redundancy)和生态系统多功能性之间有何关系？

(4) 生态系统的稳定性，包括变异性、抗性和弹性是如何对放牧、火烧、养分添加和降水波动做出响应的？不同生态系统过程，如生物量、NEE、土壤呼吸、N 矿化、凋落物分解、土壤水分变化等，对不同干扰的响应是否存在着临界阈值(critical threshold)效应？它们各自沿着什么样的轨迹变化？

(5) 生态系统不同营养级组分(家畜–植物–土壤动物和微生物)中，家畜和植物是如何自上而下地对土壤动物(如线虫)和微生物群落结构(如细菌和真菌)、多样性及相关的地下过程进行调控的？土壤动物和微生物又是如何自下而上地影响植物性状、种间相互作用和生态系统过程的？

根据生态学基本原理和国内外相关研究的成果，对上述科学问题提出以下假设和预测(prediction)作为制定研究方案的依据：

假设 1：根据生态位互补性(niche complementarity)理论，生态系统功能(e.g., 初级生产力、碳固持、养分循环、水分保持能力)主要依赖于功能多样性(functional diversity)，而功能多样性的高低则是由基于植物个体的功能性状(functional traits)及其在群落中的多度和均匀度决定的。在生态系统水平，当只考虑单个生态系统功能时，生态系统功能先随功能多样性增加而增加，然后随着功能多样性的进一步增加而逐渐达到饱和，即出现功能冗余(functional redundancy)。当同时考虑多个生态系统功能时，维持生态系统功能所需要的功能多样性则随着生态系统功能数量的增加而增加，即功能冗余会随着生态系统功能数量的增加而降低（图 11.5-5）。

预测 1：如果该假设成立，生态系统功能会随着功能多样性的下降而降低。对于某一个指定的生态系统过程，其变化主要受某一个功能性状或一些功能性状组合的影响。因此，不同生态系统过程对功能多样性改变的响应存在着差异，一些功能性状的改变对与其相关的生态系统过程影响较大，但对与其关系不大的一些生态系统过程，其影响则相对较小或没有影响。建群种和优势种的功能性状及相对多度的改变，会同时对多个生态系统过程产生重要影响。

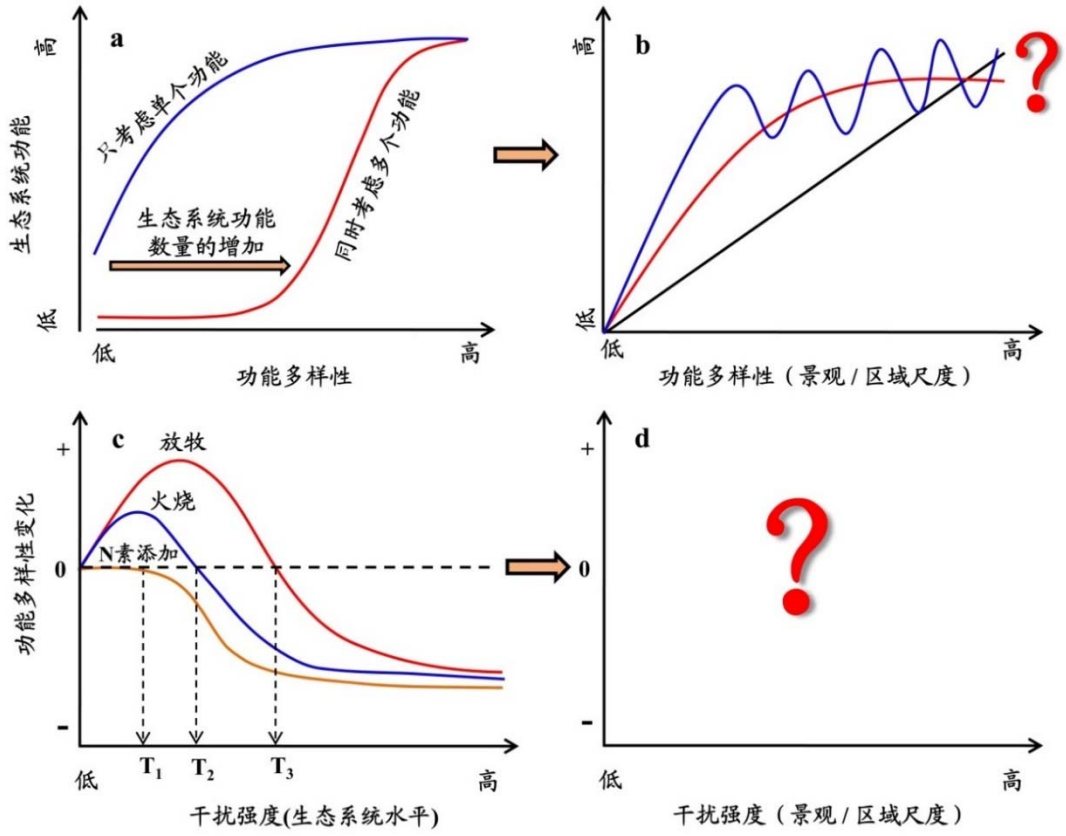


图 11.5-5 功能多样性与生态系统功能的关系及其对干扰的响应

图 11.5-5 中：a. 基于生态位互补性理论的功能多样性–生态系统多功能性关系；b. 景观/区域尺度上，生态系统功能与功能多样性的关系；c. 在生态系统水平，功能多样性对放牧、火烧和 N 素添加的响应。T1、T2 和 T3 分别表示功能多样性开始下降时的临界干扰强度或资源水平，即临界阈值(critical threshold)；d. 景观/区域尺度上，功能多样性对干扰强度的响应。

假设 2：在生态系统水平，功能多样性对不同干扰（放牧、火烧）和资源水平（N 素添加）的响应方式、变化轨迹和阈值不尽相同。适度的放牧和火烧会导致功能多样性的增加，但 N 素添加会引起功能多样性的降低（图 11.5-5）。同时，放牧、火烧和 N 素添加引起的植物功能多样性的改变，会影响到其他营养级组分的多样性、组成和相关生态系统过程，包括土壤线虫和微生物群落的结构和多样性，以及土壤呼吸、N 素矿化、硝化和反硝化等过程。

预测 2：如果该假设成立：（1）放牧、火烧和 N 素添加将引起植物功能性状、物种多度、功能多样性、ANPP 和 NEE 等的变化；（2）植物功能多样性的变化将通过光合产物的分配、凋落物、根系及其分泌物对地下过程产生影响，如土壤呼吸、N 矿化、硝化作用和甲烷氧化作用；（3）生态系统地上和地下组分的变化，使自上而下和自下而上的调控与反馈作用发生改变，并对生态系统的稳定性产生重要的影响；（4）功能多样性和物种组成改变引起的生态系统功能变化，将影响家畜的食物来源、数量和质量，进而影响畜产品的产量、质量和草原生态系统的可持续性。

假设 3：在景观/区域尺度上，沿着年降水量由低到高的水分梯度，生态系统功能先随着功能多样性的增加呈线性增加，当功能多样性达到一定水平后，生态系统功能是否会继续呈线性增加，或出现功能冗余，或者呈现无规则的震荡，需要通过实验和调查数据来进一步验证（图 11.5-5）。同时，由于受气候、土壤等环境梯度和资源水平的影响(土壤有机质、N 素有效性)，功能多样性对放牧、火烧、土地利用方式改变的响应方式、变化轨迹和阈值（如果存在阈值的话）则更加复杂，存在着很大的不确定性，目前尚不清楚（图 11.5-5）。

研究方法

（1）在景观和区域尺度上，采用样带调查的手段，研究蒙古高原草原生态系统植物的功能性状、物种多样性和功能多样性的格局与尺度特征，以及他们对气候、土壤、放牧、火烧等因子的响应与适应机制。

（2）在生态系统水平（局地尺度），利用已有的控制实验平台，研究基于个体水平的植物功能性状、功能多样性和生态系统过程对放牧、火烧、N 素添加及其交互作用的响应与适应机制。回答科学问题(3)、(4)和(5)，并对假设 1 和 2 进行验证。

（3）在上述研究的基础上，对样带调查数据和实验数据进行多尺度整合分析，从多个尺度阐明蒙古高原草原生物多样性的格局、尺度特征及其在气候、土壤、放牧、火烧等因子综合影响下的维持机制，回答项目提出的科学问题，并对 3 个假设进行验证。

主要发现

植物功能性状之间的权衡（trade-offs）关系，反映了植物通过自身内部结构与功能的调整，为适应胁迫环境，在资源获取、利用和分配方面的策略，也反映了群落内物种的竞争和共存机制(Sterck, Markesteijn et al. 2011)。基于锡林河流域草甸、草甸草原和典型草原三种不同类型草原中植物叶片、个体、物种、功能群（生活型和水分生态型）和群落多个组织水平的研究发现，随着组织水平的上升，放牧对草甸中植物功能性状的影响逐渐减弱，而对典型草原植物性状的影响逐渐增强（图 11.5-6）。叶片大小和数量之间的权衡关系，以及植物采用躲避型策略和忍耐型策略，是放牧对不同类型草原影响差异的主要原因(Zheng, Ren et al. 2010)。

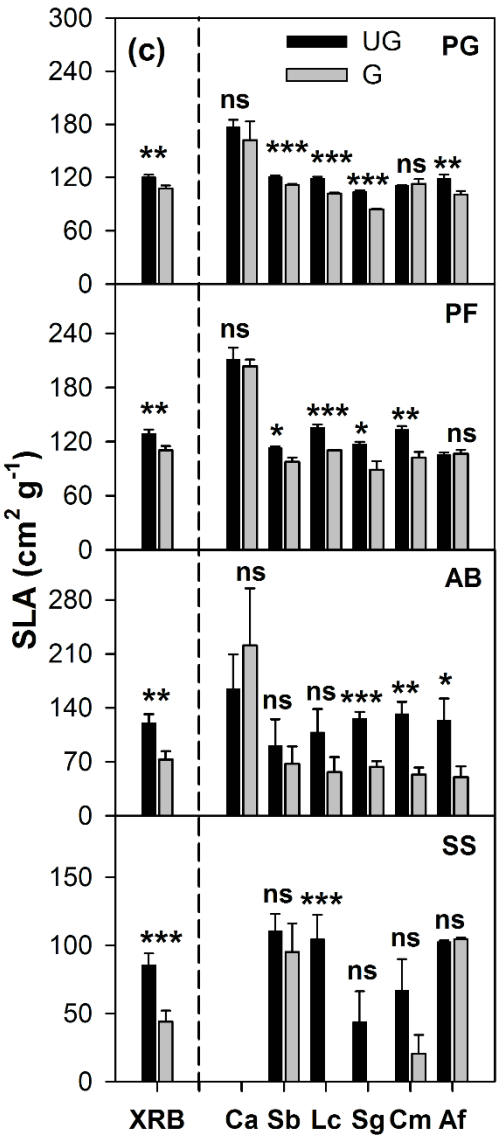


图 11.5-6 放牧对 6 个群落中不同功能群植物比叶面积（SLA）的影响。PG，表示多年生禾草；PF，表示多年生杂类草；AB，表示一二年生植物；SS，表示半灌木和灌木。Ca，*Carex appendiculata*，灰脉薹草草甸；Sb, *Stipa baicalensis*，贝加尔针茅草甸草原；Lc，*Leymus chinensis*，羊草典型草原；Sg，*Stipa grandis*，大针茅典型草原；Cm，*Caragana microphylla*，小叶锦鸡儿典型草原；Af，*Artemisia frigida*，冷蒿典型草原。 XRB，指六类群落的平均值。（引自 Zheng et al. 2010）

基于蒙古高原样带调查的研究发现，沿着东北-西南方向养分和水分可利用性逐渐减少的环境梯度，物种水平上，植物的比叶面积和比根长表现为适应旱生环境的特征，随着水分减少，比叶面积和一级根的比根长均降低；群落水平上，根系性状对环境筛选更为敏感，而地上性状主要由群落组成和环境因子的交互作用所决定(Cheng, Chu et al. 2016)。

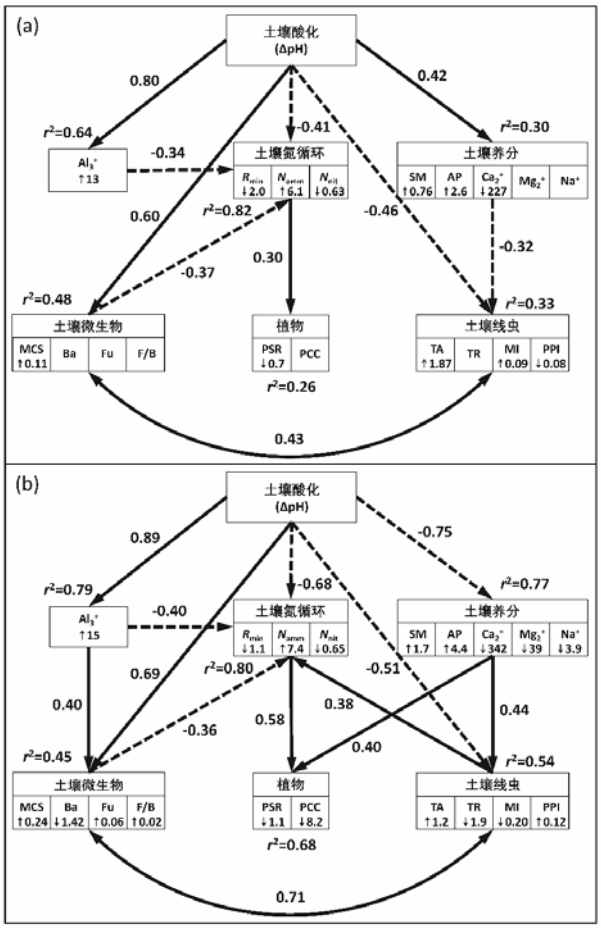


图 11.5-7 长期氮添加对草地生态系统土壤生物食物网组分（微生物和线虫）和植物群落的影响。a，2010 年；b，2011 年。R_{min}，氮矿化速率；N_{amm}，土壤铵态氮；N_{nit}，土壤硝态氮；SM，土壤含水量；AP，土壤有效磷；MCS，微生物群落结构；Ba，细菌；Fu，真菌；F/B，真菌/细菌比；PSR，植物物种丰富度；PCC，群落盖度；TA，线虫丰富度；TR，分类群多样性；MI，成熟度指数；PPI，植物寄生线虫成熟度指数。（改自 Chen et al. 2013a）

长期氮素添加和土壤酸化都降低土壤呼吸和土壤有机质分解呼吸但增加根系呼吸，其中有机质分解呼吸的降低主要是由于酸化降低了微生物生物量和真菌细菌比，而根系呼吸的增加是由于酸化增加了根系生物量和物种水平根系呼吸(Chen, Wang *et al*. 2015)；另外，氮添加对土壤微食物网的影响主要来源于土壤氮素添加所导致的土壤酸化过程，而并非由于土壤氮素增加所引起的土壤氮输入增加(Wei, Yu *et al*. 2013, Chen, Li *et al*. 2016, Ying, Li *et al*. 2017)，而氮素积累引起的微生物限制因素的转换改变了土壤有效态资源的化学计量比率，弱化了植物和微生物间的互利关系，导致了土壤碳氮循环的解耦和(Wei, Yu *et al*. 2013)；此外，土壤酸化实验证实土壤酸化导致的植物多样性和生产力的降低受土壤氮循环直接调控，土壤生物主要起间接调节作用，而土壤毒害离子的增加也并不是导致植物多样性和生产力降低的直接因素(Chen, Lan *et al*. 2013)（图 11.5-7）。

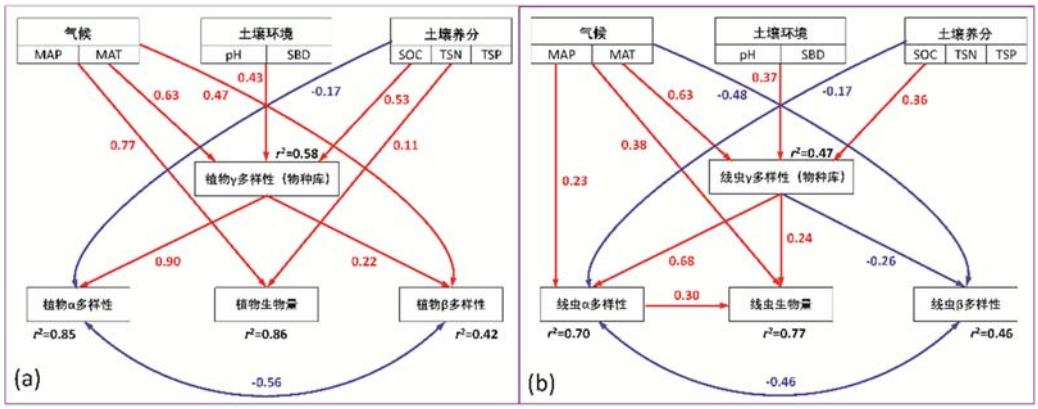


图 11.5-8 草地生态系统环境因子对植物（a）和土壤线虫（b）多样性组分的影响以及环境因子和多样性组分如何影响生产力。气候因子：MAP，年平均降雨量；MAT，年均温；土壤环境：SBD，土壤容重；土壤养分：SOC，土壤有机碳；TSN，总氮；TSP，总磷。（改自 Chen *et al*. 2016a）

基于蒙古高原 220 个样方调查的数据发现，土壤生物的 PDR 与植物群落的 PDR 存在较大差异(Chen, Cheng *et al*. 2016)。其中，土壤线虫生物量与线虫多样性（α-和 γ-）存在与植物群落相似的线性正相关关系，而线虫 β 多样性与土壤线虫生物量之间是负相关关系。另外，土壤线虫多样性-生物量之间的关系强于植物群落，当考虑环境因子（气候、土壤环境、土壤养分）对多样性和生物量的共同作用后，植物的多样性-生物量关系消失，而土壤线虫的多样性-生物量的正相互关系依然存在（图 11.5-8）。这些结果表明，多样性与生产力的关系在不同生物类群间存在差异，要得到普适性的多样性-生物量的关系需要考虑更多的生物类群。

本章小结

由于频繁的物种灭绝（包括局部性和全球性）、物种引入以及多度变化，地球的物种多样性正在迅速变化。然而，我们才刚刚开始了解这些变化对生态系统的影响。许多物种具有通过对有限资源的供应或周转、微气候、营养相互作用和干扰机制的影响而强烈影响生态系统过程的特性。这些物种特征对生态系统过程的影响取决于物种的丰度、与群落中其他物种的功能相似性以及在生态系统尺度上影响重要特征表达的物种相互作用。

物种特征对生态系统过程的影响通常是非常强烈，以至于生态系统的物种组成或多样性的变化可能会改变它们的功能，尽管这些变化的确切性质往往难以预测。功能多样性本身在生态上可能是重要的，如果它导致不同物种对资源的互补利用或增加包括具有特定生态影响的物种的可能性。由于属于同一功能效应类型的物种对环境的响应通常不同，因此在面对环境的时间变化或方向变化时，功能效应类型内的响应多样性可能会稳定生态系统过程。相反，引入具有不同功能效应的物种，则可能加速生态系统的变化速度。

推荐阅读文献：

Adair, E. C., Hooper, D. U., Paquette, A., Hungate, B. A. 2018. Ecosystem context illuminates conflicting roles of plant diversity in carbon storage. Ecology Letters 21:1604-1619.

Bai, Y. F., Han, X. G., Wu, J. G., Chen, Z. Z., Li, L. H. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431:181-184.

Cadotte, M. W., Carscadden, K., Mirotchnick, N. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079-1087.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59-67.

Díaz, S., Symstad A. J., Chapin F. S., Wardle, D. A., and Huenneke, L. F. 2003. Functional diversity revealed by removal experiments. Trends in Ecology & Evolution 18:140-146.

Flombaum, P., and Sala, O. E. 2008. Higher effect of plant species diversity on productivity in natural than artificial ecosystems. Proceedings of the National Academy of Sciences of the United States of America 105:6087-6090.

Grace, J. B., Anderson, T. M., Smith, M. D., Seabloom, E., Andelman, S. J., et al. 2007. Does species diversity limit productivity in natural grassland communities? Ecology Letters 10:680-689.

Grime, J. P. 1997. Biodiversity and ecosystem function: the debate deepens. Science 277:1260-1261.

Hooper, D. U., Chapin, F. S. III, Ewel, J. J., Hector, A., Inchausti, P., et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge and needs for future research. Ecological Applications 75:3–35.

Keller, A. B., Phillips, R. P. 2019. Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests. New Phytologist 222:556-564.

Krause, S., Le Roux, X., Niklaus, P. A., Van Bodegom, P. M., Lennon, J. T., et al. 2014. Trait-based approaches for understanding microbial biodiversity and ecosystem functioning. Frontiers in Microbiology 5: art 251. doi: 10.3389/fmicb.2014.00251.

Loreau, M., de Mazancourt, C. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecology Letters 16:106-115.

Sharp, S.J., Angelini, C. 2020. Predators enhance resilience of a saltmarsh foundation species to drought. Journal of Ecology. doi: 10.1111/1365-2745.13525.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277:1300-1302.

Wardle, D. A., Bardgett, R. D., Callaway, R. M., Van der Putten, W. H. 2011. Terrestrial Ecosystem Responses to Species Gains and Losses. Science 332:1273-1277.

Weisser, W. W., Roscher, C., Meyer, S. T., Ebeling, A., Luo, G. J., Allan, E., et al. 2017. Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. Basic and Applied Ecology 23:1-73.

第十二章 时间动态

人类在过去的 50 年里对生态系统的改变，比人类历史上任何时期都要迅速和广泛。这些变化是由于呈指数增长的人口、对资源的消耗以及我们不断增长的改变地球环境和生态系统的技术能力。也许生态系统生态学最迫切的需求是提高我们对生态系统中控制恢复力和变化的因素的理解。我们如何为这些正在发生的干扰的类型和严重性的变化做准备？例如，预计气温变暖会提高海面温度，从而加大飓风强度，影响沿海城市，如卡特里娜飓。风。预计世界干旱地区更温暖更干燥的条件会导致类似澳大利亚、南欧和美国西部发生的干旱、野火和昆虫爆发等。预计洪水更经常发生在潮湿和低洼的沿海地区。生态系统如何应对经常遇到的干扰？如何应对新的干扰？生态系统的哪些特性增强了它们维持自身结构和功能以应对不断变化的干扰机制的能力？由于人类引起的气候变化，干扰机制脱离了其历史模式，生态系统生态学家将在理解干扰模式改变的原因和后果方面发挥关键作用，这既是为了生命财产的保护，也是为了维持生态系统的多样性和其他生态属性。

第一节　生态系统过程的波动

1.1 生态系统总是能够在过去的变化中恢复

生态系统在当下所处的环境中从未达到平衡状态。

时间滞后性：在等候时间过程中性能发生变化。

恒稳态：即生态系统属性没有方向性的改变。

1.2 日间变化

即便是在同一环境下，光合作用在早晨强于午后。植物在清晨处于强烈的碳“饥饿”状态。

1.3 季节性变化

春季，植物生长加速；秋季，植物开始凋谢，对应于物种的光合周期。

1.4 年际间变化

环境变化：气候的周期变化反映了潜在的可预测过程，几个典型事例：

厄尔尼诺现象：通常是指热带太平洋中东部海水温度大范围持续异常升高，引起气候异常并造成鱼类大量死亡的现象。厄尔尼诺是西班牙语中“圣婴”的意思。

拉尼娜（La Nina）现象：厄尔尼诺过后，热带太平洋有时会出现与上述情况相反的状态，称为拉尼娜现象。拉尼娜是西班牙语中“小女孩”的意思。

以赤道太平洋东部和中部海平面平均温度连续 6 个月以上高于或低于正常值的 0.5□分别作为厄尔尼诺和拉尼娜。

生态系统内部动态：生态系统的内部动态也在生态系统过程中产生巨大的年际波动。

例如：食植动物种群密度能在几年内变化上百倍，引起植物生物量、营养循环和其他过程的巨大波动。如下图所示，旅鼠影响喜食植物的丰富（图 12.1-1）。

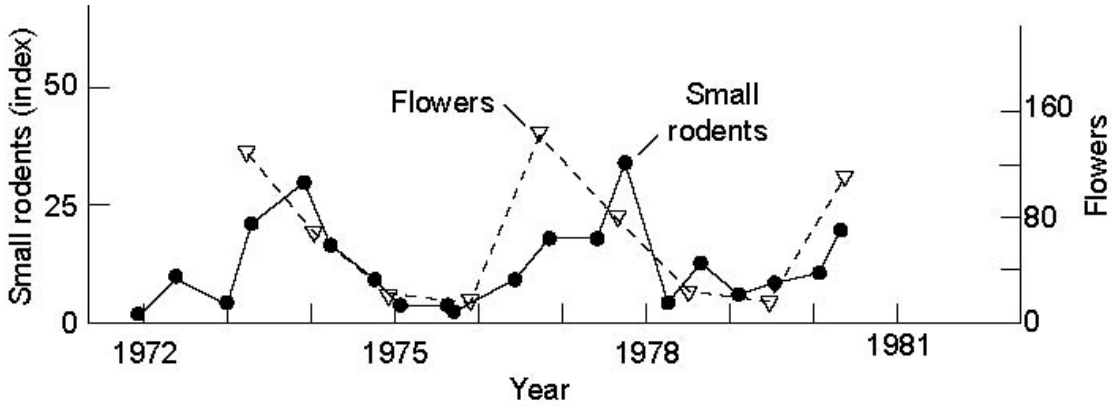


图 12.1-1 芬兰北部林下灌木（*Vaccinium myrtillus*）中开花的密度以及小型啮齿动物的密度的年际变化。这些食植动物和所食植物的多度存在一个约 4 年的周期。数据来源于 Laine and Henttonen (1983).

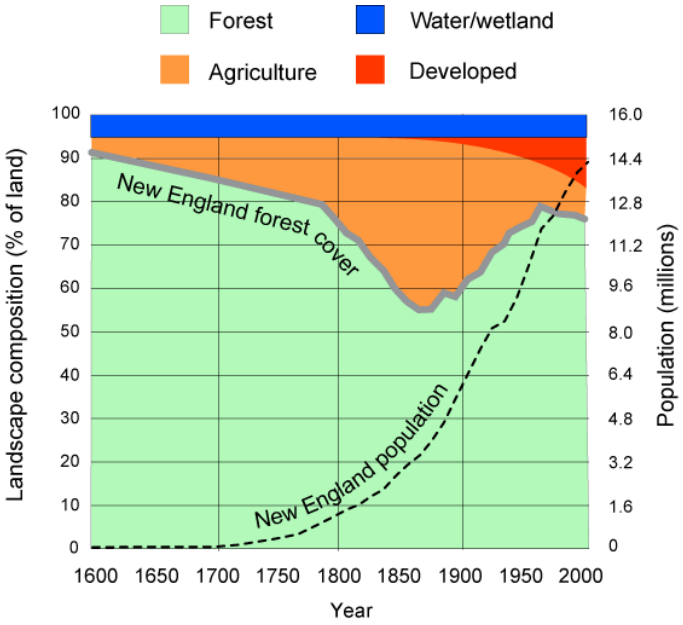


图 12.1-2 自欧洲殖民以来新西兰种群景观组成的变化 在 1850 年，这个区域大多数的森林曾经是耕地，最近发展成了城市和灌木地。数据源于 Foster et al. (2010)

1.5 长期变化和遗留效应：如图 12.1-2 所示分析结果

多稳态：既定环境总能够支撑多于一个的某生态系统的潜在状态。

遗留效应：过去环境中发生的各类事件的持续影响，在广泛的时间尺度上影响着生态系统过程。

1.6 全球变化

气候变化导致的增温效应非常显著 (图 12.1-3)。

全球平均空气温度和海洋温度均增加；世界范围上的冰雪融化引起全球海平面升高。

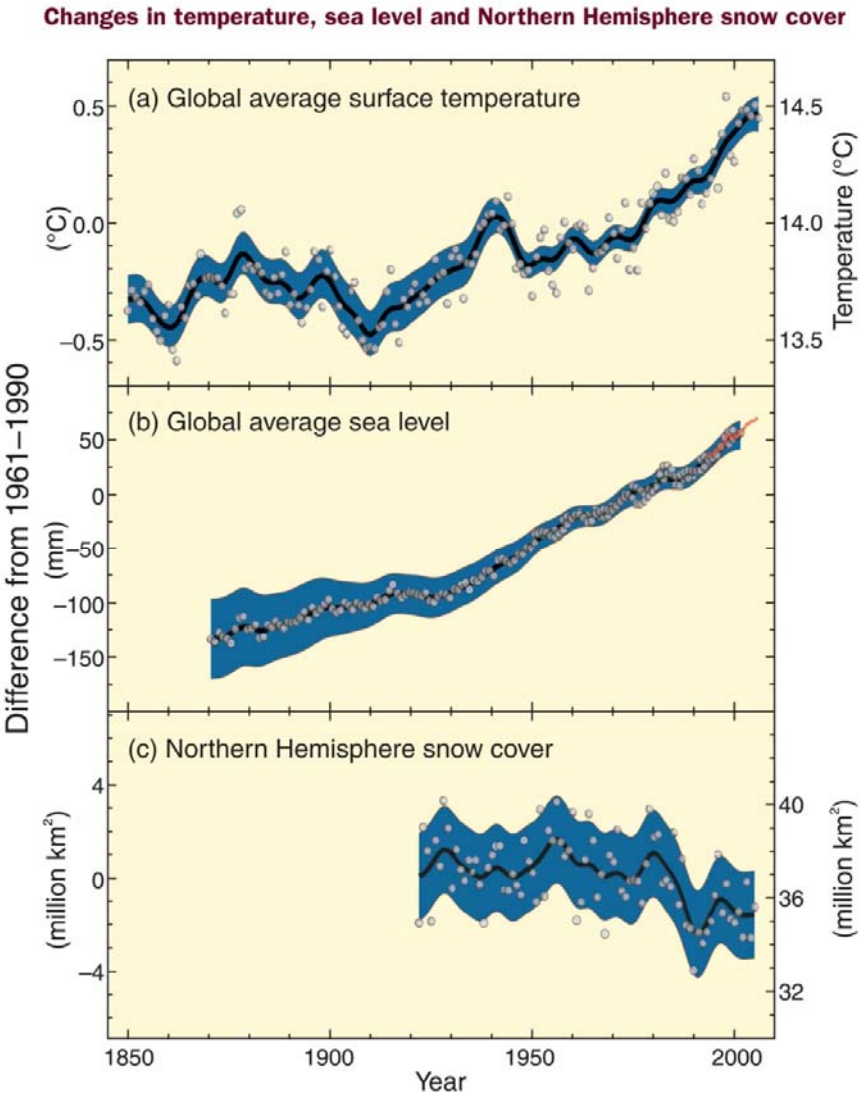


图 12.1-3 地球表面平均温度、海平面和北半球积雪覆盖的变化 （IPCC 2007）

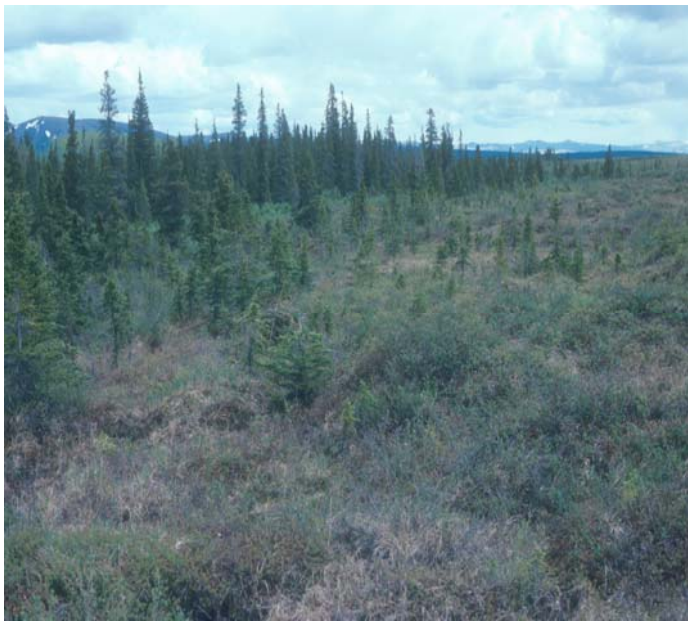
气候变化的驱动因子：自 1750 起，人类的剧烈活动导致全球温室气体(CO_2, CH_4, and N_2O)大气含量急剧增加；1750 年时 CO_2 值为 280ppm，然而到 2014 年，已达到 397.7ppm。

1.7 长期变化和遗留效应

气候变化：已在上节中提及。

植被变化：例证 1：加州海岸的北美红杉 (图 12.1-4) 个体能生存数千年，曾占据北美西部大部分暖湿环境。现在，它们的分布范围则被限制在仅仅某些山谷地区，那里海岸浓雾将夏天的干旱压力降至最低。例证 2：后冰川漂移 (图 12.1-5)，从 1949 年到 2000 年间，北极地带美国阿拉斯加州灌丛密度从无到大量增加。

土壤变化：例如，农耕废弃地有不少恢复为森林，耕作层在这些森林中仍然很明显，造成土壤过程和营养供给的垂直断层；再比如，西伯利亚湖当中的沼气流 (图 12.1-6)，热喀斯特湖在气候较温暖时期，冰层融化，土壤下层，形成了富含有机沉淀物的湖泊，形成湖泊大量的甲烷排放。



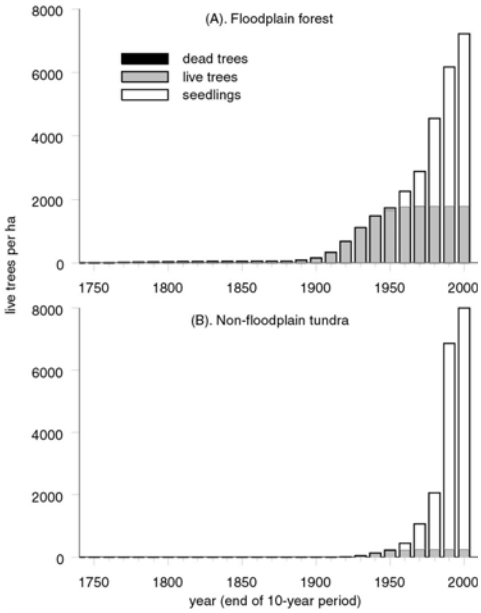


图 12.1-4 Bear Creek 的森林边界线照片。前面表示确定的红杉密度 插图表示的是涝林和非涝林年龄结构

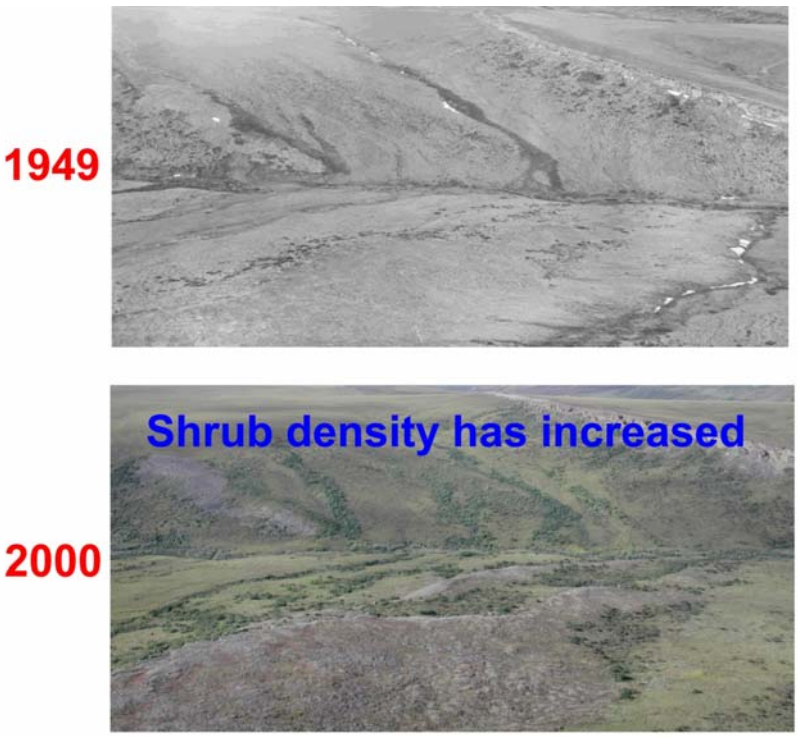


图 12.1-5 证据表明阿拉斯加北极地带景观正趋于灌丛化

图 12.1-6 热喀斯特湖和冰川融楔，导致甲烷排放

第二节　生态系统的弹性和变化

2.1 多稳态 (Alternative Stable States)

定义：是指在相同条件下，系统可以存在结构和功能截然不同的稳定状态。相同条件指的是外界条件不变；结构不同指的是系统的结构发生较大变化；而功能不同则指的是随着结构的改变，系统响应的物质流、能量流以及信息流功能发生变化，结果也会造成生态系统服务价值的变化。稳定状态在动力学理论上指的是系统的解在一定条件下稳定，在生态学意义上指的是在一定的时间和空间尺度上，生态系统保持现有的结构和功能不变。

2.2 弹性和阈值 (Resilience and Thresholds)

生态系统弹性：即指系统受到一系列冲击和扰动后，保持其基本功能、结构和反馈作用的能力 (Holling 1973, Chapin et al. 2009)。

抗性：描述系统在受到扰动时维持一定结构和功能的能力 (图 12.2-1)。

响应：指受到扰动后系统变化的方向和幅度。

弹性：系统受扰动后回到原状态的速率。

恢复：指系统恢复到原始状态的程度。

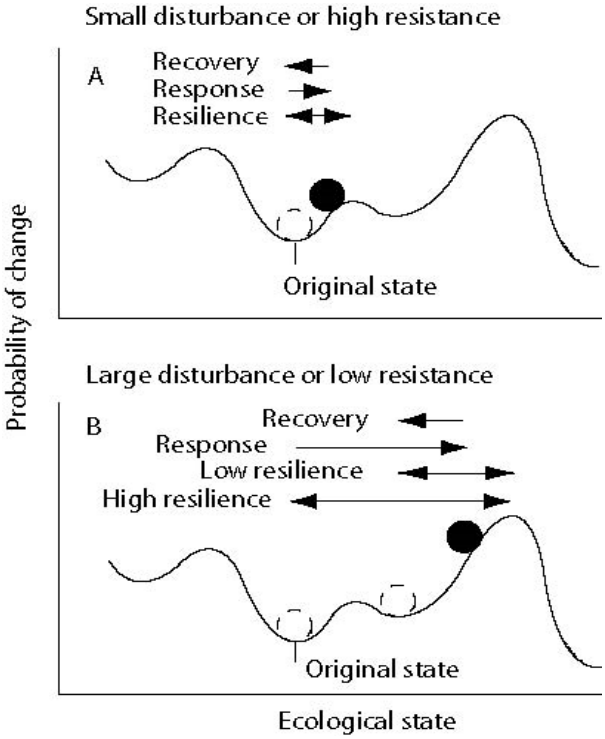


图 12.2-1 弹性和属性变化系统对干扰的响应取决于它的弹性和干扰强度，以及扰动发生后可能变化的多种状态。

2.3 生态系统适应范围

生态系统适应范围：系统容差极限的上限和下限之差 (图 12.2-2)。

体系转换：一套新的反馈作用和环境响应出现，产生可变状态的弹性。

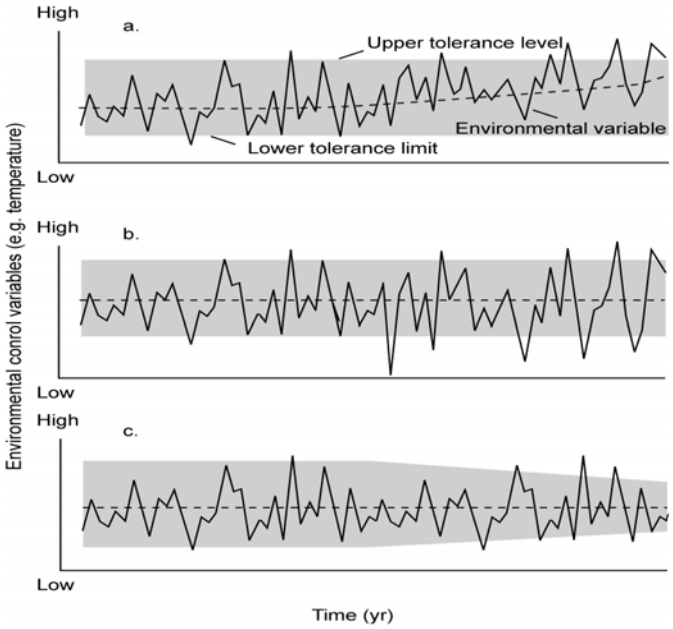


图 12.2-2 对于某重要的环境控制（例如：温度）条件下生态系统适应范围的时间变异 (a) 环境控制方向性变化 (b) 变化不定, 或者 (c) 适应范围下降。数据来源于 Smit and Wandel (2006)

第三节　干扰

3.1 概念框架 (Conceptual Framework)

定义：影响种群、群落和生态系统结构以及造成资源可利用性和物理环境变化的、时空上相对独立的事件 (Pickett and White 1985, Pickett *et al*. 1999)

干扰是造成生态系统的结构和机能长期波动的主要因素之一。干扰包括食草动物爆发、树木倒下、火灾、飓风、洪水、冰川推进和火山爆发。干扰和正常功能之间的分界线有些随意。例如，食草动物通常被视为生态系统稳态动力学的一部分，而灭绝林分的昆虫爆发则被视为干扰。干旱范围也从轻微的水分胁迫到严重的导致植物死亡和引发风蚀的水分限制。正常功能和极端干扰在大小、严重程度和频率上是连续的。干扰不是一个生态系统“发生”的外部事件。像其他交互控制一样，干扰是所有生态系统功能的一个组成部分，它响应并影响关键生态系统过程。自然发生的干扰是生态系统的正常属性，不能称之为“坏的”，如火灾和飓风。但是，通常由于人类与生态系统相互作用的变化，导致它们对社会产生负面影响时，会被视为灾害。

人类活动改变了许多自然干扰的频率和规模，如火灾和洪水，并产生了新类型的干扰，

如大规模伐木、采矿和战争。许多人类干扰具有类似于自然干扰的生态效应，因此对自然或人类干扰的研究为生态系统过程的调节和人类对这些过程的影响提供了见解。自然和人类的干扰与环境梯度相互作用，创造了景观中的许多空间模式。

受到干扰后，生态系统经历演替，即生态系统组成、结构和功能的定向变化。例如，移除活的或死的有机物质的扰动被植物定殖，这些植物逐渐减少土壤表面的光的可用性，并改变水和养分的可用性。如果没有进一步的干扰，演替将走向稳定状态。由于演替的路径依赖性质，这种稳定状态可能类似于干扰前的生态系统，也可能向其他终点移动。例如，在 1988 年 Yellowstone 公园的大火中被烧毁的洛奇坡松林，根据原生种子的可用性(取决于种子在球果中的保留和火灾的严重程度)和幼苗的建立，沿着非常不同的林分密度、养分可用性和生产力的轨迹移动。然而，在实践中，新的干扰或环境变化通常发生在演替达到稳定状态之前。尽管如此，干扰后植被方向变化的概念为分析干扰在生态系统过程中的作用提供了一个有用的框架。

Steward Pickett

简介：

Steward T.A. Pickett 是纽约米尔布鲁克凯里生态系统研究所的杰出资深植物生态学家。他于 1977 年获得伊利诺伊大学博士学位。他领导着巴尔的摩生态系统研究长期生态研究项目。他的研究重点是城市地区的生态结构和植被的时间动态，包括原始森林、美国东部农田和南非的河岸林地。他出版了关于生态异质性，人类是生态系统的组成部分，保护生态学，桥梁生态学与城市设计，生态哲学，连接生态学和生态伦理学等书籍。

代表性论文：

- Pickett, S.T.A., et al. 1987. Models, mechanisms and pathways of succession. Botanical Review 53:335-371.
- Pickett, S.T.A., et al. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129-136.
- Pickett, S.T.A., et al. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127-157.
- Pickett, S.T.A., et al. 2005. Biocomplexity in coupled naturalhuman systems: A multidimensional framework. Ecosystems 8:225-232.
- Pickett, S.T.A., et al. 2009. Altered resources, disturbance, and heterogeneity: A framework for comparing urban and non-urban soils. Urban Ecosystems 12: 23-44.
- Pickett, S.T.A., et al. 2011. Domain and propositins of succession theory. Pages 185-216 in S.M. Scheiner and M.R. Willig, editors. Theory of ecology. University of Chicago Press, Chicago

3.2 干扰事件的影响 (Impact of a Disturbance Event)

干扰特征：干扰对生态系统过程的影响取决于它的程度、频率、类型、大小、时令和强度。干扰的这些属性共同构成了干扰体系。

干扰事件的影响取决于三个干扰属性：干扰类型、生态系统系统的敏感度以及干扰严重程度或强度（图 12.3-1）。

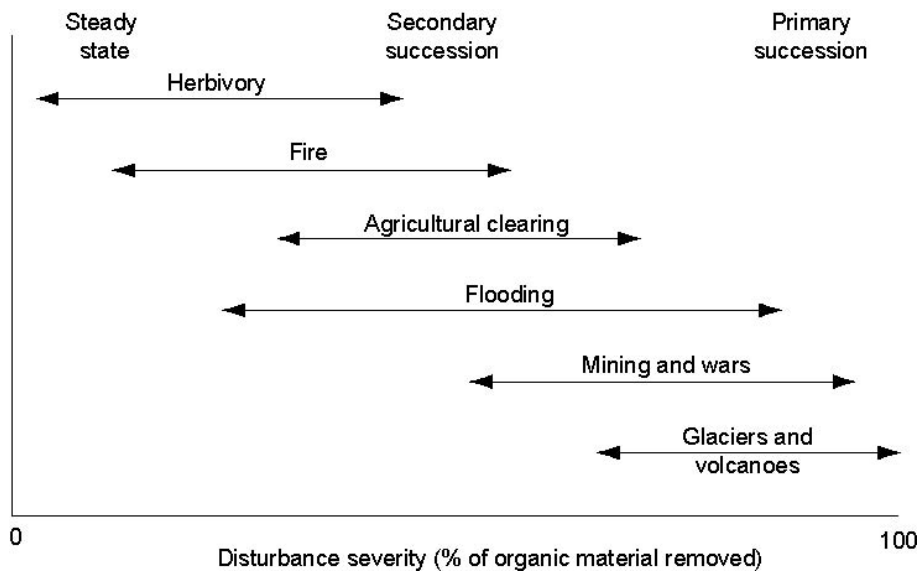


图 12.3-1 不同干扰类型的干扰程度谱（范围从生态系统正常稳态的机能执行到原生演替）

不同的干扰类型对生态系统的影响截然不同。火可以去除活的和死的有机物，并将环境温度提高到致命的水平。不合时宜的冰冻也可能产生致命的温度。洪水和滑坡会移除或增加土壤，消耗掉土壤中的氧气。飓风、风暴潮和伐木会移除或破坏生物体。物种通常能够承受进化史中相对频繁发生的干扰，但可能容易受到新型干扰的影响。例如，尽管海底生物会从驱逐个体的严重风暴中迅速恢复，但海底生物群落可能会从只刮擦表层沉积物的拖网中缓慢恢复。许多高地物种不耐受洪水，而潮湿环境中的树木通常能耐受周期性洪水，但树皮较薄，会被火烧死。

对特定干扰类型的敏感性取决于干扰时的系统特性。物种性状，如生根深度或应对霜冻、火灾或干旱的耐受性会影响个体生物的敏感性。此外，系统特性，如植物的密度或配置会影响火、病原体或害虫的传播，从而影响景观对干扰的敏感性。

干扰严重程度是由干扰引起的生物量、土壤资源和物种损失的程度。强度是单位面积和时间释放的能量。原生演替发生在严重的干扰之后，这些干扰移除或掩埋了生态系统过程的大部分产物，留下很少或没有留下有机物或有机体。导致原生演替的干扰包括火山爆发、冰川退缩、滑坡、采矿、洪水、海岸沙丘形成和湖泊排水。

次生演替发生在以前植被覆盖的地区，经过火灾、飓风、伐木和农业耕作等干扰后。这些干扰移除或杀死大量地上生物量，但留下一些土壤有机质和植物或植物繁殖体。干扰严重程度可能是决定干扰后植被发展速度和轨迹的主要因素。例如，一场杀死所有植物的严重火灾，对植被恢复的影响不同于一场只燃烧地表凋落物、允许幸存的植被重新生长的火灾。在大规模的落叶事件和由毛虫啃食单片叶子之间，或在滑坡掩埋和蚯蚓掩埋地表凋落物之间，干扰的严重程度也是连续的。 换句话说，在生态系统的日常功能与引发原生演替的事件之间，干扰的严重程度是连续的。

3.3 干扰后的恢复和更新 (Recovery and Renewal after Disturbance)

干扰后的弹性和随之发生的连续轨迹不只有赖于最初的干扰影响，而且也受控于干扰大小、干扰格局和景观矩阵，这些因素同时也会影响到干扰后的更新。

从干扰中幸存下来的生物的性状和丰度对干扰后的演替至关重要。根据干扰的类型和严重程度以及生态系统对干扰事件的敏感性，不同数量的个体和物种将生存、生长和繁殖。新个体也很重要。一些性状使物种能够对特定类型的干扰做出反应，例如火后一年生灌木由于热诱导发芽。其他性状使物种能够在多种干扰下定殖。例如，杂草物种会产生大量的小种子，这些种子会分散到很远的地方，或者在一次又一次的干扰中保持休眠状态。它们的发芽通常是由温度和养分的波动引起的，这是大多数受干扰地区的性状。

干扰大小变化很大。例如，林窗相演替发生在一株或几株植物死亡造成的小间隙中。例如，许多热带湿润森林或潮间带群落是不同年龄的缝隙的镶嵌。类似地，地鼠在草原上造成不规则的干扰。其他生态系统的发育可能在面积达到数百平方公里的群丛代替干扰之

后。干扰大小主要通过对景观结构来影响生态系统，景观结构影响物质、生物有机体和干扰在景观斑块间的横向流动。例如，干扰大小会影响火灾后的种子输入速率。小火灾之后很容易从周围未燃烧的地方的种子吹进来，或者被哺乳动物和鸟类携带进入，从而建立新的种群。然而，在大火、田地或空地的中间地带，植物的再生可能会受到种子较少而受到限制，并且主要被散布在远处的小而轻种子物种所占据。干扰的大小也会影响早期生境中的食草动物和寄生生物的扩散。景观上的干扰格局影响干扰事件的有效大小。干扰通常会留下未受干扰的植被岛屿，或形成不规则的性状与传播源之间的距离不同，导致干扰的有效大小远小于其面积范围所能显示的大小。

对干扰的恢复力还取决于受干扰生态系统所处的景观的特性，特别是其生态系统类型和年龄的多样性，这些生态系统是干扰后定殖的潜在繁殖体来源。例如，一个与农业或城市区域的自然保护区或森林林分，与在不同年龄的森林林分区域中的类似林分相比，其繁殖体较少，恢复力也较弱。同样，多样化的景观比单一的景观更能适应各种各样的干扰类型，这将在下一节进行描述。这表明，通过种植统一年龄的单一物种林分来提高收获的管理会降低景观恢复力。

3.4 干扰体系 (Disturbance Regime)

干扰体系是一个影响出现生物的种类的过滤器，因此也改变了生态系统的结构和机能执行。系统中干扰的作用有赖于多个干扰类型的频度和交互作用、单个干扰事件的本质以及支配弹性和更新的景观格局。随着时间的推移，大多数生态系统经历了不同频率和严重程度的各种干扰类型。这些共同构成了生态系统的干扰机制。

