Responses of Species Abundance Distribution and Community Similarity to Nitrogen and Phosphorus Addition in Subalpine Meadow Plant Communities: Postprint

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Abstract

This study took subalpine meadows of the Qinghai-Tibet Plateau as the research object, using a randomized block design to examine the variation characteristics of community species richness, species abundance distribution patterns, and community similarity under different fertilization treatments (N, P, N+P) through 4 consecutive years of N and P addition. The results showed: (1) After 4 consecutive years of N and N+P addition, grassland plant community species richness gradually decreased with increasing N addition levels ($P<0.001$); the slope of the species abundance distribution curve gradually increased; the effects of N+P addition treatments on plant community species richness and species abundance distribution (SAD) curves were more significant than those of N addition alone, for example, under the N15P15 treatment, the reduction in community species richness was the greatest, reaching 65.5% of the control community; (2) In single N or N+P treatments, vegetation composition diverged among different addition rates, while vegetation composition converged among the same addition rates (stress level=0.152); (3) N and N+P addition caused bunchgrasses with fibrous root systems to gradually become dominant in the plant community; (4) P addition had no significant effects on community species richness, species abundance distribution curves, community similarity, and the composition and proportion of different growth forms; (5) Plant growth form characteristics and N/P addition treatments could explain 56.97% of the species abundance distribution characteristics of plant communities. These results indicate that N addition in subalpine meadow regions causes reordering of plant community composition, changes in dominant species, gradual steepening of SAD curves, and increased community similarity; when N is enriched, P addition increases the use efficiency of N, and community structure is influenced

by N and P supply levels.

Full Text

Preamble

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Responses of Species Abundance Distribution and Community Similarity to Nitrogen and Phosphorus Additions in a Subalpine Meadow

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Abstract

Nitrogen (N) and phosphorus (P) addition can cause species richness loss in grassland ecosystems. However, few studies have reported changes in species abundance distribution (SAD) patterns and the developmental trajectory of plant communities after fertilization. In the present study, we conducted a four-year randomized block design experiment using N and/or P fertilizers at different concentrations in a subalpine meadow on the Qinghai-Tibet Plateau. Using data from the fourth year of observation, we analyzed the effects of N, P, and N+P additions on species richness, SAD patterns, and community similarity. We also evaluated the contributions of species richness and plant growth form to community structure and species abundance.

Results indicated that within the N or N+P addition treatments, community species richness significantly decreased ($P < 0.001$), and the slope of SAD patterns tended to become steeper with higher levels of N addition after four years of treatment. The community species richness and SAD curve responses were more significant in treatments with combined N+P addition than in those with only N addition. For example, in plots with N supply, mean species richness was 44 at an N level of 5 g/m², 33 at 10 g/m², and 30 at 15 g/m². In contrast, in plots with N+P supply, mean species richness values were 37, 29, and 16 at the three N+P addition levels, respectively. Plots with 15 g/m² N+P addition showed the largest extent in species richness loss, which could be 65.5% of the mean control plot species richness.

Another result was that in plots with the same resource (single N or combined N+P) addition, vegetation composition diverged among treatments with different N concentrations, whereas vegetation composition converged between treatments with the same N concentrations (stress level = 0.152). Furthermore, in

the N and N+P addition plots, gramineous plants with brushy roots and caespitose stems gradually became dominant, while plants with rosette-like leaves and straight branches, stems, rhizomes, and roots gradually decreased in the plant community. In addition, the responses of community species richness, SAD curves, and community similarity to P addition were not significant ($P > 0.05$). Finally, 56.97% of SAD could be explained by differences in plant growth forms and changes of species richness induced by the different treatments. Species richness was positively related to plants with rosette-like leaves and rhizomes, but a remarkable negative correlation existed between species richness and plants with brushy roots and caespitose stems.

These results suggest that N addition induces a series of changes in plant community composition, including species loss and rearrangement, dominant species turnover, and changes of relative abundance of community species (i.e., a change in the slope of the SAD curve). Furthermore, communities tend to be more similar at the same level of N supply and more divergent at different levels of N addition. Under the condition of N accumulation, P addition could promote the use efficiency of N, and this effect can be amplified with increasing concentrations of N supply. Overall, the community structure was affected by multiple resources and resource supply levels in this subalpine meadow.

Keywords: Qinghai-Tibet Plateau; N, P additions; species richness; biodiversity; community structure; growth forms

Introduction

Biotic interactions and competition for abiotic factors jointly determine the local distribution and abundance of plant species. Species abundance distribution (SAD) patterns are fundamental metrics for describing ecological community structure that visually display the proportions of species within communities. Since ecologists began utilizing SAD patterns to characterize animal, plant, and microbial communities, they have attempted to explain their underlying mechanisms with theoretical models. While SAD patterns emphasize overall community composition rather than differences among specific species, communities with identical SAD patterns may have different species compositions. Ordination analysis based on community similarity can more clearly reveal structural differentiation characteristics of plant communities caused by differences in species composition and proportions.