不同生态系统和不同干扰类型之间的干扰频率差异很大。食草动物在大多数生态系统中持续存在。相反，在某些地方可能从未发生过火山喷发或洪水。平均火灾发生频率从一些草原每年一次到一些热带森林几千年一次不等。生态系统通常对频繁发生的干扰最具弹性。例如，经历频繁火灾的生态系统比不频繁发生火灾的生态系统支持更快恢复生物量的适应火灾的物种。人类活动经常通过引发或抑制干扰来改变干扰频率。拦河筑坝可以消除春季洪水冲刷河道沉积物和碎屑，导致河流食物网和养鱼能力发生巨大变化。加州内华达山脉的巨型红杉(*Sequoiadendron gigantea*)的灭火措施使这个生态系统更容易受到火灾的影响，因为林下树木的生长形成了一个从地面到树冠的消防阶梯。虽然厚皮红杉能抵抗地面火灾，但它们很容易受到延伸到树冠层的火灾的伤害。通过这种方式，灭火增加了灾难性火灾的风险，而灾难性火灾可能会消灭巨大的红杉。

干扰的时令往往会决定这干扰的影响程度。发生在抽芽期间的严寒或火灾比此前两周发生相同事件的影响更大。同样，1993 年生长季节发生在密西西比河洪水造成的厌氧条件导致了严重的根和树的死亡，如果洪水发生时，根处于不活跃期的话，影响会小很多。水电站大坝可能会消除降雨或融雪造成的季节性洪水，并根据电力需求调节水流量，这通常会导致干扰时间与生物体适应的干扰状态不匹配。

干扰是一种控制生态系统过程的关键性的交互控制，它通过影响其他交互控制(微环境、土壤资源供应和生物功能类型)来起作用。例如，火后的植物群丛通常有温暖潮湿的土壤，和较高的含水量，这是因为被烧焦的表面反照率低，而蒸发水分、遮蔽土壤的叶面积减少。火灾是氮元素以挥发的形式流失氮，又以灰烬的形式将无机氮和其他养分返回土壤，从而改变了土壤资源供给。火灾的净效应通常是提高养分的有效性，尽管这种影响的大小取决于养分和火灾的严重程度和强度。火灾通过其对火后环境中差异生存和竞争平衡作用来影响生态系统中植物的功能类型。由于对其他交互控制的敏感性和影响，干扰状态的变化会改变生态系统的结构和功能。

第四节　演替

4.1 基本概念

演替：生态系统结构和功能沿某一方向发生变化称为演替。干扰之后，生态系统经历演替。资源供给中由生物驱动的变化所造成的，生态系统结构和机能执行上的定向改变。

原生演替：由移植动态控制的群落向资源竞争控制的群落变化。

次生演替：干扰过后的生境很快就会有现存的先锋物种移植。

4.2 生态系统结构与组成 (Ecosystem Structure and Composition)

原生演替：剧烈干扰之后发生原生演替，这样的干扰移走或掩埋了生态系统过程的大多数产物，很少甚至根本不留下任何的有机质或生物有机体（图 12.4-1）。发生原生演替地点的初始物种组成取决于植物应对与低氮有效性和有机贫瘠土壤的低持水能力相关的环境压力的能力。能够共生固氮的维管植物物种在原生演替的早期最常出现(约 75%的研究地点)，尽管它们仅占植被约 25%。这些物种最常见于冰川冰碛和泥石流，介于尾矿、滑坡、洪泛区和沙丘之间，在火山和岩石上出现的最少。当早期演替的定殖者固定了大量的氮，其净效应通常是促进(增强)后期演替物种的建立和生长。

由于缺乏植物和植物繁殖体，主要的演替被分散到该地点的物种所占据。大多数最初的定殖者都有易被风吹散的小种子。例如，新鲜的熔岩或冰碛首先被风传播的藻类、蓝细菌和地衣孢子占据，形成壳状地衣稳定的土壤。随后是靠风力传播的维管植物(主要是木本植物)，到达率很大程度上取决于到种子源的距离。而演替后期的物种种子较重，通常来得较慢。

早期定殖的物种身份强烈影响着长期的演替轨迹。例如，在夏威夷火山爆发后，演替通常缓慢进行，从以藻类、草本植物和小灌木为主的低矮植被，到以缓慢生长的树蕨和树木为主的森林。然而，外来的鸟类传播的固氮树 *Morella faya*，可以添加足够的氮来显著地改变氮的供应、生产、物种组成，从而改变植被的演替轨迹。

阿拉斯加冰川湾冰川退缩后，演替轨迹也发生了类似的变化，但原因不同。1800 年冰川

首次开始退缩时，杨树（*Populus*）和云杉（*Picea*）是主要的初始定殖者。然而，冰川的进一步退缩将早期演替栖息地带到固氮桤木的散布范围内，这种桤木随后成为重要的演替早期物种。桤木增加了氮输入和演替后期阶段的长期生产力。因此，冰川湾旧址上的演替晚期的森林，与年轻生境中上由桤木支撑的森林相比，有着不同的(生产力较低的)演替轨迹。人类活动强烈影响着干扰后的环境和繁殖体的可用性，因此未来的演替轨迹可能不同于与目前占主导地位的演替。

次生演替：次生演替发生在原来有植被的地点。这些干扰移走或杀死了绝大多数地上生物，但是留下一些土壤有机质与植物或植物的繁殖体（图 12.4-2）。

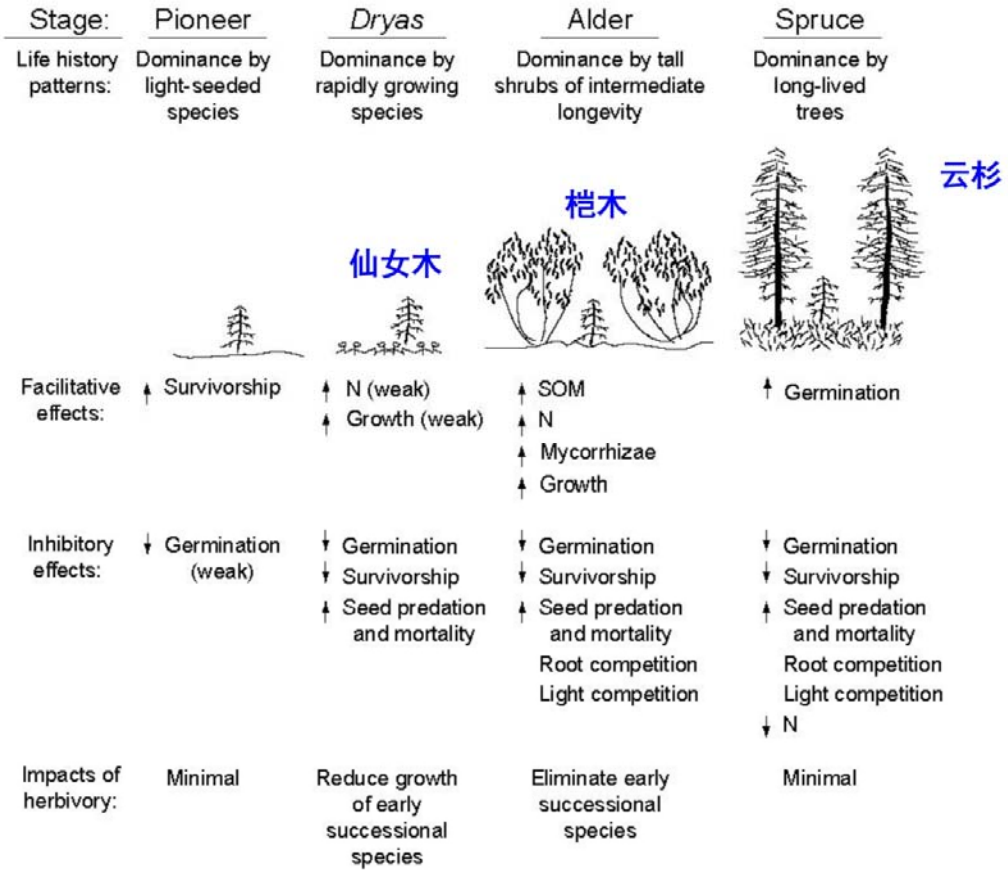


图 12.4-1 阿拉斯加冰河湾的冰川消退引起的演替变化中，生活史类型、促进作用、抑制作用以及草食行为之间的相互关系

次生演替：次生演替发生在原来有植被的地点。这些干扰移走或杀死了绝大多数地上生物，但是留下一些土壤有机质与植物或植物的繁殖体（图 12.4-2）。次生演替始于植被下发育的土壤。由于缺乏植物吸收矿化释放的养分，干扰后通常会出现养分有效性的波动。

次生演替与原生演替的不同之处在于，现存的物种很快在干扰后的生境上定殖。它们可能从经历过干扰的根或茎中重新发芽，或者从土壤种子库中发芽——产生的种子在之前的干

扰事件后在土壤中保持休眠状态，直到干扰后的条件(例如光照、较大的温度波动或高含量的土壤硝酸盐)刺激其发芽。许多森林也有物种的幼苗库(高级再生)，在林冠浓密的树荫下生长几乎是静止的，但在树木倒后形成的空地上会迅速生长。其他次生演替的定殖者从相邻地区扩散到受干扰的地点。这些物种包括风传的小型种子和动物传播的大型种子。最初的定殖植物生长迅速以开发使用干扰带来的资源。林窗相演替很少受繁殖体可用性的限制，而大型范围的干扰生境的演替轨迹可能取决于分散到该生境的物种。如果干扰是不均匀的，以致未干扰的种源在干扰区域内分布良好，那么即使是较大的干扰也可能不会受到限制。

某生境在被最初的植物定殖后，物种组成发生变化的原因在于：1.定殖者固有的生活史性状，2.促进作用，3.竞争的相互作用，4.食草动物，5.环境中的随机变化。生活史性状包括种子大小和数量、潜在生长率、最大个体大小和寿命。这些性状决定了一个物种到达一个新地方的速度，生长速度能多块，能长得多高，以及能存活多久。与演替晚期的物种相比，大多数次生演替早期物种在干扰后很快到达，通常生长迅速，相对矮小，寿命较短(图 12.4-2)。即使在演替过程中没有发生物种间的相互作用，由于到达速率、个体大小和寿命的差异，生活史性状本身也会导致物种优势从演替早期物种向演替晚期物种转移。

促进作用包括演替早期物种使得环境更有利于演替晚期物种生长的过程。在恶劣的物理环境中促进作用尤其重要，例如原生演替中，演替早期物种的固氮能力和土壤有机质的增加改善了环境，提高了其他物种幼苗定殖和生长的可能性。竞争是指使用相同限制性资源(资源竞争)或在寻找资源过程中相互伤害的两个生物或物种之间的相互作用(干扰竞争)。竞争作用和促进作用的相互作用在植物群落中都很普遍；它们在演替过程中引起物种组成变化的相对重要性可能取决于环境的严重程度。植食性动物和病原体是演替过程中植物死亡的主要原因。哺乳动物的选择性取食通常以演替早期物种为目标，从而减少与演替晚期物种的竞争，因此加快演替变化的速度。在潮间带群落中，鱼类和无脊椎动物如笠贝的捕食产生了类似的效果。昆虫在爆发期间发挥最大的影响，使具有生态重要性的植物物种减少生长或增加了其死亡率。例如，在演替的中期和晚期，当植物对水和养分的需求很高时，周期性的干旱胁迫会降低植物对昆虫的抗性并导致昆虫爆发，就像北美西部的山松甲虫爆发一样。

一般来说，生活史性状决定了物种通过演替的变化格局，而促进、竞争和食草作用决定了这种变化的速度。这些过程与其他干扰相互作用，在自然生态系统中创造了的演替多样性。

幼苗建立的机会通常会随着演替而减少。例如，在许多森林中，所有的树种都在演替早期过程中定殖下来，演替变化的优势度反映了快速生长的小型植物逐渐过渡到更高的、生长更慢的物种。在其他情况下，演替晚期的物种可能会逐渐建立起来。随着演替的进行，土壤被凋落物覆盖，形成了一个不太有利的苗床，幼苗之间对光和养分的竞争加剧。

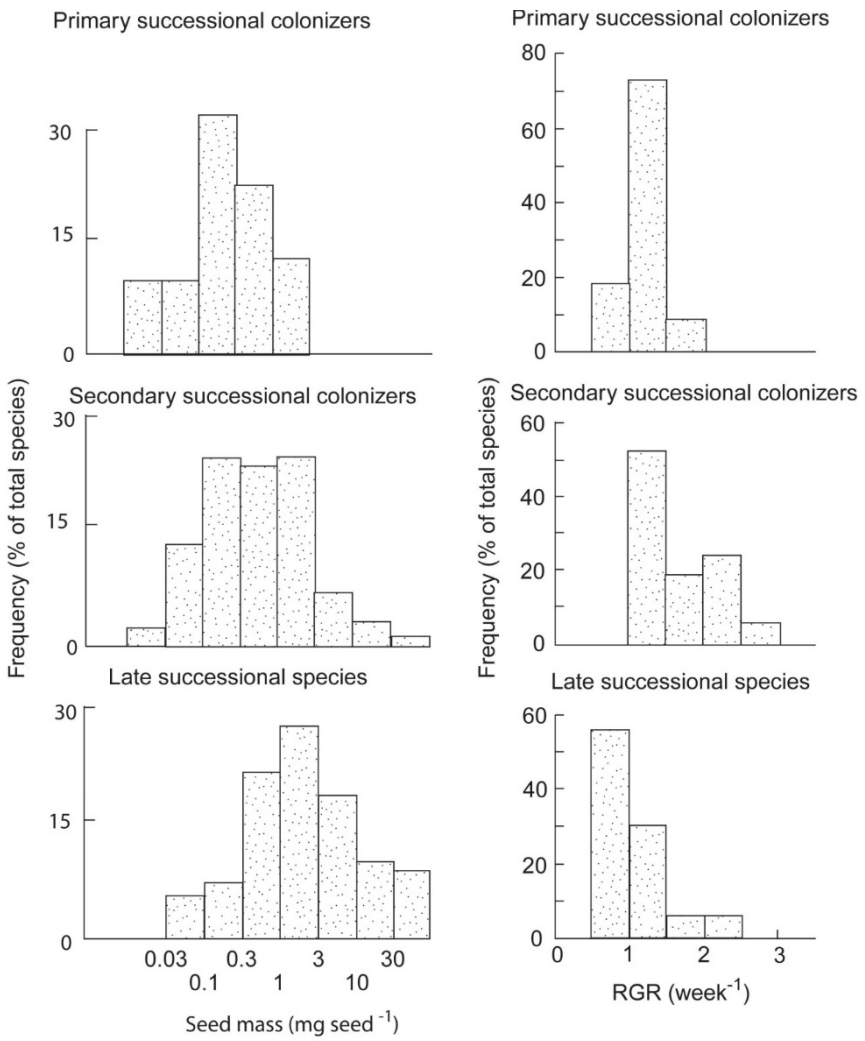


图 12.4-2 原生演替、次生演替以及演替晚期的英国生态系统中物种种子质量和相对生长速率的频度分布

4.3 水分与能量交换 (Water and Energy Exchange)

由于干扰减少了植物的生物量，所以会通过降低蒸腾作用导致径流的增加。干扰后降低的蒸腾作用导致径流增加，如图 12.4-3 所示。

通过减少蒸发增加径流来消除植物生物量的干扰。砍伐森林或过度放牧的一个最严重的后果是在低流量和洪水泛滥期间，流向溪流和河流的径流增加。这导致一些资源管理者建议将砍伐森林作为增加水产量的一种方式，以满足社会对水的需求。然而，这些排放量的增加往往是短暂的。随着植被在演替过程中重新生长，径流通常在 5 年或更短时间内下降到收获前的水平(甚至更低)。相对于收获前的植被，森林收获后径流变化的速度和格局取决于植被恢复的格局。次生演替早期的高氮有效性、高光合速率和高叶面积可导致比未受干扰的林分更高的蒸散和更低的径流。在干旱生态系统和旱季，即人类对水的需求最大的情况下，森林收获后短期内排放收益通常最小，这表明森林收获不是增加人类用水产量的有效策略。随着

根系在演替过程中的增殖，更多的水分被植物吸收，而流向地下水和溪流的水分减少。随着树冠高度和复杂性的增加，更大比例的太阳能被截留，减少了反照率，增加了可用于驱动蒸散的能量。高大复杂树冠的高表面粗糙度增加了树冠内的机械流动和在冠层之间的混合。所有这些因素都有助于蒸散量在演替过程中的快速恢复。

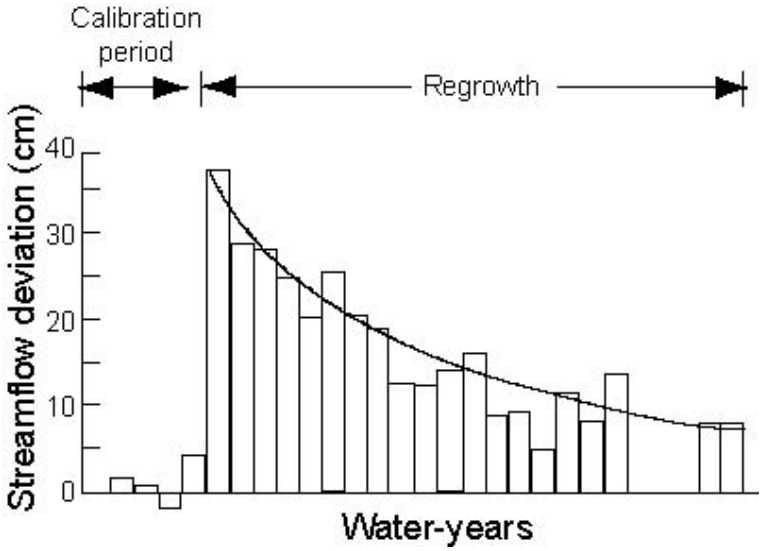


图 12.4-3 自然状态下（标准时期）和森林被砍伐后，美国东南部北卡罗来纳州森林中的一个小流域的地表径流状况。植被消失后，径流量猛增，但 20 年内又恢复到看罚钱的水平

大火干扰之后反射率增加。落叶林和针叶林有较高的反射率 (图 12.4-4)。

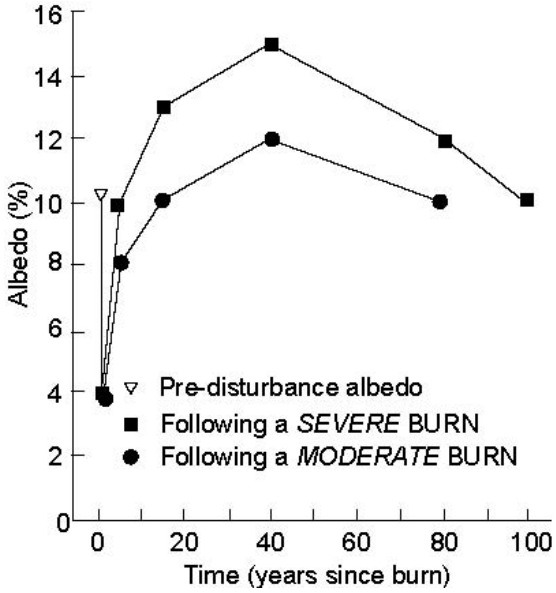


图 12.4-4 阿拉斯加北部森林遭受火灾以后，反射率的演替变化。火灾后的黑色地表造成反射率的降低。在演替的草本植物阶段和落叶林阶段，反射率逐渐增加，演替晚期变为针叶林之后又有所下降。在中度的火灾之后，因为落叶树种被针叶树种替代的速度更快，所以这一演替变化过程发生的更快

演替中期植被传递较少热量到大气中 (图 12.4-5)。

高反射率即低热吸收；较高的蒸腾作用；低热感。

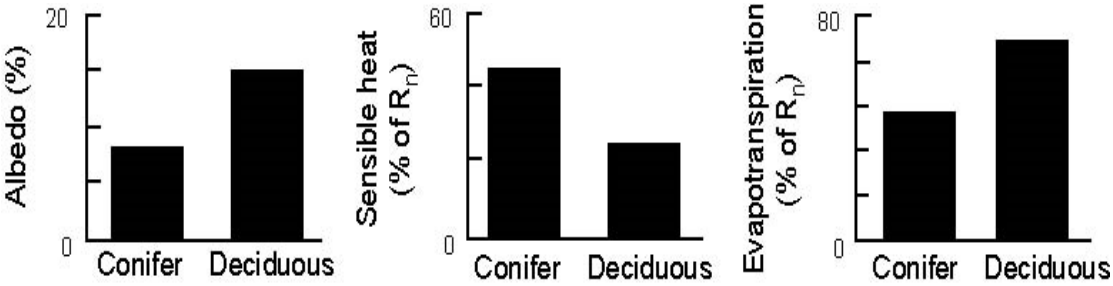


图 12.4-5 来自北方落叶林和针叶林的显热通量和潜热通量对比

4.4 碳平衡 (Carbon Balance)

原生演替中，生产力和分解速率在演替中期通常是最大的 (图 12.4-6)，然后随最大叶面积指数 LAI 逐步减少。主要特征包括降低根系水导率和营养可利用性。

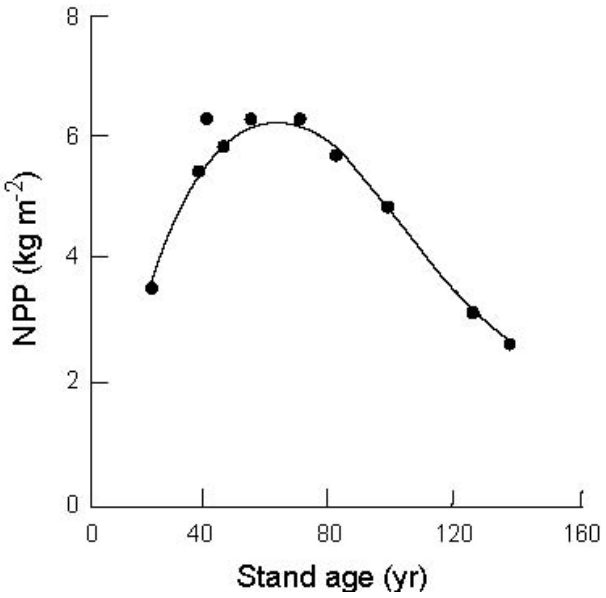


图 12.4-6 俄罗斯东部云杉地上部分生产力的演替变化。NPP 在森林年龄为 60 年时，LAI 达到最大值后开始下降。

植被碳库的常见变化格局 (图 12.4-7)。

包括：NPP 和 GPP 约一半的植物呼吸。

植物生物量在演替晚期停止生长：5 月达到峰值，之后下降。例如：阿拉斯加森林演

替过程。

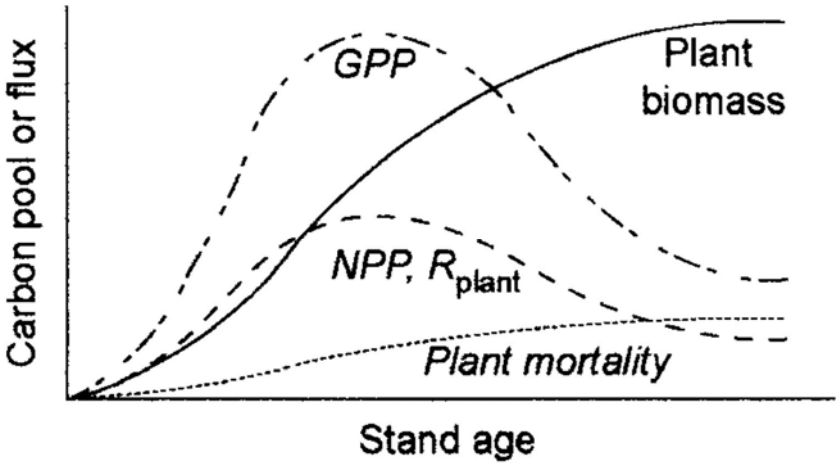


图 12.4-7 森林中植物生物量、NPP、植物呼吸 (*Rplant*),和植物死亡率的演替变化理想模式

由于土壤有机质缺乏，在原生演替开始时分解率几乎为零。土壤中的低有机质含量致使其持水力和阳离子交换能力 CEC 都很低 (图 12.4-8)。

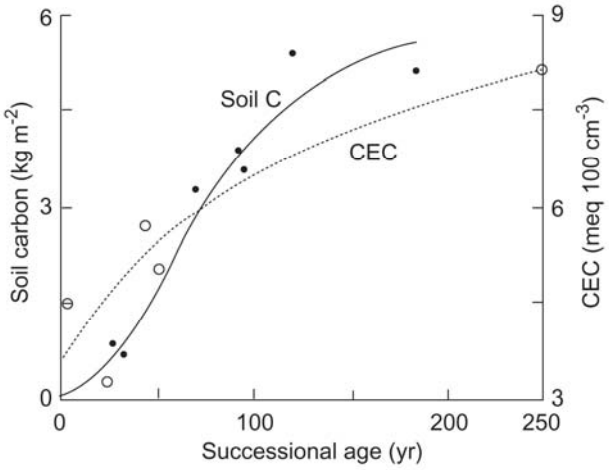


图 12.4-8 阿拉斯加冰河湾冰川消退后，土壤有机碳在演替中的积累 (Crocker and Major 1955)，以及相关的土壤矿物质阳离子交换能力 (CEC) 的变化 (Ugolini 1968)

老龄林生长能够累积土壤中的碳，例如：Zhou et al. 2006. Science 314:1417-1417。

通过演替，植物和土壤碳库增加（图 12.4-9）。干扰引起植物碳库减少，而土壤碳库或减少（比如火情干扰）或增加（比如飓风干扰）。

演替导致碳通量发生变化（图 12.4-9）。演替中期 NPP 达到最大值前，NPP 一旦超过分解作用，生态系统就会开始积累碳。演替晚期，生态系统要么达到碳平衡，要么继续以低速率积累碳，这取决于环境对 NPP 和分解的限制。NEP 表示 NPP 和分解作用达到平衡。

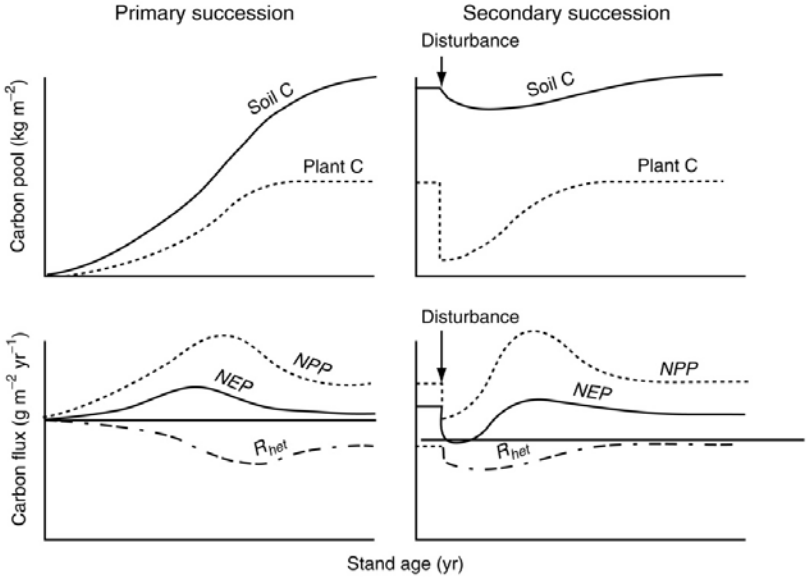


图 12.4-9 原生演替和次生演替中碳库（植物和土壤）和碳通量 (*NPP*, R_{het}, and *NEP*) 的理想模式。原生演替早期，由于 NPP 大于异养呼吸，植物和土壤的碳缓慢积累，所以生态系统净生产量（NEP）为正。次生演替早期，由于干扰后异养呼吸流失的碳超过了 NPP 的积累，土壤碳含量下降，因而 NEP 大致为零。在原生演替和次生演替中，都是演替中期时 NEP 和 NPP 达到最大。如果淋溶损失和其它碳通量作用很大，生态系统净碳积累会因显示的格局不同而不同。

4.5 养分循环 (Nutrient Cycling)

养分循环的演替变化依赖于必须元素和限制性元素在演替中期保持最大（图 12.4-10）。原生演替改变养分循环，演替过程中的养分动态既是 NPP 与分解作用之间的动态相互作用的原因，也是其结果。次生演替下的养分循环：受到自然干扰后的次生演替不同于原生演替，因为它通常含有较高的营养可利用性。可利用营养的脉冲式增加，植物生物量和摄取能力减少，使得生态系统容易流失营养。营养元素流失途径出现的可能性或流失的强度取决于氮矿化以及植物和微生物摄取之间的平衡。此外，干扰后的生态系统容易流失营养元素。营养的流失轻度通常取决于干扰时可利用营养元素的量以及再生植被摄取营养的能力。

4.6 营养级动态 (Trophic Dynamics)

在演替早期至中期，被食植动物所消耗的初级生产量的比例是最大的。在原生演替和次生演替的早期，食植动物的消耗速率可能很低，因为食物的密度较低，植被不足以为草食脊椎动物提供藏身之处，冠层也不足以为无脊椎食植动物的活动提供潮湿、不易失水的生态环境。草食性脊椎动物既可以促进演替，也可以阻碍演替的进行，这取决于它们对演替早期物种和晚期物种的相对影响。

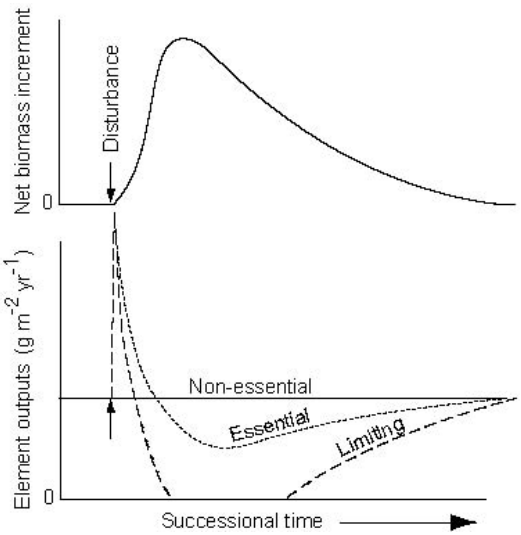


图 12.4-10 演替过程中，植被净生物量的增加以及限制性、必需和非必需元素流失的变化。在演替的早期，当生物量的年增长量很大时，生物量生产所必需的营养元素（特别是限制生长的元素）主要积累在新生植物和微生物生物量中，因此这些元素不会由于淋溶而从生态系统中流失。在演替晚期，当新生植物和微生物生物量积累所需的元素与死有机质分解所释放的元素相平衡时，生态系统的营养输入和输出基本平衡，而同植被是否对营养元素有需要无关。

第五节　生态系统过程的时间尺度推绎

5.1 时间上的外推判断需要对重要生态过程的典型时间尺度的认识

5.2 生态系统过程的绝对控制取决于时间尺度推绎

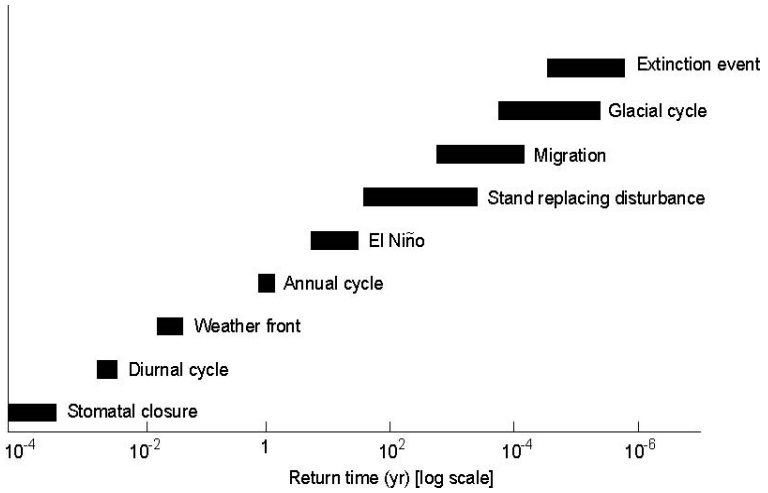


图 12.5-1 强烈影响生态系统过程的变量复原时间的变异。对于任何特定过程如 NPP，都存在可以忽略不计的快变量（如气孔关闭），强烈影响该过程的慢变量（如厄尔尼诺现象和群丛替代干扰），以及可以当做常数处理的极慢变量（如冰期循环）。

第六节　研究案例

6.1 观测和实验在长期生态学研究中的作用

6.2 为什么需要长期生态学研究

在生态学研究中，生态系统水、土、气、生要素的长期定位观测和数据积累具有极其重要的地位，也是长期生态学研究的重要手段之一。这是因为：第一、了解生态系统的变化历史是深入理解生态系统的现状和准确预测其未来变化趋势的关键。第二、生态环境问题的发生和发展通常是一个较缓慢的过程，如果没有生态系统的长期观测数据作为基准，很难去识别这些问题并找到正确的解决方案。第三、在许多生态系统中，一个偶然事件能够重新启动植被演替或者使地形地貌的的剧烈变化。例如，2008 年 1 月 3 日起发生在我国南方 20 多个省（区、市）的低温、雨雪和冰冻事件，森林受损面积 2.7 亿亩，森林生态系统的物种组成和群落演替轨迹产生了巨大影响。第四、典型生态系统的多站点长期联网观测对识别区域乃至国家尺度生态系统格局、过程和服务的变化及其人为和自然驱动因子，科学地制定生态系统管理和恢复对策，将发挥越来越重要的作用。

发达国家十分重视生态系统水、土、气、生要素的长期定位观测和联网研究，特别是在长期观测和实验样地建设，以及观测仪器和装备的自动化方面，具有引领作用。其中具有代表性的国内外野外站及样地建设包括：

英国洛桑实验站(Rothamsted Experimental Station)是世界著名的农业生态系统研究站，该站于 1843 年和 1856 年建立的 9 长期实验样地，至今已有 170 多年的长期观测数据和样品积累，为农学、土壤学、植物营养学、生态学和环境科学的发展做出了重要贡献。例如，该站 1856 年建立的牧草和草地实验，最初用以验证长期施用化肥和有机肥对牧草产量和物种组成的影响，该实验的建立比达尔文发表《物种起源》早了三年，开创了国际长期生态学实验研究之先河。基于这些实验样地 140-160 年的观测数据研究发现，传统的实验处理可能低估了土壤酸化对生物多样性的影响，减少氮素添加、控制酸化和割草处理可以使生物多样性逐步得到恢复(Silvertown et al., 2006; Storkey et al. 2015, 2016)。

Hubbard Brook 森林生态系统研究站建于 1955 年，以北方云杉和冷杉硬木林生态系统为研究对象。1964 年，该站建立了 5 个完整集水区的实验样地(whole watershed experiments)，总面积 3160 公顷，通过长期观测数据准确量化森林生态系统物质、水分和元素的输入输出及收支变化，开创了国际上基于集水区的技术和方法研究生态系统过程之先河。60 多年来，该站系统地研究了森林和水生生态系统的动态，为理解和揭示温带森林生态系统生态、水文、能量、生物地球化学过程做出了重要贡献，其研究成果多次写入教科书和美国 LTER 研究报告(Likens, 2004; Fahey et al., 2015)。

Cedar Creek 生态研究站是美国明尼苏达大学建立的野外研究站，该站是美国长期生态研究网络（LTER）的重要成员，生态学经典研究站（Nee and Lawton 1996）。从 1994 年开

始，以 David Tilman 为代表的科学家建立了多个草地生物多样性与生态系统功能(BEF)关系长期控制实验样地，研究生态系统组成、动态、功能和服务的基础过程和原理，以及它们对生物多样性丧失、氮沉降、CO2 浓度升高、气候变暖、降雨格局改变、外来种入侵的响应机制(Tilman et al. 1996, 2001, 2006; Isbell et al. 2011)。该站的研究成果有力地推动了现代生态学理论的建立和实验生态学的发展，开创了国际 BEF 实验研究之先河。

中国科学院内蒙古草原生态系统定位研究站（以下简称“内蒙草原站”）始建于 1979 年 3 月，是我国在温带草原区建立的第一个生态系统长期定位研究站。内蒙草原站的主要研究方向包括：（1）草原生态系统结构与功能、生物多样性与生态系统稳定性、全球变化等方面的生态学基础研究；（2）草原生态系统水、土、气、生等要素的长期监测和资料积累；（3）生态系统管理，特别是退化草地恢复、人工草地建设、放牧和割草地管理、生物多样性保育等方面的应用研究。内蒙草原站拥有长期野外观测样地和实验平台总面积 500 余公顷，包括站区综合观测场、辅助观测场，羊草草原、大针茅草原、退化羊草草原恢复等长期监测样地，以及放牧、养分添加、生物多样性与生态系统功能、草原火生态、降水控制、凋落物添加与移除等长期控制实验平台，以及植物和土壤样品长期保存库等研究设施。2017 年以来，建立了草原生物多样性监测和草原灌丛化监测与研究大样地，总面积 160 余公顷。长期监测样地和实验平台的建设，有力地支撑了该站的观测、研究和示范工作。建站 40 年来，内蒙站共发表各类研究论文 2400 余篇，其中在 Nature、Science、PNAS、Ecology Letters、Ecological Monographs、Ecology、Global Change Biology 等 SCI 期刊发表论文 830 余篇，出版论著 30 余部，研究成果获得国家科技进步一等奖 1 项，国家和中国科学院自然科学奖 10 项。内蒙古草原站取得的重大原创性基础研究成果包括：（1）基于近 40 年的草原生态系统水、土、气、生等要素长期监测和实验数据，揭示了内蒙古草原生物多样性与生态系统稳定性的维持机制；（2）通过长期放牧控制实验，阐明了放牧对生态系统生产力、碳氮循环、温室气体排放和草原蝗虫暴发的调控机理；（3）基于近 20 年的控制实验数据和长期监测数据，揭示了草地生态系统服务对全球变化关键驱动因子敏感性及其响应和适应机制。内蒙古站始终坚持将研究和试验示范成果服务于社会，服务于内蒙古草原的保护、建设和草地畜牧业可持续发展。2001 年以来，先后建立了沙地综合治理、退化草地恢复、天然草场合理利用、人工草地建植、生态草牧业等多个试验示范区，受到了国家和相关部门及内蒙古自治区各级政府的高度重视。取得的重要技术研发和试验示范成果包括：（1）围封休牧、延迟放牧与划区轮牧技术体系；（2）多年生混播人工草地草种配置与建植技术；（3）浑善达克沙地和沙化草地“三分之一治理，三分之二封育自然恢复”模式。这些试验示范成果为国家“京津风沙源治理工程”“退牧还草”工程、“草原生态保护奖励补助机制”提供了重要的科技支撑 (中国科学院内蒙古草原生态系统定位研究站 2017)。2001 年以来，连续三次获得中国生态系统研究网络综合评估“优秀野外站”。国务院副总理曾培炎、全国人大副委员长彭珮云、路甬祥、乌云其木格、陈竺、丁仲礼、武维华，全国政协副主席黄孟复、李兆焯、罗富和、王志珍，水利部部长汪恕诚、内蒙古自治区党委书记储波、王君，政府主席巴特，科技部副部长邓楠等先后考察和调研了内蒙站的试验示范工作，并给予了高度评价(白永飞和王扬 2017; 中国科学院内

蒙古草原生态系统定位研究站 2017)。

中国科学院于 1988 年提出并创建了中国生态系统研究网络（Chinese Ecosystem Research Network, CERN）及其标准样地。该网络是一个涵盖中国主要区域和生态系统类型，根据我国自然区划特点系统设计，集生态监测、科学研究科技示范为一体的标准化、规范化和制度化的研究网络，是世界上体量最大、功能最强、运行效率最高的国家尺度生态系统观测研究的综合网络。成为我国及世界长期生态网络建设、观测、研究和示范的引领者。生态网络积累的科学数据成为国家科技共享平台的特色数据资源，其学术理论成果在 Nature、Ecology Letters、Global Change Biology 等国际顶级学术刊物发表。为中国生态建设和农业生产做出了巨大贡献，显著推动了我国资源环境领域科技发展。

中国森林生物多样性监测网络(CForBio) 建于 2004 年，是全球森林生物多样性研究最活跃的组成部分。已经建立的大型森林监测样地 18 个, 1-5 ha 的辅助样地 50 多个, 比较好地代表了中国从寒温带到热带的地带性森林类型， 样地面积达到 538.6 ha，监测木本植物 227.9 万株，隶属于 1,737 种。截至 2017 年 2 月底, 基于 CForBio 大样地网络, 已经发表论文 370 多篇, 其中 SCI 论文 195 篇, 在国内外同行中产生了非常积极的影响。大型森林动态样地已经从建立之初以植物群落生态学研究为主发展成多学科交叉的生物多样性科学综合研究平台。良好的综合研究平台促进了物种共存机制研究的快速发展(马克平, 2017; Huang et al., 2018; Chen et al., 2019)。

6.3 哪种类型的研究需要长期观察结果

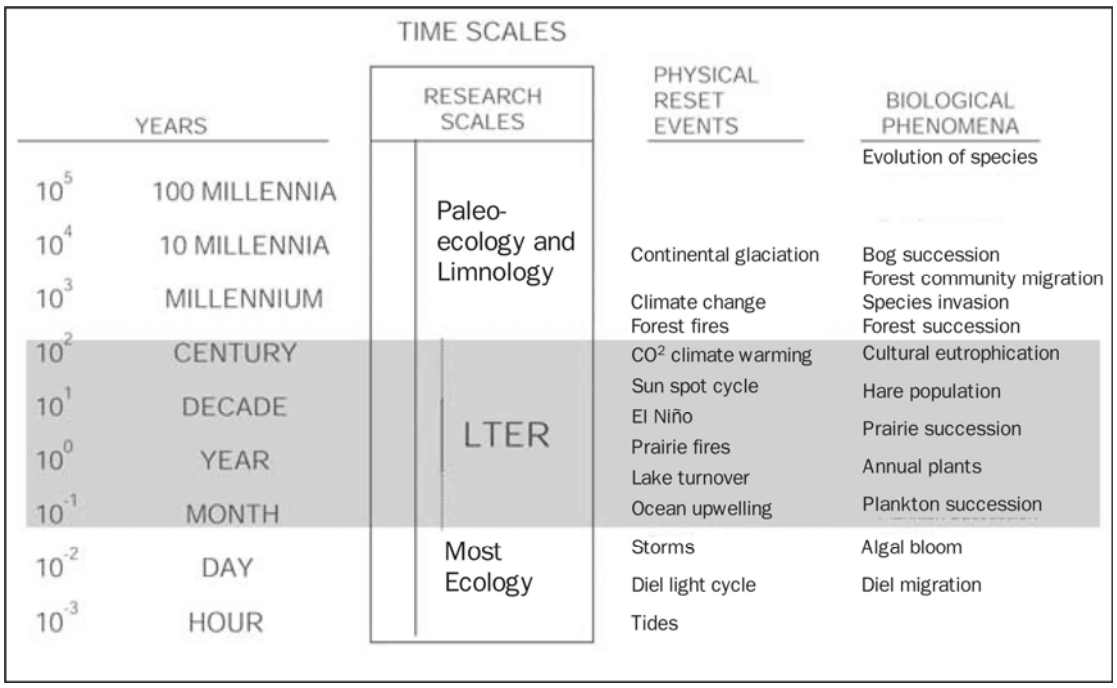


图 12.6-1 长期生态学研究的时间尺度和生态学问题

6.4 长期生态学研究的两个策略

实验性研究：即调查者针对性的改变一个或多个因子并研究其影响；这样的研究就是设计实验并实施，然后论证一个或多个解释变量和反应变量之间的因果关系。

观察性研究：不涉及任何干扰因素；调查者只观察、记录和分析结果；基于自然群落的变化观察其长期格局和生态系统过程以及相关的非生物因素；此外，有机体反应和自然系统时空变化间的相关性产生生态系统作用关系的有效信息，发生了什么？即将会发生什么？

6.5 长期生态学研究的里程碑

I. Rothamsted 长期实验

1) 引言

9 个长期田间试验开启于 1843 年和 1856 年，有一个在 1878 年时终止。最初该试验的主要目的是验证无机化合物包括 N，P，K，Na 和 Mg 元素以及有机物（家畜粪尿）对作物产量、土壤肥力和土壤酸化（通过土壤 pH 值的变化表征）影响。该试验是世界上最古老的、连续性的农业生态系统实验（图 12.6-2）。

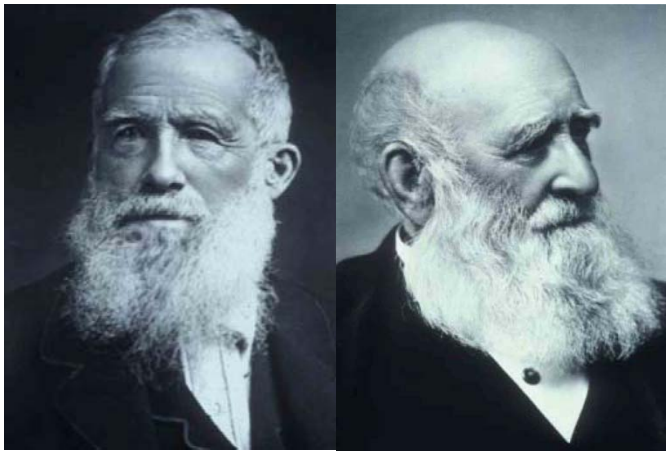


图 12.6-2 Rothamsted 长期实验之父，John Bennet Lawes（左）和 Joseph Henry Gilbert（右）

科学家简介：

Sir John Bennet Lawes 于 1814 年 12 月 28 日出生在英国哈福德郡罗桑斯塔)， 1900 年 8 月 31 日死于罗桑斯塔。英国农学家，他创立了人工肥料工业和世界上最古老的农业研究站—罗桑斯塔实验站。Sir Joseph Henry Gilbert 于 1817 年 8 月 1 日生于英国约克郡赫尔，1901 年 12 月 23 日死于赫特福德郡哈彭登；英国化学家，他最重要的贡献是研究了氮肥对作物的影响。1822 年，继承了他父亲的罗瑟姆斯特德庄园。1842 年，他在庄园里对盆栽植物和大

田作物进行了长期的粪肥试验后，他用硫酸处理磷矿产生过磷酸钙的方法获得了专利。那一年，他开了第一家化肥厂，开创了人工肥料产业。第二年，化学家 Gilbert 加入了他的行列，他们开始了长达半个多世纪的合作。两人一起研究了不同肥料对作物的影响。他们还研究了动物营养，包括不同饲料的价值和动物脂肪的来源。1867 年，英国皇家学会联合授予 Lawes and Gilbert 一枚皇家勋章。1882 年，Lawes 被尊为 baronet。七年后，他建立了 Lawes 农业信托基金，确保了罗瑟姆斯实验的继续进行。

2) 牧草和草地实验

1856 年建立，占地 2.8 公顷——早于达尔文发表《物种起源》3 年。该实验最初的目的是验证化肥和堆肥对牧草产量、物种组成和多样性的影响。最终验证了所有处理对植物学组成的实验小区的影响（图 12.6-3）。

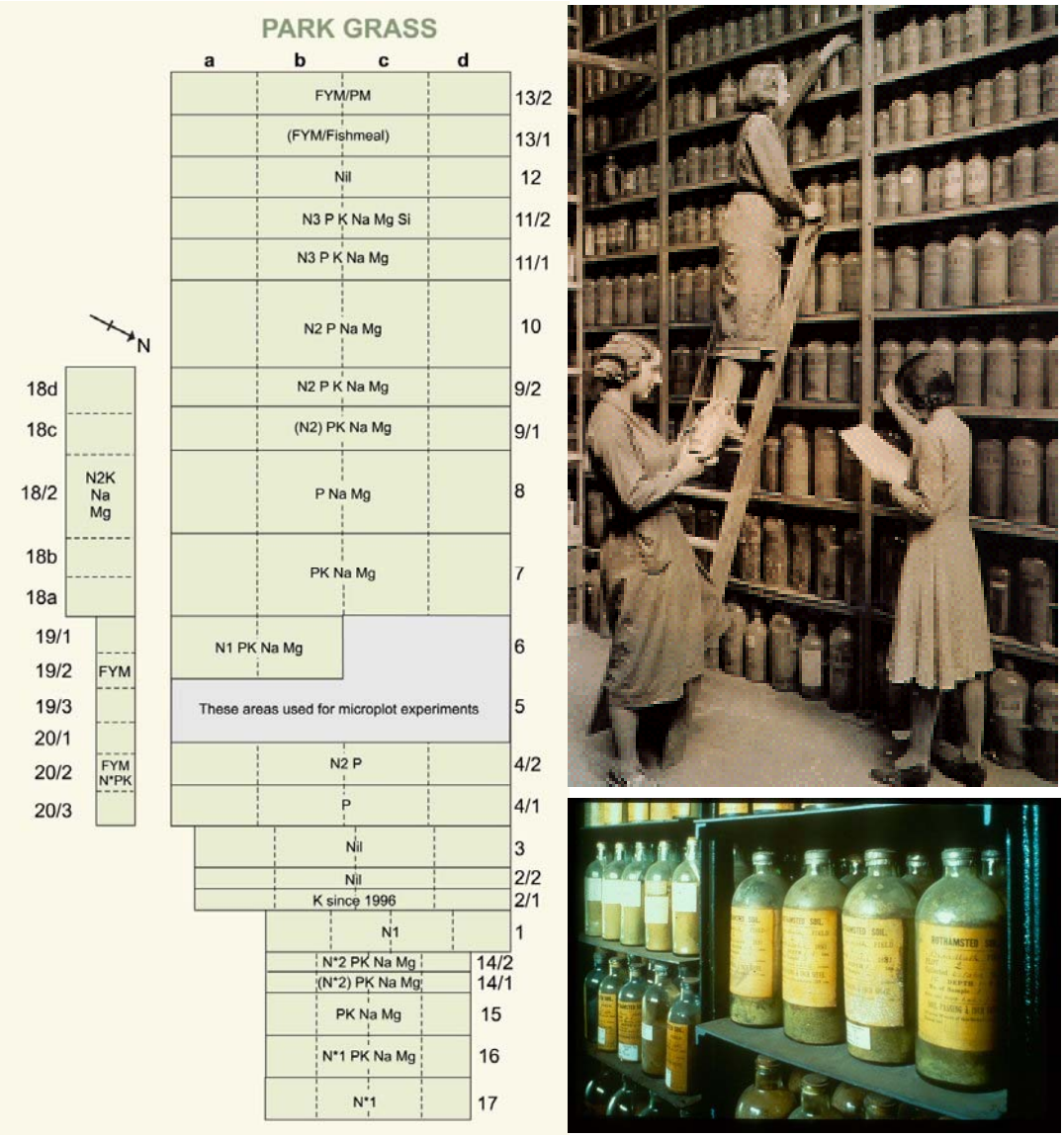


图 12.6-3 园区牧草试验 (Silvertown et al. 2006)

3) 牧草和草地试验的主要发现

（1）样地保护实验可能低估了长期变化对物种多样性的影响，比如土壤酸化；（2）物种丰富度、和生物量的变化与 pH 值得变化是相关的；（3）物种间竞争使得气候变化对群落的影响更加显著；(4)提供了首个有关不同选择压力下进化改变微生物群落组成的证据；(5）土壤和干草样品已用于追溯大气变化历史，包括核辐射事件。

II. Hubbard Brook 生态系统研究

1) 引言

Hubbard Brook 森林实验 (HBEF) 由美国农业部（USDA）森林服务机构于 1955 年建立，主要是北方云杉。

1964 年，F. H. Bormann 和 G. E. Likens 提出了在试验水域测定流水中多种物质的含量。共进行了 5 个全水域实验，面积覆盖 3160 公顷（图 12.6-4）。这些实验开创了基于小流域即集水区技术研究生态系统过程的先河。

基于某森林的水文、生物学、地理学、化学数据和与它相关的水生生态系统，样地研究进行了一些最广最长时间的连续数据积累（图 12.6-5）。

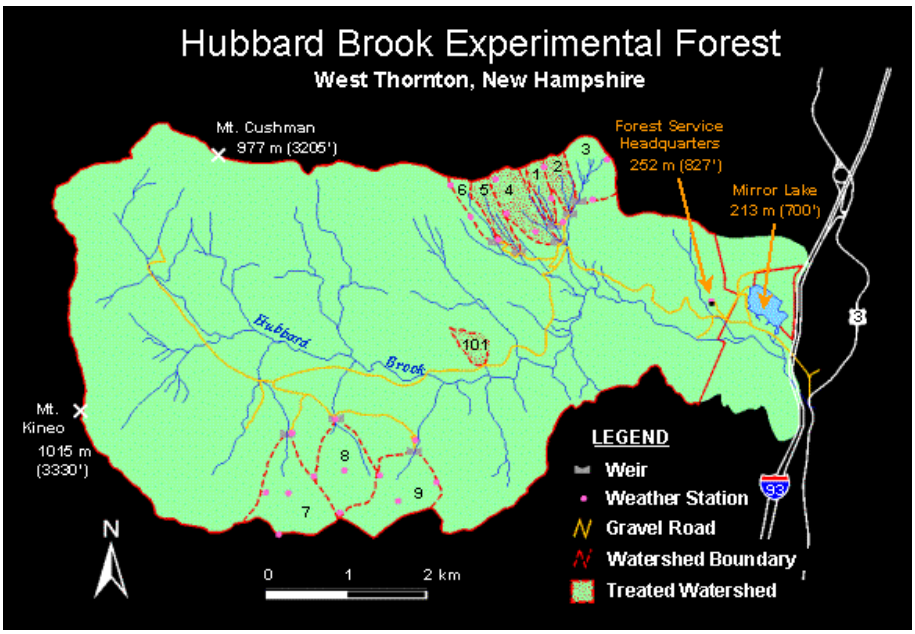


图 12.6-4 实验地分布图

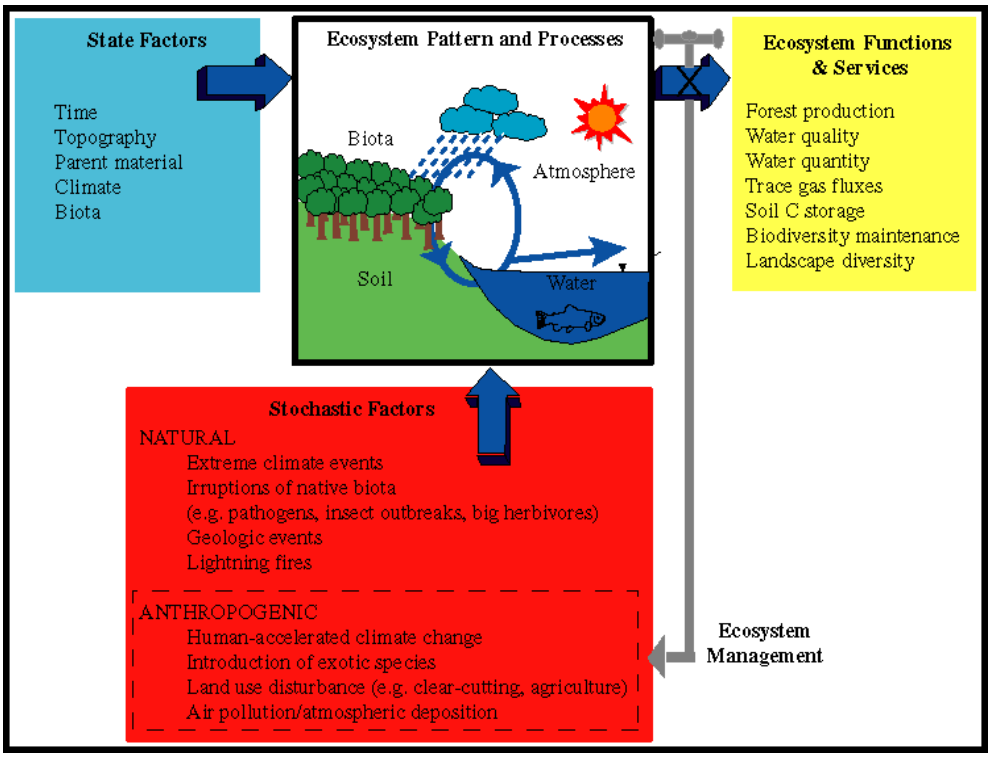


图 12.6-5 研究框架

2) 在 Hubbard Brook 生态系统研究过程中发表的论文统计 (图 12.6-6)

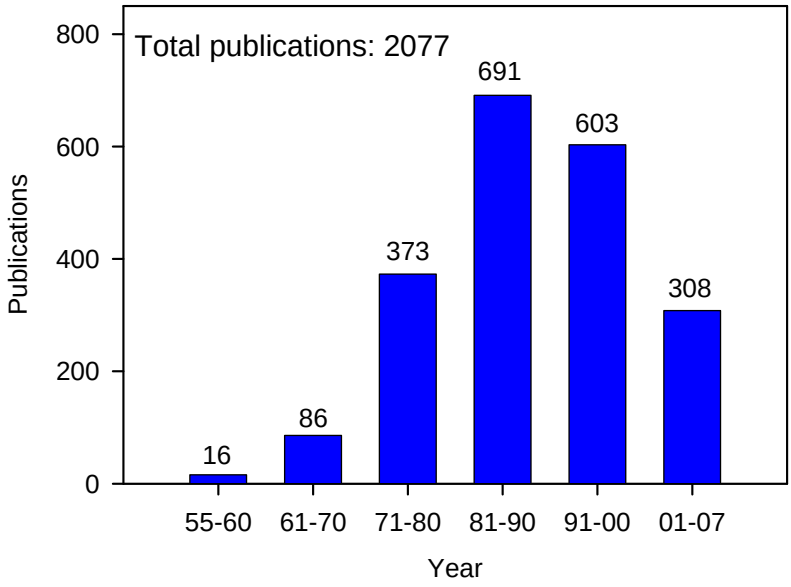


图 12.6-6 不同阶段论文发表情况

III. 生产力，生物多样性和生态系统功能——明尼苏达大学，锡达克里克

试验开始于 1994 年，该项目得到了美国 NSF 的长期资助，共发表相关研究论文近 200 篇，其中在 Science，Nature 和 PNAS 上发表论文 50 余篇，在国际上产生了重要的影响（图 12.6-7）。

图 12.6-7 明尼苏达野外实验

1) 代表性成果

生物多样性和生态系统属性（Tilman et al. Science 278:1866-1869）。

基于长期草地实验的生物多样性和生态系统稳定性研究（Tilman, D., P. B. Reich, and J. M. H. Knops. Nature 441:629-632）。

北美大草原上长时间的低氮沉降对物种损失的影响（Clark, C. M., and D. Tilman. Nature 451:712-715）。

Ⅳ. 放牧对草地生产力、生物多样性和生态系统功能的影响

实验开始于 2005 年，维持至今，覆盖面积约 160 公顷，位于中国科学院内蒙古锡林郭勒盟草原生态系体统定位研究站。该项目得到了德国 DFG、DAAG 和中国科学院国家基金委 NCFC 的资助，目前为止发表相关研究论文近 200 篇，在国际上产生了重要的影响（如表 12.6-1）。

表12.6-1 与放牧作用和气候变化相关的系统结构和动态分析成果

Structures and dynamics	Years	Method	Reference
Soil and Greenhouse gas fluxes			
Aggregate stability	2004, 2007	Ultrasound loading frame	Steffens et al., 2009b, Reszkowska et al., 2011b, Wiesmeier et al., 2012b
Ah-horizon thickness	2004, 2008	Soil auger	Steffens et al., 2009a, Wiesmeier et al., 2009
Air- and hydraulic conductivity, Pre-compression stress, Shear strength, Water repellency	2004 −2008	Oedometer, Infiltrometer, Glass pipette, Vane tester	Zhao et al., 2007, Kruemmelbein et al., 2008, 2009, Reszkowska et al., 2011b, c
Element contents and stocks (SOC, C_t, N_t, S_t)	2004, 2008	Dry combustion	Steffens et al., 2008, 2009a, b, 2011, Wiesmeier et al., 2009, 2012a
Gas fluxes (N_2O, NO_X, CH_4, CO_2)	2004 −2009	Chamber-gas chromatography systems	Holst et al., 2007a, b, Wolf et al., 2010, 2011, Chen et al., 2010, 2011b
N and SOC mineralization	2004,2008	Incubation experiments	Koelbl et al., 2011, Wiesmeier et al., 2012b, Wu et al., 2012
pH	2004	$CaCl_2$ solution	Steffens et al., 2008
Plant available inorganic N	2004 −2006	Ion-exchange resin, Soil extractions	Giese et al., 2011
Soil heat flux	2004 −2010	Ceramic pressure plate assembly, Simulation	Zhao et al., 2010, Gan et al., 2012b
Soil pores (volume, size distribution)	2004 −2005, 2007 −2009	Simulation	Kruemmelbein et al., 2009, Zhao et al., 2010, Reszkowska et al., 2011b, Gan et al., 2012a
Soil temperature	2005 −2009	Platinum ground Temperature probes	Gan et al., 2012a,b
Soil texture, Bulk density	2004, 2008	Steel cylinders, Sieving, pipette, Sedigraph	Zhao et al., 2007, Steffens et al., 2008, 2009a, Wiesmeier et al., 2012a
Soil water (budgets, content, drop penetration, hydr. conductivity, plant available, retention, spatio-temporal dynamic)	2004 −2010	HH2 Moisture Meter, Theta-probes, TDR, Simulation (e.g. SHAW model, HYDRUS-1D)	Zhao et al., 2007, 2010, 2011b, Schneider et al., 2008, 2011, Kruemmelbein et al., 2009, Gan et al., 2012a,b, 2013, Wang et al., 2012,
Wind erosion, Dust deposition	2004 −2006, 2011	Dust samplers, ^{137}Cs Tracer, Kite,	Hoffmann et al., 2008a,b,c, Funk et al., 2012, Reiche et al., 2015
Plants			
Aboveground biomass -production, Dry matter yield, Litter accumulation	2004 −2010	Destructive samplings	Schiborra et al., 2009, Brueck et al., 2010, Schoenbach et al., 2011, Fanselow et al., 2011, Li et al., 2011, Wiesmeier et al., 2012a, Gao et al., 2013, Ren et al., 2016
Belowground biomass -production, Live root biomass, Root turnover	2004 −2006	In-growth core, soil coring	Gao et al., 2008, Schiborra et al., 2009, Brueck et al., 2010, Li et al., 2011, Zhao et al., 2011b
Decomposition root/shoot	2004 −2006	Litter bags	Giese et al., 2009
Heights of standing community, Plant density	2004 −2007	Calculated, Visual estimation	Hoffmann et al., 2008c, Gao et al., 2009, Fan et al., 2009, Schoenbach et al., 2011
Herbage (mass, accumulation, production)	2005 −2010	Destructive samplings	Glindemann et al., 2009, Schoenbach et al., 2009, 2012a, Dickhoefer et al., 2014, Müller et al., 2014
Leaf area index	2004 −2008	Leaf-area meter (LI-COR)	Fan et al., 2009, Brueck et al., 2010, Zhao et al., 2010, Wiesmeier et al., 2012a
Plant species, richness and composition	2008 −2009	Destructive samplings	Liu et al., 2011, Wan et al., 2011, Ren et al., 2012
Nitrogen-/Rain use-/Water use- Transpiration-efficiencies	2004 −2006	Simulation	Brueck et al., 2010, Gong et al., 2011, Gao et al., 2013
Root length density	2004, 2007	Line intersection	Gan et al., 2012a
Tillers ratio and density	2007	Destructive samplings	Wan et al., 2011
Livestock			
Acid and Neutral detergent fiber, Crude protein, Lignin concentrations, Metabolisable energy	2005 −2010	Destructive samplings	Glindemann et al., 2009, Schoenbach et al., 2009, 2012a, Müller et al., 2012, Bösing et al., 2014, Dickhoefer et al., 2014, Ren et al., 2016
Herbage allowance, Live weight gain		Destructive samplings, Height plate meter, Animal weighing	Lin et al., 2012, Schoenbach et al., 2012a, Dickhoefer et al., 2014, Müller et al., 2014
Intake and digestibility of organic matter		Faecal collection, External marker application	Glindemann et al., 2009, Fanselow et al., 2011, Dickhoefer et al., 2014, Müller et al., 2014
Cross disciplines			
C footprint and GHG balance	2005 −2008	Review, calculations	Schoenbach et al., 2012b
N balance and cycling	2004 −2009		Giese et al., 2013

注：引自Hoffman, Journal of Arid Environment, 2016

1) 实验设计

实验地覆盖面积 158 公顷，随机区组设置，平地和坡地两种地形区块，每个区块中随机分布 7 个放牧强度处理和 2 个系统处理。放牧强度由单位面积的载畜量区分，从围封不放牧到 9 只羊每公顷，1.5 只羊每公顷递增，共 7 个梯度；放牧系统分为连续放牧系统和混合放牧系统，连续放牧系统每年生长季 6 月-9 月持续放牧，混合放牧系统进行放牧和刈割的年际间变换，图 12.6-8 表示实验地的小区布设。

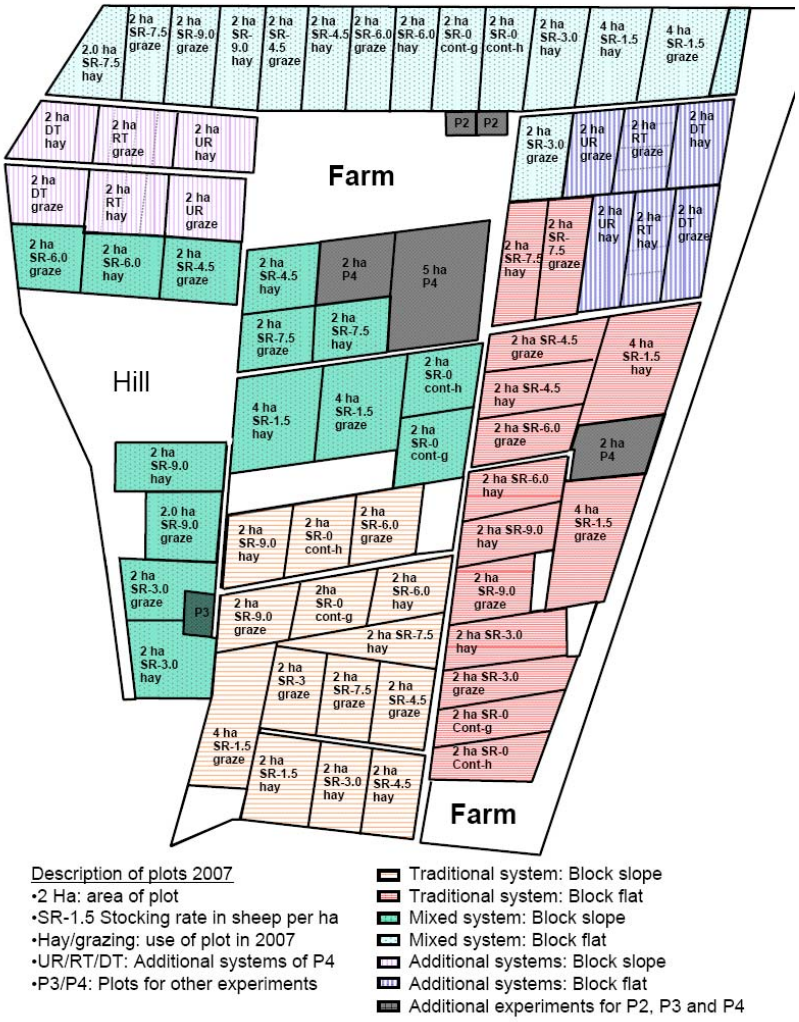


图 12.6-8 实验地小区布设图

2) 最新研究成果

放牧作用直接影响草地生态系统的多功能性，而非通过间接影响植物或微生物群落组成。因草地生态系统的各个功能对放牧压力的感应程度不同，合理的放牧强度应是能够保持草地多功能性的最大化而非单个功能的提高（比如生产力）（图 12.6-9）

除放牧强度外，不同放牧系统（连续放牧系统 vs 刈割/放牧交替系统）对本土优势功能群相互作用和生态系统稳定性的影响不同，结果表明系统生产力稳定性短期内没有随物种丰富度减少和降低，而是因优势功能群之间的补偿作用和竞争平衡保持相对稳定，如图 12.6-10。增强的放牧强度减弱了物种多样性的时间稳定效应，强调了在最大化草地稳定性时，优势功能群生产力优于物种丰富度的作用。

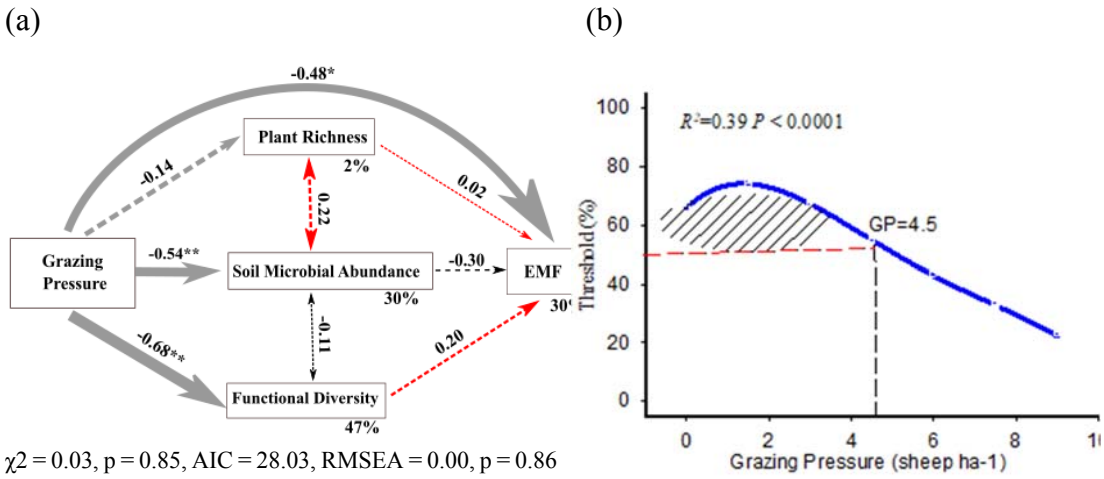


图 12.6-9. (a) 结构方程模型构建放牧强度、物种丰富度、微生物丰度、植物功能多样性与生态系统多功能性（EMF）的作用关系 (b)放牧强度对生态系统多功能性阈值的影响

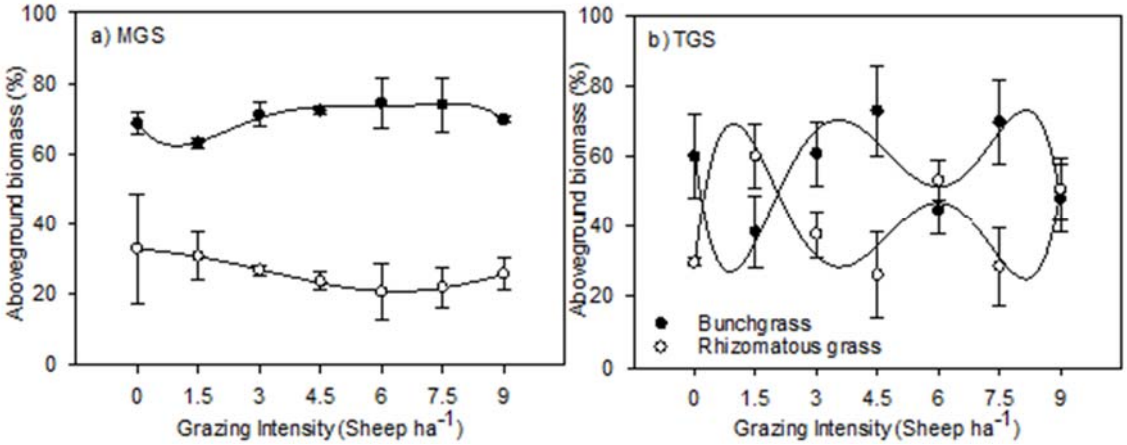


图 12.6-10.优势功能群根茎型禾草和丛生型禾草相对生物量在混合放牧系统 MGS 和连续放牧系统 TGS 中随放牧强度的变化

本章小结

生态系统过程在不断地调整以适应过去发生在所有时间尺度上的变化，从持续几毫秒的阳光照射到持续数百万年的土壤发育。缓慢发生的生态系统过程（如土壤有机质的形成）受过去事件的影响最大。生态系统过程对可预测的环境变化（如日变化和季节性变化）具有很强的弹性。

由于干扰是所有生态系统的一个自然组成部分，因此干扰后生态系统过程的演替变化对于理解生态系统动力学的区域格局具有重要意义。生态系统的演替变化对干扰的严重性、频率和类型特别敏感。通过原生演替，碳在植被和土壤中积累，由于分解变化滞后于NPP的变

化，导致正的NEP。森林中的NPP往往在演替的中期最大。次级演替开始时NPP较低，分解迅速，负NEP较大，但中晚期演替碳循环模式与初级演替相似。

随着氮素固定以及向生态系统中添加氮，养分循环通过早期原生演替发生变化。其他元素的循环与氮的循环成比例。然而，在次生演替中，氮通常在演替早期的有效性最高。在这个时候氮和其他元素很容易流失，直到植物和微生物吸收养分的潜力超过净矿化的速度。在演替中期，当营养矿化速率限制了植被的吸收速率时，生态系统内的循环最为强烈。

在不同的生态系统类型和不同的演替阶段，草食动物在演替过程中发挥的作用是不同的。哺乳动物往往通过消除或降低演替早期物种的竞争能力来加速森林的早期演替变化。然而，在草原上食草动物阻止了木本物种的建立，否则草原就会变成灌木和森林。有些昆虫在演替后期具有最大的影响，特别是在森林中，它们可能是导致死亡的重要因素。

推荐阅读文献：

Bormann, F. H., and Likens, G. E. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York.

CaraDonna, P. J., Burkle, L. A., Schwarz, B., Resasco, J., Knight, T. M., et al. 2020. Seeing through the static: the temporal dimension of plant-animal mutualistic interactions. Ecology Letters. doi: 10.1111/ele.13623.

Chapin, F. S. III, Walker, L. R., Fastie C. L., and Sharman L. C. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs 64:149-175.

Colom, P., Traveset, A., Carreras, D., and Stefanescu, C. 2020. Spatio-temporal responses of butterflies to global warming on a Mediterranean island over two decades. Ecological Entomology. doi: 10.1111/een.12958.

Connell, J. H., and Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119-1114.

Crocker, R. L., and Major, J. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. Journal of Ecology 43:427-448.

Fastie C. L. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. Ecology 76:1899–1916.

Fukami T., and Wardle D. A. 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. Proceedings of the Royal Society B-Biological Sciences 272:2105-2115.

Merila, J., and Hendry, A. P. 2014. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evolutionary Applications 7:1-14.

Parmesan, C., and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., et al. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. BioScience 58:501–517.

Sterenczak, K., Mielcarek, M., Modzelewska, A., Kraszewski, B., Fassnacht, F. E. et al. 2019. Intra-annual Ips typographus outbreak monitoring using a multi-temporal GIS analysis based on hyperspectral and ALS data in the Bialowieza Forests. Forest Ecology and Management 442:105-116

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833-2849.

Vitousek, P. 2004. Nutrient Cycling and Limitation: Hawai'i as a Model System. Princeton University Press, Oxford.

第十三章 景观异质性与生态系统动态

第一节　景观异质性的概念

1.1 空间格局和异质性的重要性

空间异质性是指某种生态学变量在空间分布上的不均匀性及复杂程度。生态系统间的空间异质性对于单个生态系统和整个区域的功能都是至关重要的。在一个区域中，生态系统的空间格局也影响生态系统过程。例如，旱地农业系统和河流之间的河岸生态系统可能更有利于硝酸盐和其他污染物进入河流。在较精细的尺度上，干旱生态系统中养分循环和有机质的积累在下层比灌木之间发生得更快。生态系统被其他类型的小块分割成更小的单元，影响着动物的丰富度和多样性。生态系统中所有的过程和机制都具有重要的空间维度。空间格局对各个尺度的生态学过程都会起到关键控制作用。其中一些景观斑块有较快的变化速率，被称为生物地球化学循环的热点地区。不同斑块间的相互作用受到斑块大小、形状和分布的影响。

人类土地利用变化使世界各地的景观支离破碎，往往改变了平衡，使管理过的小块土地成为广泛存在的基质，其中较少管理的小块土地继续存在。这些碎片的边缘与面积之比的增加改变了整个斑块的物理环境，而斑块之间连通性的丧失降低了它们支持许多物种的能力。随着全球对粮食需求的增加，我们如何管理景观以满足这些需求并维持景观中自然斑块的功能？不同管理强度的土地的可持续比例是多少？如果超过这个比例会发生什么？什么样的自然景观和管理才能最好地满足自然和社会的需要？

1.2 景观和景观异质性的概念

景观的概念一直在不断的发展。Forman & Godron (1986)将景观定义为：由不同类型生态系统所组成的、具有重复性格局的异质性地理单元（通常在几十千米至几百千米的范围内）。Naveh (1987)将景观定义为：景观包括物理、生态和地理单元，结合了所有自然和人为形成的格局和过程。Urban et al. (1987)将景观定义为：斑块的镶嵌，格局的组成部分。而广义上景观的定义是指不同生态学属性的斑块组成的镶嵌单元。

景观生态学的定义也在不断完善。景观生态学研究景观的结构、功能和变化 (Forman 1981)。景观生态学强调空间格局和生态过程之间的相互关系，即，不同尺度下产生空间异质性的原因及其结果(Turner et al. 2001)。景观生态学是研究和改善空间格局与生态和社会经济过程相互关系的整合性交叉学科。 (Wu and Hobbs 2007)。

景观结构单元包含斑块、廊道和基底。其中，斑块泛指与周围环境在外貌或性质上不同，并具有一定内部均质性的空间单元 (Forman 1995)。廊道是指景观中与相邻两边环境不同的线性或带状结构。基底是指景观中分布最广、连续性最大的背景结构。

1.3 格局和过程

格局和过程是景观生态学中的重要概念。其中，格局通常是指景观组成单元的类型、数目以及空间分布与配置。例如，不同类型的斑块可在空间上呈随机型、均匀型或聚集型分布。与格局不同，过程强调事件或现象的发生、发展的动态特征。但是，格局和过程具有尺度依赖性。在相似的尺度上，格局和过程可能相互作用和相互依赖。

1.4 尺度

尺度是指某一研究某一物体或现象时采用的空间或时间单位，往往以粒度和幅度来表达（图 13.1-1）。空间粒度指景观中最小可辨识单元所代表的特征长度、面积或体积。比如，栅格数据中的一个像素。时间粒度指某一现象或事件发生的频率或时间间隔。通过所识别斑块的大小能够决定粗糙度（例如，细粒度景观包含很多小斑块，而粗粒度景观包含很多大斑块）。

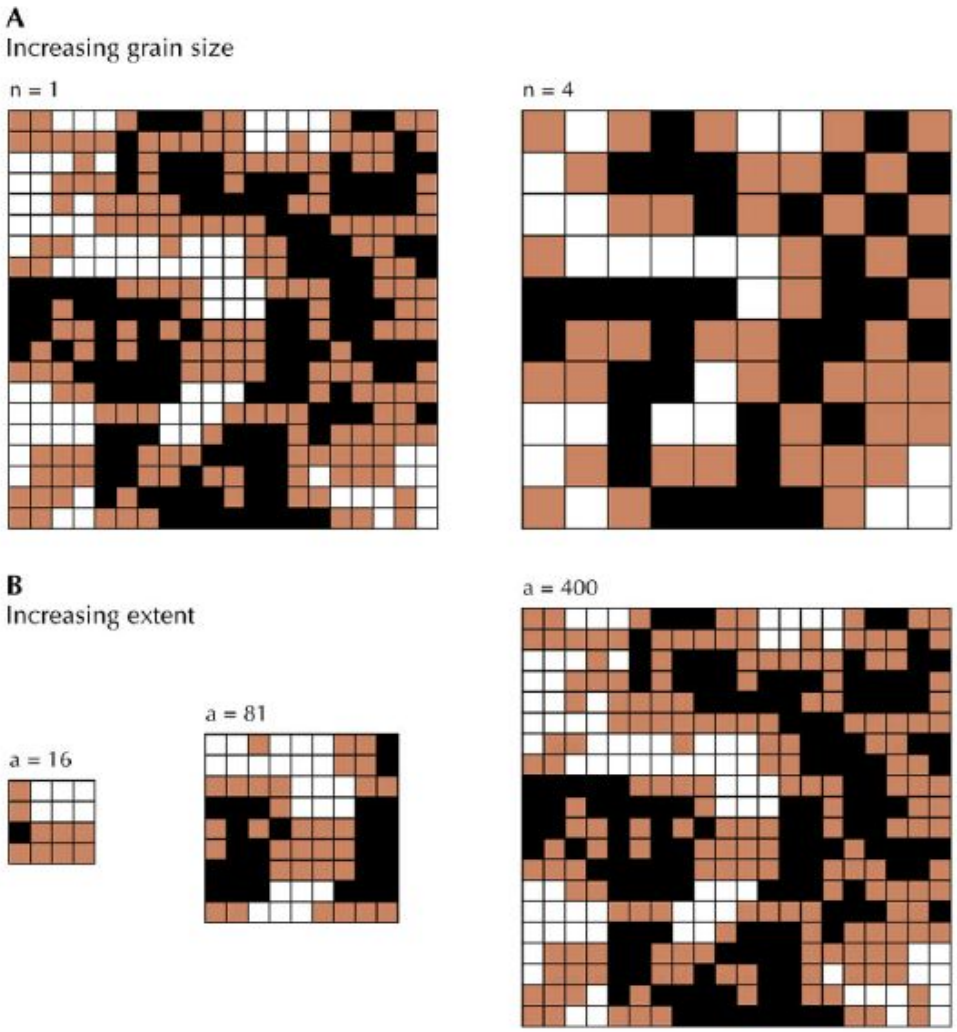


图 13.1-1 格局、粒度和空间范围之间的关系

幅度：指研究对象在空间或时间上的持续范围或长度。具体而言，所研究区域的总面积决定该研究的空间幅度，而研究项目持续多久，则确定其时间幅度。

邬建国 教授

科学家简介：

邬建国，《景观生态学》主编，亚利桑那州立大学生命科学学院和可持续发展学院院长特聘教授。他的研究领域包括: 景观生态学、城市生态学和可持续发展科学。他发表 295 篇学术论文和 14 本专著。自 2005 年以来，他一直担任《景观生态学》杂志的主编。他也是内蒙古大学中美节能、能源与可持续发展科学中心（2007-）和北京师范大学人类环境系统可持续发展中心（2012-）的创始主任。

代表性论文及论著：

- Wu, J. G. and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology 70:439-466.
- Wu, J. G. and R. Hobbs. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecology 17:355-365.
- Wu, J. G., K. B. Jones, H. B. Li, and O. L. Loucks. 2006. *Scaling and Uncertainty Analysis in Ecology*. Springer, Dordrecht, The Netherlands.
- Wu, J. G. and R. J. Hobbs. 2007. *Key Topics in Landscape Ecology*. Cambridge University Press, Cambridge.

第二节　空间异质性的起因

2.1 空间异质性的调查与分析

景观异质性源于环境变异，种群和群落过程，以及干扰。状态因子（如地形和母质）的空间变异和交互控制（如干扰和优势物种）决定了生态系统空间变异的自然基质(Holling 1992)。人类活动是引起生态系统空间异质性变化的一个重要原因。

异质景观的结构和某些功能可以通过遥感进行测定。许多有趣的空间异质性并不是发生在从地面单一点观察到的空间尺度上。遥感提供了一套技术—从低技术水平的航空观测和摄影到重复的卫星图像—使我们能够同时看到整个大区域的生态系统。遥感方面最近的发展改变了我们分析生态系统异质性的能力。例如，集成的机载激光雷达（光探测和测距，用于测量地形，树冠高度和植被结构），利用高空间分辨率光谱法可以对植物结构和化学的空间变化进行高分辨率的测量，在数千公顷的范围内几乎同时进行（Asner et al. 2007）。当应用于陆地生态系统时，该方法可用于直接检测、绘制和分析生态系统结构和功能方面的空间异质性。这种方法也可以用于理解生物地球化学热点的分布、动态和后果，例如非洲大草原上的白蚁土堆和夏威夷热带雨林中的固氮入侵生物。

2.2 状态因子和交互控制

气候梯度，例如温度和降雨量在不同区域是不同的。它们决定了区域尺度上的净初级生产力、土壤有机质等。地理阻隔，可以形成截然不同的斑块类型。地形格局，则决定了较小尺度上的斑块变异。

非生物特征和相关生物过程的差异解释了景观变化的基本基质。温度、降水、母体物质和地形在地球表面各不相同。其中一些状态因素，如岩石类型，显示出尖锐的边界，因此可以划分成不同的斑块。其他变量，包括气候变量，变化更连续并在生态系统结构和功能上产生梯度，由这些底层梯度控制的过程之间的反馈放大常常会在生态系统结构和功能上产生明显的边界。对这些景观等级和梯度的分析表明，不同的因素在不同的空间尺度上控制着空间格局。例如，草原植被、净初级生产（NPP）、土壤有机质、凋落物质量和养分有效性的区域尺度模式与降水和温度的区域梯度有关(Burke et al. 1989)。相比之下，地形、土壤质地和土地利用历史解释了几公里范围内的大多数变化。夏威夷群岛热带森林相关方面生态系统过程和广泛的海拔在很大程度上受气候的控制，而当地的气候变化又影响着母质的类型和年龄。由此产生的土壤差异导致氮循环、磷循环和氧化亚氮排放的差异一致。这些比较研究为根据非生物因子的基本空间矩阵将生态系统过程外推到区域尺度提供了基础。

2.3 群落过程和历史遗留效应

建立者效应，影响生态系统过程的物种。能够反映种群定居的随机格局。生态系统过程不仅依赖于当前环境，也会受到历史上的土地利用格局的影响。

历史遗留效应、随机散布事件和其他群落过程可以改变环境和物种分布之间的潜在关系。生态系统过程不仅取决于当前的环境，而且还取决于过去的事件，这些事件会影响一个地点的物种。例如，在黄石国家公园，火灾严重程度的景观变化和球果（种子保留在球果中的程度）导致美国海滩松火烧后补苗的范围在 0- > 500,000 stems ha^{-1} 之间，这反过来强烈影响了火后生产力和养分循环。在干旱和半干旱生态系统中，土壤过程受到单个植物存在或缺失的强烈影响，导致植物冠层下的“资源岛”。物种在一个景观上的分布是物种的生境需要、历史遗留效应和随机事件的综合结果。一旦这些模式建立起来，如果物种效应很强，它们可以持续很长一段时间。例如，几千年前在密歇根发展起来的铁杉和糖枫树的精细分布得以维持，因为每一种树都能产生有利于其自身持久性的土壤条件。

2.4 干扰

干扰能够形成不同年龄的斑块。一些干扰是非常巨大的或者不常见的，会改变生态系统的结构与过程。例如，火烧是一种自然干扰。人类的活动，比如耕地和修路。改变了自然格局的异质性和斑块动态。自然干扰在生态系统中是普遍存在的，并在许多尺度上产生空间模式。景观斑块动力学反应了扰动和扰动后演替的循环(Turner 2010)。

2.5 动态镶嵌体稳定状态

在相对稳定的条件下，这产生了一个动态稳定状态镶嵌体，其中景观中任何一点的植被总是在变化，但是在足够大的平均面积上，景观在每个演变期的比例保持相对恒定。虽然景观的每个点可能处于不同的演变期，但景观作为一个整体可能接近稳定状态。动态稳定状态镶嵌体产生于（1）在环境均匀的地区，扰动是景观变异性的主要来源；（2）当扰动相对于景观的大小较小时；（3）当恢复速率与扰动的返回时间相似时。当扰动很小以及恢复迅速时，大部分景观将处于演替中后期阶段。例如，在哥斯达黎加的原始热带雨林中，经常发生树木周期性倒掉导致树木的最大年龄只有 80-140 岁。间隙期扰动有助于维持森林的生产力和养分动态。光照和养分利用率增加了林窗，为那些对资源需求较高的物种提供了快速生长的资源，并在森林镶嵌体中维持自己的生存。草原和灌木地动物的干扰也可以产生一个动态的稳定镶嵌体。例如，地鼠会扰乱加利福尼亚草原，造成草原每 3-5 年翻耕一次。

2.6 非稳定状态镶嵌 (Non-steady-state mosaics)

一些干扰非常巨大或者少见，导致生态系统结构和功能改变，造成某一类型斑块的扩张，形成了非稳定状态的嵌合体。例如，在 1989 年波多黎的雨果飓风之后，飓风路径上的大多数树木被折断、被风刮倒或大部分叶子脱落，导致碳和营养物质从植被大量转移到土壤中。高质量凋落物的大脉冲增加了更大面积上的分解率(Scatena et al. 1996)。火也可以在景观上形成单个演替阶段的大斑块(Johnson 1992)。1988 年，野火烧毁了黄石国家公园约三分之一的土地。这样规模和强度的火灾每隔几个世纪就会发生一次。长期的人为灭火已经增加了许多以地面火灾为特征的森林（如美国西部的黄松或红杉）中晚期演替群落的比例。这就产生

了一种更加均匀、空间连续、富燃料的环境，在这种环境中火灾可以大面积燃烧。以取代树冠植物（例如黄石公园的海滩松）为特征的森林很快再生出足够的燃料再次燃烧。因此，灭火对这些森林的火情影响不大。即使是大范围受干扰地区，其内部也往往是斑块状的，形成了一种功能镶嵌体，即斑块之间的功能差异是非常重要的景观。例如，火灾通常会产生未燃烧的植被岛和燃烧严重程度不同的地块，这些地块在再生树木的密度、生产力和氮循环率方面往往存在显著差异。未烧毁的岛屿作为火灾后演替的种子来源和野生动物的保护地，大大减少了干扰的有效规模。在许多情况下，斑块在演替过程中变得不那么明显，因此在非稳态镶嵌体中，空间异质性可能随时间而下降。

人为干扰改变了自然格局和景观异质性的大小。人类影响的特征很容易在景观格局中发现。单独的土地利用变化可能通过在主要是自然植被的基质中创造小块的景观异质性。然而，人类活动已经改变了多达 75%的无冰地表。我们清除或选择性地砍伐森林；将草原和热带大草原转变为牧场或农业系统、排干湿地、河流高地和灌溉旱地。随着土地利用变化的日益广泛，以人为主导的斑块成为孤立的自然生态系统碎片嵌入其中的基质，减少景观异质性，导致景观结构和功能发生质的变化。人类活动对景观异质性的这些对比影响可以从农业转移的实践中得到说明。

农业转移是低人口密度下景观异质性的一个来源，但随着人口的增加，景观异质性会减少。移动农业，也被称为刀耕火种农业或 swidden 农业，包括砍伐森林种植作物，然后是森林再生的休耕期，在此之后循环往复。农业转移在热带地区广泛使用，过去在欧洲和北美东部的森林砍伐中发挥了重要作用。小面积的森林通常会被清除掉大部分的树木，并被焚烧以释放有机结合的养分。农作物是混合种植的，有多种种植和收获。由于土壤肥力下降，昆虫和植物害虫侵入，通常在 3-5 年内，农田被放弃，森林再生。农业转移在许多尺度上产生景观异质性，从森林中的不同年岁斑块到农田中的不同作物种类。由于人口密度适中，可以有足够长的休耕期和明智地选择耕地，农业转移持续了数千年，而生物地球化学循环没有任何变化。

随着人口密度的增加，土地变得越来越稀少，休耕期缩短或消失，导致农业景观更加单一。在这种情况下，农业阶段的营养和有机质损失无法弥补，系统退化，需要更大的地区提供足够的粮食。当景观被活跃的农田或演替早期的杂草物种所主导时，演替中期物种的种子来源被消灭，阻止了森林的再生，进一步降低了景观异质性的潜力。例如，在印度东北部，当轮作周期下降到 10 年以下时，这种农业转移似乎是不可持续的。

2.7 各种异质性来源间的相互作用 (Interactions among Sources of Heterogeneity)

干扰发生的可能性依赖于景观异质性和干扰历史。干扰能够受到负反馈和正反馈的作用。其中，负反馈作用可以降低干扰发生的可能性。例如，火烧在生态系统中产生了演替早期的植被斑块，这些斑块比演替后期的植被对火更不敏感。再比如，病原体引起森林中古老树木的死亡，但同时增加了光照，氮矿化和营养元素，有利于新生森林抵抗将来的侵害，降低病

原体爆发的可能性 (图 13.2-1)。相反，正反馈作用会增加干扰发生的可能性。例如，虫害导致树木死亡，增加了森林的易燃性，即火烧干扰的发生概率。此外，为了降低火烧发生的概率，人们会对死亡树木进行砍伐，导致形成新的斑块。多种干扰都可能发生，使得景观异质性和干扰难以预测。

在内蒙古草原，蝗虫灾害始终是生产中的一个重要问题。特别是上世纪 80 年代以后，随着放牧活动的增加、草地退化严重，蝗虫灾害发生频度有明显增加的趋势。中国科学院动物研究所康乐和美国亚利桑那州立大学 James Elser 研究组通过分析亚洲小车蝗（*Oedaleus asiaticus*）的饮食结构，发现高氮食物会显著降低亚洲小车蝗的大小和生存能力，而重度放牧由于导致植物含氮量降低、而有利于蝗虫的生长和发育(Cease, Elser *et al*. 2012)。该研究证明了过多的蛋白质可能不利于亚洲小车蝗的生长，提出与目前观点相反的新观点：过度放牧降低了植物氮素浓度而加剧了蝗虫爆发，这一成果颠覆了传统的氮浓度增加导致蝗虫爆发的观点(William J. Mattson 1980)。该研究部分解释了内蒙古草原退化与蝗虫成灾的关系，不仅对内蒙古草原蝗虫的控制具有意义，对世界其它地区草原蝗虫的控制也具有启发和借鉴意义。

人类活动产生的干扰也会改变景观的斑块结构和功能。例如，公路增加了土地利用发生改变的可能性。道路是一种能够很好反映人类对土地利用改变的预测指标。从另一个角度来说，景观异质性也会影响人类对景观的利用方式。例如，平原地区更适宜发展机械化农业，大部分转变为农田，而山地地区不适宜发展机械化农业，主要由小农场主所有，维持着土地利用的异质性。

第三节　景观中斑块间的相互作用

景观斑块间的相互作用影响着单个斑块的功能和景观整体的功能。景观斑块通过横向运动的水，能量，营养物质，或生物跨越边界从一个斑块到另一个斑块。这是通过地形控制的相互作用，通过大气转移、生物转移和干扰扩散而发生的。这些转移对于生态系统的长期可持续性至关重要，因为它们代表了捐赠生态系统的损失和对接受生态系统的补贴。这些转移的巨大变化构成了资源投入和产出的变化，因此改变了生态系统的功能。

3.1 地形和陆地-水体相互作用 (Topographic and Land–Water Interactions)

由地形控制的物质再分配是物质在生态系统之间移动的主要物理途径（图 13.3-1）。重力是一种重要的景观作用力量，它导致水向山下移动，携带溶解和颗粒物质。重力也是滑坡、土壤移动和其他形式的土壤运动的驱动力。这些由地形控制的过程可以把物质从陆地运输到水生生态系统，从淡水生态系统再到海洋生态系统（Naiman et al. 2005）。集约化农业地区和大量氮沉降的地区将大量的硝酸盐和磷转移到河流、湖泊和地下水中。例如，河流中的硝酸盐负荷与世界主要流域的总氮输入量密切相关在更局部的尺度上，土地利用和城市化的模式影响到湖泊和河流的养分输入。这些增加的溶解氮对环境造成多种后果，包括健康危害、酸化、富营养化以及下游淡水和海洋生态系统的生物多样性减少。

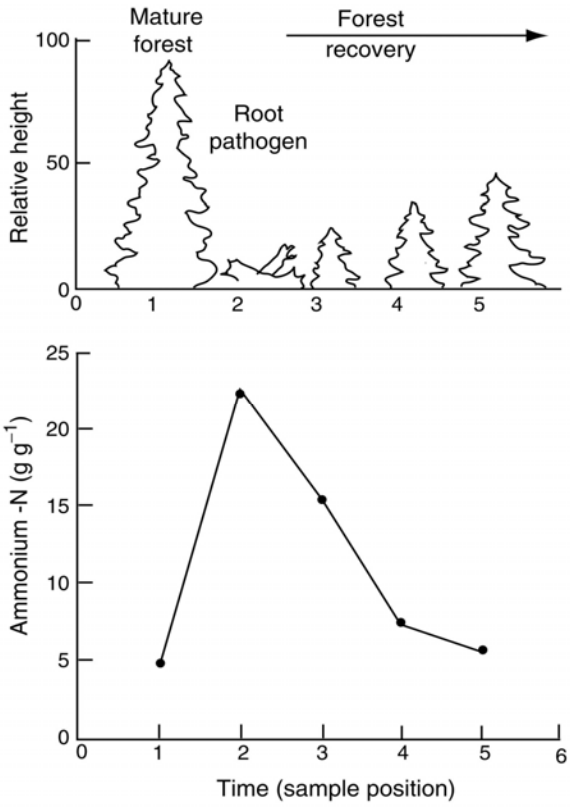


图 13.2-1 美国西北部铁杉林的树高和由根部病原体干扰引起的净氮矿化速率截面（Matson & Boone 1984）

侵蚀将含有营养物质和有机物的颗粒物质从一个生态系统中移动到另一个生态系统中。侵蚀范围从悬浮在水中的泥沙到整个山体滑坡运动。移动的物质数量取决于许多物理因素，包括斜坡位置、斜坡坡度、岩石和土壤下的松散物质的类型以及侵蚀类型。生态系统的生物学特性也至关重要。植被类型、根系强度、干扰、管理和人类发展与坡度或母质一样重要。例如，美国西北部陡峭山坡上的森林收获增加了山体滑坡的频率。同样，旱地农业经常增加泥沙淤积以及与之相关的营养物和污染物的转移（Syvitski et al. 2005）。通过使用覆盖作物、减少耕作和其他管理措施对上坡系统进行适当管理，可以减少物质的侵蚀转移。

景观格局也会影响物质在生态系统之间的转移。在有管理和没有管理的景观中，生态系统沿着地形序列相互作用，从高地过滤的养分为中坡或低地生态系统提供养分补贴（Shaver et al. 1991）。这些生态系统在景观中的组合决定了养分再分配的模式及其对地下水和河流的输出。包括湿地和平原森林在内的河岸植被带，对从高地流向溪流的水和物质起到了过滤器和沉积物收集器的作用。河岸带在农业流域中起着特别重要的作用，因为它们带走了肥料产生的氮和磷，侵蚀了沉积物。大多数河岸地区所特有的质地细密、富含有机物质的土壤和湿润的条件也促进了流入的硝酸盐的反硝化作用。植物吸收和反硝化作用共同解释了硝酸盐浓度的下降，因为地下水从农田通过河岸森林流向小溪。磷主要通过植物和微生物对营养物质的吸收和对土壤的物理吸附而保留在河岸地区，因为磷没有气体损失途径。

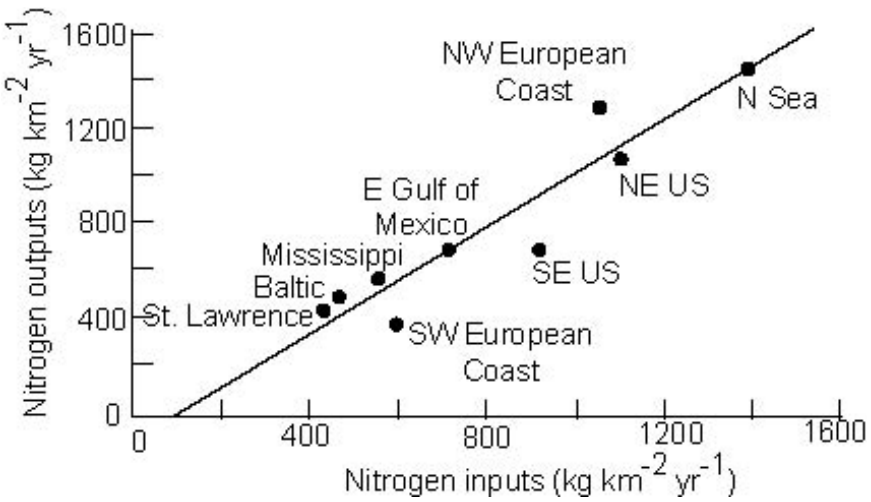


图 13.3-1 世界上主要流域氮的人工施用量和河流中硝酸盐浓度的关系

3.2 大气传输 (Atmospheric Transfers)

通过大气传输，可以使不同生态系统在长距离和大尺度上建立联系。比如，氨气和氮氧化物等气体传输（图 13.3-2）。同时，大气传输还可以通过灰尘对一些元素进行传输，如钙、镁、钠、钾、磷等。从管理的或自然的生态系统排放的气体在大气中被处理，可以被运输到其他地方。一旦沉降下来，它们可以改变生态系统的功能（图 13.3-2），就像地形控制的转移一样。

在农业的下风地区，NH_3 和 NO_x 在氮沉降中占很大比例。例如，荷兰希思兰的氮沉降量至少是自然沉降量的 10 倍。这些输入量的大小与每年通过植被循环的氮量相似，极大地增加了氮循环的开放性。工业和化石燃料的下风地区主要以氮氧化物的形式吸收氮。包括二氧化硫在内的含硫气体也由化石燃料燃烧产生，相对于氮氧化物的排放和沉降，改进的法规减少了含硫气体的排放。

向生态系统输入的大量氮对 NPP、养分循环、微量气体通量和碳储存有重要影响。长期沉降最初通过增加氮循环速率、叶面氮浓度和 NPP 来降低氮限制。然而，超过某个阈值，生态系统就会饱和。当过量的硝酸盐和硫酸盐从土壤中滤出时，它们会携带阳离子来维持电荷平衡，从而造成植被中的钙和镁贫乏(Driscoll et al. 2001)。在过去的半个世纪中，瑞典南部超过一半的植物可用阳离子已经从 70 厘米以上的土壤流失，至少部分原因是长期暴露在酸雨中。交换络合物由锰、铝和氢离子占主导地位，增加土壤酸度和铝毒性的可能性。这一系列的土壤变化通常会增加对霜冻的敏感性，损害根系生长，促进食草动物采食，导致欧洲和美国东北部许多地区的森林退化。然而，让人惊讶的是，一些森林对酸雨的适应能力非常强，往往能在几十年内保持生态系统中的大部分氮输入，并维持它们的生产力和碳储存。

生态系统对酸雨的脆弱性部分取决于投入的大小（与污染源的距离和收到的降水量有关）和最初的土壤酸度，而土壤酸度又取决于母质和物种组成。例如，在美国东北部，花岗岩基

岩地区的森林生产力已经下降，特别是在高海拔地区（土壤碱性阳离子库最小）(Fahey et al. 2005)。糖枫（sugar maple）是一种对钙敏感的树种，也是重要的冠层优势种，这与土壤中钙的流失和糖枫生长的降低和死亡率的增加有关。向流域添加钙会增加糖枫菌根侵染、组织钙浓度和幼苗的生长，特别是在高海拔地区。酸雨还增加了流入河流的氮，降低了湖泊的酸中和能力。湖泊酸度的增加在基岩中阳离子含量较低的流域最为明显。在这些湖泊中，酸性降低了鱼类的体积、存活率和密度，部分原因是由于减少了它们的食物供应(Driscoll et al. 2001)。

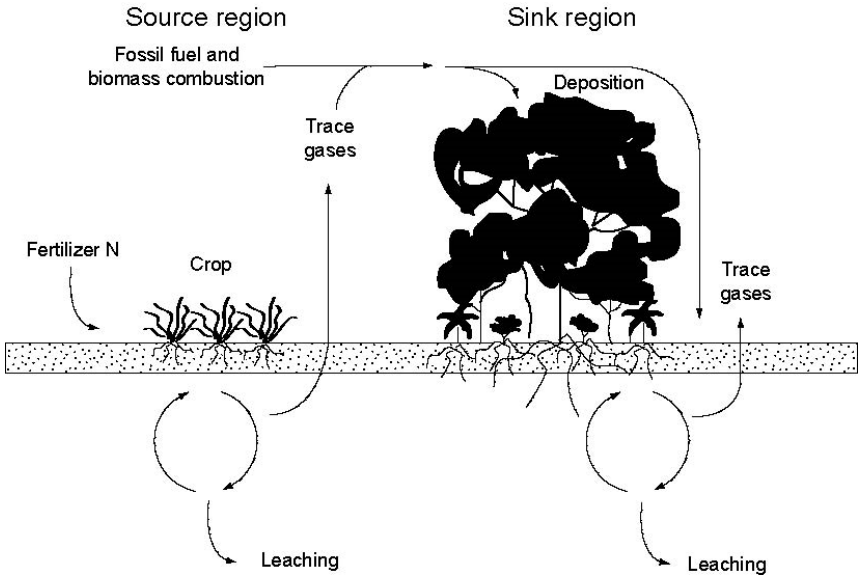


图 13.3-2 气体、溶液和颗粒物在生态系统间的大气传输。输入来自化石燃料和生物物质的燃烧，以及自然和人工生态系统中的痕量气体排放。

几乎所有关于人为氮的转移、沉降和生态系统后果的研究都是在温带区进行的。然而，氮沉降的进一步增加可能主要发生在热带和亚热带(Galloway et al. 1995)，在那里植物和微生物的生长往往受到除氮以外的元素的限制。因此，这些生态系统可能会在微量气体中表现出更直接的氮损失或氮沉降响应。另一方面，土壤属性如如高粘土含量或阳离子交换能力，可能使热带土壤在氮流失之前隔离大量的氮。

生物量燃烧直接将营养物质从陆地库转移到大气中，然后转移到顺风生态系统中。大约有一半的干生物量是由碳组成的，因此释放的主要气体是处于不同氧化阶段的碳化合物，包括二氧化碳、甲烷、一氧化碳和少量的非甲烷碳氢化合物。氮也会以不同的氧化状态释放出来，包括氮氧化物（NO和NO_2，统称为NO_x）和氨（NH_3）。这些形式的排放比例还取决于燃烧强度，氮氧化物通常占排放的大部分。含硫气体、有机烟灰和其他气溶胶粒子、元素碳以及许多微量碳、氮和硫也具有重要的区域和全球影响。

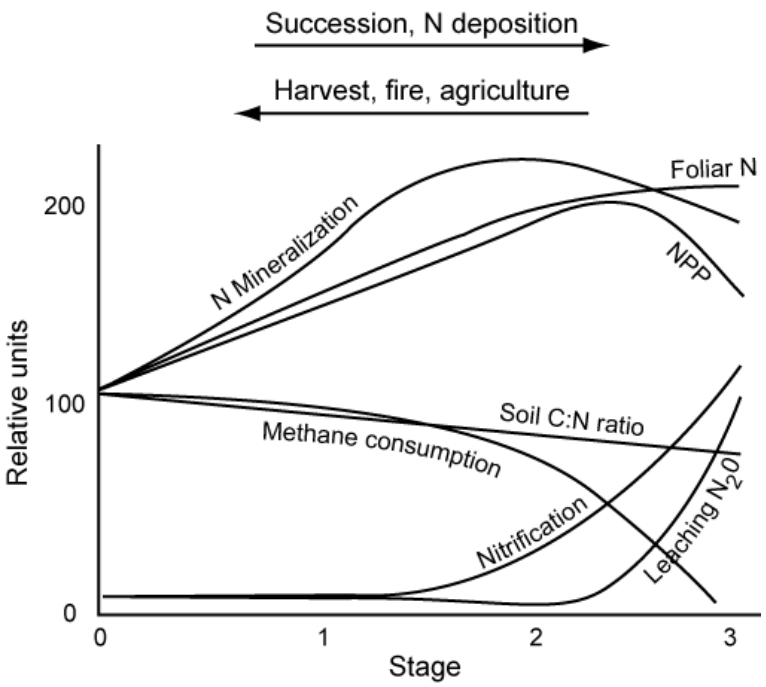


图 13.3-3 森林经历了长期的氮沉降与饱和之后出现的变化

由自然和人为因素产生的被风吹来的颗粒在景观上连接着生态系统。大气在生态系统中作为运输途径的作用因元素而异。对于某些碱性阳离子（Ca^{2+}、Mg^{2+}、Na^{+}和 K^{+}）和磷，粉尘的输送是生态系统之间的主要大气联系。在地方到区域的尺度上，来自道路或河流的灰尘可以改变土壤的 pH 值和其他土壤属性，从而导致植被的区域分带性和陆地-大气交换。在全球范围内，撒哈拉沙漠的沙尘被热带东风带过大西洋，沉降在亚马逊河上。虽然每年的沙尘输入量很小，但从长期来看，它对土壤的发育有很大的影响(Okin et al. 2004)。同样，来自戈壁沙漠的灰尘以 1.25 g m^{-2} $year^{-1}$ 的速度沉降在夏威夷群岛的潮湿森林中。在古老的土壤，即> 200 万年的土壤中，粉尘输入可能是磷的最大来源。在美国西部，1860 年至 1900 年间铁路的修建，加上美国西南部牛羊高强度放牧，增加了大气中的粉尘负荷，导致圣胡安山脉积雪持续时间缩短。同样，亚洲的大沙尘暴可以传播到远至美国西部，导致更快更早的积雪融化，而用于灌溉、城市和落基山脉滑雪胜地的水却更少。

在一个地方，陆地-大气的水和能量交换会影响顺风气候。海洋和大湖通过降低极端温度和增加降水来缓和邻近陆地地区的气候。人类对陆地表面改变的范围很广，它也对顺风生态系统产生了重大影响。例如，澳大利亚灌木林转为农业使得灌木林的降水量增加，而农业地区的降水量减少了 30%。亚马逊地区的森林砍伐减少了区域的蒸发蒸腾。水循环的降低减少了盆地其他地方可用于降水的水分，使得气候对热带雨林不利。在全球范围内，为农业清理土地减少了区域反照率和蒸散发，导致更大的感热通量(Field et al. 2007)。在所有空间尺度上，从一个生态系统到另一个生态系统的大气热量和水蒸气的传递强烈地影响着顺风生态系统的生态系统过程。在评估这些管理项目的潜在影响时，很少将气候对水库下风生态系统的影响、干旱土地灌溉和土地利用变化纳入其中。

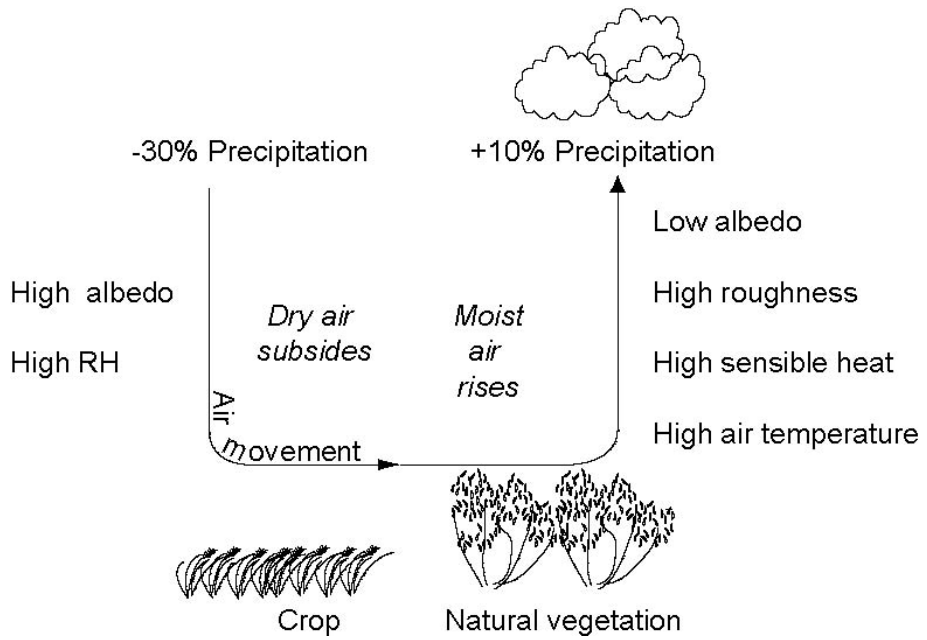


图 13.3-4 澳大利亚西南部荒地变成麦田后对当地气候的影响（Chambers 1998）。荒地比相邻的麦田能吸收更多的辐射，将更多的能量传导到空气中，使得荒地上的空气上升，然后从周边灌溉的农田吸收潮湿空气，造成了农田上方空气下沉。潮湿空气的上升使荒地的降雨量增加了 10%，而农田地区干燥空气的下沉导致降雨量减少了 30%。

3.3 动、植物在景观中的迁移 (Movement of Plants and Animals on the Landscape)

动物、植物的迁移和传播可以连接景观中的多个生态系统。大型动物通常从高质量的小块区域摄取草料，并在它们休息或睡觉的地方沉积粪便和尿液。例如，新西兰绵羊在山下采食，然后在山顶排泄粪便，从而把养分从山下向山顶进行迁移。海鸟将大量的磷从海产食物转移到陆地上，以至于沉降在它们传统筑巢区域的鸟粪成为了磷肥的主要来源。溯河鱼类，也就是进入淡水繁殖的海洋鱼类，也会将海洋衍生的营养物质输送到陆地生态系统。这些鱼把营养物质带到河流和溪流中，成为陆地掠食者的重要食物，而陆地掠食者又把从海洋中获得的营养物质运送到河岸和高地的陆地生态系统中。反过来，这些来自海洋的营养物质促进了树木的生长，提供了更多的阴凉，更少的河岸侵蚀，更大的粗木屑；因此，与没有鲑鱼的溪流相比，可能有更好的鲑鱼栖息地。同样，以海藻和其他海洋碎屑为食的昆虫是岛上蜘蛛的重要食物来源，它们将海洋和陆地的食物网结合在一起。

动物也通过皮毛和粪便来移植植物，特别是种子。许多植物已经进化出了利用这种有效传播方式的生活史策略。这种扩散机制促成了入侵植物的扩散。例如，夏威夷热带雨林中的一种非本地草食动物—野猪，会传播诸如西番莲之类的入侵植物的种子，从而改变营养循环的模式。因此，从一个生态系统到另一个生态系统的植物和动物的入侵可以促成各种生态系统的变化。

在斑块间移动的动物会对不同斑块类型产生不同的影响。边缘专家如鹿，可能会集中在一种栖息地觅食，但为了寻求保护，以躲避捕食者，并将营养物质储存在另一种栖息地(Seagle 2003)。捕食者-被捕食者的动态也可能造成营养成分的不均一，这取决于捕食发生的地点和尸体的存放地点，例如，当驼鹿以富含氮的水生植物为食而在高地被狼杀死时（Bump et al. 2009）。在更大的尺度上，候鸟在不同的生态系统类型之间进行季节性迁移。例如，体型较小的雪雁在美国南部过冬，在加拿大的北极地区繁殖。由于越冬地对农作物（水稻、玉米和小麦）的使用增加和狩猎压力的减少，该物种的数量增加了一个数量级以上。这一物种现在已经超过了其夏季繁殖地的承载能力，并且已经把北极多产的盐沼变成了没有植被的荒地。

人类是生态系统间物质横向转移的一个日益增加的原因，通过添加肥料、杀虫剂等，引进入侵物种的繁殖体，移除作物和森林产品，以及水的转移。由此产生的水生系统的养分输入发生在河岸带和其他生态适应者经常退化或缺乏的地方。粮食从农村向城市地区的营养转移是巨大的。欧洲的食品进口是欧洲碳平衡尤其是氮平衡的重要组成部分(Ciais et al. 2008)，而食品进口是沿海流域氮的主要来源(Driscoll et al. 2003)。人类的引水大大改变了干旱地区土地利用变化的速度和模式，损害了河流和湿地。在今后几十年，由于水越来越稀少，引水的压力可能会增加。

3.4 干扰的传播 (Disturbance Spread)

斑块的大小和配置决定了干扰在景观内的传播（图 13.3-5）。扰动是对生态系统过程的一种关键的交互控制，它受到从一个斑块到另一个斑块的水平扩散的强烈影响。例如，不可滑动植被的燃料防护罩可以降低城市-荒地交界面的火灾风险。火灾会自己产生燃料，因为火灾后的植被通常比火灾前的植被不易燃烧。理论模型表明，当少于一半的地形易受干扰时，在消除干扰的影响方面，严重程度比频率更重要。然而，当景观的很大一部分容易受到干扰时，干扰的频率就变得越来越重要。斑块的大小也影响扰动的扩散。大斑块占主导地位的景观往往发生大火灾的频率较低，而大火灾又会产生大斑块。面积小的景观有更大的边缘面积比，所以火灾倾向于更频繁地蔓延到不易生长的植被中(Rupp et al. 2000)。这样，景观往往会维持其特有的干扰状态，直到受到其他因素（例如气候或土地利用变化）的影响。

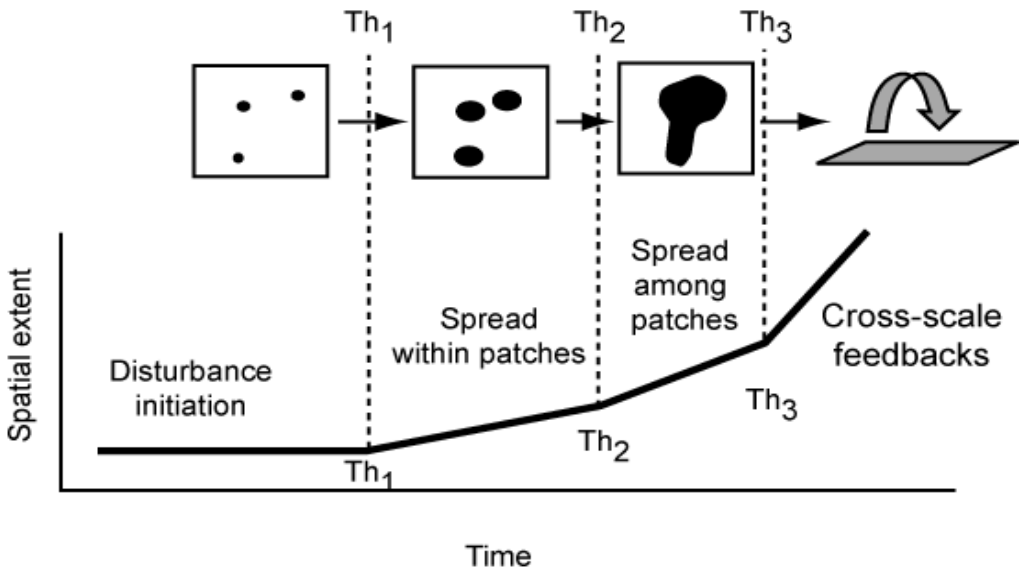


图 13.3-5 多尺度交互作用影响干扰的非线性传播

与大规模连续单一栽培相比，零星的农业景观不太容易传播病虫害和病原体。集约化农业在多个方面减少了景观的斑块。单个牧场的平均规模和农业用地占总面积的比例普遍增加，使用相同的品种也是如此。这可能导致害虫在整个景观上迅速蔓延。

第四节　土地利用变化和景观异质性

4.1 人类对景观的改变从根本上改变了生态系统在区域尺度和全球尺度过程中的角色

人类活动可以改变自然植被，砍伐森林，将草原转换为牧场、农田，使原本的自然生态系统从基底变为了斑块。因此，如果不考虑人类活动，是无法理解景观过程的。人类是区域系统中的重要组成部分。人类活动在很大程度上降低了景观异质性，改变了斑块动态的自然格局。以刀耕火种的轮耕农业为例（图 13.4-1）。在人口密度较低时，人类可以长时间休耕，这种情况下能够维持长期的轮耕农业，保持稳定状态的斑块。而人口迅速增加以后，休耕期不断缩减，导致均质化的农业景观，产生了非稳定状态的斑块。

4.2 扩大化 (Extensification)

土地利用变化包括土地利用转换（land-use conversion）和改变（land-use modifiation）(Meyer and Turner 1992)。土地利用的转换是指生态系统从一种类型转化到另一种由不同物理环境或植物功能群类型占优势的类型，例如，从森林到牧场或从河流到水库的变化。土地利用改变是指人类对生态系统的改变，其方式对生态系统过程、群落结构和种群动态产生重大影响，而不会从根本上改变自然环境或主导植物的功能类型。例如，将天然林改为管理森林，将热带草原管理为放牧地，以及将传统的低投入农业改为高强度农业。

表 13.4-1 印度东北部多个农业系统间生态系统过程的比较

Ecosystem	Nitrogen input (g N m^{-2} yr^{-1}) b	NPP (g m^{-2} yr^{-1}) c	Litterfall (g m^{-2} yr^{-1}) c	Soil erosion (g m^{-2} yr^{-1}) d
Natural forest	15.5	2360	118	800
Shifting agriculture				
5-yr cycle	5.7	550	48	6900
10-yr cycle	9.2	670	71	3000
30-yr cycle	10.9	1480	98	1500
Mixed crop	-	100	-	100
Intensive agriculture				
Coffee	12.4	50	-	1200
Tea	28.4	100	-	2600
Ginger	21.3	190	-	20000

图 13.4-1 刀耕火种的景观

森林砍伐是一种在热带地区很广泛的转化方式。森林覆盖率约占陆地面积的 25%，是农业用地总面积的 2-3 倍。自前农业时代以来，全球森林面积减少了约 15%（即减少了 900 万平方公里）。例如，欧洲和印度的大部分亚大陆在历史上都被森林覆盖，但是在过去的 5 到 10 个世纪里已经支持了大面积的农业。同样，从大西洋海岸到密西西比河，北美曾经是毗邻的森林，但欧洲殖民者砍伐大片森林的速度与现在热带森林的特征相似(Dale et al. 2000)。

大多数原始热带森林（地球上最大的生物区系）将会在我们的有生之年消失。这样的变化也同时发生在加拿大和俄罗斯的北部森林（地球上第二大的生物区系）。相反，一些温带地区的国家在之前的农业弃耕地上重新造林，从而改变景观。

如今，在潮湿的热带地区，将森林变为牧场或农业用地是主要的土地利用变化之一。这种土地利用变化的程度是不确定的，但随着遥感技术和适用性的提高，这种不确定性正在减弱(Chambers et al. 2007)。直到 1990 年代，只有最大的砍伐面积可以通过遥感进行准确监测，但是，新开发的工具和分析可以探测选择性砍伐以及砍伐和转换的区域。例如，Asner 等人（2010）使用机载激光雷达和卫星系统的多尺度方法评估了秘鲁亚马逊地区 430 万公顷区域的碳储量和损失，空间分辨率为 0.1 公顷。他们的分析表明，在这一相对偏远的地区，由于土地使用的变化，在十年的碳损失量仅相当于现有生物量的 1%多一点，而在分析中包括选择性伐木，使得计算出的碳损失增加了近 50%。在更精细的空间尺度上，对森林结构的重复激光雷达测量可用于在景观尺度上直接估计林窗形成和填充的速率(Kellner et al 2009)。最终，这些森林周转量的直接测量将适用于更大和更不均匀的地区。

森林砍伐导致的景观变化轨迹取决于原始森林的性质和随后的土地利用。原始森林存在于偏远地区，如亚马逊和中非的大部分地区可能比其他地方存在的时间更长。森林向管理生态系统的永久或长期转变涉及燃烧或去除大部分生物量，往往导致系统中碳、氮和其他营养元素的大量损失。相比之下，伐木只砍伐了具有商业价值的树木，并可能减少土壤中的碳和养分流失。伴随森林砍伐而来的养分流失可以改变邻近的生态系统，特别是水生生态系统，并通过微量气体通量以及水和能量交换的变化影响大气和气候。它们还可能影响干扰后的森林再生(Davidson et al. 2004)。

再生森林的特征也取决于以前的土地利用类型。长期和密集的农业耕作会使土壤变得密实，改变土壤结构和排水能力，耗尽土壤有机质，降低土壤保水能力，降低养分利用率，耗尽本地物种的种子库，并引入新的杂草物种。因此，在这些土地上再生的森林可能与原始森林或在管理较不集中的土地上再生的森林有很大的不同。放牧强度和随之而来的土地管理做法也影响到可能的植被恢复，因为放牧越密集的系统往往需要更长的时间才能恢复森林生物量。在这种情况下，自然造林可能进展缓慢，或者根本无法进行。

利用草原、热带稀树大草原和灌木地放牧牲畜是目前发生的对自然生态系统最广泛的改变，和森林砍伐一样，现在可以通过遥感监测和分析。在全球范围内，每年都有数千平方公里的热带草原被烧毁，以维持放牧的生产力。尽管草原和放牧都是中土草原的自然组成部分，但燃烧和放牧的频率或严重程度的变化改变了生态系统过程(Knapp et al. 1998)。燃烧释放养分，刺激新叶子的产生，这些叶子含有更高的蛋白质，对食草动物来说更可口。相反，食草动物通过减少草的生物量和落叶层的积累来减少火灾发生的可能性。火和食草动物都阻止了大多数树木的建立，否则热带大草原就会变成林地或森林。然而，当火灾发生频率大幅增加时，系统中碳和氮的损失会降低土壤肥力和水分保持力（从而降低生产力）。火灾还会影响区域的示踪气体在顺风生态系统中的分配和沉积，以及营养物质和沉积物向水生生态系统的

转移。

海洋食物的扩张已经改变了全球范围内的海洋食物网，对大多数生态系统过程产生了级联反应。世界海洋被积极捕捞的面积大幅增加，部分原因是技术进步使鱼类和底栖无脊椎动物的捕捞更加有效，在回归市场之前可以更长久地储存。地球上大部分的大陆架，最具生产力的海洋生态系统，现在都在积极捕捞，高纬度开放海洋盆地也是如此。鱼类的消失对远洋生态系统具有级联效应，因为鱼类的捕食对浮游动物的生物量和种类构成有巨大的自上而下的影响，而这反过来又通过浮游植物和水体内营养的循环来影响初级生产力。捕捞底栖无脊椎动物，如蛤蜊、蟹类和牡蛎，也会对生态系统产生巨大影响，因为这些生物的栖息地受到直接干扰，并对碎屑食物网和底栖生物分解产生影响。海洋渔业全球化的影响比我们预期的更为广泛，因为许多大型鱼类具有高度的流动性，可以迁徙数千公里(Berkes et al. 2006)。因此，这些鱼类种群的巨大变化会对整个海洋产生生态影响，就溯河洄游鱼类而言，甚至会影响淡水生态系统。

4.3 集约化 (Intensification)

农业集约化通常降低了景观异质性，增加了向相邻生态系统中养分和其他污染物的输送。农业集约化一般包括使用高产作物品种，并结合耕作、灌溉、工业生产的肥料，通常还有杀虫剂和除草剂。集约化使粮食生产能够满足人口的快速增长。虽然这种做法减少了农业所需的土地面积，但它几乎消除了一些自然占据高土壤肥力地区的生态系统类型。集约化农业在比较平坦的地区最发达，例如适合灌溉和使用大型农业机械的平原和草原。这种设备的高成本要求大面积种植，很大程度上消除了景观异质性的自然格局。

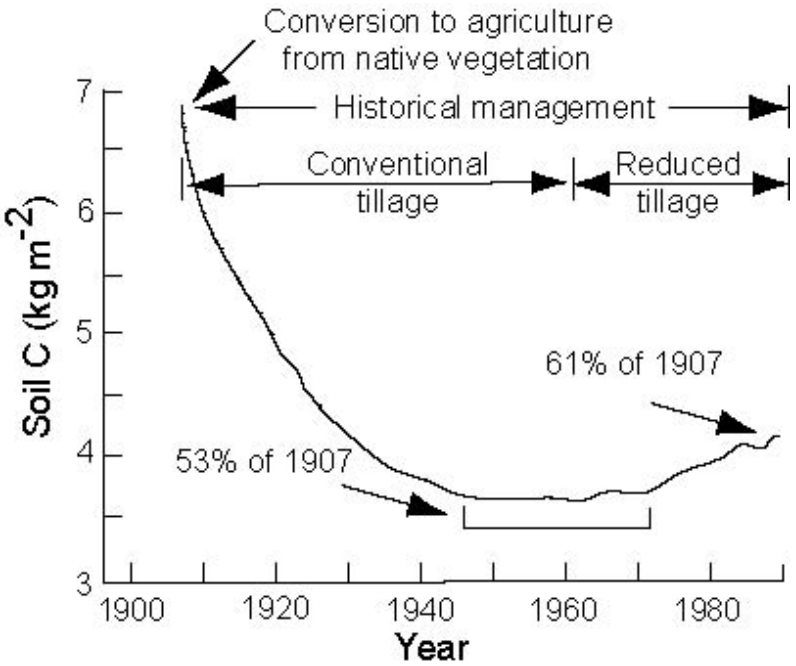


图 13.4-2 草地转化为农田几十年后导致近一半土壤有机质损失

农业集约化产生生物地球化学热点，改变生态系统过程，影响当地、区域和全球环境(Matson et al. 1997)。维持集约化农业所需的大量定期养分投入增加了在全球氮循环中发挥重要作用的氮微量气体的排放，并将这些生态系统与顺风生态系统连接起来。陆地上的养分负荷增加了邻近水生生态系统的非点源污染。陆地上磷的增加对湖泊有特别大的影响，至少有以下两个方面的原因。首先，大多数湖泊的初级生产在根本上受到磷的限制，因此对即使是少量磷的添加也反应灵敏。其次，添加到农田中的磷大多经过化学处理，所以添加到农田中的磷往往比作物吸收的多。例如，在中国北部平原，磷的添加量是农作物中去除量的三倍。大量添加的磷代表着一个巨大的磷储存库，在农民停止施肥后很长一段时间，磷将继续进入水生生态系统。来自人类污水和牲畜粪便的磷输入也具有同样持久的影响。在某些情况下，农民可以“开采”过去增加的肥料以满足作物的需求。例如，中西部许多农场现在施用的磷比作物去除的少，并且依赖于以前施用磷的残留物(Vitousek et al. 2009b)。

20 世纪土地利用变化对生态的影响比任何其他全球变化都大。因此，了解和预测土地利用在未来变化对预测和管理地球系统的未来变化至关重要。土地变化科学家在气候学家、地理学家、生态学家、农学家和社会科学家之间建立了有效的跨学科合作，以评估土地利用和土地覆盖变化的比率、原因和后果(Lambin et al. 2003)。这些合作可以为未来土地利用/土地覆盖变化制定可行的方案。假设不断增长的人口将得到粮食而不是死于饥荒、战争或疾病流行的乐观设想项目继续在土地使用方面发生巨大变化，特别是在发展中国家。当然，未来实际发生的情况是不确定的，但这些和其他情景表明，土地利用变化将继续是未来几十年全球环境变化的主要原因。生态学家与决策者、规划者和管理者一起工作，有机会开发出将未来景观变化的影响最小化的方法。这一设想必须认识到土地利用变化对景观过程的巨大影响，它们对当地到全球规模的影响，以及与人类活动和行为的关系。

第五节　空间异质性与尺度推绎

5.1 空间和时间尺度是理解生态系统改变造成全球性结果的关键（图 13.5-1）

生态学研究需要考虑研究对象的空间和时间尺度。比如，我们的一个研究样地只是是全球生态系统的一小部分。而我们希望能够在不同的尺度上理解生态系统变化的机制。

5.2 生态系统过程的主要控制因素会随时间和空间的尺度发生改变

快速，小尺度的过程为大尺度的过程提供了机理。慢速，大尺度的过程是基本不变的，为快速和小尺度的过程提供了背景(图 13.5-2)。

5.3 空间尺度推绎的方法

“数字绘画”的方法。通过计算每种斑块的均值，乘以斑块所占的面积，来估算更大区域的通量和库容。这种测量的可行性依赖于多个方面。首先，测量值的代表性。其次，该生态系统类型面积的准确性。然后，所包含的热点区域。最后，某一生态系统类型过程的均质性。

通过建立回归关系是一种推绎的方法。例如，构建 NPP 与 NDVI 之间的关系函数。

基于过程的模型也是一种推绎的方法(图 13.5-3)。在模型的构建过程中，必须理解时间和空间尺度上重要的控制因素，必须理解重要的生态学过程。

大尺度测量也是一种推绎的方法，可以给尺度推绎研究提供基础。例如，涡度协方差技术可以测量碳交换。在几十米到几十公里的尺度上测量生态系统通量，对通过景观中热点和冷点地区的通量进行整合。

另一种推绎方法是通过模型反演。例如，基于大气运输模型可以用反演模型来估算二氧化碳或甲烷通量的区域和全球格局。

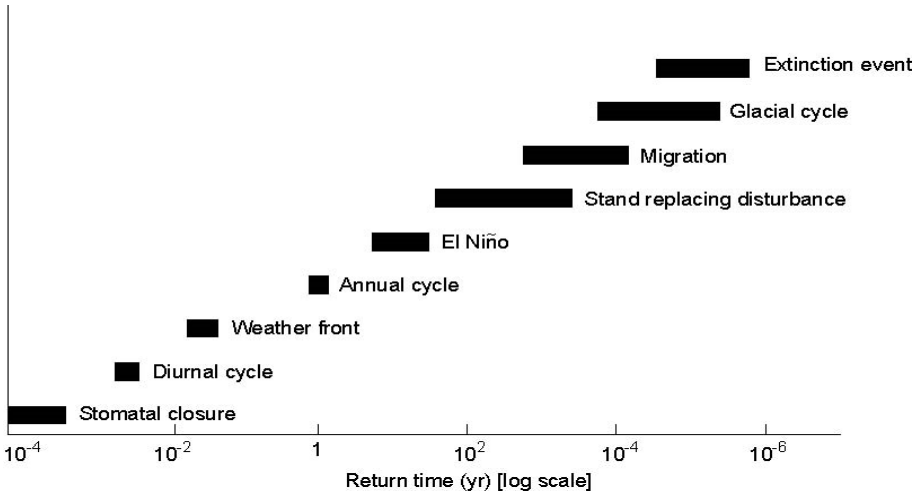


图 13.5-1 影响生态系统过程的主要控制因素依赖于时间尺度

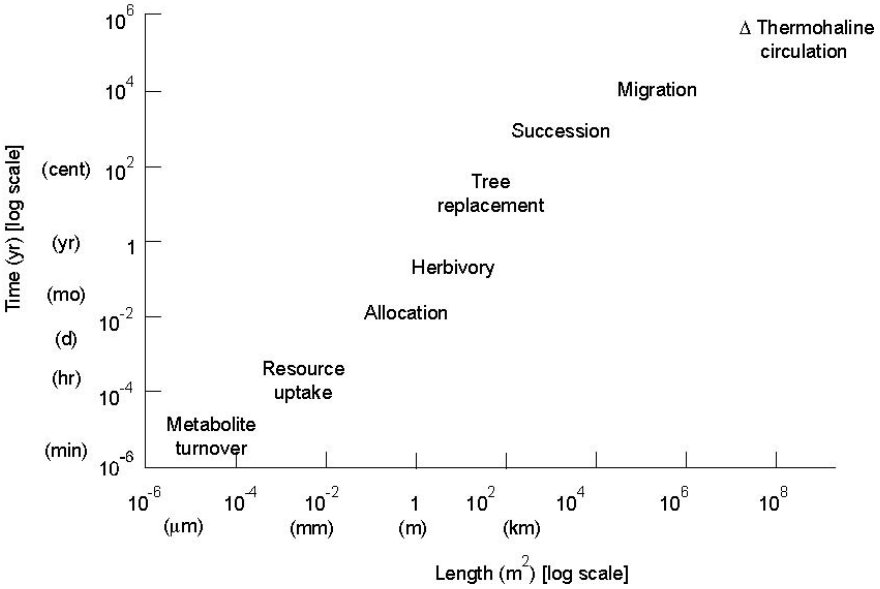


图 13.5-2 影响生态系统过程的主要因素会随这空间和时间尺度的改变而发生变化

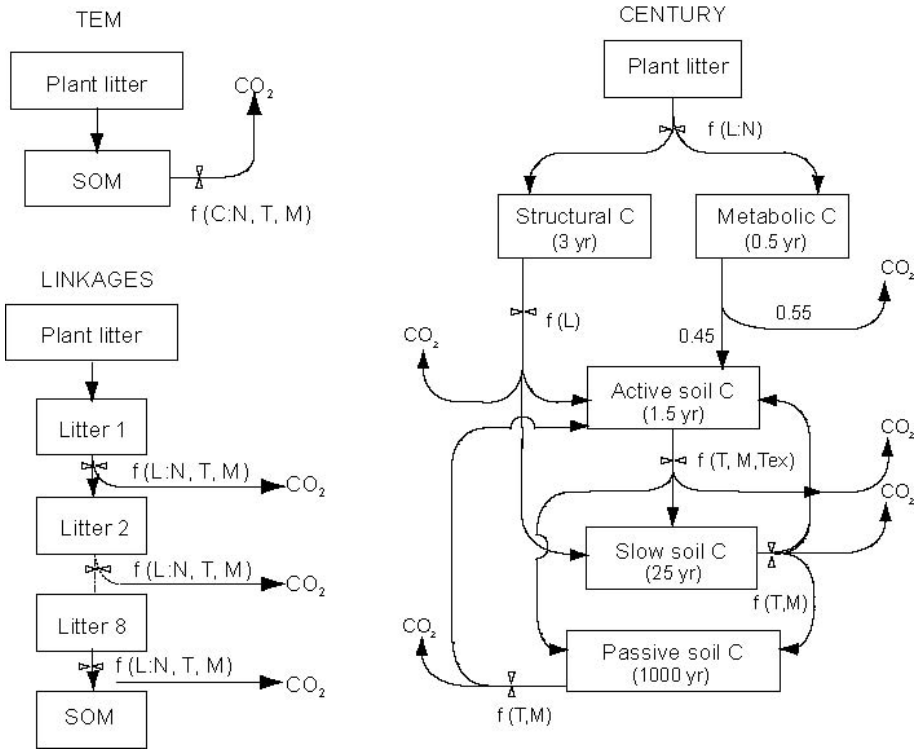


图13.5-3 两种生态系统模型中有关分解的部分：TEM (McGuire et al. 1995b) and CENTURY (Parton et al. 1987).

第六节　研究案例

案例 1 放牧对生态系统功能和群落结构阈值的影响

研究背景

生态阈值是指生态响应发生突然转变时对应的点或者区域(Huggett 2005; Groffman et al. 2006)，这一概念在水生生态系统和陆地生态系统中都越来越受到关注，尤其是草地研究中(Brenden et al. 2008; Hoover et al. 2014; Ratajczak et al. 2014)。在过去的 50 年里，过度放牧引起了世界范围内生物多样性和生态系统服务功能的广泛下降((Milchunas and Lauenroth 1993; White et al. 2000; Díaz et al. 2007)。例如，过度放牧降低了植物物种多样性和生产力(Bai et al. 2007)并且改变了典型草原的 C、N、P 库以及化学计量关系(Bai et al. 2012)。通过对群落结构和生态系统功能阈值的识别，能够避免这样不利的影响发生(Briske et al. 2006; Lohmann et al. 2012)。但是，三个方面的因素可能限制了我们对阈值的检测。首先，大多数放牧实验只包含放牧与不放牧的处理(Milchunas and Lauenroth 1993; Adler et al. 2004; Frenette-Dussault et al. 2012)，无法识别阈值。其次，之前的大多数研究中只是单独地检验群落结构或功能阈值(Sasaki et al. 2008; Augustine et al. 2014; Ratajczak et al. 2014)，很少有实验同时结构和功能的阈值。最后，物种性状的差异可能导致物种对放牧产生正的、负的或非线性响应(McIntyre et al. 2003)，从而使群落水平对放牧的响应变得更加复杂(Díaz et al. 2007)。因此，考虑不同放

牧强度和物种性状的研究能够使我们更好地理解群落结构和生态系统功能阈值间的联系，为草地可持续利用提供指导。

科学问题

第一，放牧如何影响群落结构阈值和生态系统功能阈值，这种影响如何随地形位置变化（平地与坡地）？第二，物种对放牧的响应在常见种和稀有种之间，以及不同的放牧强度之间有何差别？第三，不同植物功能性状对物种阈值的影响？

研究方法

实验样地位于内蒙古自治区锡林浩特市，中国科学院内蒙古草原生态系统定位研究站（43°38' N，116°42' E）。长期放牧控制实验开始于 2005 年 6 月，占地面积近 300 hm^2。实验处理包括两种草地利用方式，即传统利用方式（放牧小区和割草小区分开，放牧小区每年生长季放牧，割草小区每年秋季割草）和混合利用方式（放牧小区和割草小区每年进行轮换）。每种利用方式包括 7 个放牧强度（grazing intensity，GI）水平（0、1.5、3.0、4.5、6.0、7.5、9.0 sheep·ha^{-1}），采用羊标准单位。为了评价放牧如何影响植物群落的物种组成和结构，我们在 2009 年 8 月测定了物种的多度。每个小区内随机设置 3 个 10 m × 10 m 的样方，每个样方进一步划分为 25 个 2 m × 2 m 的亚样方。在每个亚样方内，识别所有的物种并且对每个物种的个体数进行计数。此外，为了量化放牧对地上净初级生产力的影响，我们于 6 月放牧之前在每个小区内设置 3 个 2 m × 3 m 的围笼，并且每个月在羊采食过的区域中移动一次。在放牧对照小区中，8 月份群落地上生物量的峰值用来估算地上净初级生产力(Bai *et al*. 2004)，而放牧小区中的地上净初级生产力则是根据每月移动的围笼内外测得的生物量进行估算(Schönbach *et al*. 2011)，具体计算公式如下：$ANPP=W_{1g}+(W_{2u}-W_{1g})+(W_{3u}-W_{2g})+(W_{4u}-W_{3g})$，其中，Wi 是取样时间 ti 时对应的烘干的地上生物量（i = 1，2，3，4：分别对应于六月，七月，八月，九月的开始时期）。指数 u（未放牧）和 g（放牧）表示围笼内和围笼外的样方。为了评价放牧对照中初始的植物性状如何影响物种对放牧的响应，我们在 2007 年 8 月采集了相邻的未放牧样地中的植物，该样地自 1979 年起围封。对于每个物种，我们随机选取 30 个成熟个体进行分析(Cornelissen *et al*. 2003)。考虑到性状之间的自相关性和内在维度的关联(Laughlin 2014)，我们测定并计算了 4 个与初级生产力相关的功能性状(Cornelissen *et al*. 2003)，即植株高度，比叶面积，茎叶比和叶片氮含量。我们计算了性状均值和种内性状可塑性来确定它们在物种对放牧响应中的作用(Díaz *et al*. 2001)。

主要研究结果

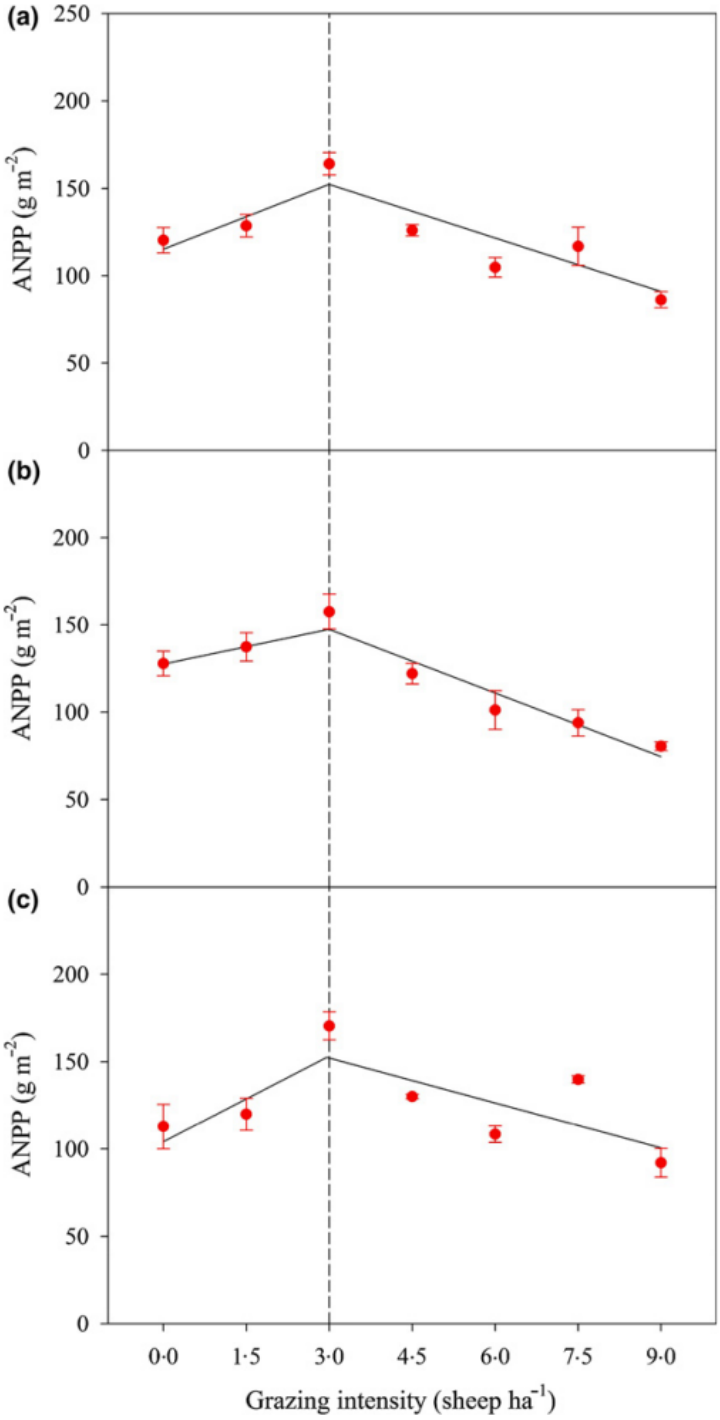


图 13.6-1 放牧对生态系统功能阈值变化的影响。（a）整个系统，（b）平地系统，（c）坡地系统。每个放牧强度下（GI）的地上净初级生产力（ANPP）通过计算三个移动围栏的平均值得到（误差线代表标准误差）。垂直虚线表示地上净初级生产力变化的放牧强度阈值。

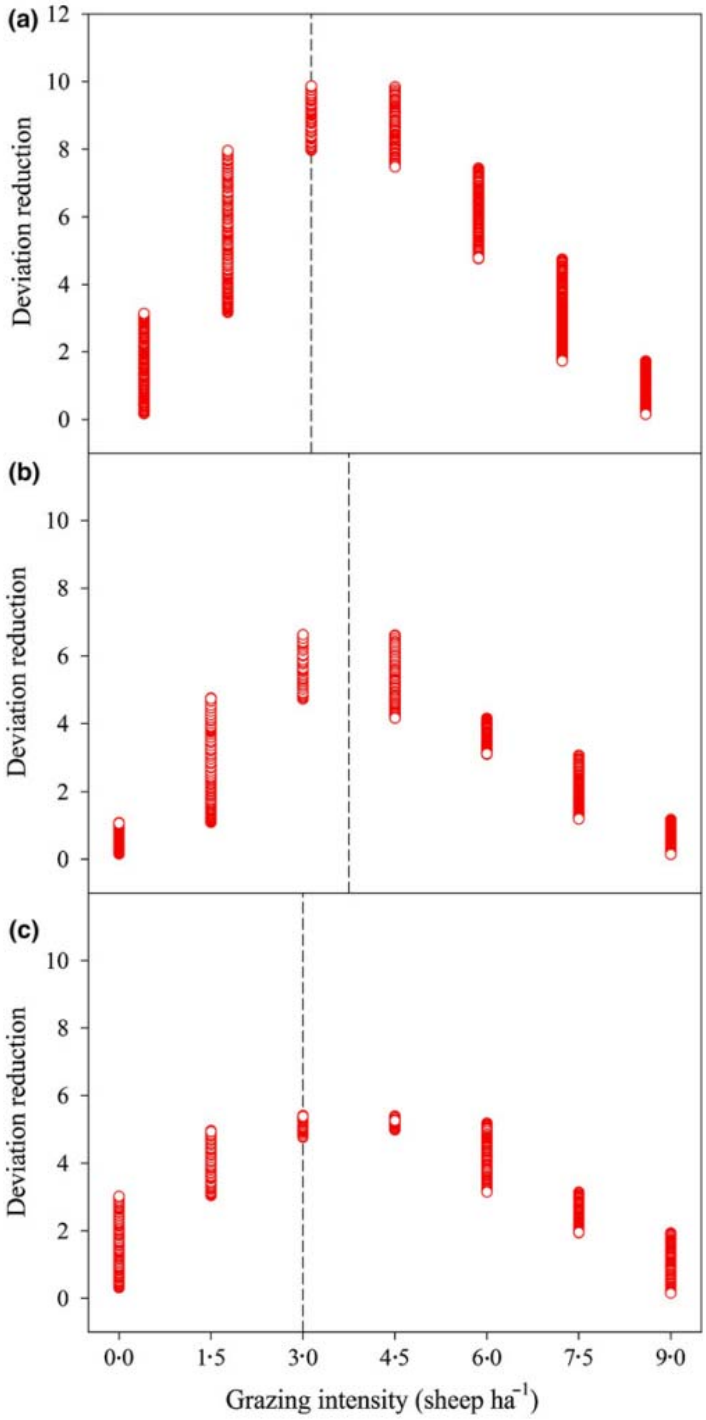


图 13.6-2 群落结构对放牧强度响应的拐点分析（nCPA）。（a）整个系统，（b）平地系统，（c）坡地系统。基于 2m x 2m 样方多度数据，每个符号代表用于分组的候选拐点（阈值）。虚线代表群落结构变化对应的放牧强度阈值。

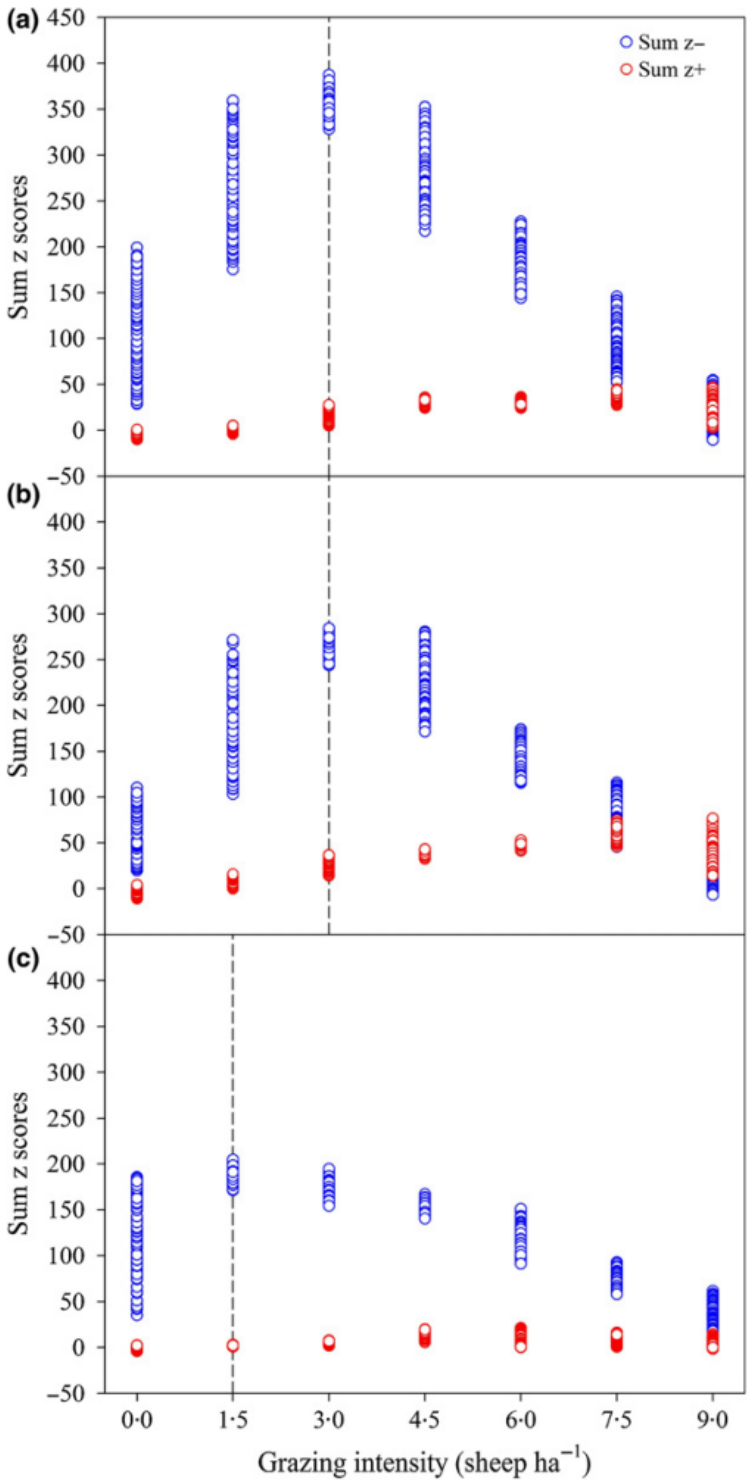


图 13.6-3 放牧对物种多度累积负响应和正响应的影响。（a）整个系统，（b）平地系统，（c）坡地系统。蓝色和红色符号分别代表累积负响应和正响应。虚线代表最大累积负响应对应的放牧强度阈值。

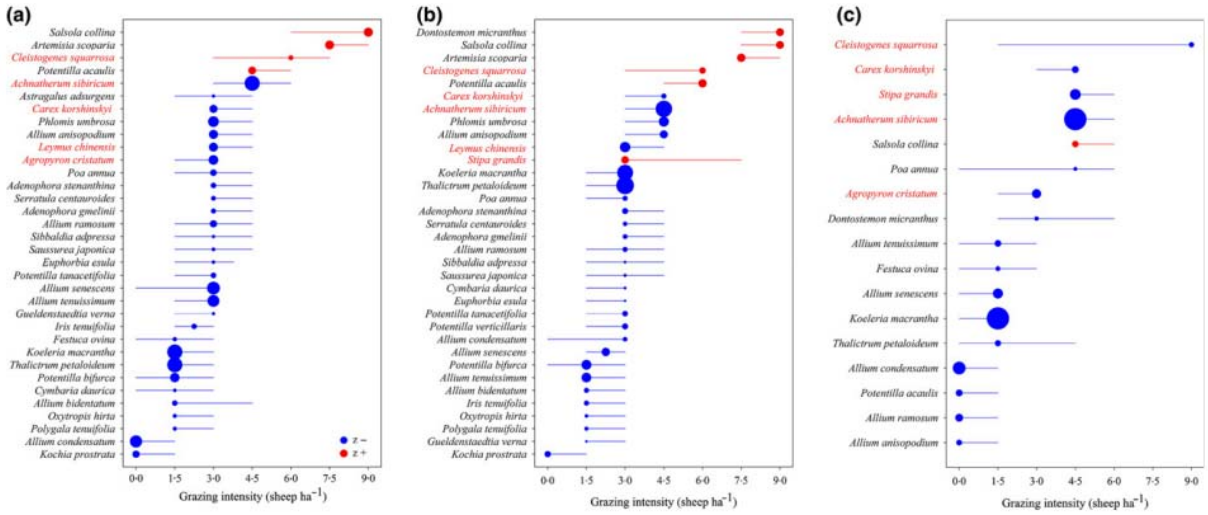


图 13.6-4 物种相对多度与物种相对频度相结合的阈值指示分类分析。（a）整个系统，（b）平地系统，（c）坡地系统。基于 2m x 2m 样方多度数据。蓝色和红色符号分别表示对放牧产生负响应和正响应。符号大小与 z 值成正比，符号较大则表明物种的多度或出现概率有较大变化。对于每个物种，实线代表 95% 置信区间。红色标识的物种为常见种。

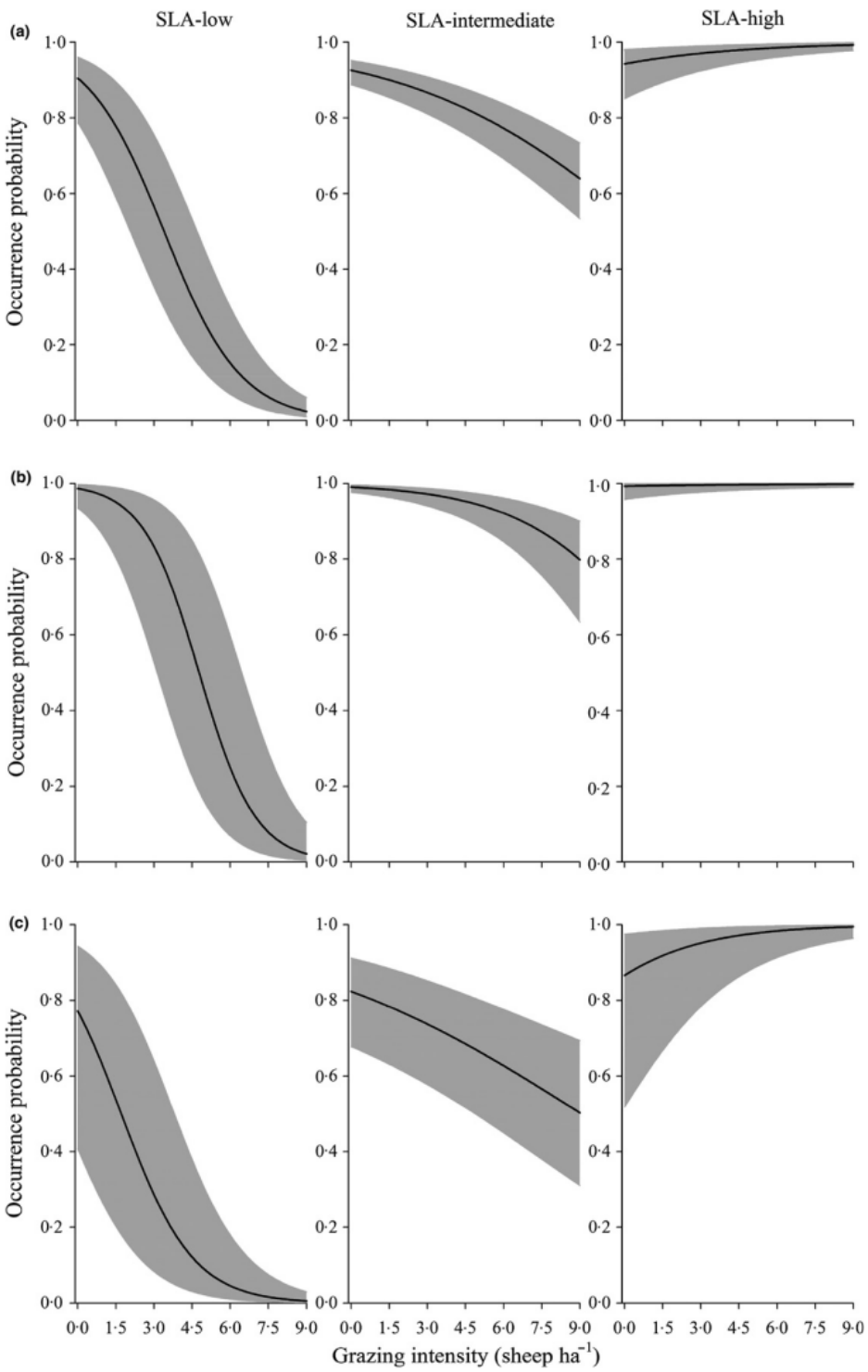


图 13.6-5 不同比叶面积的物种随放牧强度增加的出现概率。（a）整个系统，（b）平地系统，（c）坡地系统。低：SLA≤60 cm^{2}g^{-1}，中：60<SLA≤120 cm^{2}g^{-1}，高：120<SLA≤180 cm^{2}g^{-1}。灰色条带表示 95%置信区间。

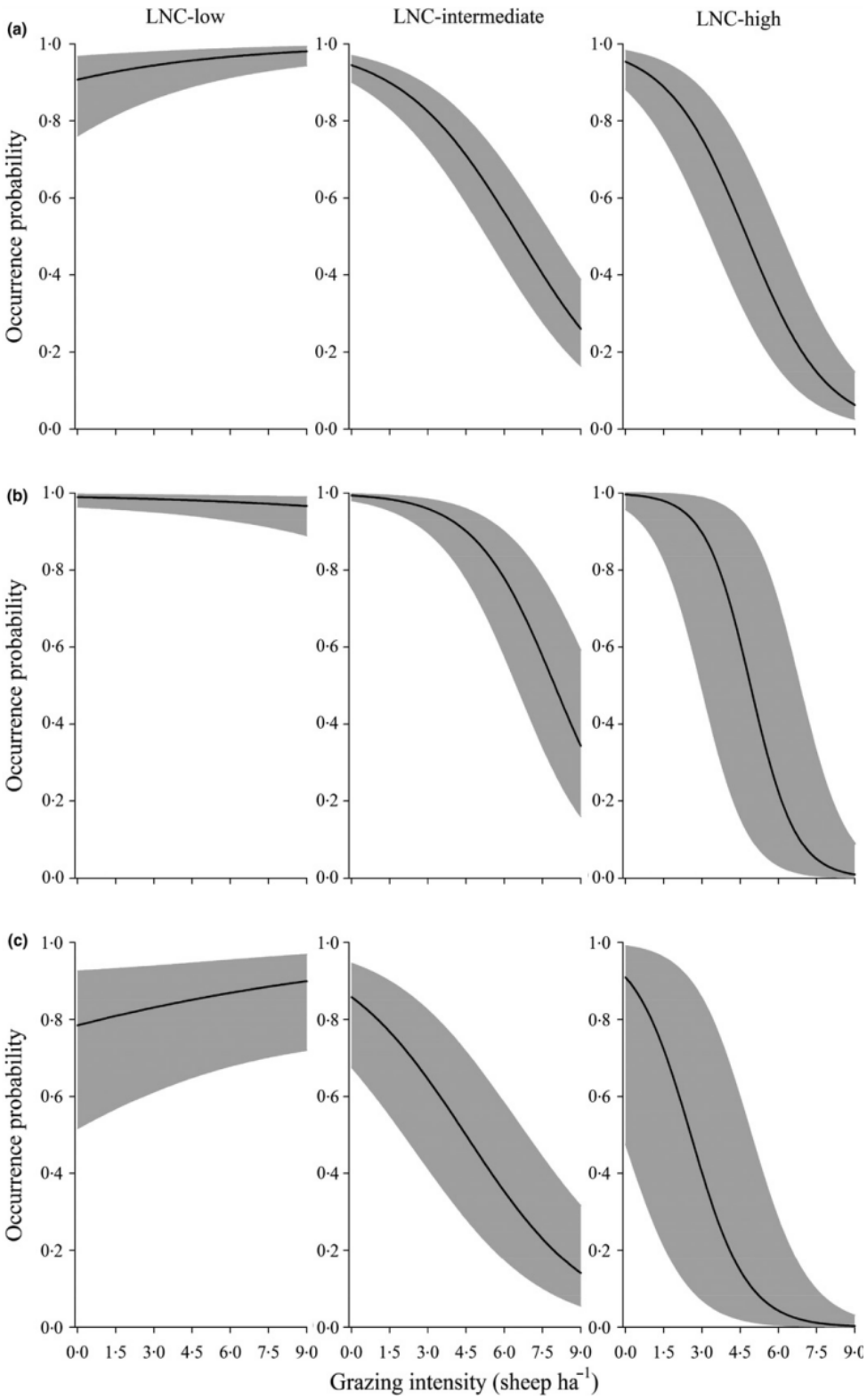


图 13.6-6 不同叶片氮含量的物种随放牧强度增加的出现概率。（a）整个系统，（b）平地系统，（c）坡地系统。低：LNC≤2 %，中：2<LNC≤2.75 %，高：2.75<LNC≤3.5 %。灰色条带表示 95%置信区间。

通过研究我们发现：1）半干旱典型草原群落结构和生态系统功能对放牧的响应都存在生态阈值，但是，不同地形下群落结构阈值的变化主要受物种数的影响，而功能阈值的变化主要受常见种生物量的影响；2）群落结构阈值的变化是由于物种水平对放牧的响应引起的，并且地形起到了明显的调控作用；3）比叶面积和叶片氮含量可以很好地指示预测物种对放牧的响应，比叶面积较低和叶片氮含量较高的物种受高放牧强度作用时其出现概率会显著降低，而比叶面积较高和叶片氮含量较低的物种其出现概率受放牧影响较小。本研究通过整合植物功能性状和阈值分析的方法，为草地管理中确定可持续的放牧强度以及半干旱草地多样性保护提供了重要的理论依据。

案例 2 生态系统的长期变化案例研究——以中国科学院植物研究所内蒙古草原生态系统定位研究站为例

研究背景

探求草原生态系统过程与变化，是当代干旱半干旱地区生态学的重要问题之一。内蒙古草原是欧亚大陆草原的重要组成部分，是我国重要的草牧业基地和重要的水源涵养区，同时也是我国北方的重要生态屏障。由于近几十年的过度利用，该区域有 90%左右的草地处于不同程度的退化之中，其中严重退化草地占 60%以上。人为因素和气候干旱，特别是长期的过度放牧是导致内蒙古草地退化的主要因素。长期过度放牧使草地的植被覆盖度和初级生产力降低，生物多样性减少，土壤养分和水分保持能力下降，土壤侵蚀和水土流失加重，对气候变化的敏感性增强等，严重地影响了不同时空尺度的生态系统功能，加速了草地的退化演替，从而使草地的生态服务功能日益衰减，虫鼠害和沙尘暴等自然灾害频繁发生，严重威胁了我国北方及其周边地区的生态安全，成为实现区域经济可持续发展、边疆稳定和构建和谐社会的关键制约因素。中科院内蒙古草原生态系统定位研究站（以下简称内蒙古站），是我国在温带草原区建立的第一个草原生态系统长期定位研究站。长期以来，内蒙古站围绕草原生态系统生态学基础研究，生态系统长期监测，以及生态系统管理等应用研究开展了大量的试验研究，在草原生物多样性与生态系统稳定性的维持机制、放牧对生态系统生产力和碳氮循环的影响，以及草地生态系统服务对全球变化的响应等方面取得了众多的研究成果。

研究方向

草原生态系统结构与功能、生物多样性与生态系统稳定性、全球变化等方面的生态学基础研究；

草原生态系统水、土、气、生要素的长期监测和资料积累；

生态系统管理特别是退化草地恢复、放牧和割草地管理、人工草地建设、生物多样性保育等方面的应用研究。

研究方法

1) 建立长期监测样地

内蒙古站的试验观测场主要包括综合观测场、辅助观测场和气象观测场。除了试验观测场的主辅样地外，内蒙古站还设有多个研究样地，主要包括：①羊草群落系列研究样地（1979 年围封区、1999 年围封区、2001 年围封区和自由放牧区）；②退化草地恢复生态学研究样地（1983 年围封区和外侧自由放牧区）；③浑善达克沙地大样地（2013 年，建于锡林郭勒盟正蓝旗桑根达来镇以北 30 公里的浑善达克沙地腹地，样地面积为 1000 米×1000 米）。

2) 建立长期实验平台

随着生态学研究的不断深入，野外长期定位研究的实验生态学受到各国生态学家的高度重视。以科学问题为导向的大型野外控制试验平台，已经成为内蒙古站基础研究的主要基地。2000 年以来，按照严格的统计学要求，内蒙古站设计实施了多个大型生态学实验平台（图 13.6-7）。

长期养分添加实验平台：自 2000 年开始实施，包括不同水平、不同时期氮素、磷素和有机肥添加的处理 50 个，每个处理 9 次重复，共 450 个小区。该实验对于揭示养分驱动的生态系统的响应机理以及草原生态系统的元素生物地球化学循环具有重要意义。

退化草地生态系统火因子调控实验平台：该实验平台建于 2005 年，包括 81 个处理、648 个实验小区。其研究结论有助于了解草原的退化机理、退化草地恢复的驱动因子、并为阐明火因子在草地生态系统结构和功能维持中的作用提供重要的实验证据。

生物多样性与生态系统功能实验平台：该实验平台是由内蒙古站与美国哥伦比亚大学、亚利桑那州立大学等单位的科学家共同设计的，包括 96 个处理，每个处理 8 次重复，共 768 个小区，2005 年启动。该实验不仅可以检验现有的生态学的重要理论，深入揭示草原生态系统结构、功能、过程相互之间的关系，特别是对于回答生物多样性与生态系功能的关系这一颇具争议的科学热点问题具有重要意义。

长期放牧实验平台：长期放牧实验平台是由中国和德国双方科学家于 2004 年共同建成的，36 个实验处理，实验小区总面积 200 多公顷，是迄今世界上具有多个放牧梯度的最大的长期受控放牧实验样地。主要研究不同放牧率对草地生态系统生产力和物质通量的影响，其研究结论对于指导我国北方典型草原生态系统的适应性管理具有重要理论价值。

降水实验平台：该实验平台建于 2013 年，包括大型防雨棚试验区和遮雨架试验区。该实验平台主要用于研究内蒙古典型草原生态系统对极端降水事件的响应阈值和应答机理以及对长期干旱的适应机制。

凋落物实验平台：该实验平台建于 2013 年，设置凋落物移除和添加两种实验处理，每种处理下设 0、50%和 100%三个处理梯度，共计实验小区 126 个。该实验平台主要研究

凋落物在维持草地生态系统生物多样性和生态系统功能稳定性方面的维持机制，为改善草地生态系统以及加速退化草地恢复提供理论依据。

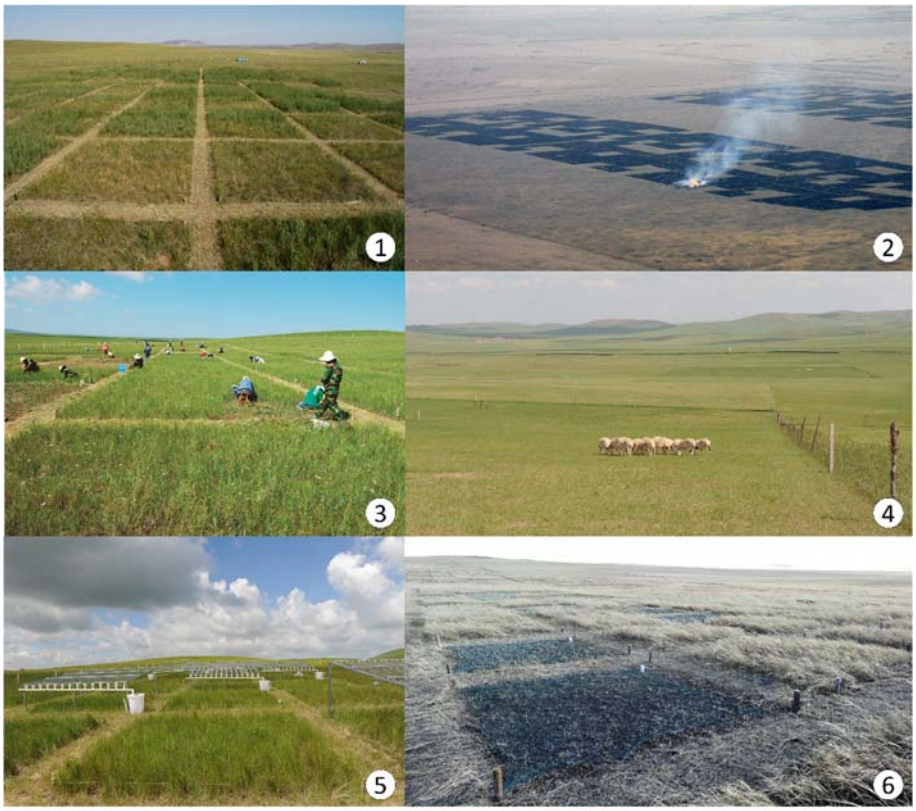


图 13.6-7 内蒙古站主要实验研究平台

注：①长期养分添加实验平台；②火烧处理实验平台；③生物多样性与生态系统功能试验平台；④长期放牧实验平台；⑤降水实验平台；⑥凋落物实验平台。

主要发现

建站以来，内蒙古站共发表各类研究论文 2100 余篇，其中在 Nature、Science、Ecology Letters、Ecological Monographs、Ecology、Global Change Biology 等 SCI 期刊发表论文近 700 篇，出版论著 30 余部，研究成果获得国家科技进步一等奖 1 项，国家和中国科学院自然科学奖 10 项。取得的重大原创性基础研究成果包括：1）基于近 40 年的长期监测和实验数据，揭示了内蒙古草原生物多样性与生态系统稳定性的维持机制；2）通过长期放牧控制实验，阐明了放牧对生态系统生产力、碳氮循环、温室气体排放和草原蝗虫爆发的调控机理；3）基于 20 年的控制实验数据和长期监测数据，揭示了草地生态系统服务对全球变化关键驱动因子敏感性及其响应和适应机制。

本章小结

生态系统内部和之间的空间异质性对单个生态系统和整个区域的功能至关重要。景观是由不同生态特性的斑块组成的嵌合体。例如，一些斑块是生物地球化学的热点地区，具有重要的地位。景观斑块的大小、形状、连通性和布局影响着它们之间的相互作用。例如，较大的斑块具有更多的资源和环境异质性，即较小的边缘生境比例。斑块的形状和连通性影响了它们的面积和异质性，影响方式因生物和生态过程而存在差异。景观斑块的分布很重要，因为它决定了相邻斑块之间物质转移和对邻近生态系统的干扰。斑块的边界具有与斑块中心不同的物理和生物特性，斑块的大小和形状不同，具有不同的内缘比，会影响斑块内生态过程的平均速率。

在景观中，生态系统并不是以孤立形式存在的。通过水、空气、物质、生物体的移动和干扰的传播，它们之间发生相互作用。

推荐阅读文献:

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., Turlure, C. 2013. Individual dispersal, landscape connectivity and ecological networks. Biological reviews 88:310-326.

Fahrig, L., Arroyo-Rodriguez, V., Bennett, J. R., Boucher-Lalonde, V., Cazetta, E., et al. 2019. Is habitat fragmentation bad for biodiversity? Biological Conservation 230:179-186.

Forman, R. T. T. 1995. Land mosaics: The ecology of landscapes and regions. Cambridge University Press, Cambridge.

Lovett, G. M., Jones, C.G., Turner, M.G., and Weathers, K. C. 2005. Ecosystem function in heterogeneous landscapes. Springer, New York.

Matson, P. A., Parton, W. J., Power, A. G., and Swift, M. J. 1997. Agricultural intensification and ecosystem properties. Science 227:504–509.

McDowell, N. G., Coops, N. C., Beck, P. S. A., Chambers, J. Q., Gangodagamage, C., et al. 2015. Global satellite monitoring of climate-induced vegetation disturbances. Trends in plant science 20:114-123.

Meyer, W. B., and Turner, B.L., III. 1992. Human population growth and global land-use/cover change. Annual Review of Ecology and Systematics 23:39-61.

Perino, A., Pereira, H. M., Navarro, L. M., Fernandez, N., Bullock, J. M., et al. 2019. Rewilding complex ecosystems. Science 364:351-358.

Pickett, S. T. A., and Cadenasso, M. L. 1995. Landscape ecology: Spatial heterogeneity in ecological systems. Science 269:331–334.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Wu, J. G. and Hobbs, R. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecology 17:355-365.

Wu, J. G. and Hobbs, R. J. 2007. Key Topics in Landscape Ecology. Cambridge University Press, Cambridge.

Wu, J. G. and Loucks, O. L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology 70:439-466.

Wu, J. G., Jones, K. B., Li, H. B., and Loucks, O. L. 2006. Scaling and Uncertainty Analysis in Ecology. Springer, Dordrecht, The Netherlands.

第十四章 地球系统的变化

生物地球化学循环：化学元素和分子通过生物的（生物圈）和非生物的（岩石圈、大气圈、水圈）地球组分的移动途径。理解 H_2O，C，N，P，P 的循环对于理解生态系统、生物圈和整个地球系统非常关键。化石燃料的燃烧会增加 CO_2、NO 和几种含硫气体的排放。采矿和农业：改变 C, N, P, S 的可利用性和移动性。

人类活动改变了全球范围内的生物地球化学循环，从而改变了地球作为生态系统的功能。自工业革命开始以来，人类活动极大地改变了元素循环。特别是化石燃料的燃烧增加了二氧化碳、一氧化氮和几种含硫气体的排放。采矿和农业也改变了碳、氮、磷和硫的可利用性和流动性。这些生物地球化学循环的变化改变了地球的气候，加速了全球水文循环，反过来又反馈到其他生物地球化学循环。这些变化一起改变了从单个生物体到整个生物圈等多种尺度的生态系统。

人类活动的综合效应已经改变了全球尺度的生物地球化学循环。化石燃料的燃烧使大气中的二氧化碳浓度增加了 35%，也使海洋的酸度增加了类似比例。海洋酸化引起的大多数问题我们无法直接观察到，但是，通过溶解海洋生物的碳酸钙结构如珊瑚、海洋无脊椎动物如贻贝和螃蟹以及显微镜下的有孔虫类（它们是海洋食物链的重要基础），从而对海洋生态系统产生深远影响。许多海洋珊瑚礁已经受到温度上升变暖导致的珊瑚白化以及陆地上的营养和沉积物径流的威胁。人类的多重影响如何交互影响珊瑚礁的发展和它们所支撑的多样的生态系统？改变世界海洋的食物基础的潜在后果是什么？海洋生产力的变化如何对地球二氧化碳浓度和气候做出反馈？与陆地生物圈影响气候的能力变化相比，这些影响是大还是小？把这些重要问题放在一个综合的背景下去理解全球生物地球化学循环，可以指示人类社会行为的交互后果。

第一节　全球水循环

1.1 水库和通量 (Water Pools and Fluxes)

全球的水仅有 0.01%存在于土壤，这些水被植物获取并且支撑了陆地生命的活动。地球上大多数水存在于海洋（96.5%）、冰冠和冰川（2.4%）和地下水（1%）。大约 90%的从海洋中蒸发的水会以降雨的形式返回海洋。另外 10%以湿润水汽的形式穿过陆地，形成降雨并且通过江河径流返回海洋（图 14.1-1）。陆地蒸发量（65, 000 km^3 $year^{-1}$）约占全球蒸发量的 15%，虽然陆地约占地球表面的 30%；这表明陆地上的平均蒸发蒸腾速率大约是海洋上的一半。与气候有关的陆地和海洋的蒸发率具有很大的区域差异；就陆地而言，水的了利用性和植被的蒸腾速率同样具有很大的区域差异。陆地降水（110, 000 km^3 $year^{-1}$）中，约 40%来自海洋（45, 000 km^3 $year^{-1}$），60%（65, 000 km^3 $year^{-1}$）来自陆地和再循环。蒸发和降水在区域和季节上

都有很大的变化。

大气中的水量仅为每年在大气中循环蒸发和蒸腾水量的2.6%，平均周转时间约为10天。因此，在数小时到数周的时间尺度上，降水与逆风生态系统的蒸散发密切相关。土壤水分的平均周转时间在2个月左右，具有较大的区域变异性，因此植物水分利用对降水的季节变化非常敏感。地下水的平均周转时间约为200年。这使它成为比地表水分更可靠的水源，但也意味着如果过度开采用于灌溉或其他用途，地下水的补充需要很长时间。随着持续的气候变暖，湿润地区预计将变得更加湿润，洪涝更加频繁，干燥地区可能会变得更加干燥。

1.2 人类活动引起的水循环变化 (Anthropogenic Changes in the Water Cycle)

人类活动已经改变了全球水循环，主要通过改变改变契合和地球能量收支（图14.1-1）。当地球的空气变暖时，它会携带更多的水分，导致更大的蒸发，增加降水的可能性。例如，在20世纪，陆地上的降水在北纬30度以北呈现增加趋势。土地利用变化也通过改变（1）能量吸收量；（2）能量损失途径和（3）大气水分和温度来改变水文循环。例如，从热带雨林到牧场的转变导致能量吸收减少，因为反射率增加，而且更大比例的能量以显热而不是潜热的形式耗散到大气中。温暖干燥的大气带来较少的降水，有利于草场的持久生长，而不是雨林的演替。当土地利用变化加剧时，由于大气环流的大规模调整，它们往往在远离土地覆盖变化区域的地点对温度和降水产生大陆尺度的影响。例如，东南亚的土地覆盖变化通过大气远距联系对全球范围的气候产生了特别大的影响。陆地生态系统一般对土壤湿度比对降水更敏感。在降水量减少的地区和蒸发增加多于降水量的地区，土壤水分可能会下降。模型一般预测高纬度地区和海洋岛屿的土壤湿度增加，大陆内部的夏季土壤湿度减少，这是由于较高的温度和不充分降雨增加（或减少）。目前许多对农业非常重要的大陆地区，比如乌克兰和美国中西部，可能特别容易在未来遭遇干旱，而粮食产区可能会向极地迁移。适宜农业的土壤水分位置的变化将对区域和国家产生重大的经济和社会影响。

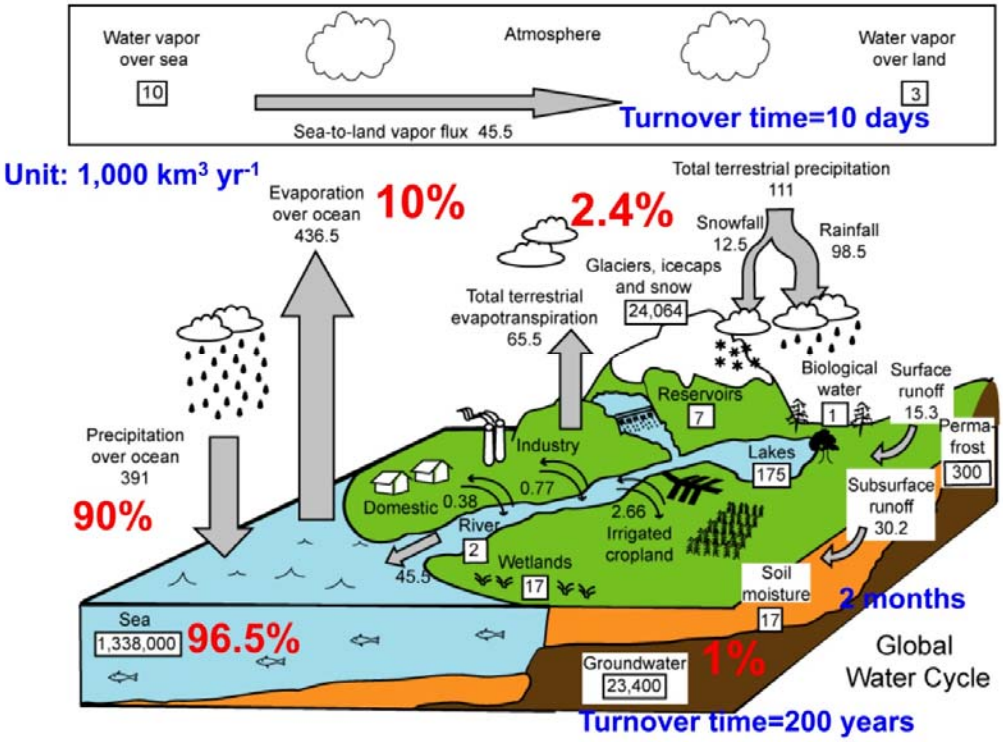


图 14.1-1 全球水循环图。图中展示了主要的库（1000km³；方框）和通量（1000km³ 年⁻¹；箭头）。大多数水以海水、冰川、地下水的形式存在，从而不能直接被陆地生物利用。主要的水通量形式是降水、蒸发、径流。修改自 Carpenter and Biggs (2009)。

1.3 水循环改变的后果 (Consequences of Changes in the Water Cycle)

人类社会大多数直接依赖于在水循环中一些最小和最脆弱的库（图 14.1-2）。

例如，非灌溉农业依赖于降水产生的土壤水分，这是一个相对较小的库，对降水和蒸散发之间平衡的变化迅速作出反应。在一些地区，从降水中获得的土壤水分通过灌溉补充，即从湖泊、河流和地下水中获取水分。在 20 世纪，灌溉农田增加了 5 倍，支撑着全球 40%的作物产量。在过去的一个世纪里，用于支持人类活动的用水量增加了 8 倍；与此同时，人口增加了 4 倍，人均用水量增加了 50%。现在人们使用了 25%的大陆径流，其中大部分用于水力发电和灌溉。在世界非常贫穷地区有选择地扩大灌溉农业是减轻饥饿和贫穷的一个重要机会。缺水只是社会面临的水文挑战的一部分。2004 年，40%的世界人口无法获得适当的卫生设施，17%的人没有干净的饮用水。洁净水的短缺在世界发展中国家尤其严重，这些国家未来的人口增长和对水的需求可能是最大的。人类对淡水需求的预计增长将对水生生态系统产生强烈的影响，因为淡水将被用于灌溉，水坝和水库将改变水田灌溉系统。这些影响可以通过提高社会用水和营养的效率来最小化。

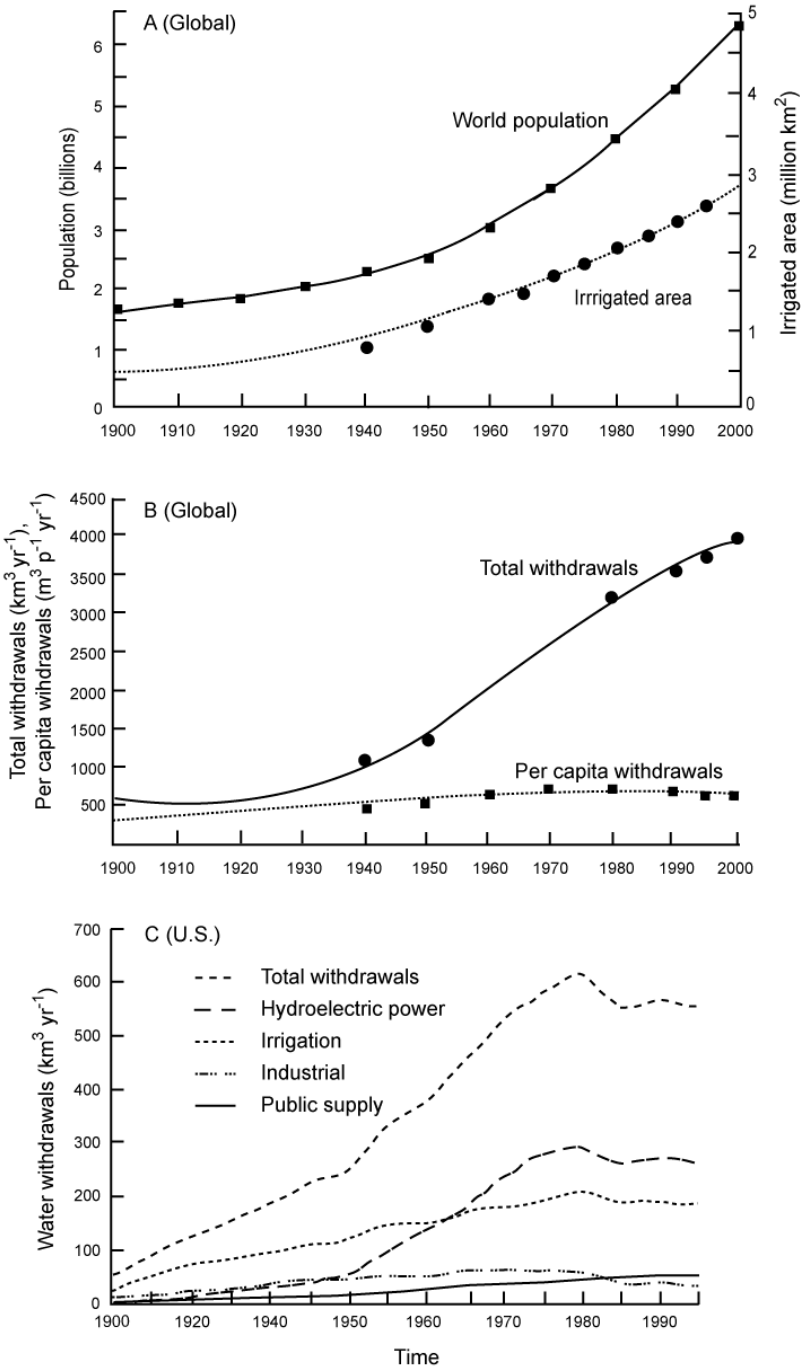


图 14.1-2（a）世界人口和全球灌溉土地面积的年际变化趋势，（b）全球用水总量和人均量的年际变化趋势，（c）美国不同经济活动的取水量年际变化趋势。Gleick(1998)重绘。

第二节　全球碳循环

2.1 碳库和通量 (Carbon Pools and Fluxes)

从大气和海洋中吸收碳的光合作用为大多数生物过程提供了燃料。这些被还原的碳约占地球有机物质质量的一半。反过来，生物系统在使用有机碳作为维持和生长的能源时，呼吸释放二氧化碳。对碳循环的控制取决于时间尺度，从秒到几百万年，循环由光合速率和地表空气交换控制，循环由地壳运动控制。碳分布在四个主要的资源库中（图 14.2-1）:大气、海洋、陆地(土壤和植被)、沉积物和岩石。大气碳库主要由二氧化碳组成，是这些碳库中最小但最具活力的。它大约每 5 年周转一次，主要是通过光合作用去除，然后通过呼吸作用返回。因此，生物体的新陈代谢是推动全球碳循环的动力，其时间跨度从几秒到几个世纪不等。

碳以可溶解有机碳（DOC）、可溶解无机碳（DIC）和颗粒有机碳（POC）的形式存在于海洋中，其中既有活的生物体，也有死的物质。大部分碳是无机形式（98%），主要是碳酸氢盐（90%），其余大部分是碳酸盐。大多数海洋初级生者直接使用的游离二氧化碳在无机库中所占比例不到 1%。这三种类型的 DIC 处于依赖于 pH 的平衡状态。海洋生物只占 3 Pg（3×10^{15} g）的碳，尽管它们每年循环的碳几乎和陆地植被一样多。海洋生物群中的碳大约每 3 周就会周转一次。

陆地生物圈含有最大的生物碳库。陆地植被中的碳含量几乎与大气中的一样多，土壤中的有机碳含量是大气中的 2-3 倍。冻土（永久冻土）也含有一个巨大的碳库，直到最近，碳库的周转非常缓慢。陆地上的 NPP 略大于海洋中，但由于陆地上的植物生物量大得多，陆地上植物碳的周转期约为 11 年，而海洋中为 3 周。在陆地和海洋中，NPP 约为 GPP 的一半。土壤碳库平均每 25 年更新一次。这些平均循环时间掩盖了陆地碳循环各组成部分在循环时间上的巨大差异。在光合作用过程中，叶绿体中的碳通过光呼吸在数秒的时间尺度内周转。树叶和根的周转需要几周到几年的时间，木材的周转需要几十年到几百年的时间。土壤有机质成分的周转期也有很大的不同，不稳定形态的土壤周转期在几分钟内，腐殖质的周转期在几十年到几千年之间。

岩石和沉积物中的碳占地球碳总量的 99%以上（107 Pg）。碳库的循环极其缓慢，循环时间长达数百万年。控制这些库周转的因素是与岩石循环有关的地质过程，包括大陆板块运动、火山活动、隆升和风化作用。

人类活动现已成为全球碳循环的重要组成部分。从 1990 年到 2008 年，人类燃烧化石燃料产生的碳排放增加了 40%。土地利用变化每年通过物质燃烧和提高分解额外释放 1.5 Pg 的碳。这些人为碳排放总量约占陆地或海洋碳循环总量的 15%，使人类碳排放成为由生物控制的大气碳排放总量的第三位。

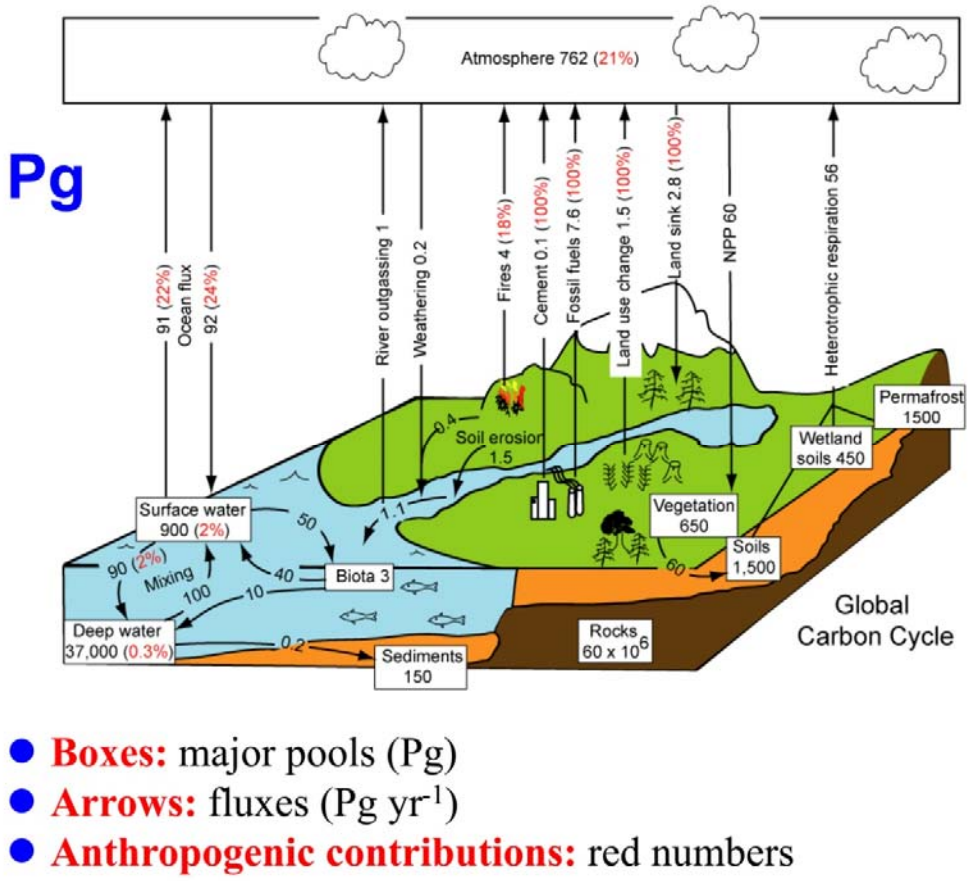


图 14.2-1 全球碳循环图。图中所示主要的碳库（方框）和碳通量（箭头）。1 Pg 等于 1 ×10^{15}g。括号内的红色数字是人类对碳库和碳通量的影响（相对于工业革命之前 1750 年）。数据来自 Sabine et al.(2004), Sarmiento and Gruber (2006)和 IPCC(2007)，2002-2006 年人类的碳通量数据卡 Canadell et al. (2007)。在过去几十年到几百年中，对于碳循环有贡献的碳库包括大气、陆地（植被和土壤）和表层海水。在陆地上，CO_2 升高和氮沉降对碳收获的施肥效应稍微大于土地利用改变带来的碳支出。相近数量的陆地碳被侵蚀进入河流，其中有一半进入大气，另一半被截获在海洋。从大气进入海洋的碳通量稍大于从海洋进入大气的碳通量。这些陆地和海洋的碳汇低于化石燃料燃烧释放 CO_2 的一半，导致大气中 CO2 累积。陆地生物圈贡献了 50-60%的全球 NPP。大多数（80%）的海洋 NPP 固定的碳通过异氧呼吸释放到环境中，剩余的 20%通过生物泵进入海洋中。海洋的提升作用将这部分深海碳库重新带回到表层海水。

2.2 大气 CO_2 的变化 (Changes in Atmospheric CO_2)

碳循环中的关键过程能够在在多个时间尺度上对环境作出响应。在数秒到数年的时间尺度上，对碳循环的关键控制是光合作用和呼吸；从年到世纪时间尺度上的 NPP、SOM 周转转和扰动；从数千到数百万年的隆升、风化和海洋沉积。在地球的历史上，大气中的二氧化碳浓度变化了至少 10 倍，从工业化前的 280 ppmv 到 3000 ppmv 以上。地球化学过程决定了大气中二氧化碳在地质时间尺度上的变化。其中包括硅酸盐岩石的风化（消耗二氧化碳并释放碳酸氢盐），有机碳在沉积物中的埋藏，以及火山作用（释放二氧化碳）。生物过程

在许多方面影响地球化学循环，例如增加风化速率。虽然在长期尺度上至关重要，但这些地球化学过程的速率与人为变化相比非常缓慢，因此它们不影响大气中二氧化碳变化的当前轨迹。

在过去的 65 万年中，太阳输入的变化与地球轨道的变化导致的与冰期-间冰期循环相关的大气二氧化碳浓度的循环变化。二氧化碳浓度在冰期下降，在间冰期上升。这些二氧化碳浓度的变化远远大于简单的光强和温度的变化，以响应改变的太阳输入。大的生物圈变化必然是地球系统中生物地球化学反馈放大的结果。

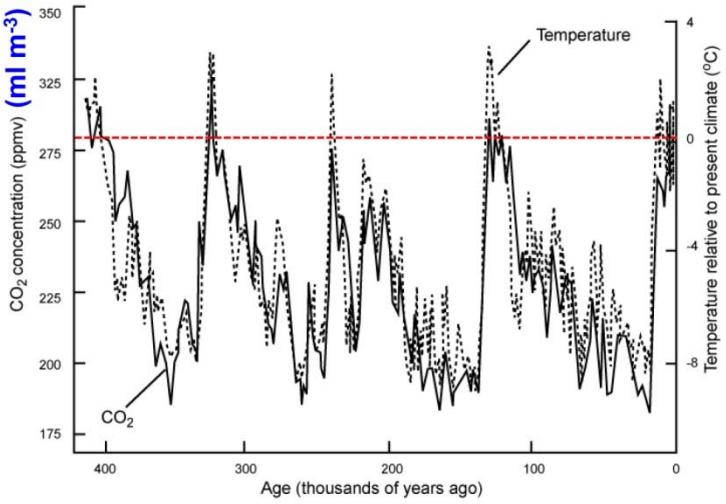


图 14.2-2 从北极冰芯的气泡中推测的温度和大气 CO_2 浓度的变化趋势。重绘 Folland *et al*. (2001)。

（1）冰期从植被少的大陆上增加的沙尘转移可能增加了铁、磷、硅的输移和 NPP 的增强，导致二氧化碳吸收增加，并通过生物泵转移到深度。（2）南极洲周围广泛的冬季海冰可能减少了富含二氧化碳的深水区释放出二氧化碳。（3）在冰河时期，更多的碳可能被储存在陆地上—无论是由于海平面下降而暴露在大陆架上，还是高纬度地区的永久冻土层上。然而，在冰河时期，由于草原、沙漠、苔原和冰原取代了森林，陆地系统也失去了碳。尽管所有这些变化的净效应是不确定的，但在冰川循环的过程中，已经有了大量的碳在陆地、大气和海洋之间重新分配。对控制全球碳库再分配的更好理解，可以表明地球系统将如何应对当前温度和大气二氧化碳浓度的上升趋势。

就像空气温度一样，大气中的二氧化碳浓度在过去的 12000 年里一直相对稳定，在前工业时代从大约 260 到 280 ppmv。然而，在过去的一个世纪里，二氧化碳浓度的增长速度是过去 2 万年里任何时候的 10 倍。2011 年二氧化碳的浓度为 390 ppmv，至少是 65 万年，也可能是过去 2000 万年中最高的。尽管最近作出了减少排放的努力，大气中的二氧化碳仍在以越来越快的速度上升。这主要是由于排放量的增加，特别是在中国和印度等快速发展的国家，以及美国、日本和欧洲等发达国家持续的高排放率。最近由人类活动引起的碳和其他元素的全球循环变化大到足以表明地球已经进入了一个新的地质时代。

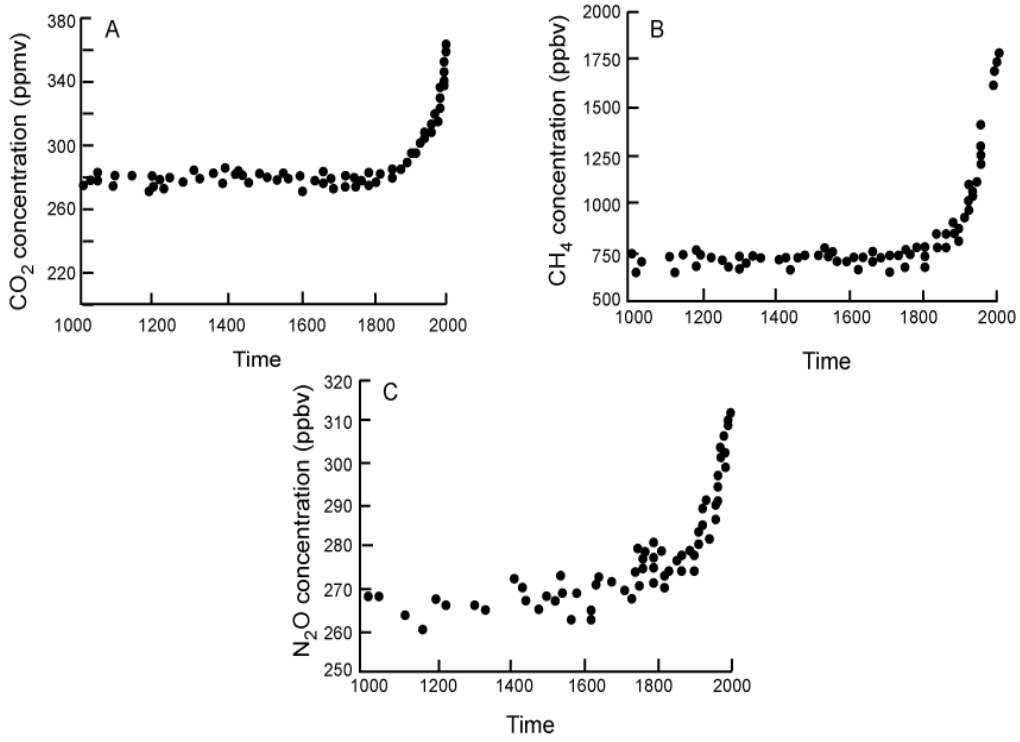


图 14.2-3 三种温室气体在大气中的浓度在最近一千年受到人类活动的显著影响。

2.3 海洋 CO_2 汇(Marine Sinks for CO_2)

海洋会通过溶解在海水和海洋生物的光合作用以移除大气中的 CO_2。二氧化碳在海洋中的溶解是二氧化碳流向海洋的主要原因，当它与碳酸氢盐和碳酸根离子平衡时产生氢离子（H^+）。溶解二氧化碳浓度的上升以及由此导致的海洋酸度 30%的增加至少会带来两个重要后果。它会溶解海洋无脊椎动物和硅藻的碳酸盐壳，改变海洋生态系统的功能。此外，它还降低了二氧化碳在海洋中溶解的速度——也就是说，使海洋成为更弱的二氧化碳吸收区。这使得化石燃料碳的比例越来越大，而化石燃料碳仍作为温室气体存在于大气中.

表 14.2-1 2000-2006 年的人类碳排放的年均量和流向。改自 Canadell et al. (2007) and Le Quere et al. (2009)

Sources and sinks of anthropogenic carbon	Annual net flux (Pg C year^{-1})
Anthropogenic carbon sources	9.1
Fossil fuel and cement production (8.7 in 2008)	7.6
Land-use change	1.5
Carbon sinks (190-2000)	9.1
Storage in the atmosphere	4.1
Oceanic uptake	2.2
Terrestrial uptake	2.8

4 陆地 CO_2 汇(Terrestrial Sinks for CO_2)

土地利用变化、二氧化浓度增加、氮沉降和各种气候效应都有助于二氧化碳被陆地吸。在二十世纪中期以前，中高纬度地区的土地利用变化主要是将森林转为农业用地。如今，废弃农业土地上的森林再生增强了碳储存，尤其是在欧洲和北美。广泛的抑制野火也增加了中纬度的碳汇，因为它减少了火灾的排放，并允许木本植物侵入草原。这些可能是北温带陆地生态系统作为净碳汇的最重要原因。与此同时，热带地区森林砍伐率的增加减少了低纬度地区的碳汇。

表 14.2-2 全球陆地区系分布及其植物生物量中总碳

Biome	Area (10^6 km^2)	Total C pool (Pg C)	Total NPP (Pg C yr^{-1})
Tropical forests	17.5	340	21.9
Temperate forests	10.4	139	8.1
Boreal forests	13.7	57	2.6
Mediterranean shrublands	2.8	17	1.4
Tropical savannas and grasslands	27.6	79	14.9
Temperate grasslands	15	6	5.6
Deserts	27.7	10	3.5
Arctic tundra	5.6	2	0.5
Crop	13.5	4	4.1
Ice	15.5		
Total	149.3	652	62.6

光合作用的二氧化碳增强也有助于碳储存，尽管不如光合作用对二氧化碳的短期反应所暗示的那么多。从长远来看，二氧化碳的吸收会受到养分的限制，因为营养物质被隔离在活的和死的有机物中。二氧化碳浓度升高对碳储存的影响似乎比温带重新造林的影响要小，但在热带地区，二氧化碳浓度升高似乎足以抵消毁林造成的碳化能力的损失。氮肥的施用或化石燃料燃烧产生的氮氧化物等空气污染物在大气中的沉积，刺激了光合作用，减少了呼吸作用，导致一些地方有更大的碳储存量。

最后，气候变化（包括温度、湿度和辐射的变化）通过影响碳输入（光合作用）和输出（呼吸作用）影响碳储存。这些影响因区域而异，难以一概而论，因为直接的气候影响（例如，温度升高对呼吸碳损失的刺激）往往被间接影响所抵消。植被的碳氮比（160:1）通常比土壤有机质（14:1）高得多，因此，一定数量的氮从土壤向植物的转移促进了碳的储存。

陆地生物圈中增大碳储存的各种机制的相对重要性尚不确定，但它们加在一起可能足以解释观测到的一小部分人为二氧化碳从大气向和陆地的移动。正如海洋那样，陆地碳汇的强度似乎正在减弱，这表明，各种碳汇机制（森林再生、二氧化碳施肥、氮添加和气候效应）

正开始饱和，可能在未来只能从大气中去除较少的二氧化碳。因此，稳定大气中二氧化碳浓度的最有效机制是减少人为排放。

5 CO_2 对气候的影响 (CO_2 Effects on Climate)

增加的化石燃料产生的CO_2将会在大气中存在数百年至数千年。如果今天所有人为排都停止，30年内约有一半将被陆地和海洋吸收，其中约30%将在大气中存留几个世纪，剩下的20%将在大气中存留数千年。二氧化碳从大气中缓慢消失的原因至少有四个:（1）如前所述，陆地和海洋的吸收效率正在减弱；（2）深海是二氧化碳的长期主要碳汇，与表层海洋和大气的平衡非常缓慢；（3）稳定反馈尽量减少生态系统碳库的变化-例如，由于光合作用增加和凋落物投入增加而产生的分解增加；硅酸盐岩石是陆地上长期吸收二氧化碳最多的地方，其风化过程非常缓慢。因为二氧化碳是导致气候变暖的最大人为因素，过去的二氧化碳排放已经使我们的地球变暖，关于未来排放的决定将强烈影响持续的气候变暖的程度。此外，由于温室气体浓度增加而吸收的大部分热量已经进入海洋，并将返回到大气中，即使自然循环或某些（尚不清楚）技术解决方案立即将所有化石燃料中的碳从大气中移除。这种对未来变暖的长期承诺加剧了人们的担忧，即地球已经接近或可能超过了“危险气候变化”的临界值，需要迅速而有力地努力减少对大气的碳排放。

6 全球甲烷收支 (The Global Methane Budget)

人类活动是大气中甲烷浓度增加的原因。虽然大气中甲烷的浓度（1.8 ppmv）远低于二氧化碳（390 ppmv），但CH_4作为一种温室气体，其每个分子的效率是二氧化碳的23倍。与二氧化碳一样，大气中的CH_4浓度自工业革命开始以来呈指数级增长。甲烷的增加占大气温室效应增加潜力的20%。因此，记录大气中CH_4的主要全球来源和汇，对于了解最近全球气温的上升和未来气候变暖的可能性十分重要。

甲烷只能在厌氧条件下产生。湿地占自然产生的CH_4的85%，其余主要来自淡水沉积物、动物肠道的发酵，以及各种地质来源。人为产生的甲烷比自然产生的甲烷要大2.5倍，这说明了尽管甲烷具有很高的反应性和快速的循环（9年），但它仍能在大气中积累。化石燃料的提取和提炼；废物管理（废弃物、动物废弃物及生活污水处理）；农业来源（稻田、生物质燃烧、家畜等家畜的肠道发酵）都是重要的CH_4来源。大气中的浓度和积累速率已经相当精确了，但不同源和汇的相对贡献仍然是争论的主题。重要的新来源仍在被发现，包括高纬度的融冰湖泊和有机物丰富的水库。在阳光的照射下，CH_4很容易与大气中的OH自由基反应。这种光化学过程是大气中CH_4的主要汇储，占CH_4消耗量的85%。另外的甲烷会混入平流层，与臭氧发生反应，或者被土壤中的甲烷营养物去除。每年大气中CH_4的蓄积约为人为年氟氯化碳的10%，而二氧化碳的蓄积约为50%。

表14.2-3 全球甲烷的源和汇。数据来自Wang et al.(2004), Chen and Prinn (2006), IPCC (2007)

Methane sources and sinks	Annual flux (Tg CH_4 year^{-1})
Natural sources	168
Wetlands	145
Termites and ruminants	23
Anthropogenic sources	428
Coal combustion	48
Oil and gas combustion	36
Landfills and waste	70
Fermentation by cattle	119
Rice agriculture	112
Biomass burning	43
Total sources	596
Sinks	581
Reaction with OH	511
Removal by soils	40
Removal by soils	30
Atmospheric increase	1-22

第三节　全球氮循环

许多自然生态系统的生产力，不管是陆地还是海洋的，不论是人工管理的农业还是森林生态系统，都受到氮元素的限制。在过去一个世纪，人类活动导致陆地生态系统和大气之间的氮循环速率增加了 1 倍。许多含氮痕量气体从地球向大气的排放应该归咎于人类活动。

3.1 氮库和通量 (Nitrogen Pools and Fluxes)

许多陆地和海洋生态系统的生产力在一定程度上受到可用性氮供应的限制。几乎所有与生物地球化学有关的氮都在一个单一的库（大气）中，在海洋、岩石和沉积物中含量相对较少（图 14.3-1）。有机氮库相对于大气库是极小的，主要存在于土壤和陆地植被中。虽然氮占大气的 78%，但它几乎全是 N_2，对大多数生物来说都是不可用的。通过土壤和水生系统中的细菌或与植物共生的细菌的固氮作用，氮被转化为生物可利用的形式。全球自然生态系统每年的固氮量很不确定，陆地生态系统估计为 100 Tg year^{-1}，海洋生态系统估计为 40～200 Tg year^{-1}。闪电可能会给可利用氮库增加 3 Tg year^{-1} 的氮。在人类改变之前，通过固氮进入生物圈的氮与通过反硝化作用和埋藏在沉积物中返回到不可用库中的氮大致达到了平衡。在冰期，铁和其他微量营养元素的输入可能导致氮含量超过反硝化作用量，降低了海洋中的氮限制程度。在间冰期，例如现在，反硝化作用可能超过固氮作用。目前海洋固氮与反

硝化作用的平衡或不平衡程度存在较大争议(Falkowski et al. 1998)。与碳相比，氮在陆地生态系统中循环得非常紧密，其年吞吐量通常至少是输入和损失的四倍。

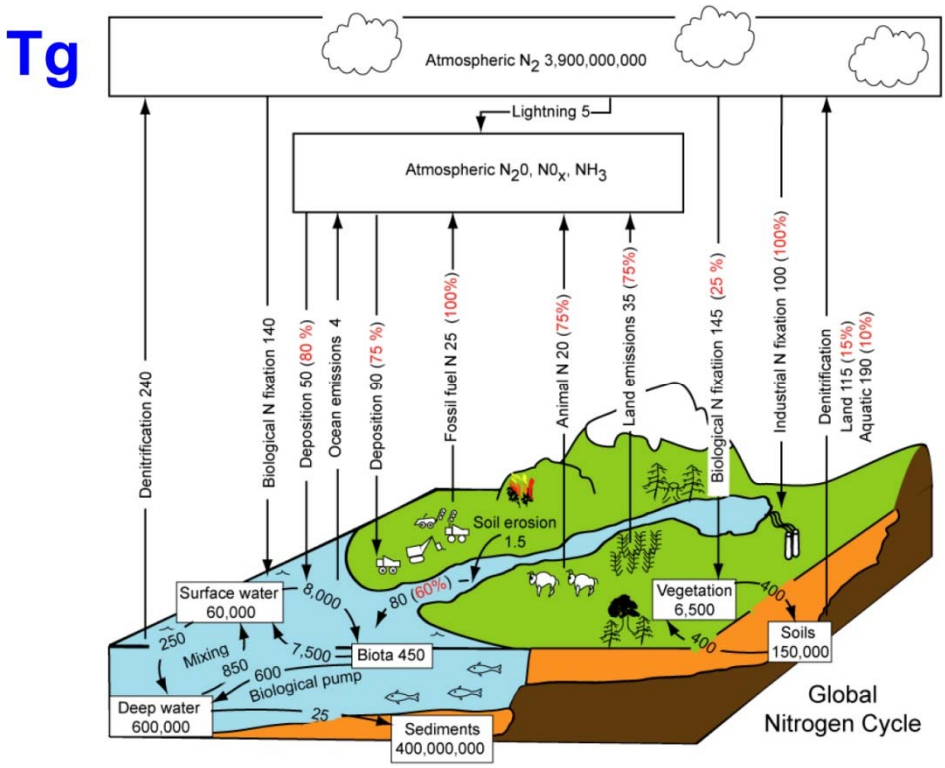


图 14.3-1 全球氮循环图。图中表明主要的氮库（方框）和氮通量（箭头）。1 Tg 等于 1×10^{12}g. 括号内的数字代表人类活动对这些氮库和氮通量的贡献。数据来自 Reeburgh(1997), Chapin *et al*.(2002), Galloway et al. (2004), Gruber and Galloway (2008). 为了保证全球循环在不同元素间的一致性，生物的氮源和通量的数据来自于全球碳收支的换算，并且将海洋生物的 C:N 比赋值 6.6，陆地植被的 C:N 比赋值 100 和陆地凋落物的 C:N 比赋值 150（Sterner and Elser 2002）。该计算结果与全球氮收支直接估测数值接近。大气包含了地球上最多的单元所。 通过陆地非农作物植被的氮元素总量比固氮输入量多 4 倍。在海洋中，每年通过生物的氮循环通量是固氮输入量的 60 倍。反硝化是氮进入大气的主要途径。人类活动通过生产废料、种植固氮作物和燃烧化石燃料，增加了氮元素输入。人类活动也会增加含氮痕量气体的排放（NO_2, N_2O，NH_3），例如化石燃料燃烧、土地利用（农业、火烧、土地利用方式改变）、畜牧业等人类活动。

3.2 人类活动引起的氮循环变化 (Anthropogenic Changes in the Nitrogen Cycle)

氮沉降会影响许多生态系统过程。人类活动会增加陆地生态系统的氮损失和向水生生态系统的氮转移。Haber 过程是利用化石燃料中的能量将 N_2 转化为 NH_3 来生产肥料，它固定的氮比任何其他人为过程都多。20 世纪 40 年代，利用 Haber 法工业固氮开始大幅增加（14.3-2），1970 年达到 30 Tg year^{-1}, 2000 年达到 100 Tg year^{-1}。预计到 2050 年为 165 Tg year^{-1} (Galloway et al. 2004)。最初，大部分氮肥在发达国家施用，但从 2000 年到 2009 年，全球氮

肥使用量增长的 80%发生在中国和印度。预计化肥使用的大部分增加将发生在发展中国家。

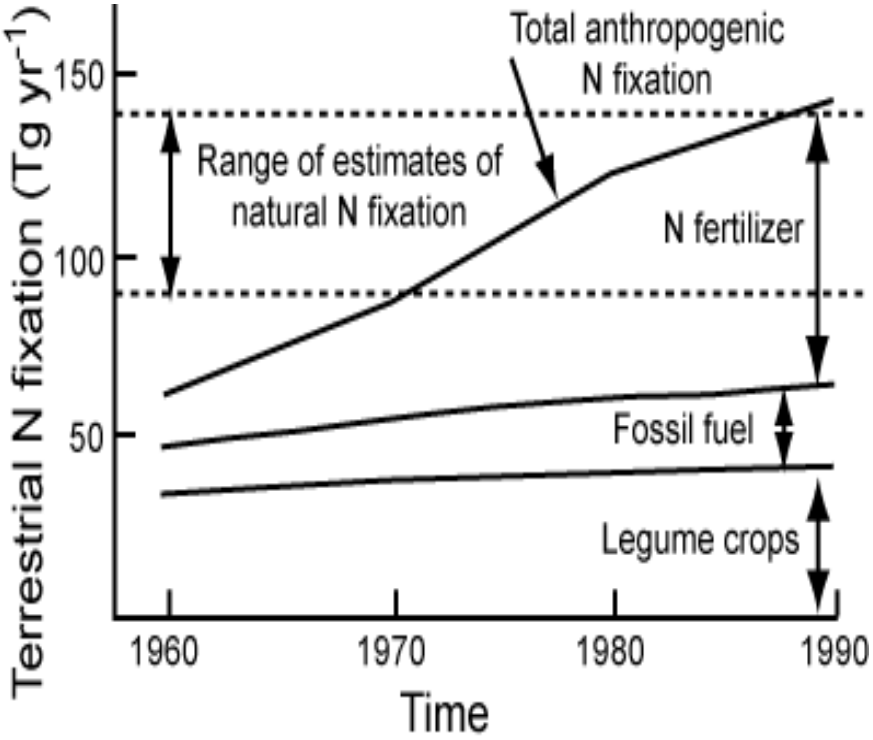


图 14.3-2 陆地生态系统中人类固氮量的年际变化趋势，与陆地自然固氮量的估算范围做比较。重绘 Vitousek et al.(1997)。

从地球转移到大气中的含氮气体大部分是由人类活动造成的。除了大量相对不活跃的氮气外，大气中还含有几种氮微量气体，包括 NO_x(NO 和 NO_2)、N_2O 和 NH_3。虽然这些氮微量气体的库和通量比 N_2 的要小得多，但它们在大气化学中起着非常积极的作用，受到人类活动的影响更大。一氧化二氮（N_2O）以每年 0.2-0.3%的速度增长，是一种惰性气体，其温室效应是二氧化碳的 200 倍，对温室效应的影响约为 6%(IPCC 2007)。海洋和热带土壤中的硝化作用和反硝化作用是 N_2O 的主要自然来源(Schlesinger 1997, Galloway et al. 2004)。人类活动使从地球到大气的氧化亚氮通量增加了近一倍，主要是通过农业施肥。其他人为的一氧化二氮来源包括牛和饲养场、生物质燃烧和各种工业来源。氧化亚氮在平流层中分解，催化平流层臭氧的破坏。人类活动使陆地到大气中的氨通量增加了两倍 (Galloway et al. 2004)。家畜现在是全球最大的氨来源；农业施肥、生物质燃烧和人类污水也是其他重要来源。耕地仅占无冰土地面积的 10%，约占从土壤到大气的氨通量的一半。总之，与农业有关的活动（畜牧业、化肥添加和生物质燃烧）是氨向大气输送增加的主要原因，占全球通量的 60%。氨是许多大气反应的反应物，形成气溶胶和产生空气污染。氨也是大气中主要的酸中和剂，它会提高降雨和气溶胶的 pH 值。大部分释放到大气中的氨以降水的形式返回地球。

氮沉降导致的自然生态系统养分增加是全球变化的重要内容。研究表明氮沉降显著影响

干旱区和半干旱区的植物多样性、群落生产力、土壤生物结构组成和土壤碳氮循环等多个陆地生态系统过程和功能(Suding and Collins et al. 2005, Clark and Tilman 2008, Yang et al. 2012, Hautier et al. 2014)。非热带生态系统中普遍存在的氮限制或植物生产的共同限制导致在生态系统中沉积的大量人为氮被保留下来，特别是在正在植物中积累养分的年轻、生长活跃的森林中。氮沉降通常通过刺激氮限制地点的初级生产和减少富氮地方的异养呼吸来促进碳存储(Magnani et al. 2007, de Vries et al. 2009, Janssens et al. 2010)。氮素在生产和有机质储存中的积累不能持续增加。经过长期的氮输入，氮素供应可能会超过植物和微生物的需求，导致氮素饱和(Driscoll et al. 2001)。当生态系统氮饱和时，流向水流、地下水和大气的氮流失会增加，最终接近氮输入量。在欧洲(Schulze 1989)和美国(Aber et al. 1995, Fahey et al. 2005)，氮饱和通常与森林生产力下降和针叶林树木死亡率上升有关。

温带森林在接近氮饱和的速率方面因区域而异，这取决于氮输入的速率和土壤缓冲这些输入的能力(Juice et al. 2006)。在热带森林中，氮的利用率相对于植物和微生物的需求通常较高，人为氮沉降可能会导致氮的流失(Hall and Matson 1998)，这可能会对植物和土壤过程产生潜在的负面影响(Matson et al. 1999)。一般来说，森林生态系统保持氮的能力与其生产潜力和氮的限制程度有关。有限营养物质的添加会改变物种的优势地位，减少生态系统的多样性。例如，草原或石南丛生地的氮添加增加了喜氮植物的优势，从而抑制了其他植物物种(Berendse et al. 1993)。这些物种的变化可以将营养贫乏、多样化的石楠丛地转变为物种贫乏的森林和草原。

第四节　全球磷循环

在大量元素的循环中，磷循环很独特，因为它仅有极小部分是气态的，并且缺乏可以将新的磷元素带入到生态系统的生物途径。海洋和淡水沉积物、陆地土壤占据了大部分的地表磷元素分布。全球磷循环（不考虑人类活动）的主要磷通量是通过从陆地向海洋的水动力运输。

4.1 磷库和通量 (Phosphorus Pools and Fluxes)

与碳和氮不同，磷只有微小的气体成分，没有生物途径将新的磷带入生态系统。因此，直到最近，生态系统才从有机形式中获得磷，磷在陆地生态系统中循环得非常紧密。和氮一样，磷也是一种经常短缺的必要营养物质。海洋和淡水沉积物以及陆地土壤是地球表面磷的主要来源(图 14.4-1)。这些储存大部分不能直接进入生物群，而是主要以不溶性的形式存在，如钙或磷酸铁。大部分有机磷存在于植物或微生物中。有机物死后的循环利用是磷的主要来源，生物体可以直接利用这一部分磷。

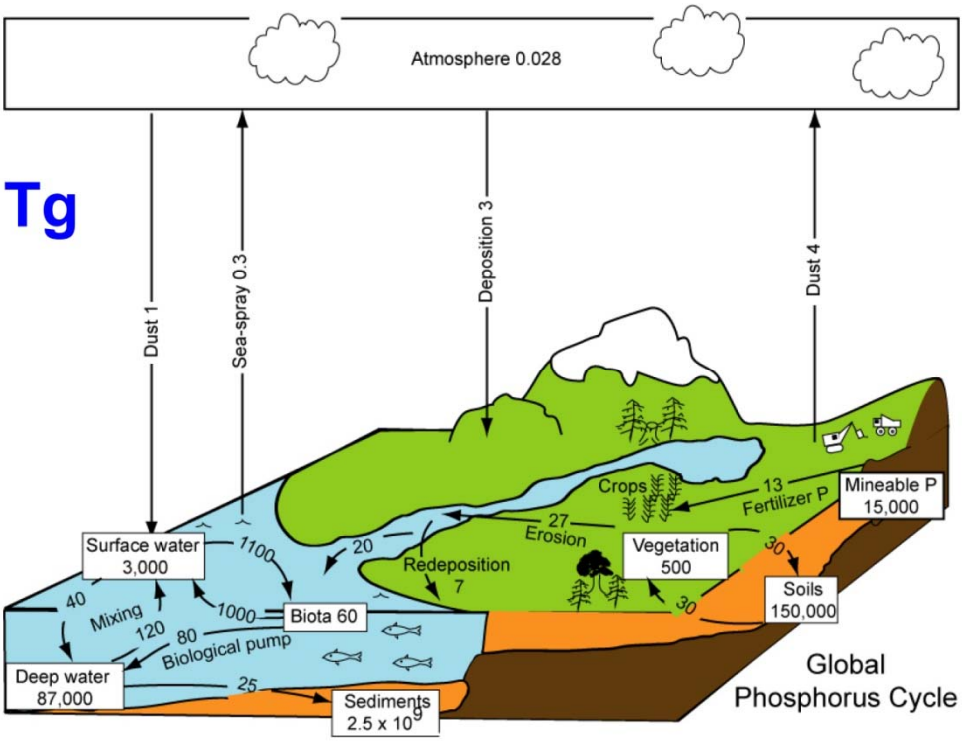


图 14.4-1 全球磷循环图。图中所示主要的库（方框）和通量（箭头）。1 Tg 等于 1×10^{12}g。数据来自 Reeburgh(1997), Chapin et al.(2002), Galloway et al. (2004), Gruber and Galloway (2008). 为了保证全球循环在不同元素间的一致性，生物的磷源和通量的数据来自于全球碳收支和氮收支的换算，并且将海洋生物的 N:P 质量比赋值 7.2，陆地植被的比赋值 100 和陆地凋落物的 C:N 比赋值 12.6（Sterner and Elser 2002）。该方法的结果和直接估算的海洋生物磷收支接近，但是小于陆地生态系统生物磷收支的直接估算值 (Ruttenberg 2004)。大多数磷元素在数十年、数百年的时间尺度上参与到生物地球化学循环中，包括土壤、沉积物、海洋之间。磷循环再陆地上与植物和土壤紧密联系，在海洋中与海水和海洋动物紧密联系。人类活动对全球磷循环的影响已经被用于化肥（接近自然植被磷通量的三分之一）和作物和牧场的磷损失。

磷在全球范围内的物理转移受到缺乏主要大气气体成分的限制。由于磷的低溶解度，自然生态系统的淋溶损失也很低。相反，磷在全球范围内的流动主要是通过风的侵蚀以及河流和溪流中的微粒流入海洋。全球磷循环的主要通量（不包括人类活动）是通过从陆地到海洋的水文运输。在海洋中，这些含磷微粒中的一部分被海洋生物循环利用，其余的被埋在沉积物中。因为海洋和陆地之间没有大气联系，所以在短时间尺度上，这种流动是单向的(Smil 2000)。在地质时间尺度上（数千万到数亿年），含磷沉积岩暴露并风化，向生物圈补充磷 (Ruttenberg 2004)。

4.2 人类活动引起的磷循环变化 (Anthropogenic Changes in the Phosphorus Cycle)

人类活动已经显著增加了磷元素的移动性和自然循环，通过增加侵蚀和风、水传播。无机磷肥料自 19 世纪中期开始生产，但自 20 世纪中期以来产量和使用量急剧增加（图 14.4-2）。在 1850 年到 2000 年之间，农业系统吸收了大约 550 Tg 的新磷。每年用于农业生态系统的磷用量(10-15 Tg $year^{-1}$)大约是所有陆地生态系统中自然循环的三分之一。

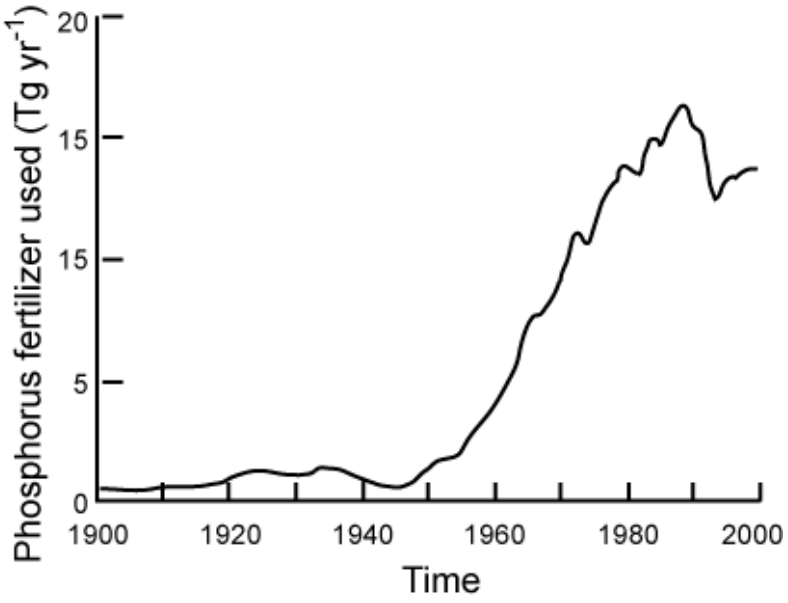


图 14.4-2 在 20 世纪全球使用无机磷肥料的年际变化。重绘 Smil (2000)。

人类土地利用的变化也增加了生态系统中磷的流失。水蚀和风蚀导致全球农田每年损失 15 Tg $year^{-1}$ 的磷，这个数字与每年的化肥投入量相似。过度放牧还增加了侵蚀损失，从放牧地吸收了大约 12 Tg $year^{-1}$ 的磷(Smil 2000)。总之，这些变化增加了磷在世界各地的输送(Howarth et al. 1995)。由于磷通常限制湖泊的生产，淡水生态系统无意中施磷可能导致富营养化，并对水生生物和社会造成相关的负面后果。被风吹来的沙尘输送的磷也会影响像南大洋这样的顺风生态系统。

与氮（N）的生物地球化学循环不同，磷（P）循环属于沉积型循环，其可再生性远低于N，因此P越来越成为植物生产力的限制因子(Elser et al. 2000)。特别是在全球变化的大环境下，人类活动加剧了N沉降使得自然生态系统中N的有效性加倍(Vitousek et al. 1997)，而N有效性的增加会改变生态计量化学平衡，导致P的相对限制增加(Elser et al. 2009)。目前对生态系统N作用的研究远远多于P(Marklein and Houlton 2012)，且始终未形成统一的N、P关系理论体系。由于生态学研究对象在时间、空间上差异很大，对于部分研究，例如N、P限制，N、P添加生物多样性的影响等均有较大争议；而在养分和水分条件发生显著改变的背景下，生态系统优势物种和生态系统功能对P限制的响应如何，是急需了解的问题。内蒙古站自2009

年开展N、P添加实验，主要研究了在N沉降背景下P的限制性和对物种、群落及生态系统的影响。在自然环境下，单纯的P添加处理并不能显著提高植物叶片的N及P含量（或浓度），也不改变N: P比；但在N和P同时添加的情况下，植物的P含量却显著提高了，说明P有效性的增加高度依赖于土壤的N含量，这可能与N添加造成土壤pH减低，从而引起P的有效性增加有关(Long et al. 2016)。进一步对N、P共同添加在不同组织水平影响的详细分析表明：在物种水平上，N添加虽然提高了植物叶片的N:P比，但也加剧了P的相对限制；在群落水平上，由于土壤有效N、P含量的年际间变异，正常降雨年份群落处于N限制，而相对湿润的年份则受到N和P的共同限制，表明P的限制性会受到水分，氮素等因子的调节；此外，从植物叶片、根系到微生物，其N:P比的稳定性逐渐增加(Zhan et al. 2017)。随着N沉降的日益加剧，未来生态计量化学比的平衡会被逐渐打破，而P将会成为草地生态系统的主要限制因子。

第五节　全球硫循环

全球硫循环与全球氮循环和磷循环具有一些相似特点。硫循环和氮循环一样，具有重要的大气成分。大气中气态的浓度很低，但起着重要的作用。和磷一样，硫主要来自岩石。海水、沉积物和岩石是硫的最大储层（图 14.5-1）。大气中含硫很少。在过去几个世纪的人类活动之前，硫主要通过沉积黄铁矿的风化作用进入生物圈。一旦风化，硫通过水文运输或排放到大气中，以减少硫气体或含硫颗粒的形式通过全球系统移动。在前工业化世界中，大约 100 Tg $year^{-1}$ 的硫，主要以溶解的硫酸盐的形式移动，通过河流运输到沿海边缘或开阔的海洋(Galloway 1996)。

在湿地和沿海沉积物等厌氧环境中，硫可被还原为硫化物或其他微量含硫气体。海水和海洋排放的硫酸盐和含硫微量气体大约是大陆排放的 100 倍（图 14.5-1）。海洋生物排放包括二甲基硫化物(DMS)，这是大气硫酸盐的主要来源之一；火山爆发释放的二氧化硫是另一个主要的自然来源。排放到大气中的硫通常停留时间很短。它与氢氧根反应被氧化成硫酸盐。硫酸在几天内就会像下雨一样从下风流出。硫酸迅速凝结形成云滴中的硫酸盐，而云滴很快蒸发形成硫酸盐气溶胶。这些气溶胶对地球的能量收支有直接和间接的影响。它们的直接影响是反向散射（回流）入射的短波辐射，从而减少太阳能的输入，并倾向于降低全球温度。它们的间接影响更为复杂和难以预测。作为微粒，它们通过提供一个水可以凝结的表面来充当云凝结核，从而影响云的形成、云的寿命、云滴的大小以及云的反照率。硫酸盐气溶胶对气候的多重影响的方向和程度的不确定性是人们关注全球硫循环中人为变化的一个关键原因。

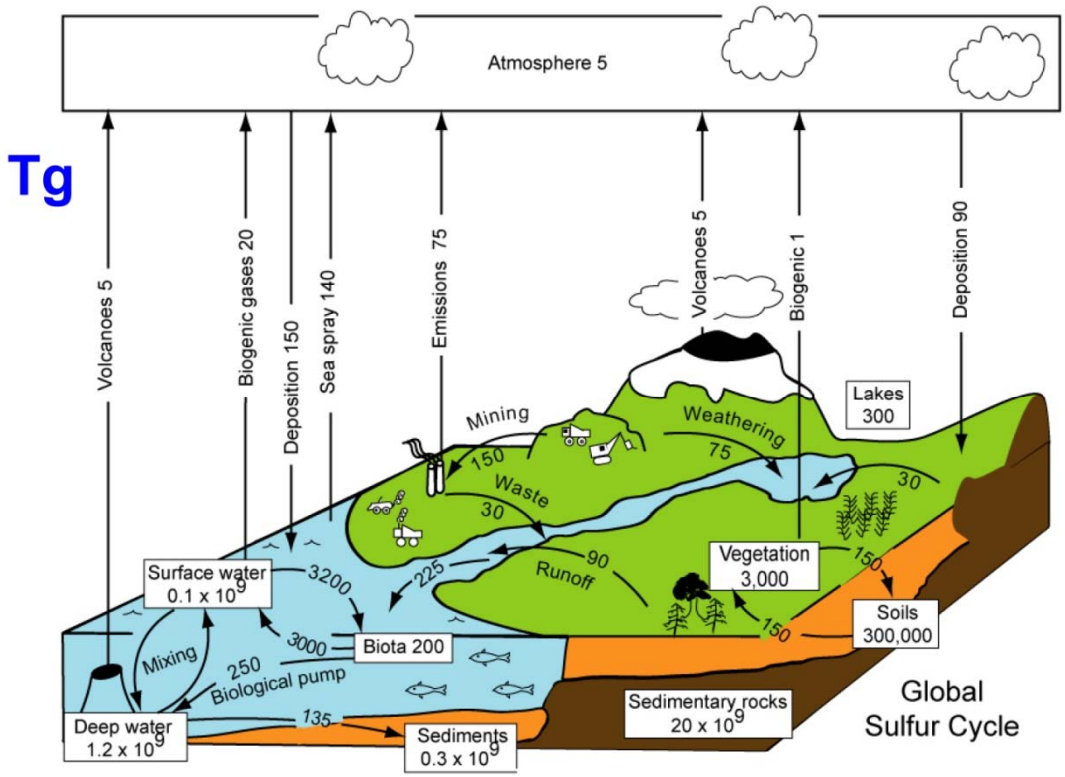


图 14.5-1 全球硫循环图。图中所示主要的库（方框）和通量（箭头）。1 Tg 等于 1×10^{12}g。数据来自 Galloway (1996), Reeburgh (1997), Schlesinger (1997), and Brimblecombe (2004).为了保证全球循环在不同元素间的一致性，生物的磷源和通量的数据来自于全球碳收支和氮收支的换算（图 14.5，14.8），并且将生物的 N:S 质量比赋值 7.2 (Bolin *et al*. 1983)。硫元素主要存在于岩石、沉积物和海水。硫通量主要通过生物和不同的痕量气体通量。人类活动加倍了全球硫通量，通过采矿和增加气体排放。

现在，人类活动将大约135 Tg year^{-1}的硫转移到大气和海洋中，使自然循环速率增加了约50%（图14.5-1）。其中一半的硫来自化石燃料燃烧和矿石精炼，其余的来自农业、畜牧业、暴露沉积物的侵蚀和其他来源的粉尘中的硫。许多人为产生的硫在大气中流动，沉积在陆地上，在土壤或生物体中积累，或者以溶液的形式排放到海洋中。从冰芯重建的全球温度记录表明，火山释放的二氧化硫是长期尺度上的年际气候变化的主要原因。因此，由人为排放引起的硫气溶胶的急剧增加无疑将在未来的气候变化中发挥重要作用。硫排放及其相关的直接和间接影响的降温效应可能在0-1.5 W m^{2}之间，部分抵消了温室气体造成的变暖(IPCC 2007)。

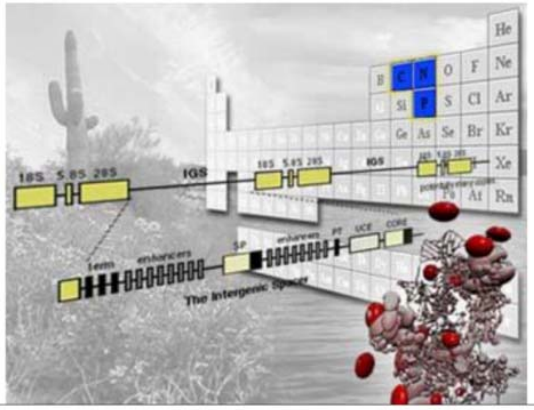
第六节　研究案例

6.1 生态化学计量学(Ecological Stoichiometry)

生态化学计量学(ecological stoichiometry)概念最早由Redfield提出，后来由Robert Sterner和 James Elser 建立了生态化学计量学的基本理论和方法体系[11]。其基本原理是通过定量研究基因、个体、种群、群落和生态系统水平生命有机体的元素组成比例及变化，揭示植物、动物、微生物和土壤系统的养分限制与养分平衡，进而阐明不同营养级间的养分转移和循环规律。

Redfield A. C. 1934. *On the proportions of organic derivatives in sea water and their relation to the composition of plankton*. In: Daniel R J. James Johnstone Memorial Volume. Liverpool, U.K.: Liverpool University Press. 176-192

Redfield, A. C. 1958. The biological control of chemical factors in the environment. *American Scientist* 46:205-221.



$H_{375,000,000}$ $O_{132,000,000}$ $C_{85,700,000}$ $N_{6,430,000}$ $Ca_{1,500,000}$ $P_{1,020,000}$ $S_{206,000}$ $Na_{183,000}$ $K_{177,000}$ $Cl_{127,000}$ $Mg_{40,000}$ $Si_{38,600}$ $Fe_{2,680}$ $Zn_{2,110}$ Cu_{76} I_{14} Mn_{13} F_{13} Cr_{7} Se_{4} Mo_{3} Co_{1}

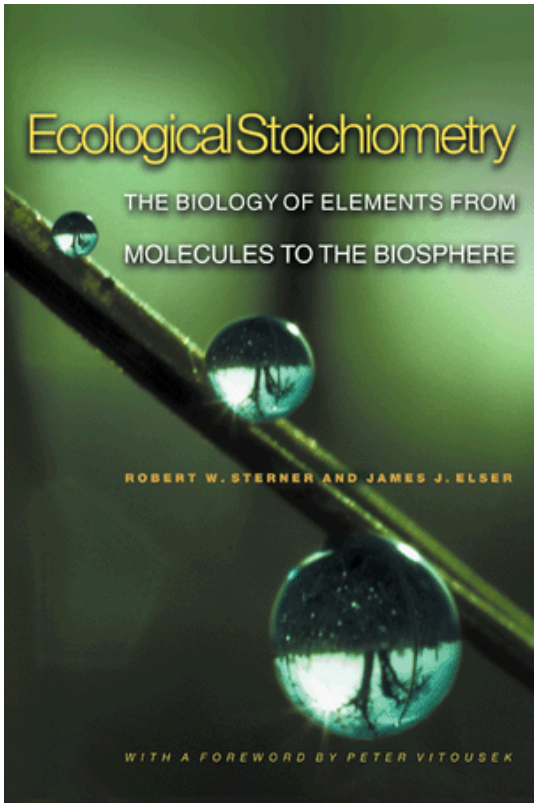
That is, there are about 375 million H atoms for every Co atom in your body (the formula is based on "wet weight"). This formula combines all compounds in a human being into a single abstract "molecule." This formula sets the value of the scarcest substance (cobalt, mass in humans ≈ 1 mg) equal to a stoichiometric coefficient of 1 and shows relative amounts, not absolute ones. Most stoichiometric analyses are in fact concerned with

图 14.6-1 人体中各种元素的原子数比

6.2 生态化学计量学和生物化学计量学

生态化学计量学：研究生态系统中能量和多种化学元素平衡，例如竞争、食植、互惠、食物网、生物地球化学（图 14.6-2）。

生物化学计量学：研究生物系统中能量和多种化学元素平衡，例如细胞代谢、生长和法语、生理内稳定性、进化改变，生态学等。



Robert W. Sterner and James J. Elser

图 14.6-2 生态化学计量

科学家简介：

James Elser，湖泊学家，他最著名的工作是发展和检验生态化学计量学理论。他出生于波特兰，在康涅狄格州的诺格塔克长大。Elser 在加州大学戴维斯分校获得博士学位。Elser 的研究重点是发展和检验生态化学计量学理论，特别关注营养限制在生态学中的作用。最近，他将该理论扩展到生态学以外的生物化学计量学，并应用于进化生物学。他目前的研究主要集中在 Pinhead 湖以及蒙大拿州西部和中国西部的山区湖泊。具体的研究包括不同尺度的观测和实验工作，包括实验室培养、短期野外实验。2019 年，Elser 博士被选为美国国家科学院院士，以表彰他的研究成就。

Robert W. Sterner，湖泊学家，他最著名的工作是发展和检验生态化学计量学理论。他的研究将生态系统科学（例如营养通量）与种群和群落过程（如竞争和捕食）结合在一起。

基本元素如氮和磷的含量在种间和种内都不同，这一事实引起了他的兴趣。这一观测结果有助于将群落结构与营养过程的研究结合起来。他在实验室的工作主要包括: 淡水浮游动物的营养（特别是矿物元素限制）；循环氮磷对藻类和细菌的重要性；藻类生长的营养限制；鱼类在湖泊营养循环中的作用以及消费者营养循环的数学模型。工作范围包括从纯粹的数学模型到精心控制的实验室实验以及整个生态系统实验。

代表性论文：

- Elser, J.J. 2012. Phosphorus: a limiting nutrient for humanity? Current Opinion in Biotechnology 23:833-838.
- Elser, J.J. 2011. A world awash with nitrogen. Science 334:1504-1505.
- Elser, J.J. et al. 2011. Stoichiogenomics: the evolutionary ecology of macromolecular elemental composition. Trends in Ecology and Evolution 26:38-44.
- Elser, J.J. et al. 2009. Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science 326:835-837.
- Elser, J.J. et al. 2009. Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition. Ecology 90:3062-3073.
- Elser, J.J. et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10:1135-1142.
- Elser, J.J. et al. 2000. Biological stoichiometry from genes to ecosystems. Ecology Letters 3:540-550.
- Elser, J.J. et al. 2000. Nutritional constraints in terrestrial and freshwater food webs. Nature 408:578-580.
- Sterner, R.W. et al. 2020. Ecosystem services of Earth's largest freshwater lakes. Ecosystem Services 41:101046.
- Sterner, R.W. 2015. Ocean stoichiometry, global carbon, and climate. Proceedings of The National Academy of Sciences USA 112:8162-8163.
- Sterner, R.W. et al. 2008. Scale-dependent carbon : nitrogen : phosphorus seston stoichiometry in marine and freshwaters. Limnology and Oceanography 53:1169-1180.
- Sterner, R.W. et al. 2000. Carbon, nitrogen, and phosphorus stoichiometry of cyprinid fishes. Ecology 81:127-140.

6.3 在食物网基础上的生态化学计量特征变化

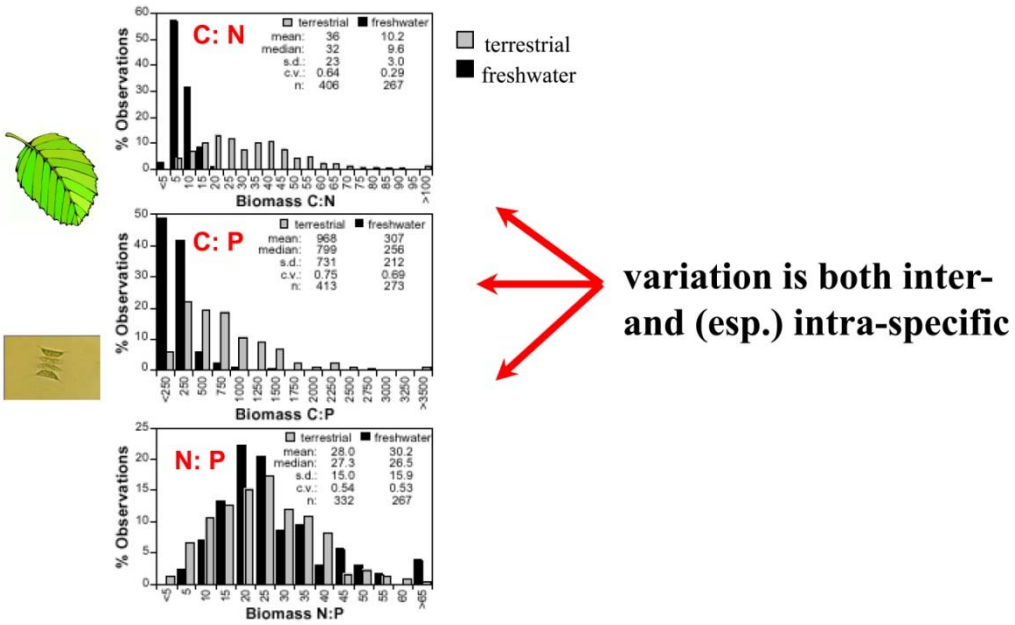


图 14.6-3 陆地草叶和淡水悬浮物（引自 Elser, J. J. et al. 2000. Nature 408: 578-580）

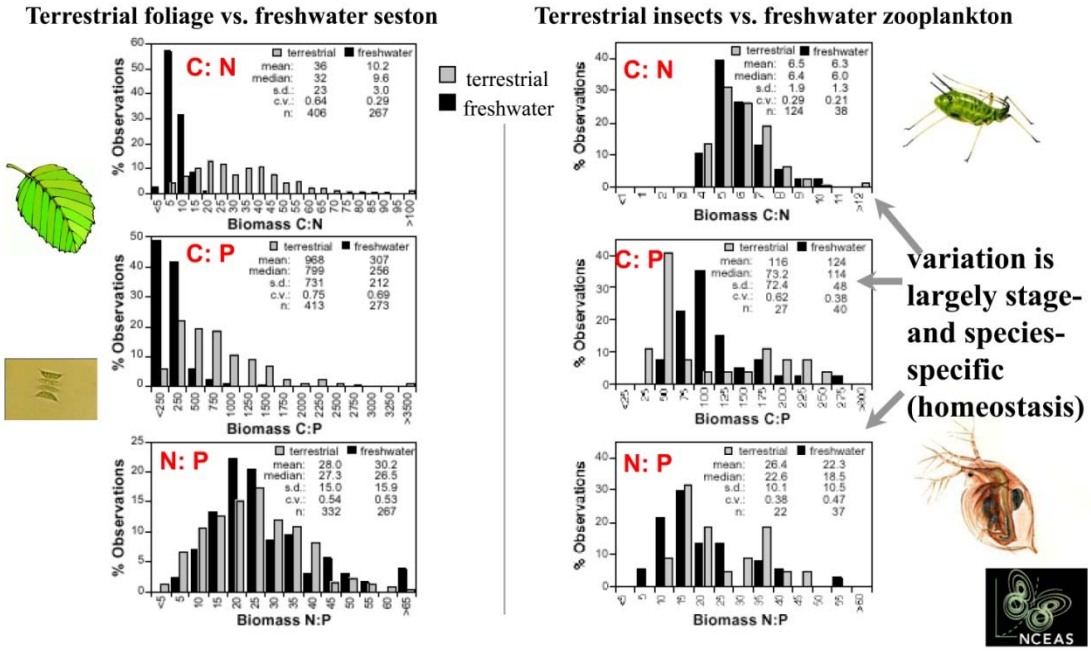


图 14.6-4 陆地昆虫和水生浮游动物的内稳定性（引自 Elser, J. J. et al. 2000. Nature 408: 578-580）

本章小结

生态过程和人类活动在大多数生物地球化学循环中起着重要作用。生物和人类对生态系统过程的影响在全球范围内是巨大的。大部分水存在于海洋、冰和地下水中，陆地生物无法直接获得这些水源。主要的水分通量是降水、蒸散发和径流。人类活动加快了全球水文循环的速度，因为全球温度升高增加了蒸散发，从而增加了降水量，并将大量可获得的淡水转移给人类使用。如果按照目前人口增加趋势继续下去，对社会来说，淡水将是一种日益稀缺的资源。

生物过程（光合作用和呼吸作用）构成驱动全球碳循环的引擎。大气、陆地、海洋和地表沉积物是碳循环长达数十年至数百年的四大碳库。在陆地上，植被固定的碳略大于呼吸释放的碳，导致陆地为碳储存。输入海洋的净碳量也略大于返回大气的净碳量。海洋的初级生产与陆地的基本相同。大部分（80%）的 NPP 通过呼吸作用释放到环境中，剩下的 20%通过生物泵进入深海。海洋上升流将大部分碳元素返回到海洋表层水域；只有少量沉积在沉积物中。人类活动通过燃烧化石燃料、水泥生产和土地利用变化，导致碳释放到大气中。这种通量相当于陆地异养呼吸的 14%。

地球上的氮绝大多数都存在于大气中。每年在陆地植被中循环的氮量是氮固定量的九倍。在海洋中，通过生物体内的氮年循环是氮固定量的七十倍。反硝化作用是氮想大气的主要输入。人类活动如生产肥料、种植含氮作物和燃烧化石燃料，使陆地生物圈含氮量增加了一倍。

在几十年到几百年的生物地球化学循环中，大多数磷存在于土壤、沉积物和海洋中。磷在陆地上的植被和土壤之间以及海洋生物和海洋表层水体之间紧密地循环。人类对全球磷循环的主要影响是化肥的施用（相当于植被自然循环的 40%）以及农田和牧场的侵蚀损失（相当于每年植被循环的一半）。大部分硫存在于岩石、沉积物和海水中。硫中主要是通过生物区系和各种微量气体流动。人类活动通过采矿和增加气体排放，大幅度增加了全球硫的排放量。

推荐阅读文献：

Aber, J., McDowell, W., Nadelhoffer K., Magill A., Berntson G., et al. 1998. Nitrogen saturation in temperate forest ecosystems: Hypotheses revisited. BioScience 48:921 - 934.

Balesdent, J., Basile-Doelsch, I., Chadoeuf, J., Cornu, S., Derrien, D., et al. 2018. Atmosphere-soil carbon transfer as a function of soil depth. Nature 559:599-602.

Battin, T. J., Luyssaert, S., Kaplan, L. A., Aufdenkampe, A. K., Richter, A., et al. 2009. The boundless carbon cycle. Nature Geoscience 2:598-600.

Bousquet, P., Ciais, P., Miller, J. B., Dlugokencky, E. J., Hauglustaine, D. A., et al. 2006. Contribution of anthropogenic and natural sources of atmospheric methane variability. Nature 443:439-443.

Carvalhais, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., et al. 2014. Global covariation of carbon turnover times with climate in terrestrial ecosystems. Nature 514:213 - 217.

Davidson E. A., and Janssens I. A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165 - 173.

Drake, B. G., GonzalezMeler, M. A., and Long, S. P. 1997. More efficient plants: a consequence of rising atmospheric CO_2? Annual Review of Plant Physiology and Plant Molecular Biology 48:609 - 639.

Flerchinger, G. N., Fellows, A. W., Seyfried, M. S., Clark, P. E., and Lohse K. A. 2020. Water and carbon fluxes along an elevational gradient in a sagebrush ecosystem. Ecosystems 23:246-263.

Gaitan, J. J., Maestre, F. T., Bran, D. E., Buono, G. G., Dougill, A. J., et al. 2019. Biotic and abiotic drivers of topsoil organic carbon concentration in drylands have similar effects at regional and global scales. Ecosystems 22:1445-1456.

Keenan, T. F., Hollinger, D. Y., Bohrer, G., Dragoni, D., Munger J. W., et al. 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature 499:324-327.

Luo, Z. K., Feng, W. T., Luo, Y. Q., Baldock, J., and Wang, E. L. 2017. Soil organic carbon dynamics jointly controlled by climate, carbon inputs, soil properties and soil carbon fractions. Global Change Biology 23:443-4439.

Magnani, F., Mencuccini, M., Borghetti, M., Berbigier, P., Berninger, F., et al. 2007. The human footprint in the carbon cycle of temperate and boreal forests. Nature 447: 848 - 850.

Medlyn, B., and De Kauwe, M. 2013. Carbon dioxide and water use in forests. Nature 499:287-289.

Oki, T., and Kanae, S. 2006. Global hydrological cycles and world water resources. Science 313:1068–1072.

Schindler, D. W. 1973. Eutrophication and recovery in experimental lakes: implications for lake management. Science 184:897 - 899.

Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. Science 195:260–262 .

Schindler, D. W., Hecky, R. E., Findlay, D. L., Stainton, M. P., Parker, B. R., et al. 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37 - year

whole-ecosystem experiment. Proceedings of the National Academy of Sciences of the United States of America 105: 11254 - 11258.

Schlesinger, W. H. 1997. Biogeochemistry: an analysis of global change. Academic Press, San Diego.

Smil, V. 2000. Phosphorus in the environment: Natural flows and human interferences. Annual Review of Energy and the Environment 25:53-88.

Tilman, D., Wedin, D., and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720.

Vitousek, P. M. 1994. Beyond global warming: ecology and global change. Ecology 75:1861–1876.

第十五章 生态系统的管理和维持

第一节　可持续的社会生态体系

人类依靠全球生态系统所提供的食物、庇护所以及其他的重要的物品和服务。生态系统除了为人类提供包括木材、食物、燃料、药物以及工业产品的原材料外，还提供一些如水和化学物质的再循环，减缓洪涝灾害的发生，为植物授粉，净化大气等。人类活动范围和活动强度的不断增大，意味着全球所有的生态系统都将受到人类活动的直接或间接影响。生态系统的功能是相互联系的，其正常发挥受邻近地区甚至全球范围内人类活动的影响。人类活动使几乎所有的生态过程在交互控制方面都发生了全球性变化：气候变暖、氮沉降、土地利用变化、物种入侵和灭绝。许多情况下，在区域水平上，这些全球变化各成分之间发生相互作用，并于当地的变化发生相互作用。因此在生态系统控制下所有的生态系统都朝着一定的方向发生变化，从而产生新的环境条件。这些交互控制的变化将不可避免地改变着生态系统的属性，其中的一些变化对人类社会也将产生不良影响。由于人类活动已经并且持续影响着地球上的生态系统，如何进行管理人类活动以维持生态系统属性和它们为人类社会提供的服务？

1.1 可持续性 (Sustainability)

可持续性是利用环境和资源用于满足现在人的需求，而且不以损害后代的需求为代价。可持续性要求对影响当今和未来社会生态系统的选择所产生的权衡作出认识（图 15.1-1）。大多数对生态系统产生负面影响的决定都不是恶意的，而是为了追求某些社会经济利益的逆流选择。例如，采矿和过度放牧通常是通过努力满足人们对矿产和食物的需求而发生的。与短期的社会或经济利益相比，这些行动的生态后果有时不那么明显或对决策者不那么紧迫。生态学家可以通过记录影响生态和社会风险的潜在权衡从而在这些决策中发挥重要作用。可持续性为澄清社会所面临的选择的后果提供了一个重要的框架。这些选择对发展中国家来说尤其严峻，因为那里人类社会直接依赖生态系统生存。

1987 年，布伦特兰委员会（1987 年世界经济会议）向联合国提出了一个可持续性框架，以解决满足生态保护和人类发展需要的双重挑战。可持续性并不要求生态系统保持不变，而这在一个迅速变化的世界是不可能的。此外，我们不能肯定地知道后代想要什么。可持续性只是要求以使子孙后代有机会作出自己选择的方式来维持可提供给他们的生产基础。

人类社会所依赖的生产基础具有生态和社会经济两个维度。可持续性要求系统的总资本或生产基础（资产）是可持续的。自然资本包括不可再生的资源（如石油储备）和可再生的生态系统资源（如植物、动物和水），它们支持社会所依赖的商品和服务的生产。建造资本包括在自然界之外的物质生产手段（如工具、衣服、庇护所、水坝和工厂）。人力资本是指人们实现自己目标的能力;它可以通过各种形式的学习来提高。这些资本形式共同构成了这

个体系的财富，即社会可获得的生产基础（资产）。虽然社会资本没有被正式纳入财富的范畴，但它是另一项重要的社会资产。它是一群人共同行动解决问题的能力。每一种资本形式的组成部分都会随着时间而变化。例如，可以通过改善生态系统的管理，包括恢复或更新退化的生态系统或建立海洋保护区网络来增加自然资本；通过对桥梁或学校的投资建立资本；通过教育和培训获得人力资本；并通过发展新的社会资本伙伴关系来解决问题。这一生产基础的增加构成了真正的投资。投资是资产数量乘以其价值的增长。可持续性要求真正的投资是积极的，也就是说产基础不会随着时间的推移而下降。这为评估管理是否可持续提供了客观的标准。

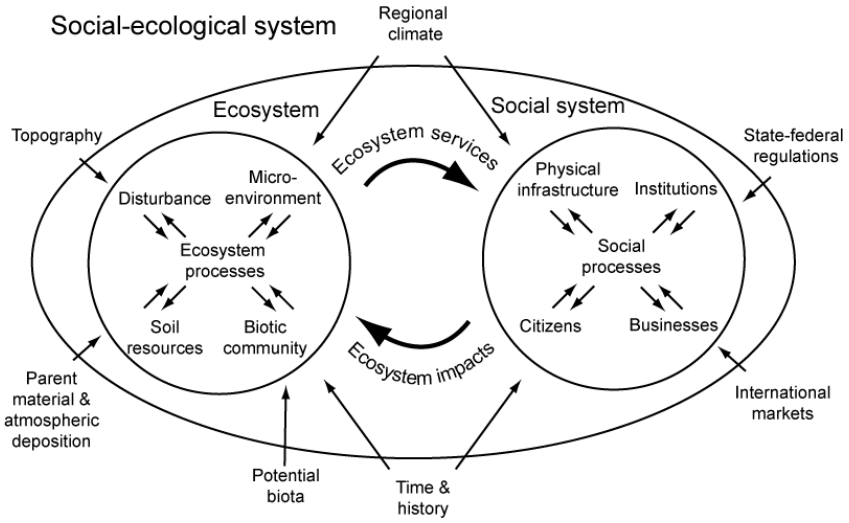


图 15.1-1 社会-生态系统的功能的调控因子。人类活动对生态系统的影响受到多种社会过程的调控，并且社会受益于生态系统提供的服务。改编自 Whiteman et al. (2004)。

在某种程度上，不同形式的资本可以相互替代，例如天然湿地可以提供净水功能，否则就可能需要建造昂贵的水处理设施。见多识广的领导可能能够对某一特定问题实施具有成本效益的解决办法（用人力资本代替经济资本）。然而，不同形式的资本可以被替代的程度是有限的。例如，水和食物是生存所必需的，任何其他形式的资本都不能完全替代它们。因此，当它们变得稀缺时，它们对社会具有极高的价值。类似地，其他形式的资本也不能轻易地弥补农业土壤为作物生产保留足够水分的能力的下降、为重要作物授粉的物种的存在、文化认同感或社会对其领导地位的信任。许多形式的人力、社会和自然资本的损失具有很多问题，因为不可能提供适当的替代品，或成本极高。因此，我们特别注意如何维持资本的这些关键组成部分，否则后代就无法满足其需要。

如果一个体系的生产基础得以维持，后代就可以自己选择如何最好地满足他们的需求。这违反了决定某些实践在不断变化的世界中是否可持续的标准。从资本的数量和对社会的价值两方面衡量各种形式资本的变化，存在着重大的挑战。尽管如此，目前最好的估计表明，在过去 50 年里，大多数国家的制造业和人力资本有所增加，但由于可再生和不可再生资源的消耗以及污染和生物多样性功能效益的丧失，自然资本有所下降。在一些较贫穷的发展中

国家，自然资本的损失超过了制造资本和人力资本的增加，表明了一条明显不可持续的发展道路。

1.2 生态维度和可持续性 (Ecological Dimensions of Sustainability)

经验的框架-多生态系统服务：生态系统服务提供了一个管理生态可持续性的经验框架。虽然自然资本是衡量生态系统满足社会长期需求能力的基本指标，但它对寻求解决特定社会生态问题（如林业或海洋的多用途管理）的生态系统管理者无法提供指导。不同的生态系统配制可能反应类似水平的自然资本，但提供不同模式的生态系统服务，社会从生态系统获得的效益。生态系统提供公认的供应服务（商品），包括水、木材、饲料、燃料、药品和从生态系统收获的工业产品的原材料。生态系统还提供调节服务，如水及其化学循环利用、漂浮物的减少、作物的授粉和大气的净化，以及满足娱乐、审美和精神需求的文化服务。所有这些服务都依赖于生态系统过程，有时也称为支持服务。这些过程包括生物地球化学循环、多样性维持和干扰循环。除非能够维持这些基本的生态系统属性，否则其他服务就无法维持。

多种生态系统服务(图 15.1-2)：必须纳入关键生态系统服务；然而，决定通常强调短期经济价值，并且假定生态服务服务的丧失是免费的，因此它们的退化是零成本的。评估生态系统是一种组织信息和帮助决定的方式。

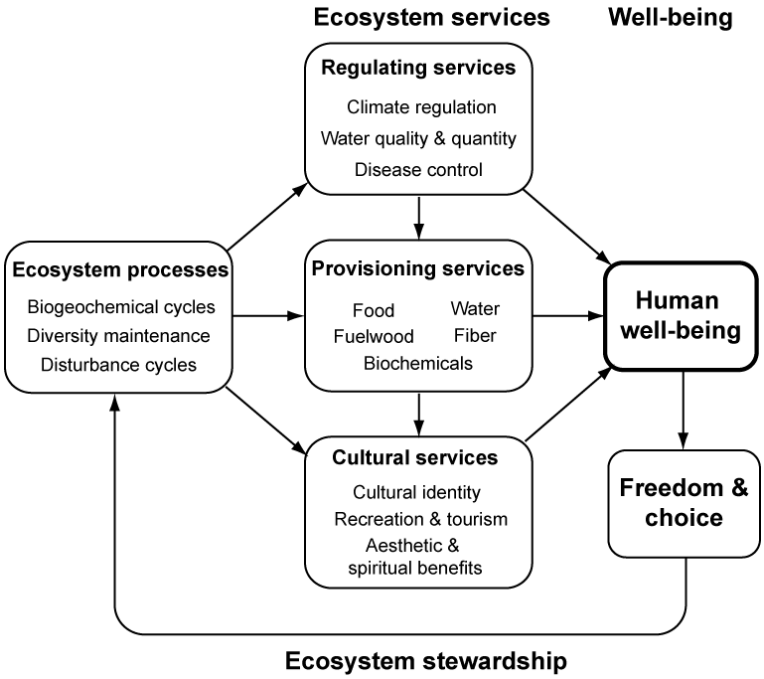


图 15.1-2 生态系统过程、生态系统服务和社会福祉之间的联系；这个关系框架是由千年生态系统评估提出的（MEA2005）。生态系统过程是生态系统服务的基础，而且生态系统服务直接被社会利用，并且较强地影响人类。人类行为会通过影响环境和生态系统而影响支持生命系统的地球。

资源的过度使用或滥用会改变生态系统的功能及其提供的服务。例如，土地利用变化会降低净化水的能力，给城市带来巨大的水处理成本。湿地的退化和丧失会增加社区遭受浮冰和风暴潮破坏的风险。传粉昆虫数量减少降低了许多作物的产量。杀人蜂、火蚁、斑马贻贝等外来物种的引进和入侵，通过人类的行为，对生物资源造成了巨大的破坏，威胁着人类的健康。人类活动还通过大气、水文系统和气候的变化间接影响生态系统的产品和服务。

管理决策通常涉及在生态系统服务之间权衡取舍的选择。例如，森林收获可以提供生森林产品，但是需要以牺牲未砍伐的森林提供的娱乐机会为代价。提高雪地机使用者娱乐价值的政策可能会降低雪地机对越野滑雪者的价值。提高雪地机使用者娱乐价值的政策可能会降低雪地机对越野滑雪者的价值。砍伐热带森林可能为当地使用者提供森林产品和土地，以支持农业，但会使土壤退化，减少子孙后代的生计机会。生态系统管理的一个重要步骤是评估决策对多种生态系统服务的潜在影响。鉴于生态系统提供的服务数量巨大，以及它们对特定行动的反应存在不确定性，因此这具有很大挑战。特别注重少数关键的生态系统服务往往是务实的，这些服务最容易受到改变，在技术或生态方面的替代选择最少，而且最受社会重视。

第二节　生态系统管理的概念框架

2.1 生态系统管理

生态系统管理追求维持和提高生态系统的功能属性，以支撑社会所需要的生物多样性和生态系统服务。生态系统管理是运用生态科学于资源管理，以促进生态系统的长期可持续性，并且传递基本生态系统产品和服务于社会。

2.2 管理原则

静态因子包含可能的管理选择（不能被管理）：控制土壤和生态系统（如气候、母质、地形、潜在生物区系、时间、人类活动）属性的独立变量。

交互影响可以被管理：保留交互作用的影响因子。

2.3 管理原则（短期目标）

保留交互作用的影响因子：维持并提高负反馈；维持自然景观联系。

2.4 管理原则（长期目标）

最大化弹性；多样性；学习的机会；适应性能力。

2.5 识别可持续的主题

为了普遍的属性（如生产对环境变化的潜力和弹性，而不是尝试阻碍所有的波动和变

化）的可持续性去管理生态系统是更能够实践的。

土壤资源、生物多样性、干扰格局是相互作用，通常被人类活动所影响，尤其是对生态系统和他们提供的服务有较强的影响。

2.6 可持续土壤资源 (Sustaining Soil Resources)

土壤和沉积物是关键的较慢的变量，通过提供生物所需要的资源来调控生态系统过程。因此，对土壤和沉积物的形成、退化和资源利用潜力的控制是健全的生态系统管理和维持社会所依赖的自然资本的核心。生态系统中土壤的数量很大程度上取决于来自风化或沉积的输入和来自侵蚀的损失之间的平衡。此外，有机体，特别是植物，通过组织和个体的死亡向土壤中输入有机质，而这些有机质也可以通过分解而被损失抵消。一般来说，植物冠层和凋落物层的存在通过减少雨滴对表层土壤的影响以及由此导致的水注入量下降，将侵蚀程度降到最低。减少植被覆盖的人类活动会使侵蚀率增加几个数量级，导致可能积累了几千年的土壤在数年到数十年之间消失。这基本上是生态系统生产力的永久丧失。同样，人类对河道的改造也会改变流向平原和三角洲的泥沙输入。例如在美国南部，沉积物输入的流失和随后的土壤沉降导致了之前保护新奥尔良免受飓风袭击的岛屿消失。

像粘土和有机物这样的细颗粒在水和养分固持中特别重要。它们通常集中在土壤表面附近，在那里它们很容易因侵蚀而流失。人类活动促进了风和水的侵蚀，例如森林砍伐、过度放牧、耕地或休耕农业，因此侵蚀土壤保持水分和营养的能力速度远远快于土壤总量的损失。因此，防止即使是轻微增加的侵蚀率，对于维持陆地生态系统的生产能力至关重要。

加速的土壤侵蚀是全球生态系统服务下降的最严重原因之一。细粒土壤的侵蚀损失是旱地沙化、土壤退化的直接原因。荒漠化可能由干旱、植被覆盖减少、过度放牧或它们的相互作用引起。例如，当干旱减少植被覆盖时，山羊和其他牲畜会更集中地吃剩下的植被。极端贫困和缺乏安全的粮食供应往往限制了在干旱时期减少放牧压力的选择，因为短期粮食需求优先于可能防止水土流失的做法。湿润地区也会经历严重的土壤侵蚀损失，特别是植被损失使土壤暴露于地表流动的地方。例如，中国的黄河每年从其源头的黄土高原农业区运输 16 亿吨泥沙。在 20 世纪 30 年代的干旱时期，美国的草原被开垦为农业用地时，也发生过类似的侵蚀损失，形成了“沙尘暴”。维持植被覆盖的管理，特别是在陡峭的地形和靠近溪流的地方，可以大大减少侵蚀潜力，从而保持陆地生态系统的生产潜力。

2.7 可持续生物多样性 (Sustaining Biodiversity)

生物多样性较强地影响了环境和生物条件的范围，生态系统过程在该范围内是可持续的。不同的生态系统包括通过利用和循环土壤资源来维持广泛的生态系统过程（多样性效应）的物种。多样化的系统还包含有可能在各种环境和生物条件下维持生态系统服务的生物体（响应多样性）。这些种生态系统服务的提供依赖于现有物种的种类（功能组成）、物种内部的遗传多样性、林分内部的物种多样性以及跨区域的景观多样性。

在没有被人类活动强烈改变的生态系统中，生物多样性倾向于“自我照顾”。物种多样性是指那些到达某个特定地点，能够在该环境中生长和繁殖，并能在面临竞争和其他物种捕食时生存下来的物种。如果一个物种从某个特定的斑块中消失，它可能会从邻近的斑块中重新定居。然而，人类活动往往通过改变土地利用和景观结构，或通过引入或消灭控制物种间竞争和营养相互作用的物种，从根本上改变物理和生物环境。例如，在历史上没有哺乳动物的岛屿上引入老鼠，消灭了不会飞的鸟类和许多本地植物。将固氮外来物种引入低氮环境有利于快速生长的杂草物种的竞争优势。捕食者的消失会导致食草动物密度的激增，从而减少植物的多样性。气候、养分沉积和侵蚀的长期趋势正在改变整个地球的物理环境，改变物种之间的竞争相互作用，并经常淘汰那些不能在这些新条件下有效竞争的物种。这些物种的消失比迁移或进化能将多样性恢复到以前的水平要快得多。人类对生物多样性的这些影响，累积起来就解释了为什么现在世界正处于地球生命历史上的第六次大灭绝事件中。此外，物种多样性的丧失可能是许多人为造成的全球变化中最不可逆的。土壤、土地覆盖或大气的组成可能需要数千年才能恢复到扰动前的状态，但灭绝实际上是永远的。

生态系统管理强烈影响生物多样性的维持或丧失。在集约化管理的森林或农业用地上，管理者通常故意减少多样性，以生产出能够有效管理和收获的水平。然而，在收获效率和这些低多样性林分对环境和生物的可变性和变化的脆弱性之间有一个权衡。这些低多样性的林分通常需要抑制自然病原体和干扰，以维持其生产力。人类无意的影响也会改变多样性。增加诸如水或养分等资源减少了植物可以竞争的潜在有限资源的数量，从而减少了可以共存的物种的多样性。在非集约化管理的生态系统中，可通过尽量减少生态系统新变化的规模和程度来促进生物多样性。这就减少了那些能够很好地适应历史环境和生物条件的物种灭绝的可能性。例如，尽量减少热带森林的土地改作农业或火灾，为本地物种维持了栖息地。原生生境的比例覆盖是一个地区生物多样性的重要预测指标。同样，防止外来物种的引入或传播，减少大规模生物多样性和生态系统变化的可能性。具有新的生态系统效应的物种（如固氮或高度易流失的物种），或在原生地躲过了控制其种群数量的疾病和捕食者的物种，它们将会对生物多样性产生强烈影响。最后，维持干扰和景观连接性的自然模式，维持景观中所有演替阶段的种群，并为迁移和干扰后的定居提供路径。

2.8 可持续的变异性和弹性 (Sustaining Variability and Resilience)

干扰塑造了生态系统的结构和功能的长期波动，因此也影响了它们对环境改变的弹性和脆弱性。扰动不是生态系统“发生”的事情，而是生态系统功能的一个组成部分，是景观时空变化的一个关键来源。物种通常会适应形成它们进化历史的扰动环境。因此，改变这种干扰状态的管理，例如通过防止漂浮物、野生动物或害虫的爆发，可以为物种创造难以适应的环境。例如，过去为防止这些自然干扰所做的努力创造了同质的后期栖息地，这些栖息地不再支持早期的演替物种。此外，演替晚期生态系统往往容易发生病虫害暴发，这些病虫害可在同质的晚期演替林分中广泛传播。允许自然小干扰发生的管理会产生空间异质性，减少干扰的扩散，从而减少大的灾难性干扰的可能性。允许小规模干扰发生在政策上往往具有很大挑

战，然而由于小干扰有时减少或破坏资源的经济价值，人们想要收获（如森林收获），创建风险居住景观（如荒地和城市分界面）或减少斑块在景观的美学价值。这些权衡最好通过长期的社会-生态规划来解决，后续会讨论。

小尺度扰动所产生的景观多样性，形成了结构和物种组成不同的生态系统镶嵌体。每一种林分类型对各种可预测和不可预测的冲击和干扰的反应可能不同，包括历史上重要的干扰和由气候变化、污染或新的干扰机制（例如，野火和洪水频率和程度的改变）引起的新情况。因此，就像林分内的遗传或物种多样性一样，景观多样性促进了对历史和新干扰的恢复力。

管理需要考虑生态系统之间相互作用的景观视角。例如，如果不考虑周围景观的养分投入，就不能对湖泊进行可持续管理；如果考虑到飓风、火灾和伐木等干扰，就可以将森林生产作为景观镶嵌体进行最可持续的管理。湖泊的恢复力和可持续性取决于一系列过程控制，这些过程控制在不同的尺度上发挥作用，以减轻扰动的影响。这些过程控制包括河岸植被和湿地的适配效应，猎渔在营养动力学中的作用，以及大型植物对营养物质的吸收。当这些组成部分完好无损时，包含湖泊的景观可以承受诸如干旱、浮冰、森林火灾和一些土地使用变化等干扰。在粗略的空间尺度上管理景观需要不同于管理单个湖泊或林分的信息。在粗略的空间尺度上，监测湖泊的食物网是不可行的，因此土地利用记录、湖泊清澈度遥感、当地居民的知识以及对捕鱼活动的调查为模型提供了有用的信息。景观聚焦的一个重要含义是它需要认识到生态系统对多种驱动力的响应。

第三节　生态系统原理在管理中的应用

生态系统管理是将生态科学应用于资源管理，以促进生态系统的长期可持续性，并向社会提供必要的生态系统产品和服务。美国林业局于 1992 年采纳了这一概念，并根据一套共同原则在理论和应用上不断发展（表 15.3-1）。在本节中，我们将说明这些原则在资源管理问题上的应用。

表 15.3-1 生态系统管理的属性，基于 Christensen et al. (1996)

Sustainability	Intergenerational sustainability is the primary objective
Goals	Measurable goals are defined that assess sustainability of outcomes
Ecological understanding	Ecological research at all levels of organization informs management
Ecological complexity	Ecological diversity and connectedness reduces risks of unforeseen change
Dynamic change	Evolution and change are inherent in ecological sustainability
Context and scale	Key ecological processes occur at many scales, linking ecosystems to their matrix
Humans as ecosystem components	People actively participate in determining sustainable management goals
Adaptability	Management approaches will change in response to changes in scientific knowledge and human values

3.1 森林管理 (Forest Management)

可持续林业面临的挑战是确定森林生态系统在生态和社会方面具有重要意义的属性，并在面临变化时最大限度地发挥这些生态系统的服务作用。森林管理者面临的管理挑战，在某种程度上是森林树木长期存在的必然结果。为多种生态系统服务而管理森林涉及对不同使用者的成本和收益的强烈权衡，其选择影响到多代人。森林提供许多生态系统服务，包括燃料木材、木材产品、供水、娱乐、物种保护以及美学和精神价值。为了维持这些服务，养分供应速率必须足以维持快速生长，但又不能太高，导致大量养分流失或物种组成发生变化。林分的收获率必须与砍伐后的再生率相平衡。应保持林分天然镶嵌所具有的物种多样性。砍伐斑块的大小和排列应提供半自然景观镶嵌体，具有可靠的种子来源和森林边缘的模式，允许自然使用和动物种群的移动。由于预测不同管理方法的长期后果比较困难，因此在不同领域使用多种方法来满足不同用户的需求，并增加这些方法产生长期良好结果的可能性是有益的。

在快速变化的条件下管理森林是一项挑战，因为在林分中每棵树的生命周期中，林分很可能遇到新的环境和社会经济条件。全球的森林生态系统都面临着来自有意和无意的人类影响的威胁，包括空气污染、入侵物种，或许最重要的是全球气候变化。由于大多数森林树木在与它们开始生长时完全不同的条件下达到成熟期，因此从不同的气候区重新播种具有一系列基因型的森林可能是合适的。这不同于过去的最佳做法，在过去，适合当地的树木基因型是重新造林的首选。

森林转换为新的土地利用方式是一种状态变化，由于森林树木和生态系统的再生时间很长，扭转这种变化需要较长时间，同时也是非常困难的。过去和正在进行的土地利用已经将大约 40%的前工业时代的森林覆盖转化为农业、建造环境和单一或有限物种（通常是外来物种）的种植。在其他情况下，大规模的农业弃用或增加森林的经济价值，例如碳封存或美学效益，可以促进再造林（分别是在最近收获的地点更新森林或在以前未被森林覆盖的地点种植新森林）。

3.2 渔业管理 (Fisheries Management)

制订渔业管理选择方案需要了解生态系统的复原力。管理选择包括海洋保护区、配额制度、根据鱼群数量大小制定放养限制的新办法，以及长期维持种群数量的经济激励措施。无限制的鱼类捕捞会降低可持续性，因为它会将种群变化的自然稳定（负面）反馈转化为放大（正面）反馈，从而使捕捞的种群减少到低水平。例如，当鱼类种群数量减少时，供求经济学和政府补贴常常会维持或增加捕鱼的强度。与此形成对比的是，在一个不受管理的生态系统中，随着猎物数量的减少，捕食压力也会减少。

通过捕鱼活动的严格管制对北太平洋鲑鱼渔场的管理，对捕鱼压力形成了稳定的（负面）反馈。只有在足够的鱼进入产卵的河流以确保足够的补充后，才允许进行商业捕鱼和自给捕鱼。维持渔业还需要保护产卵河流不受其他交互控制变化的影响。这些变化包括防止冬季浮冰的堤坝（扰动状态），通过移除被砍伐地点的河岸植被（微环境）而使河流变暖，物种引

进（功能类型），以及在农业和城市径流和污水中输入淤泥和营养物质（营养资源）。可持续管理的一个共同办法是，只捕捞超过当鱼类资源受到依赖密度的死亡率限制时将出现的产量，称为过剩产量。剩余产量的存在和大小取决于当一些鱼被捕捞时，剩余的鱼是否提高了它们的生长率或繁殖成功率。这又取决于交互控制（例如物理环境、营养和捕食压力）的稳定性，以及这些交互控制对渔业种群变化作出反应的程度。渔业管理的主要挑战是在面临不断变化的交互控制以及这些控制与鱼类种群大小之间关系的不确定性的情况下估算剩余产量。渔业生物学家就任何生态系统在受到人类持续捕捞的影响时是否具有可持续性展开了激烈的辩论。

3.3 生态系统更新 (Ecosystem Renewal)

生态系统更新通常受益于引入放大的（积极的）反馈，推动生态系统到一个新的、更理想的状态。许多生态系统由于人类的综合影响而退化，包括土壤流失、空气和水污染、栖息地破碎化、外来物种入侵。在退化的农业系统和放牧地，最具挑战的问题是使它们恢复到足够的生产状态，以便向人类提供商品和服务。在其他情况下，目标是恢复原始生态系统的自然组成、结构、过程和动态。恢复实践方面的进展包括查明妨碍恢复生态系统结构和功能的障碍，并通过经常使用或模拟自然过程和交互控制的人工干预措施克服这些障碍。干预措施可以应用于生态系统的任何组成部分，但水文、土壤和植物群落特征通常是工作的重点。土壤肥力低和有机质含量低是过度使用农牧系统和废弃矿山重建森林或草原的普遍问题。肥料和固氮植物可以恢复土壤养分和有机输入。一旦土壤特性合适，植物物种可以通过播种、种植或自然迁移重新引入。例如，在一个迅速变化的世界中，将更新的目标定位于与新兴气候条件相适应的生态系统类型，而不是试图将生态系统恢复到一个与环境日益失衡的历史状态可能更实际。在这种背景下，更新生态而不是恢复生态可能是最合适的框架。

3.4 濒危物种的管理 (Management for Endangered Species)

对濒危物种的管理需要一种景观的视角。濒危物种保护的重点一般是建立保护区，其中包括目标物种的种群和与这些物种相关的植被。然而，当人类继续影响如气候、火烧、水流以及物种引进时，建立公园可能也无法保护物种。例如，如果气候变化，动物可能会被困在一个不再有适合的气候或植被的公园里。选择具有不同海拔的公园为生物提供了垂直迁移到更高海拔的机会，以应对气候变暖。栖息地破碎化和土地利用变化也改变了公园内外生态系统之间的自然联系。因此，几乎所有的公园都需要管理来补偿人类的影响。例如，黄石国家公园的边界阻碍了麋鹿迁徙到传统的越冬地区，所以必须提供冬季食物补充。这些冬季食物的补充，加上对天敌的消灭，使麋鹿的数量脱离了自然控制。因此，管理者必须允许狩猎或重新分配麋鹿作为种群调节的替代机制。使用密集管理取代交互式控制，而不是努力维持交互式控制，是一项昂贵、复杂和困难的任务，特别是当管理有多个，经常合并的目标。

第四节　生态系统管理的社会经济范畴

有效的生态系统管理需要完整的社会-生态框架，以理解和管理变化世界中的可持续性。

4.1 满足人类的需求 (Meeting Human Needs and Wants)

生态系统管理的成功取决于生态系统服务满足人类需求的能力。

表 15.4-1 静态资源管理和生态系统管理的区别。改自 Chapin et al. (2010)。

Characteristic	Steady-state resource management	Ecosystem stewardship
Reference point	Historic condition	Trajectory of change
Central goal	Ecological integrity	Sustain social–ecological systems and delivery of ecosystem services
Predominant approach	Manage resource stocks and condition	Manage stabilizing and amplifying feedbacks
Role of uncertainty	Reduce uncertainty before taking action	Embrace uncertainty: maximize flexibility to adapt to an uncertain future
Role of research	Researchers transfer findings to managers who take action	Researchers and managers collaborate through adaptive management to create continuous learning loops
Role of resource manager	Decision maker who sets course for sustainable management	Facilitator who engages stakeholder groups to respond to and shape social–ecological change and nurture resilience
Response to isturbance	Minimize disturbance probability and impacts	Disturbance cycles used to provide windows of opportunity
Resources of primary concern	Species composition and ecosystem structure	Biodiversity, well-being, and adaptive capacity

4.2 管理生态系统服务的流动 (Managing Flows of Ecosystem Services)

经济成本和收益显著地影响了生态系统管理的可持续性。私有的自然资源和市场化的自然资源常常对于管理可持续性具有挑战性。公有自然资源常常通过政府机构管理，它们的职责是管理这些生态系统服务流。生态系统文化服务常常促进了可持续利用。

可持续生态系统管理不受限于私有的或公有的土地。资源依赖性社会常常可持续地管理自然资源，他们在缺乏私有属性或政府管理后，就会均分资源。

4.3 政策制定 (Addressing Political Realities)

资源管理者面临的最大的挑战许多都反映了他们工作的社会和政治环境。

4.4 创新和适应性管理 (Innovation and Adaptive Management)

适应性管理，包括在政策设计和运用方面的实验，是有效的生态系统管理的核心。像实验一样对待管理：管理基于假设。从经验中学习：基于结构改变管理；面对不确定性不作为是一种决定；尽量减少灾害的风险，而不是优化结果。

4.5 可持续发展: 社会-生态效益 (Sustainable Development: Social–Ecological)

整合的保护和发展计划(ICDPs)：假定保护不会具有作用，除非它对社会和经济有益；非常难权衡；始于 1980 年，在 1990 年超过了 100 个项目。

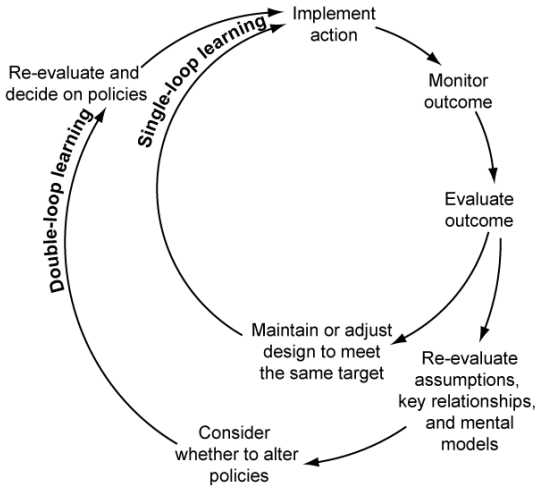


图 15.4-1 单环和双环学习。单环学习包括改变行为以满足确定的管理目标（例如改变收获量已满足规定的捕鱼量限制），通常通过反复试验。双环学习包括一个反射过程，评估内在前提和模型是定义问题的基础（例如基于近期的政策结果，修改指标和拟合模型以计算肥料输入量和作物产量的关系）。重绘 Kofina (2009)。

第五节　研究案例

案例 1 草地和荒漠生态系统服务功能的形成与调控机制

研究背景

生态系统服务功能是指生态系统提供的用以维持和实现人类生存与发展的环境条件和过程(Daily 1997)，是人类从生态系统获得的惠益(Millennium Ecosystem Assessment 2005)，是人类赖以生存和发展的基础(de Groot et al. 2002)。生态系统服务功能分为四大类：支持服务（养分循环、土壤形成、初级生产等）、供给服务（食物、淡水、木材和纤维、燃料等）、调节服务（调节气候、调节淡水、调控疾病）、文化服务（美学、精神、教育、消遣等）(Millennium Ecosystem Assessment 2005)。按照《世界资源报告》和联合国粮农组织（FAO）的定义，草地是指可以用于放牧或割草的土地，包括：天然放牧地、长久休闲地、五年以上生产草本饲

料作物的耕地、疏林地、矮木林、疏灌丛、荒漠、冻原、沿海滩涂、湿地沼泽和草甸(国际环境与发展研究所，世界资源研究所 1987)。《中国草地资源》一书采用了与 FAO 类似的概念，将草地定义为“草本和木本饲用植物与其所着生的土地构成的具有多种功能的自然综合体”(中华人民共和国农业部兽医司、全国畜牧兽医总站 1996)。草地生态系统服务功能的本质特征体现为生态功能和生产功能(de Groot et al. 2002)。生态功能指其生境、生物学性质和生态过程，为赖以生存的生命系统提供环境条件，包括气候调节、养分循环与贮存、固定 CO_2、释放 O_2、消减 SO_2、水源涵养、土壤形成、侵蚀控制、废物处理、滞留沙尘和生物多样性维持等方面(Sala and Paruelo 1997; White et al. 2000; 刘兴元 等 2001)。生产功能是为生命系统提供各种消费资源，包括家畜生产、牧草产品和药用植物等，对支撑畜牧业发展具有重要的作用。长期以来，我国在畜牧业生产中过度利用草地的生产功能，而忽视了草地的生态功能，造成了超载过牧、人-草-畜关系失衡和草地的大面积退化，并诱发了沙尘暴、荒漠化等生态灾难(国家环保总局 2006; 韩俊等 2011)。

近年来，生态系统服务功能研究已成为国际生态学研究的前沿和热点。国际上围绕生态系统服务功能的内涵和类型划分，生态系统服务功能的现状、受威胁程度和变化趋势评估，服务价值化评估，以及服务功能的关键驱动因子与相互作用机制等方面开展了大量的研究工作(Daily 1997; Daily et al. 2000; Kremen 2005; Millennium Ecosystem Assessment 2005; Bennett et al. 2009; Perrings et al. 2010; Chisholm and Wintle 2012; Bateman et al. 2013)。目前，生态系统服务功能研究的科学前沿和热点领域包括以下四个方面：

（1）生态系统服务功能的关键驱动因子及多个服务功能之间的相互作用机制是生态系统服务功能研究的科学前沿。生态系统为人类的生存和发展提供了多种服务，包括支持服务、供给服务、调节服务和文化服务等。许多研究表明，人类对一些服务功能的过度利用（例如，供给服务）可能会导致另一些服务功能（如，支持和调节服务）的显著下降、衰退甚至丧失，特别是当许多服务功能之间存在非线性关系时，其变化更加难以预测(Millennium Ecosystem Assessment 2005)。揭示管理措施（如，放牧、割草、施肥）和环境变化是如何对生态系统的多个服务功能产生影响，以及多个生态系统服务功能之间的关系与相互作用机制是当前生态系统服务功能研究的科学前沿(Carpenter et al. 2006; Bennett et al. 2009; Perrings et al. 2010)。在草地生态系统中，定量评估初级生产力、碳固定、防风固沙、保持水土和生物多样性维持功能之间的相互依赖性(interdependency)、弹性(resilience)和权衡关系(tradeoff)，可以帮助我们深入理解各种服务功能之间的依存关系及其生态学机制，同时为草地资源的保护、管理和可持续利用提供详实的科学依据。

（2）生态系统“结构－过程－服务”的相互作用机理及其反馈与调控机制是当前生态系统服务功能研究的热点。生态系统服务依赖于生态系统的结构和过程，土地利用变化、气候变化和管理措施通过改变生态系统的结构和过程，进而影响其服务功能(Bennett et al. 2009; Carpenter et al. 2009)。进入后千年生态系统评估时代，基于不同区域和生态系统类型的比较研究，揭示生态系统结构－过程－服务的相互作用机理及其反馈调节机制，成为当前乃至今

后若干年内生态系统服务功能研究的热点领域(Palmer et al. 2004; Carpenter et al. 2006; Carpenter et al. 2009; 傅伯杰等 2009; Fu et al. 2013)。

（3）生态系统服务的尺度特征与多尺度关联是生态系统服务功能研究的重点和难点。生态系统服务功能的形成依赖于一定的时间和空间尺度上的生态系统结构与过程, 只有在特定的时空尺度上才能表现其显著的主导作用和效果(Peterson and Parker 1998; Millennium Ecosystem Assessment 2005; 傅伯杰 et al. 2009; Perrings et al. 2010; Scholes et al. 2013)。近年来，对生态系统服务功能的时空特征、尺度效应和多尺度关联的研究已引起越来越多人的关注(Power 2010; Dearing et al. 2012; Quijas et al. 2012; Seppelt et al. 2013)。

（4）生物多样性与生态系统服务功能的关系是生态系统服务功能研究的重要内容。生物多样性与生态系统服务功能的关系，成为近 20 年来全球范围内倍受关注的重要领域，是生态学研究的热点(Sala et al. 2000; Loreau and Hector 2001; Hooper et al. 2005; Reiss et al. 2009; Midgley 2012; Turnbull et al. 2013)。尽管国内外学者围绕生物多样性与生态系统服务功能开展了大量研究，但由于两者的关系非常复杂，目前仍存在着很大的不确定性(Kremen 2005; 傅伯杰等 2009; Feld et al. 2010; Bullock et al. 2011; Isbell et al. 2011; Perrings et al. 2011; Larigauderie et al. 2012; Fu et al. 2013)。生物多样性与生态系统服务功能的实验研究是阐明生物多样性与生态系统服务功能关系的重要手段(Mertz et al. 2007; 傅伯杰等 2009; Geijzendorffer and Roche 2013; Vihervaara et al. 2013)。在草地生态系统中，依托大型野外控制实验平台，结合长期实验观测数据，从植物、动物和土壤微生物三个营养级水平，研究植物多样性、食草动物和土壤微生物之间的相互作用及其对生态系统过程与服务功能的反馈与调控机制，进而阐明生物多样性与生态系统生产力、稳定性和养分、水分保持能力等服务功能的内在联系，是草地生态系统生物多样性与服务功能关系研究的重要领域(Sala et al. 2000; Reiss et al. 2009)。

科学问题

（1)沿水分梯度，降水量及其季节分配是如何影响草地和荒漠生态系统结构与功能的？

（2）多种限制性养分(氮、磷、钾)是如何并在多大程度上影响生态系统生物多样性、初级生产力和服务功能的？其主要调控机制是什么？

（3）沿不同的组织水平和空间尺度，水分与养分的耦合作用是如何自下而上地影响生态系统过程和服务功能的？

（4）水分、养分和动物采食是如何影响生态系统各组分（植物地上部分、凋落物、植物根系、土壤和土壤微生物）之间的化学计量关系的？不同组分之间相互作用的强度有多大？它们是如何对生态系统格局、过程和服务功能进行调控的？

研究方法

联网实验包括三个养分（N、P、K）添加处理，每种养分设两个水平（添加和对照），采用因子设计，共八个处理；实验还包括一个草食动物剔除处理，两个水平（N、P、K 添加和完全对照），共两个处理，合计 10 个处理。N、P、K 添加处理分别为 10g $N \cdot m^{-2}$（施用 72.9 $g \cdot m^{-2}$ $CaNO_3$）、10g $P \cdot m^{-2}$（施用 44.4 g m^{-2} 重过磷酸钙）和 10g $K \cdot m^{-2}$（施用 48.2 g m^{-2} K_2SO_4），每年的施肥时间为 4 月 10 日（阜康站）和 7 月 1-3 日（其他站）进行。将 10 个处理的每个实验小区进一步划分为四个亚区：A 区为对照区；B 为预留实验区；C 为夏季增雨区；D 为冬春增雪区，具体增雨（雪）量和处理时间安排见表 1。对每个亚区，进一步划分为永久观测区（1m × 1m）、稳定性同位素标记及凋落物与根系分解实验区（1m × 1m）和生物量测定与土壤采样区（2.5m × 1m）三部分。实验采用完全随机区组设计，共 10 个一级处理（30 个二级处理），每个处理 6 次重复，共计 60 个小区，每个小区面积为 6m × 6m（草地）或 8m × 8m（荒漠）。

图 15.5-1 联网控制实验平台（野外实验设置）内蒙站，锡林郭勒草原生态系统国家野外科学观测研究站；海北站，海北高寒草甸生态系统国家野外科学观测研究站；奈曼站，奈曼沙化草地生态系统国家野外科学观测研究站；阜康站，阜康荒漠生态系统国家野外科学观测研究站。

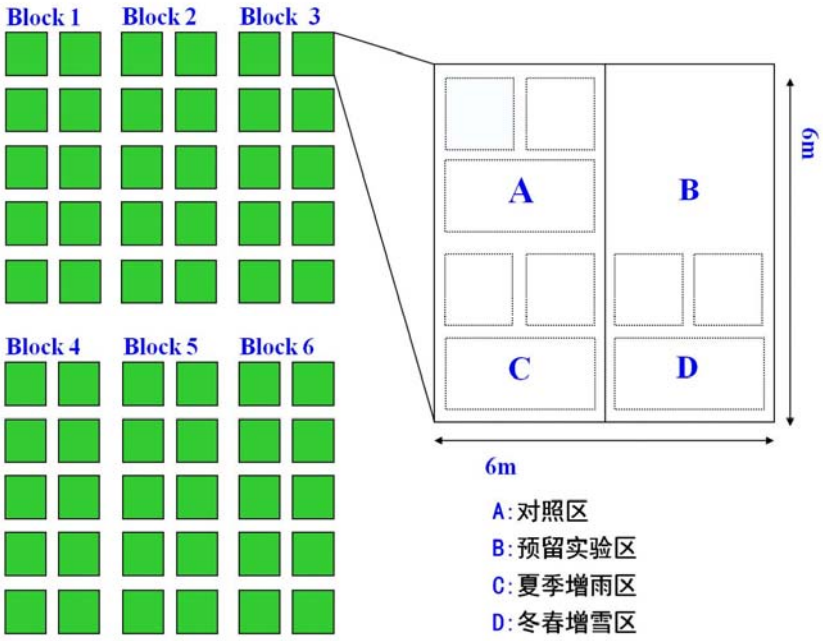


图 15.5-2 联网实验完全随机区组设计一级与二级实验处理方案。A 为对照区，B 为预留实验区，C 为夏季增雨区，D 为冬春增雪区；Block 1-6 表示 6 个实验区组重复。

观测指标体系

（1）生态系统属性：

根据草原生态系统的地上、地下组分，选取了 9 项生态系统属性指标进行观测，包括：物种组成，地上净初级生产力(ANPP)，地下生物量，生态系统净气体交换(NEE)，土壤呼吸，氮矿化作用，微生物生物量、C:N 比及群落结构，凋落物分解（图 15.5-3），氮素吸收、分配和利用。

（2）植物功能性状

植物功能性状的观测指标分为 4 类：整株性状（株高、茎和叶生物量、茎叶比、叶片密度、个体生物量和根冠比）、叶片形态性状（叶片面积、叶干物质含量和比叶面积）、叶片生理性状（光合速率、叶寿命、水分和氮素利用效率、叶片 C、N、P 含量）、根系性状（根直径、根表面积、根长密度、比根长、根系生物量、C、N、P 含量）和种子性状（种子质量），共计 26 个性状指标。

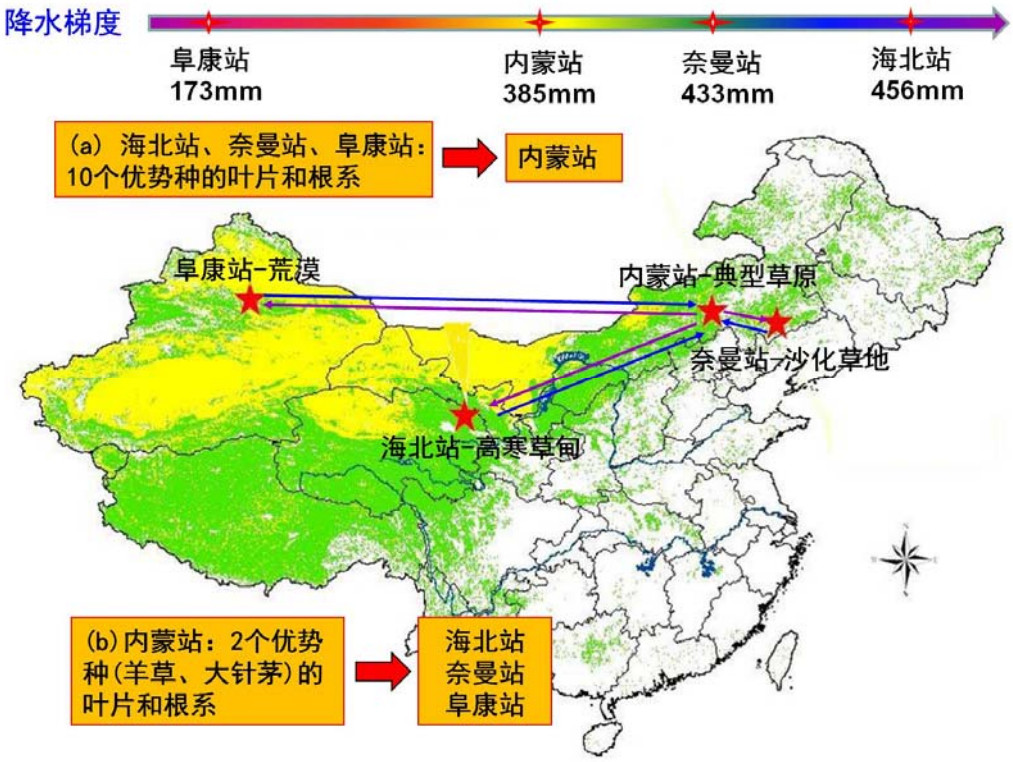


图 15.5-3 植物凋落物和根系异地分解实验：沿着降水梯度，海北站、奈曼站、内蒙站和阜康站的多年平均降雨量分别为 456、433、385 和 173mm；海北站、内蒙站、奈曼站和阜康站的代表性植被类型分别为高寒草甸、典型草原、沙化草地和荒漠。(a) 将海北站、奈曼站和阜康站的 10 个优势物种的叶片和根系样品放在内蒙站进行分解实验；(b) 将内蒙站的两个优势物种（羊草和大针茅）的叶片和根系样品放在海北站、奈曼站和阜康站进行分解实验。

主要发现

（1）养分和水分添加对高寒草地群落结构和服务功能的影响

通过在青藏高原高寒草甸连续 4 年(2009–2012 年)的养分、水分添加和 ^{15}N 稳定性同位素示踪实验，揭示了养分和水分添加对高寒草原群落结构和生产力、植物 N 吸收与分配策略及物候特征的影响机制，发现：1) N、P 添加提高了高寒草甸群落地上生物量，P 添加提高了群落地下生物量，而 N 添加对地下生物量无显著影响；N、P 添加改变了植物功能群组成，使禾草的多度增加，杂类草的多度降低（杨晓霞 等 2014）；2) 养分和水分添加改变了不同功能群植物的物候特征。N、P 添加使莎草科、禾本科、杂类草植物的返青期和枯黄期推迟，而增雪处理使杂类草植物的返青期提前，使大多数植物的开花期提前，增水处理使杂类草植物的枯黄期提前（叶鑫 等 2014）；3) 不同植物种对 N 素的吸收和分配策略具有明显的生态位分化和资源分配策略的权衡（邓建明 等 2014）；4)三江源区不同退化阶段草地土壤呼吸的研究发现，土壤温度和湿度对的土壤呼吸具有重要影响，中度退化草地生长季的

土壤呼吸速率最高，重度退化草地的土壤呼吸速率最低，土壤呼吸与地上生物量存在显著正相关关系（温军 等 2014）。

（2）养分、水分添加和放牧对典型草原群落结构和服务功能的影响

以内蒙古典型草原为研究对象，通过 N、P 添加实验和放牧控制实验，研究了养分添加、降水波动和放牧强度对典型草原群落物种多样性、初级生产力和植物功能性状的影响，发现：1) 群落净初级生产力受 N、P 元素共同限制。建群种羊草对 N、P 添加的响应因组织水平而异，同时受年际间降水波动的影响。羊草通过增加比叶面积、叶片大小和叶片 N 含量，提高整体光合能力，促进个体生长（白雪 等 2014）；2) 植物多样性对放牧的响应受降水波动和地形因素的调节，丰水年份群落 α–、β–和 γ–多样性均高于平水年份，平地对放牧的缓冲能力强于坡地，干旱会加剧重度放牧对植物多样性的影响（杨婧 等 2014）；3) 生态位分化机制对草原群落物种多度分布起着主导作用，常见种和稀有种通过不同的响应方式共同维持了群落的物种多样性（李文怀 等 2014）；4) 对群落中常见植物的根际和非根际土壤中细菌和真菌数量及群落结构的研究发现，根际土壤中的细菌和真菌数量普遍高于非根际土壤，尤其以真菌更为明显；大多数物种的根际细菌及真菌的群落结构与非根际存在显著地差异（王纳纳 等 2014）。

（3）养分和水分添加对沙化草地和荒漠群落结构和服务功能的影响

通过在荒漠和沙化草地设置养分(N、P、K)与水分(夏季增雨、冬春增雪)添加实验，研究了养分与水分添加对荒漠和沙化草地群落物种多样性和生物量分配格局、植物功能性状的影响，发现：1) 养分和水分添加降低了荒漠群落的物种多样性，改变了植物功能群组成，使禾草类植物增加, 十字花科植物减少。而水分添加、肥水交互作用对物种丰富度均无显著影响（赵新风 等 2014）；2) 施氮、增水的交互作用对荒漠建群种植物钠猪毛菜(Salsola nitraria)的功能性状具有显著的影响，施氮+冬春增雪处理使钠猪毛菜的株高、个体生物量、叶面积和比叶面积显著增加，钠猪毛菜通过形态可塑性提高其适应能力（赵新风 等 2014）；3) 施氮+夏季增雨（冬季增雪）均显著提高了一年生植物向叶片和果实的生物量分配，而对多年生植物无明显影响；施氮+冬季增雪使群落的植物叶生物量分配增加，而施氮+夏季增雨则使群落的茎生物量分配增加（毛伟 等 2014）。

今后我国草地和荒漠生态系统服务功能的研究重点应集中于以下几个方面：1）草地和荒漠生态系统初级生产力形成和维持机制；2）生物多样性与生态系统稳定性和服务功能的关系；3）生态系统服务功能对环境扰动的响应与适应机理；4）生态系统重要服务功能之间的相互依赖性、弹性、可逆性、权衡关系和尺度效应；5）水分、养分等关键限制因子及其耦合作用对生态系统结构与功能的多营养级水平和多尺度调控机理。

案例 2 氮素增加对植物多样性和群落稳定性的影响

研究背景

氮素可利用性是植物生长、繁殖最重要的限制因子之一；氮素可利用性的改变会影响许多陆地生态系统的物种组成和初级生产力(Vitousek et al. 1997; Aert and Chapin 2000; Elser et al. 2007)。由于工业和农业的生产活动，全球氮的可利用性在过去的 50 年增加了两倍，并成为世界范围内的生物多样性丧失和生态系统退化的主要原因之一 (Vitousek et al. 1997; Sala et al. 2000; Bobbink et al. 2010)。在草地上开展的控制实验研究表明，氮素增加能够持续降低物种数，并且增加少数物种（这些物种的性状让它们能够迅速利用这些添加的氮元素）的多度，改变群落的组成(Bobbink et al. 1998; Suding et al. 2005; Clark et al. 2007; Bai et al. 2010)。物种数的变化和植物功能群组成的改变对许多生态系统功能都会产生影响，例如土壤碳库和氮库固持、地上和地下生物量、生态系统的稳定性(Wedin and Tilman 1996; Tilman et al. 2006; Maestre et al. 2012)。因此，理解生物和非生物因子如何影响氮素增加导致的生物多样性和生态系统功能的改变，对于全球变化背景下的生物多样性保护和生态系统管理非常重要。

然而，至今仍不确定，氮素增加如何影响自然生态系统的稳定性（stability，本研究中表示为生物量的平均值/ 标准差）（Hautier et al. 2014）。氮素增加可能会通过以下几个途径影响生态系统的稳定性。首先，氮素增加能够增加群落的生物量的平均值（Bai et al. 2010），从而增加生物量的稳定性。但是，氮素增加提高了水分的限制性（Hooper and Johnson 1999），可能会增加生物量对年际间降雨量变化的敏感性，从而增加生物量的年际间变异，并且降低生态系统的稳定性。因此，氮素增加对稳定性的影响依赖于它对于生物量的平均值和标准差影响的相对大小。第二，由于氮素增加会降低生物多样性（Stevens et al. 2004; Suding et al. 2005; Clark and Tilman 2008; Chalcraft et al. 2008; Hautier et al. 2009; Hautier et al. 2014），从而降低物种异步性（species asynchrony），最终导致生态系统的稳定性下降（Yang et al. 2012a; Hautier et al. 2014）。第三，氮素增加往往提高了生长速度快的物种在群落中的优势度（Suding et al. 2005），但是这些物种的生物量年际变异性较高（Bai et al. 2004），因此可能导致群落的年际变异性增加、或稳定性下降。因此，只有更清楚地认识氮素增加如何影响这几个途径（例如生物多样性、生物量的变异），本研究才能够理解氮素增加如何影响生态系统的稳定性。

科学问题

本研究基于在内蒙古半干旱草原开展的氮素增加实验（>10 年）。本研究旨在解决三个问题：第一，在不同的组织水平（如物种，功能群和群落）和处理年数下，氮素增加导致物种多样性降低的阈值和格局是怎样的？第二，降雨量（湿润年与干旱年份）如何影响物种数和生物量对氮素增加的响应？第三，氮素增加如何影响生态系统功能（生物量、稳定性、干旱抗性）以及其内在的机制是什么？

研究方法

长期氮素增加实验于 1999 年开展于定位研究站的 1979 年羊草围封样地内。该样地自 1979 年开始围封。氮素增加实验按照随机区组设计（block design），共有 9 个区组。每个区组包括不同的施肥时间处理和施肥梯度处理，共 18 个处理（具体处理见第二章氮添加实验）。在本研究中，除了完全对照（control）外，本研究另外选取了其中的 6 个 7 月份施肥的处理，即 0.00, 1.75, 5.25, 10.50, 17.50, 28.0 g N m^{-2} yr^{-1}，同时每个施肥处理（除了完全对照）都添加等量的磷肥和微肥。

主要发现

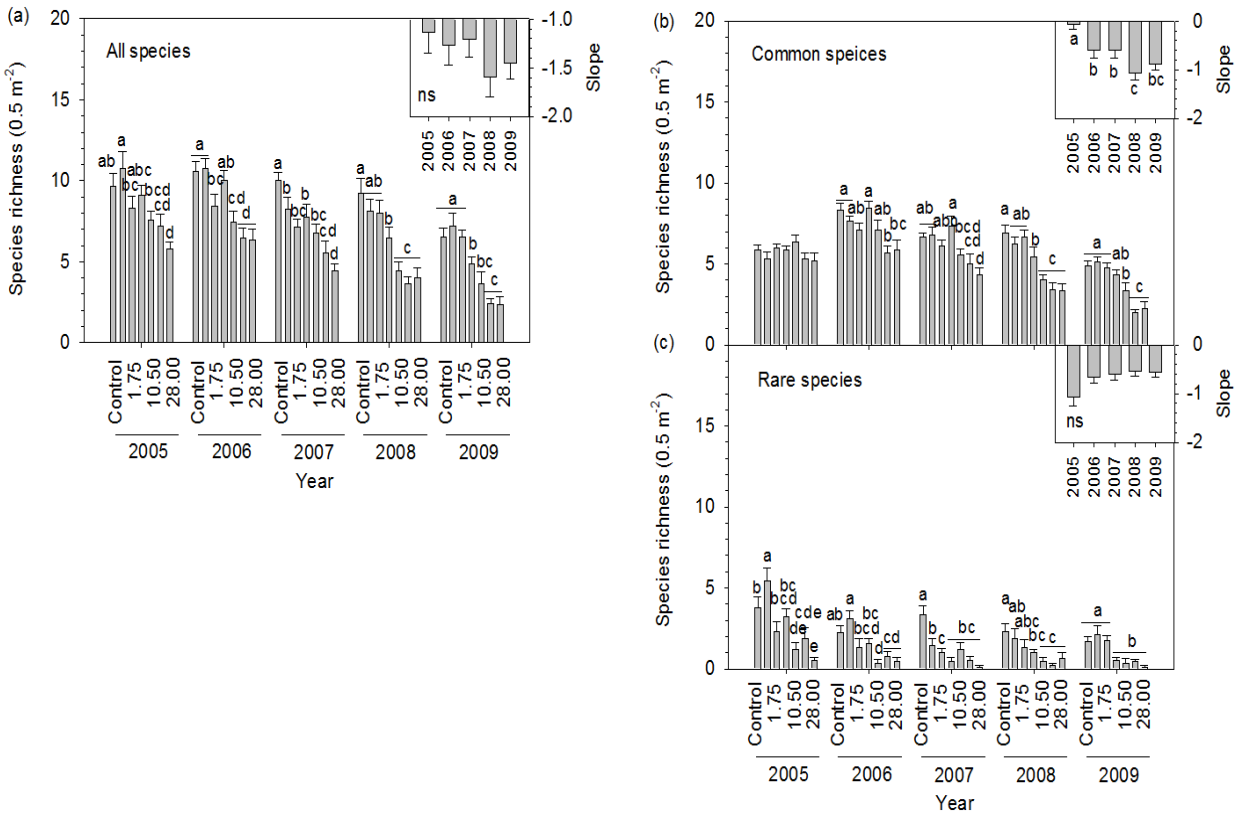


图 15.5-4 2005-2009 年氮素添加对(a)所有物种，(b)常见种和(c)稀有种丰富度的影响(平均值±标准误)。通过单因素方差分析和 Duncan's 多重比较进行处理间物种数比较，相同字母表示处理间物种数平均值没有显著差异。同时，以氮素添加量(Ln(N))为连续变量，对物种数按年份进行回归参数估计(物种数 = 截距+斜率× Ln (N)). 右上角小图表示物种数与氮素添加之间(Ln(N))斜率。相同字母表示用普通最小二乘法(OLS)拟合的斜率在年份间没有显著差异。

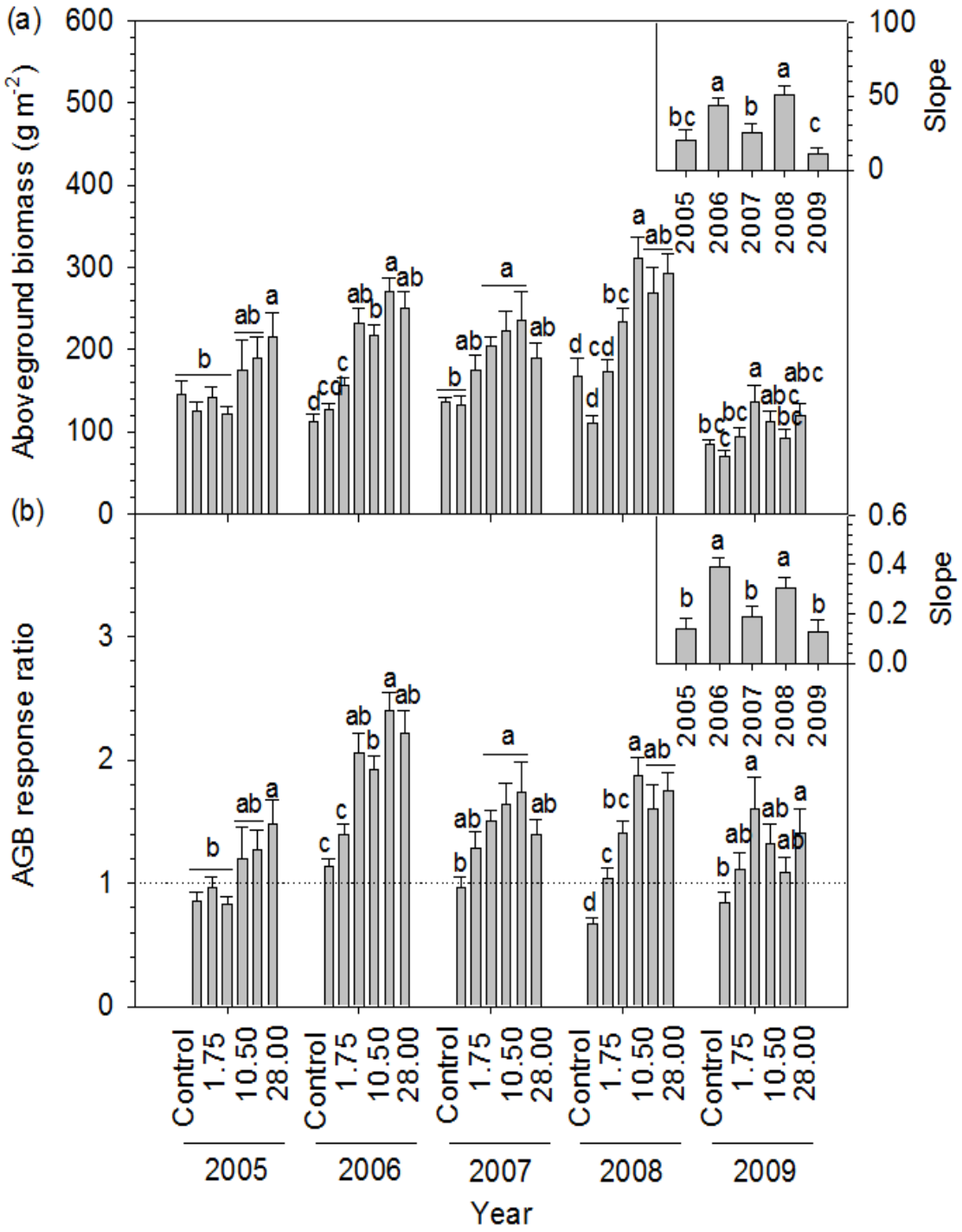


图 15.5-5 2005-2009 年氮素添加对(a)地上生物量(AGB)和(b)地上生物量响应速率(AGB response ratio)的影响(平均值±标准误)。同时，以氮素添加量(Ln(N+1))为连续变量，对物种数按年份进行回归参数估计(物种数 = 截距+斜率× Ln (N+1)). 右上角小图表示地上生物量，地上生物量响应速率与氮素添加之间(Ln (N+1))斜率。相同字母表示用普通最小二乘法(OLS)拟合的斜率在年份间没有显著差异。

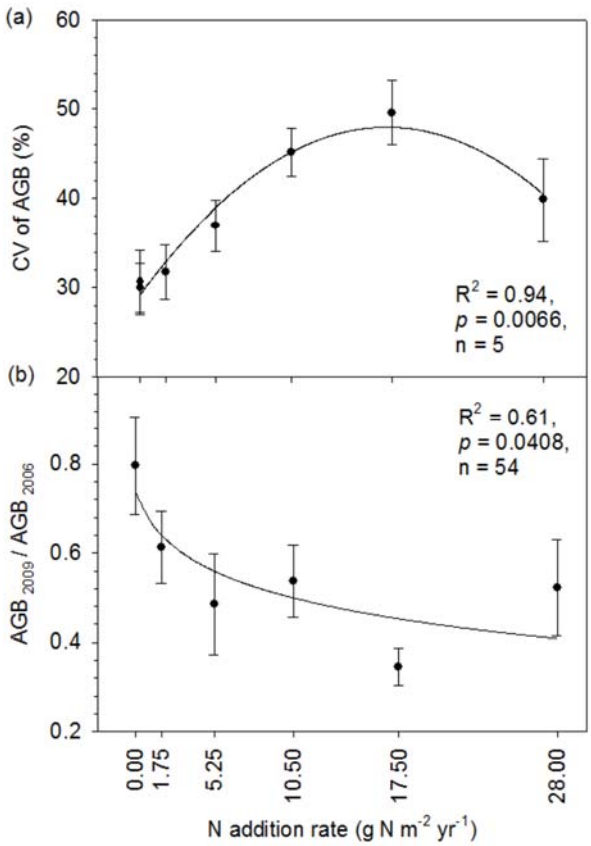


图 15.5-6 氮素添加对（a）地上生物量（AGB）年间的变异性和（b）耐旱性的（AGB_{2009}/ AGB_{2006}）影响（平均值±标准误）。

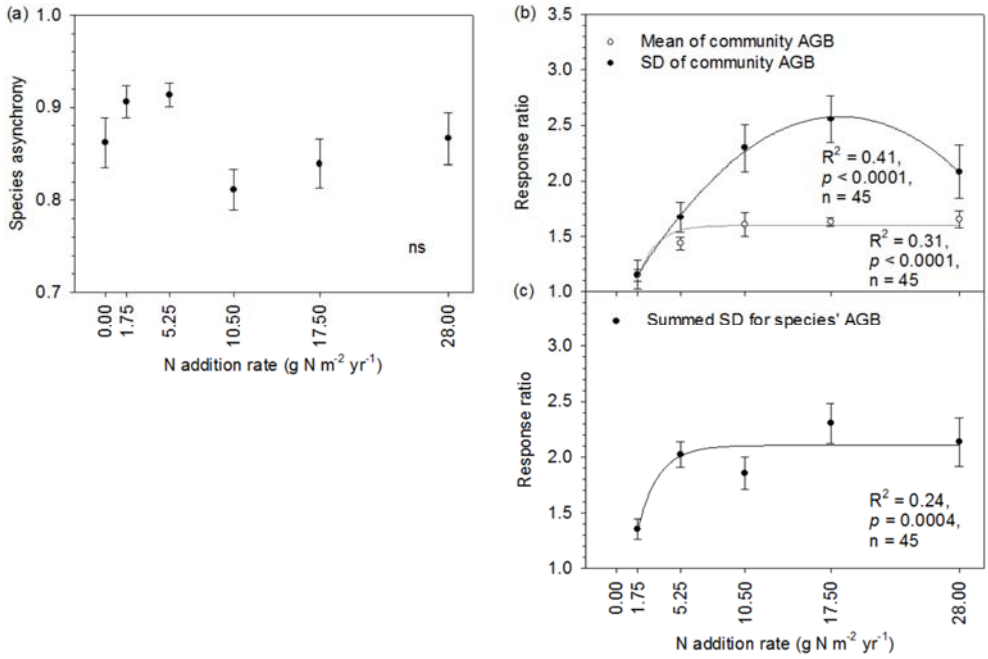


图 15.5-7 (a) 氮素添加对物种不同性的影响，(b)群落地上生物量(AGB)平均值和标准差响应速率对氮素添加的响应，(c)物种地上生物量标准差之和对氮素添加的响应速率(平均值±标准误)。

氮素增加在 1.75g N m^{-2} yr^{-1} 时显著降低物种数，预测的氮素增加导致物种多样性降低的阈值是 0.85g N m^{-2} yr^{-1}。相对于常见种，稀有种更容易丧失，具有较低的物种多样性降低阈值和较高的物种数减少的比例。氮素增加导致群落生物量增加的阈值通常低于 5.25 g N m^{-2} yr^{-1}。

处理年数增加会线性增加氮素增加导致物种多样性降低的程度。相对于较干旱的年份，在湿润年份地上生物量响应程度较高，物种多样性降低程度也较大。氮素增加显著地降低了群落的稳定性（生物量的平均值/标准差），但是主要是由于生物量的标准差的响应比例要高于平均值。

本研究对于理解氮沉降如何影响生物多样性和生态系统功能（如生产力、稳定性）有重要意义。由于氮增加的效应受到水分的调控，而未来的全球变化将可能会改变降雨量和频次，因此本研究体现了多个全球变化因子之间交互作用的重要性。

本章小结

人类活动影响地球上所有生态系统。生态系统直接受到资源采集、土地利用变化和管理等活动的影响，并间接受到人为造成的大气化学、水文和气候变化的影响。由于人类活动强烈地影响着地球上大部分的生态系统，因此我们也应该承担起照顾和保护它们的责任。一方面必须减缓全球变化的速度和程度，如气候、生物地球化学循环和土地利用变化。此外，需要对所有生态系统进行积极管理，以维持人口、物种和生态系统在面对人为变化时的功能，并维持人类从生态系统获得的商品和服务的供应。

状态因素和交互控制对生态系统过程具有较强的控制作用，以致这些控制因素的变化不可避免地改变生态系统，并降低其当前属性的可维持性。然后管理实践能够强烈影响可持续程度。如果管理的目标是提高管理和未管理的生态系统的可持续性，这就需要尽可能保存状态因素和相互作用的控制，并在生态系统内部和生态系统之间加强有助于维持这些控制的稳定（消极）反馈。许多生态系统控制的方向性变化加大了可持续管理自然资源的挑战，并威胁到各地自然生态系统的可持续性。生态系统管理方法将生态理解应用于资源管理，以促进生态系统的长期可持续性，并向社会提供必要的生态系统产品和服务。这需要从景观或区域的角度来考虑生态系统之间的相互作用，并明确将人类作为该区域系统的组成部分。生态系统管理承认随机事件的重要性，以及我们无法确定地预测未来的情况。适应性管理基于管理将如何影响生态系统的假设采取行动。根据实验结果，调整管理政策以提高可持续性。

推荐阅读文献：

Bai Y.F., Wu J.G., Clark C.M., Naeem S., Pan Q.M., et al. 2010. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands. Global Change Biology 16: 358-372.

Foley J.A., DeFries R., Asner G.P., Barford C., Bonan G., et al. 2005. Global consequences of land use. Science 309: 570–574.

Foley J.A., Ramankutty N., Brauman K.A., Cassidy E.S., Gerber J.S., 2011. Solutions for a cultivated planet. Nature 478: 337-342.

Holling, C. S., and Meffe, G. K. 1996. Command and control and the pathology of natural resource management. Conservation Biology 10:328-337.

Isbell F., Adler P.R., Eisenhauer N., Fornara D., Kimmel K., et al. 2017. Benefits of increasing plant diversity in sustainable agroecosystems. Journal of Ecology 105: 871-879.

Lubchenco, J., Olson, A. M., Brubaker, L. B., Carpenter, S. R., et al. 1991. The sustainable biosphere initiative: An ecological research agenda: A report from the ecological society of America . Ecology 72:371-412.

MEA (Millennium Ecosystem Assessment). 2005. Ecosystems and Human Well-being: Synthesis. Island Press, Washington.

Perino A., Pereira H.M., Navarro L.M., Fernandez N., Bullock J.M., et al. 2019. Rewilding complex ecosystems. Science 364: 351-358

Plieninger T., van der Horst D., Schleyer C., Bieling C. 2014. Sustaining ecosystem services in cultural landscapes. Ecology and society 19: art 59. doi: 10.5751/ES-06159-190259.

Schaub S., Finger R., Leiber F., Probst S., Kreuzer M., et al. 2020. Plant diversity effects on forage quality, yield and revenues of semi-natural grasslands. Nature Communications 11: art 1. doi: 10.1038/s41467-020-14541-4.

Steffen, W. L., Sanderson A., Tyson, P. D., Jaeger, J., Matson, P. A., et al. 2004. Global change and the earth system: a planet under pressure. Springer-Verlag, New York.

Turner B.L., Kasperson R.E., Matson P.A., McCarthy, J. J., Corell, R. W., et al. 2003. A framework for vulnerability analysis in sustainability science. Proceedings of the National Academy of Sciences of the United States of America 100:8074–8079.

Wang L., Delgado-Baquerizo M., Wang D.L., Isbell F., Liu J., et al. 2019. Diversifying livestock promotes multidiversity and multifunctionality in managed grasslands. Proceedings of the National Academy of Sciences of the United States of America 116: 6187-6192.

生态系统生态学综合作业要求

一、总体要求

围绕生态系统生态学前沿科学问题，每人选择一个问题，通过 Web of Science 对相关问题的研究历史、最新进展（近 5-10 年）、知名科学家及其代表性成果进行综述（3000 字左右），并做成 10 张左右的 PPT 进行课堂报告、互动和答疑。

成绩：50%（综述和课堂报告各占 25%）

二、各部分字数要求

1. 摘要（200 字左右）
2. 研究历史与最新进展（2000 字左右）
3. 知名科学家及其代表性成果（500 字左右）

生态系统生态学的前沿科学问题

1 生态系统特征

1) 在控制群落多样性和组成方面，随机过程和确定过程的相对重要性是什么？在不同的生态系统类型中，它们是如何变化的 (Chase 2007, Chase and Myers 2011, Sutherland et al. 2013, Wang et al. 2013)? What is the relative importance of stochastic vs. deterministic processes in controlling diversity and composition of communities, and how does this vary across ecosystem types?

2) 生态系统哪些属性对群落组成的变化最敏感?What properties of ecosystem are most sensitive to changes in community composition?

3) 我们能否基于物种的性状来预测生态系统对环境变化的响应? Can we predict the responses of ecosystems to environmental change based on the traits of species?

4) 物种性状如何影响生态网络结构(Crea et al. 2016, Tylianakis and Morris 2017)？How do species traits influence ecological network structure?

5) 生态学相互作用的网络结构如何影响生态系统的功能和稳定性 (Murphy et al. 2016)? How does the structure of ecological interaction networks affect ecosystem functioning and stability?

6) 哪些因素和机制决定了生态系统对外部扰动的弹性和恢复力？如何测度(Seddon et al. 2016)? Which factors and mechanisms determine the resilience of ecosystems to external perturbations and how do we measure resilience?

7) 我们如何知道一个生态系统何时接近临界点(Laurance 2013)？How can we tell when an ecosystem is near a tipping point? 哪些生态系统对临界点更敏感(Sutherland et al. 2013)？为什么？Which ecosystems are susceptible to showing tipping points and why?

8) 在生态系统中，滞后现象是特例还是常态(Fauchald 2010, Sternberg 2010)？Is hysteresis the exception or the norm in ecological systems?

2 生态系统输入过程

9) 初级生产者多样性在多大程度驱动了更广泛的群落多样性(Otto et al. 2008, Castagneyrol et al. 2014)? To what extent is primary producer diversity a driver of wider

community diversity?

10) 如何利用诸如个体大小和叶面积等简单性状的分布来预测群落属性及其对环境变的响应 (Wardle et al. 1998)？How well can community properties and responses to environmental change be predicted from the distribution of simple synoptic traits, e.g. body size, leaf area?

11) 植物如何对气候变化，如干旱等，做出响应 (Anderegg et al. 2019, Chardon et al. 2019, Miller and McGill 2019)？How do plants respond to climate change, e.g. drought, etc.?

12) 我们如何利用物种性状作为一个指标来预测营养级相互作用的强度(Otto et al. 2008)？How can we use species' traits as proxies to predict trophic interaction strength?

13) 干扰如何影响营养级之间的相互作用(Grabowski 2004, Sentis et al. 2015)？How do disturbances affect trophic interaction?

14) 营养级之间相互作用的变化对生态系统功能有多大影响(Schuldt et al. 2018)？How much do changes in trophic interactions affect ecosystem functioning?

3 生态系统生产过程

15) 植物固定的 C 在生长和呼吸之间的分配受什么机制控制(Atkin et al. 2000, Poorter 2002)？What mechanisms control the allocation of plant-fixed C between growth and respiration?

16) 净初级生产力和总初级生产力变化的机制是什么(Goulden et al. 2011)？What are the mechanisms for the changes in NPP and GPP?

17) C 分配的改变如何影响资源限制、资源获取和 NPP(Rennenberg 2015)？How do changes in allocation affect resource limitation, resource acquisition and NPP?

18) 生态系统中，除氮和磷(以及海洋中的铁)以外的营养物质如何影响生产力(Sutherland et al. 2013)? How do nutrients other than nitrogen and phosphorus (and iron in the sea) affect productivity in ecosystems?

4 生态系统分解过程

19) 分解作用对生态系统系统功能的意义是什么(Hattenschwiler et al. 2005)？What are the implications of decomposition for ecosystem functioning?

20) 全球变化引起的生物多样性丧失如何影响分解作用(Ball et al. 2008, Miki et al. 2014)？How does the loss of biodiversity due to global change affect decomposition?

21) 细菌和真菌在分解过程中的作用有何差异，为什么？What is the difference between the roles of bacteria and fungi during decomposition and why?

22) 由外界干扰引起的不同微生物类群（如细菌和真菌）相对比例的改变如何影响分解过程 (Peter et al. 2011)？How do the changes in the relative proportions of different microbial groups (e.g. bacteria and fungi) caused by external perturbations affect the decomposition processes?

23) 植物与微生物之间的相互作用如何影响生态系统分解过程(McCully 1999, Andrews and Harris 2000, Bais et al. 2004, Hinsinger et al. 2005)？How do plant-microbial interactions affect decomposition processes?

24) 除土壤微生物外，土壤动物对生态系统分解有什么影响(Gonzalez and Seastedt 2001)？In addition to soil microbes, what is the effect of soil animals on ecosystem decomposition?

25) 凋落物质量、环境因子和土壤微生物是影响分解过程中三个最重要的因子，其相对重要性如何(Cornwell et al. 2008, Wickings et al. 2012, Garcia-Palacios et al. 2016)？Litter quality, environmental factors and soil microorganisms are the three most important factors affecting the decomposition process, what is their relative importance？

26) 微生物对分解作用的影响是通过分泌与分解有关的酶，而不是在体内分解死有机质，为什么？Microorganisms influence decomposition by secreting extracellular enzymes rather than by breaking down dead organic matter in their body, why

27) 作为生态系统中一种重要的共生体，菌根对分解过程有何影响？不同菌根类型（如丛植菌根和外生菌根）有什么差异？As an important symbiont in the ecosystem, how does mycorrhizae affect the decomposition processes? what are the differences between different mycorrhizal types (e.g. arbuscular mycorrhizal and ectomycorrhizal)?

28) AMF 可以定殖在落叶中（不完全依赖于植物提供碳源？）(Bunn et al. 2019)，这一现象对分解作用以及其他生态系统功能有什么影响？AMF can colonize leaf litter (that is, not solely dependent on plant carbon sources) (Bunn et al. 2019). What is the implication of this phenomenon for decomposition and other ecosystem functions?

5 生态系统养分循环

29) 大气中的氮是如何进入到陆地生态系统的？How does atmospheric nitrogen enters

terrestrial ecosystems?

30) 凋落物中的氮通过什么途径才能成为植物可利用氮？By what pathways can nitrogen in litters become available to plants?

31) 氮素在陆地生态系统中的转化过程有哪些(Kuypers et al. 2018)？What are the processes of nitrogen conversion in terrestrial ecosystems (Kuypers et al. 2018)?

32) 磷进入生态系统的机制是什么？What are the mechanisms by which phosphorus enters ecosystem?

33) 全球变化引起的生物多样性丧失对养分循环有什么影响(Hobbie 1992, Hooper and Vitousek 1998, Niklaus et al. 2007)？What is the impact of biodiversity loss due to global change on nutrient cycling (Hobbie 1992, Hooper and Vitousek 1998, Niklaus et al. 2007)?

34) 不同养分在循环过程中的耦合关系如何(Gusewell 2004, Vitousek et al. 2010, Penuelas et al. 2012, Rivas-Ubach et al. 2012, Penuelas et al. 2013)？全球变化如何影响这些耦合关系 (Delgado-Baquerizo et al. 2013, Yuan and Chen 2015)？What is the coupling between different nutrients in the cycling process (Gusewell 2004, Vitousek et al. 2010, Penuelas et al. 2012, Rivas-Ubach et al. 2012, Penuelas et al. 2013)? How does global change affect these coupling relationships (Delgado-Baquerizo et al. 2013, Yuan and Chen 2015)?

6 生物多样性与生态系统功能

35) 物种丢失如何影响剩余物种的灭绝风险? How does species loss affect the extinction risk of the remaining species?

36) 局地尺度的物种组成和多样性在多大程度上受区域尺度物种库和传播限制控制(Sutherland et al. 2013)？To what extent is local species composition and diversity controlled by dispersal limitation and the regional species pool?

37) 一些我们知之甚少的生态系统，例如，深海、地下水，是否在全球具有重要的生态系统功能(Sutherland et al. 2013)? Are there globally significant ecosystem functions provided by poorly known ecosystems (e.g. deep oceans, ground water)?

38) 不同组织层次的生物多样性（基因、物种丰富度、物种属性、功能属性、功能多样性）对生态系统功能的相对贡献是什么? What is the relative contribution of biodiversity at different levels of organization (genes, species richness, species identity, functional identity, functional diversity) to ecosystem functioning?

39) 在生物多样性变化的现实情景下，生态系统功能是如何变化的(Tilman et al. 1996, Tilman et al. 2014)？How is ecosystem function altered under realistic scenarios of biodiversity change?

40) 地下生物多样性如何影响地上生物多样性，反之亦然(Sutherland et al. 2013)？How does below-ground biodiversity affect aboveground biodiversity, and vice versa?

41) 地下生物多样如何影响生态系统功能(Bardgett and van der Putten 2014, van der Heijden 2016)？How does belowground biodiversity affect ecosystem functioning?

42) 微生物多样性（功能型、物种、遗传多样性）与群落和生态系统功能之间的关系是怎样的(Sutherland et al. 2013)？What is the relationship between microbial diversity (functional type, species, genotype) and community and ecosystem functioning?

43) 生物入侵和本土物种的丧失在多大程度上造成了生态系统属性的改变? To what extent is biotic invasion and native species loss creating ecosystems with altered properties?

44) 不同时空尺度下，环境异质性如何影响生物多样性(Sutherland et al. 2013)？How do spatial and temporal environmental heterogeneity influence diversity at different scales?

45) 空间结构如何影响生态系统功能，我们如何在空间尺度内和空间尺度之间进行整合评估生态系统功能? How does spatial structure influence ecosystem function and how do we integrate within and between spatial scales to assess function?

46) 在随机或定向环境变化的背景下，哪些物种在功能上是冗余的?Which species are functionally redundant in the context of stochastic or directional environmental changes?

47) 跨越多个生态系统类型，禾草与木本植物长期共存的机制是什么(Sutherland et al. 2013)？Which mechanisms allow the long-term coexistence of grasses and woody plants over a wide range of ecosystems?

48) 稀有种对生态系统功能具有哪些重要影响(Sutherland et al. 2013)？How important are rare species in the functioning of ecological communities?

49) 顶级捕食者数量下降对生态系统有什么影响? What is the impact of a decline in the number of top predators on the ecosystem?

7 人类活动与全球变化

50) 自然栖息地破碎化与消失对生物多样性的影响是什么(Aguilar et al. 2006)？What are the impacts of fragmentation and loss of natural habitats on biodiversity (Aguilar et al.

2006)?

51) 采伐会对生态系统结构和动态产生什么样间接影响？What are the indirect effects of harvesting on ecosystem structure and dynamics (Sutherland et al. 2013)?

52) 全球变化（如大气 CO2 浓度升高、全球气温升高、土地利用变化等）将如何影响生态系统初级生产力(Cao and Woodward 1998)？How will global change affect primary productivity of terrestrial ecosystems?

53) 气候变化在多大程度上能够通过改变物候导致生态系统营养级联系解体(Edwards and Richardson 2004, Thackeray et al. 2016, Burgess et al. 2018, Renner and Zohner 2018)？To what extent will climate change uncouple trophic links due to phenological change?

54) 在全球变化下，是什么决定了物种是适应环境、改变生存范围还是走向灭绝(Onstein et al. 2018)？In the face of global change, what determines whether species adapt, shift their ranges or go extinct?

55) 种间相互作用如何影响物种对全球变化的响应(Singer et al. 2013, Mason et al. 2015)? How do interspecific interactions affect the response of species to global change?

56) 什么是灭绝债务(extinction debt)?其机制是什么？自然栖息地的破碎化和丧失对灭绝债务的影响有多大？什么时候支付？What is the magnitude of the ‘extinction debt’ following the loss and fragmentation of natural habitats, and when will it be paid (Kuussaari et al. 2009, Hylander and Ehrlén 2013)?

8 生态系统服务

57) 充分考虑生态系统结构异质性导致的态系统服务异质性对于我们准确评价生态系统服务的意义是什么(Meyer 2005, Levine et al. 2016)？What is the implication of considering the heterogeneity of ecosystem services caused by heterogeneity of ecosystem structure for our accurate evaluation of ecosystem services?

58) 生态系统服务功能空间转移的机理、载体、过程、途径、方向和强度如何(Plummer 2009, Newton and Cordingley 2012, Ferrini et al. 2015, Khan et al. 2018)？What are the mechanisms, carriers, processes, approaches, directions and strengths of the spatial transfer of ecosystem services?

59) 生态系统服务功能在转移过程中会发生何种转化？其影响是什么？What transformation will take place in the transfer process of ecosystem service? What is the impact?

60) 哪些生态系统服务会影响到生态安全？What ecosystem services will affect ecological security?

61) 生态系统服务的空间格局对生态安全格局有什么影响？What impact does the spatial pattern of ecosystem services have on the ecological security pattern?

62) 生态系统服务的状况与生态安全阈值有何关系？What is the relationship between the state of ecosystem services and ecological security thresholds?

63) 如何建立一个生态安全评价体系和预警系统（如态系统服务受损害模拟、评估和预测）？ How to establish an ecological security assessment system and an early warning system (e.g. simulation, assessment and prediction of damage to ecosystem services)?

64) 如何建立一种更精确的评价方法来评价生态系统服务(Alexander et al. 1998, Dunford et al. 2018, Harrison et al. 2018, Rincon-Ruiz et al. 2019)？How to establish a more accurate evaluation method to assess ecosystem services?

65) 全球变化对不同类型生态系统服务的影响什么？哪些生态系统服务服务对全球变化最为敏感(Schroter et al. 2005, Tallis et al. 2012, Boone et al. 2017)？What are the impacts of global change on different types of ecosystem services? Which ecosystem services are most sensitive to global change?

9 生态学中的尺度问题

66) 环境的时空异质性是如何在不同尺度上影响生物多样性？How does spatiotemporal heterogeneity of environment affect biodiversity at different scales?

67) 空间结构如何影响生态系统功能？如何在不同空间尺度之内或之间整合来评估功能？How does spatial structure affect ecosystem function? How to evaluate functionality within or between different spatial scales?

68) 如何整合多尺度和类型的监测（从区域到全球的观测）来产生稳健的生态学推断？How do we combine multiple scales and types of monitoring (from field to earth observation) to make robust ecological inferences?

69) 广泛研究的生态学格局（物种多度分布、种-面积关系）在多大程度上反映了统计结果而不是生态学过程？To what extent are widely studied ecological patterns (species-abundance distribution, species-area relationship, etc.) the outcomes of statistical rather than ecological processes?

70) 决定生态系统变化大小和方向的最适基准是什么？What are the most appropriate

baselines for determining the magnitude and direction of ecological changes?

10 新技术和新方法在生态系统生态学研究中的应用

71) 高通量测序

72) 基因组学(Swenson and Jones 2017)

73) 转录组学(Swenson et al. 2017)

74) 核磁共振技术

75) 稳定性同位素

76) 生态系统天-空-地一体化监测与研究

77) 大数据和人工智能

参考文献

Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecology letters **9**:968–980.

Alexander, A. M., J. A. List, M. Margolis, and R. C. d'Arge. 1998. A method for valuing global ecosystem services. Ecological Economics **27**:161-170.

Anderegg, W. R. L., A. T. Trugman, D. R. Bowling, G. Salvucci, and S. E. Tuttle. 2019. Plant functional traits and climate influence drought intensification and land-atmosphere feedbacks. Proceedings of the National Academy of Sciences of the United States of America **116**:14071-14076.

Andrews, J. H., and R. F. Harris. 2000. The ecology and biogeography of microorganisms of plant surfaces. Annual Review of Phytopathology **38**:145-180.

Atkin, O. K., A. H. Millar, P. Gardeström, and D. A. Day. 2000. Photosynthesis, carbohydrate metabolism and respiration in leaves of higher plants. Pages 153-175 *in* R. C. Leegood, T. D. Sharkey, and S. von Caemmerer, editors. Photosynthesis: Physiology and Metabolism. Kluwer Academic Publishers, New York.

Bais, H. P., S. W. Park, T. L. Weir, R. M. Callaway, and J. M. Vivanco. 2004. How plants communicate using the underground information superhighway. Trends in Plant Science **9**:26-32.

Ball, B. A., M. D. Hunter, J. S. Kominoski, C. M. Swan, and M. A. Bradford. 2008. Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. Journal of Ecology **96**:303-313.

Bardgett, R. D., and W. H. van der Putten. 2014. Belowground biodiversity and ecosystem functioning. Nature **515**:505-511.

Boone, R. B., R. T. Conant, J. Sircely, P. K. Thornton, and M. Herrero. 2017. Climate change impacts on selected global rangeland ecosystem services. Global Change Biology **24**:1382-1393.

Bunn, R. A., D. T. Simpson, L. S. Bullington, Y. Lekberg, and D. P. Janos. 2019. Revisiting the 'direct mineral cycling' hypothesis: arbuscular mycorrhizal fungi colonize leaf litter, but why? The ISME journal **13**:1891-1898.

Burgess, M. D., K. W. Smith, K. L. Evans, D. Leech, J. W. Pearcehiggins, C. J. Branston, K. Briggs, J. R. Clark, C. R. D. Feu, and K. Lewthwaite. 2018. Tritrophic phenological match–mismatch in space and time. Nature Ecology & Evolution **2**:970-975.

Cao, M., and F. I. Woodward. 1998. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. Global Change Biology **4**:185–198.

Castagneyrol, B., H. Jactel, C. Vacher, E. G. Brockerhoff, and J. Koricheva. 2014. Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. Journal of Applied Ecology **51**:134-141.

Chardon, N. I., C. Rixen, S. Wipf, and D. F. Doak. 2019. Human trampling disturbance exerts different ecological effects at contrasting elevational range limits. Journal of Applied Ecology **56**:1389-1399.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences of the United States of America **104**:17430-17434.

Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society B-Biological Sciences **366**:2351-2363.

Cornwell, W., J. Cornelissen, K. Amatangelo, E. Dorrepaal, V. Eviner, O. Godoy, S. Hobbie, B. Hoorens, H. Kurokawa, and N. Perez-Harguindeguy. 2008. Plant traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology letters **11**:1065–1071.

Crea, C., R. A. Ali, and R. Rader. 2016. A new model for ecological networks using species-level

traits. Methods in Ecology and Evolution **7**:232-241.

Delgado-Baquerizo, M., F. T. Maestre, A. Gallardol, M. A. Bowker, M. D. Wallenstein, J. Luis Quero, V. Ochoa, B. Gozalo, M. Garcia-Gomez, S. Soliveres, P. Garcia-Palacios, M. Berdugo, E. Valencia, C. Escolar, T. Arredondo, C. Barraza-Zepeda, D. Bran, J. Antonio Carreiral, M. Chaieb, A. A. Conceicao, M. Derak, D. J. Eldridge, A. Escudero, C. I. Espinosa, J. Gaitan, M. G. Gatica, S. Gomez-Gonzalez, E. Guzman, J. R. Gutierrez, A. Florentino, E. Hepper, R. M. Hernandez, E. Huber-Sannwald, M. Jankju, J. Liu, R. L. Mau, M. Miriti, J. Monerris, K. Naseri, Z. Noumi, V. Polo, A. Prina, E. Pucheta, E. Ramirez, D. A. Ramirez-Collantes, R. Romao, M. Tighe, D. Torres, C. Torres-Diaz, E. D. Ungar, J. Val, W. Wamiti, D. Wang, and E. Zaady. 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature **502**:672-+.

Dunford, R., P. Harrison, A. Smith, J. Dick, D. N. Barton, B. Martin-Lopez, E. Kelemen, S. Jacobs, H. Saarikoski, F. Turkelboom, W. Verheyden, J. Hauck, P. Antunes, R. Aszalos, O. Badea, F. Baro, P. Berry, L. Carvalho, G. Conte, B. Czucz, G. G. Blanco, D. Howard, R. Giuca, E. Gomez-Baggethun, B. Grizetti, Z. Izakovicova, L. Kopperoinen, J. Langemeyer, S. Luque, D. M. Lapola, G. Martinez-Pastur, R. Mukhopadhyay, S. B. Roy, J. Niemela, L. Norton, J. Ochieng, D. Odee, I. Palomo, P. Pinho, J. Priess, G. Rusch, S. R. Saarela, R. Santos, J. T. van der Wal, A. Vadineanu, A. Vari, H. Woods, and V. Yli-Pelkonen. 2018. Integrating methods for ecosystem service assessment: experiences from real world situations. Ecosystem Services **29**:499-514.

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature **430**:881-884.

Fauchald, P. 2010. Predator-prey reversal: a possible mechanism for ecosystem hysteresis in the North Sea? Ecology **91**:2191-2197.

Ferrini, S., M. Schaafsma, and I. J. Bateman. 2015. Ecosystem Services Assessment and Benefit Transfer.

Garcia-Palacios, P., E. A. Shaw, D. H. Wall, and S. Hattenschwiler. 2016. Temporal dynamics of biotic and abiotic drivers of litter decomposition. Ecology letters **19**:554-563.

Gonzalez, G., and T. R. Seastedt. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology **82**:955-964.

Goulden, M. L., A. M. S. McMillan, G. C. Winston, A. V. Rocha, K. L. Manies, J. W. Harden, and B. P. Bond-Lamberty. 2011. Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. Global Change Biology **17**:855-871.

Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. Ecology **85**:995-1004.

Gusewell, S. 2004. N : P ratios in terrestrial plants: variation and functional significance. New Phytologist **164**:243-266.

Harrison, P. A., R. Dunford, D. N. Barton, E. Kelemen, B. Martin-Lopez, L. Norton, M. Termansen, H. Saarikoski, K. Hendriks, E. Gomez-Baggethun, B. Czucz, M. Garcia-Llorente, D. Howard, S. Jacobs, M. Karlsen, L. Kopperoinen, A. Madsen, G. Rusch, M. van Eupen, P. Verweij, R. Smith, D. Tuomasjukka, and G. Zulian. 2018. Selecting methods for ecosystem service assessment: a decision tree approach. Ecosystem Services **29**:481-498.

Hattenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology Evolution and Systematics **36**:191-218.

Hinsinger, P., G. R. Gobran, P. J. Gregory, and W. W. Wenzel. 2005. Rhizosphere geometry and heterogeneity arising from root-mediated physical and chemical processes. New Phytologist **168**:293-303.

Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. Trends in Ecology & Evolution **7**:336-339.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. Ecological Monographs **68**:121-149.

Hylander, K., and J. Ehrlén. 2013. The mechanisms causing extinction debts. Trends in Ecology & Evolution **28**:341-346.

Khan, I., M. J. Zhao, S. U. Khan, L. Y. Yao, A. Ullah, and T. Xu. 2018. Spatial heterogeneity of preferences for improvements in river basin ecosystem services and its validity for benefit transfer. Ecological Indicators **93**:627-637.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology & Evolution **24**:564-571.

Kuypers, M. M. M., H. K. Marchant, and B. Kartal. 2018. The microbial nitrogen-cycling network. Nature Reviews Microbiology **16**:263-276.

Laurance, W. F. 2013. Tipping points and the vulnerability of Australia's tropical ecosystems. Pages 169-180 *in* P. H. Raven, N. S. Sodhi, and L. Gibson, editors. Conservation Biology: Voices from the Tropics. John Wiley & Sons, Ltd Chichester.

Levine, N. M., K. Zhang, M. Longo, A. Baccini, O. L. Phillips, S. L. Lewis, E. Alvarez-Davila, A. C. S. de Andrade, R. J. W. Brienen, T. L. Erwin, T. R. Feldpausch, A. L. M. Mendoza, P. N. Vargas, A. Prieton, J. E. Silva-Espejo, Y. Malhi, and P. R. Moorcroft. 2016. Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. Proceedings of the National Academy of Sciences of the United States of America **113**:793-797.

Mason, T. H., P. A. Stephens, M. Apollonio, and S. G. Willis. 2015. Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. Global Change Biology **20**:3872-3882.

McCully, M. E. 1999. Roots in soil: Unearthing the complexities of roots and their rhizospheres. Annual Review of Plant Physiology and Plant Molecular Biology **50**:695-718.

Meyer, J. L. 2005. Heterogeneity and Ecosystem Function: Enhancing Ecological Understanding and Applications. Pages 451-461 *in* G. M. Lovett, M. G.Turner, C. G. Jones, and K. C. Weathers, editors. Ecosystem Function in Heterogeneous Landscapes. Springer, New York.

Miki, T., T. Yokokawa, and K. Matsui. 2014. Biodiversity and multifunctionality in a microbial community: a novel theoretical approach to quantify functional redundancy. Proceedings of the Royal Society B-Biological Sciences **281**:20132498.

Miller, K. M., and B. J. McGill. 2019. Compounding human stressors cause major regeneration debt in over half of eastern US forests. Journal of Applied Ecology **56**:1355-1366.

Murphy, E. J., R. D. Cavanagh, K. F. Drinkwater, S. M. Grant, J. J. Heymans, E. E. Hofmann, G. L. Hunt, and N. M. Johnston. 2016. Understanding the structure and functioning of polar pelagic ecosystems to predict the impacts of change. Proceedings of the Royal Society B-Biological Sciences **283**:10.

Newton, A. C., and J. Cordingley. 2012. Cost-benefit analysis of ecological networks assessed through spatial analysis of ecosystem services. Journal of Applied Ecology **49**:571-580.

Niklaus, P. A., J. Alphei, C. Kampichler, E. Kandeler, C. Körner, D. Tscherko, and M. Wohlfender. 2007. Interactive effects of plant species diversity and elevated CO_2 on soil biota and nutrient cycling. Ecology **88**:3153-3163.

Onstein, R. E., W. J. Baker, C. Tlp, S. Faurby, L. Herrera-Alsina, J. C. Svenning, and W. D. Kissling. 2018. To adapt or go extinct? The fate of megafaunal palm fruits under past global change. Proceedings of the Royal Society B: Biological Sciences **285**:20180882.

Otto, S. B., E. L. Berlow, N. E. Rank, J. Smiley, and U. Brose. 2008. Predator diversity and identity

drive interaction strength and trophic cascades in a food web. Ecology **89**:134-144.

Penuelas, J., B. Poulter, J. Sardans, P. Ciais, M. van der Velde, L. Bopp, O. Boucher, Y. Godderis, P. Hinsinger, J. Llusia, E. Nardin, S. Vicca, M. Obersteiner, and I. A. Janssens. 2013. Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. Nature Communications **4**:2934.

Penuelas, J., J. Sardans, A. Rivas-Ubach, and I. A. Janssens. 2012. The human-induced imbalance between C, N and P in Earth's life system. Global Change Biology **18**:3-6.

Peter, H., S. Beier, S. Bertilsson, E. S. Lindstrom, S. Langenheder, and L. J. Tranvik. 2011. Function-specific response to depletion of microbial diversity. Isme Journal **5**:351-361.

Plummer, M. L. 2009. Assessing benefit transfer for the valuation of ecosystem services. Frontiers in Ecology and the Environment **7**:38-45.

Poorter, H. 2002. Plant growth and carbon economy. In: eLS. John Wiley & Sons Ltd., Chichester. https://doi.org/10.1038/npg.els.0003200.

Rennenberg, H. 2015. Communities and ecosystem functioning. Pages 77-92 *in* G.-J. Krauss and D. H. Nies, editors. Ecological Biochemistry: Environmental and Interspecies Interactions. Wiley-VCH, Weinheim.

Renner, S. S., and C. M. Zohner. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annual Review of Ecology, Evolution, and Systematics **49**:165-182.

Rincon-Ruiz, A., P. Arias-Arevalo, J. M. N. Hernandez, H. Cotler, M. A. Caso, P. Meli, A. Tauro, V. D. A. Akerberg, V. S. Avila-Foucat, J. P. Cardenas, L. A. C. Hernandez, L. G. Castro, V. A. C. Hernandez, A. C. Araque, J. Deschamps-Lomeli, J. M. Galeana-Pizann, K. G. Onate, J. A. H. Aguilar, A. D. Jimenez, L. A. L. Mathamba, L. M. Perez, M. L. M. Diaz, W. M. Marin, V. Ochoa, M. A. Sarmiento, J. D. Timote, L. L. T. Cardozo, A. T. Acosta, and T. Waldron. 2019. Applying integrated valuation of ecosystem services in Latin America: Insights from 21 case studies. Ecosystem Services **36**:12.

Rivas-Ubach, A., J. Sardans, M. Perez-Trujillo, M. Estiarte, and J. Penuelas. 2012. Strong relationship between elemental stoichiometry and metabolome in plants. Proceedings of the National Academy of Sciences of the United States of America **109**:4181-4186.

Schroter, D., W. Cramer, R. Leemans, I. C. Prentice, M. B. Araujo, N. W. Arnell, A. Bondeau, H. Bugmann, T. R. Carter, C. A. Gracia, A. C. de la Vega-Leinert, M. Erhard, F. Ewert, M. Glendining, J. I. House, S. Kankaanpaa, R. J. T. Klein, S. Lavorel, M. Lindner, M. J. Metzger,

J. Meyer, T. D. Mitchell, I. Reginster, M. Rounsevell, S. Sabate, S. Sitch, B. Smith, J. Smith, P. Smith, M. T. Sykes, K. Thonicke, W. Thuiller, G. Tuck, S. Zaehle, and B. Zierl. 2005. Ecosystem service supply and vulnerability to global change in Europe. Science **310**:1333-1337.

Schuldt, A., T. Assmann, M. Brezzi, F. Buscot, D. Eichenberg, J. Gutknecht, W. Hardtle, J. S. He, A. M. Klein, P. Kuhn, X. J. Liu, K. P. Ma, P. A. Niklaus, K. A. Pietsch, W. Purahong, M. Scherer-Lorenzen, B. Schmid, T. Scholten, M. Staab, Z. Y. Tang, S. Trogisch, G. von Oheimb, C. Wirth, T. Wubet, C. D. Zhu, and H. Bruelheide. 2018. Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nature Communications **9**:2989.

Seddon, A. W. R., M. Macias-Fauria, P. R. Long, D. Benz, and K. J. Willis. 2016. Sensitivity of global terrestrial ecosystems to climate variability. Nature **531**:229-+.

Sentis, A., J. Morisson, and D. S. Boukal. 2015. Thermal acclimation modulates the impacts of temperature and enrichment on trophic interaction strengths and population dynamics. Global Change Biology **21**:3290-3298.

Singer, A., J. M. J. Travis, and K. Johst. 2013. Interspecific interactions affect species and community responses to climate shifts. Oikos **122**:358-366.

Sternberg, L. D. S. L. 2010. Savanna-forest hysteresis in the tropics. Global Ecology & Biogeography **10**:369-378.

Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, S. R. Beissinger, T. Benton, D. D. Cameron, Y. Carmel, D. A. Coomes, T. Coulson, M. C. Emmerson, R. S. Hails, G. C. Hays, D. J. Hodgson, M. J. Hutchings, D. Johnson, J. P. G. Jones, M. J. Keeling, H. Kokko, W. E. Kunin, X. Lambin, O. T. Lewis, Y. Malhi, N. Mieszkowska, E. J. Milner-Gulland, K. Norris, A. B. Phillimore, D. W. Purves, J. M. Reid, D. C. Reuman, K. Thompson, J. M. J. Travis, L. A. Turnbull, D. A. Wardle, and T. Wiegand. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology **101**:58-67.

Swenson, N. G., Y. Iida, R. Howe, A. Wolf, M. N. Umana, K. Petprakob, B. L. Turner, and K. P. Ma. 2017. Tree co-occurrence and transcriptomic response to drought. Nature Communications **8**:1996.

Swenson, N. G., and F. A. Jones. 2017. Community transcriptomics, genomics and the problem of species co-occurrence. Journal of Ecology **105**:563-568.

Tallis, H., H. Mooney, S. Andelman, P. Balvanera, W. Cramer, D. Karp, S. Polasky, B. Reyers, T. Ricketts, and S. Running. 2012. A global system for monitoring ecosystem service change. Bioscience **62**:977–986.

Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helaouet, D. G. Johns, I. D. Jones, and D. I. Leech. 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature **535**:241-245.

Tilman, D., I. Forest, and J. M. Cowles. 2014. Biodiversity and Ecosystem Functioning. Annual Review of Ecology, Evolution, and Systematics **45**:471-493.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**:718-720.

Tylianakis, J. M., and R. J. Morris. 2017. Ecological Networks across Environmental Gradients. Annual Review of Ecology, Evolution, and Systematics **48**:25-48.

van der Heijden, M. G. A. 2016. Ecology underground networking. Science **352**:290-291.

Vitousek, P. M., S. Porder, B. Z. Houlton, and O. A. Chadwick. 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecological Applications **20**:5-15.

Wang, J., J. Shen, Y. Wu, C. Tu, J. Soininen, J. C. Stegen, J. He, X. Liu, L. Zhang, and E. Zhang. 2013. Phylogenetic beta diversity in bacterial assemblages across ecosystems: deterministic versus stochastic processes. Isme Journal **7**:1310-1321.

Wardle, D. A., G. M. Barker, K. I. Bonner, and K. S. Nicholson. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? Journal of Ecology **86**:405-420.

Wickings, K., A. S. Grandy, S. C. Reed, and C. C. Cleveland. 2012. The origin of litter chemical complexity during decomposition. Ecology letters **15**:1180-1188.

Yuan, Z. Y., and H. Y. H. Chen. 2015. Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. Nature Climate Change **5**:465-469.