Niche differentiation among species significantly influences community assembly patterns because plant competitive ability for nutrients, reproductive capacity, and other traits are closely related to growth form characteristics such as plant morphology and root distribution. Therefore, growth form characteristics differentially influence community abundance distribution patterns. Atmospheric nitrogen deposition and similar phenomena directly affect grassland vegetation community composition and structure by altering the original soil environment. Previous observational and experimental studies have repeatedly reported that nutrient enrichment produces toxic effects and reduces community species richness. Fertilizer addition typically increases community primary productivity, thereby causing loss of community species diversity.

The traditional view holds that nitrogen is the primary limiting nutrient element for grassland ecosystems on the Qinghai-Tibet Plateau. However, during nutrient cycling, nitrogen and phosphorus are inextricably linked in both terrestrial and freshwater ecosystems and co-limit community productivity. Based on numerous existing research results, we conducted corresponding studies on nitrogen and phosphorus addition. Analyzing changes in grassland plant community structure will help understand the response mechanisms of plant communities to nutrient enrichment, which has important practical significance.

This study selected a subalpine meadow community on the Qinghai-Tibet Plateau as the research object, established different addition levels of two nutrient elements, and addressed the following questions: (1) How do different levels of element supply affect the development trend of plant community structure? (2) How do different element addition treatments affect the species abundance distribution patterns of plant communities? (3) Which ecological mechanisms regulate the above changes in community structure?

1 Study Site Description

The experimental site was located at the Lanzhou University Alpine Meadow and Wetland Ecosystem Research Station (34°55 N, 102°53 E, 2900 m) in the suburbs of Hezuo City, Gannan Tibetan Autonomous Prefecture, Gansu Province. This region belongs to a subalpine humid zone with an average annual precipitation of approximately 550 mm and mean annual temperature of 2.4°C. The soil is typical calcareous soil. August is the peak plant growth period, with temperatures ranging from -22°C to 26°C. The vegetation is a subalpine meadow dominated by perennial herbaceous plants. The site has been fenced since 2006. Before grazing prohibition, the main vegetation consisted of *Kobresia humilis*, *Elymus nutans*, *Festuca sinensis*, *Potentilla anserina*, *Artemisia tangutica*, with associated species including *Taraxacum lugubre*, *Geranium pylzowianum*, and *Melissilus ruthenicus*.

2 Experimental Design and Field Survey

The addition experiment was conducted in a homogeneous 35 m × 53 m plot. Three types of nutrient addition treatments (N, P, N+P) were established, with three addition gradients for each treatment type (5, 10, 15 g/m²), creating ten treatment combinations (N5, N10, N15; P5, P10, P15; N5P5, N10P10, N15P15) plus a control (CK). Each subplot measured 5 m × 5 m, with three replicates per treatment. Urea (CO(NH) , N% = 46%) and sodium dihydrogen phosphate (NaH PO , P% = 44.60%) were selected as fertilizers and uniformly applied in late May during rainy days. A fixed 0.5 m × 0.5 m quadrat was established in each subplot for long-term observation.

Soil analysis showed total nitrogen content of (3.739 ± 0.052) mg/g and total phosphorus content of (0.649 ± 0.01) mg/g in dry soil (0–30 cm). Field vegetation surveys were conducted in late August using manual counting to identify and record species and their abundances in the fixed quadrats.

3 Data Analysis

One-way ANOVA was used to compare differences in plant community species richness among N, P, and N+P addition treatments. Differences between addition treatments and the control were also analyzed. Species abundance distribution curves for different treatments were plotted based on relative coverage data. Non-metric multidimensional scaling (NMDS) was used to test the effects of nutrient addition treatments on plant community similarity. Growth forms were classified into stem growth types (erect, rosette, branching, tufted) and root growth types (taproot, rhizome, fibrous) based on plant stem and root characteristics. Redundancy analysis (RDA) was used to test the effects of growth form and species richness on species abundance. All statistical analyses were performed using R v3.2.0 (R Development Core Team).

1 Effects of Nitrogen and Phosphorus Addition on Plant Community Species Richness and SAD Curves

Control community species richness averaged 42.6. Under N addition treatments, community species richness significantly decreased with increasing fertilizer amount ($P < 0.001$), with values of 44, 33, and 30, representing decreases of 6.3%, 29.6%, and 37.3%, respectively. Under N+P addition treatments, species richness also showed a significant decreasing trend with values of 37, 29, and 16 ($P < 0.001$), representing decreases of 21.1%, 38.7%, and 65.5%, respectively. The N+P addition treatments showed greater reductions in species richness than N addition alone. The N15P15 treatment showed the most significant decrease in community species richness, with differences among treatments being highly significant ($F = 16.4$, $P < 0.001$). P addition alone did not significantly affect community species richness ($F = 5.7$, $P > 0.05$).

With increasing N addition levels, the slope of the SAD curve pattern gradually increased. The effects of combined N+P addition on community SAD curves were more significant than N addition alone. The differences in SAD curve slopes among different P addition treatments were not significant ($P > 0.05$).

In control quadrats, the three species with highest relative coverage were *Geranium pylzowianum* (21.3%), *Astragalus polycladus* (21%), and *Thalictrum alpinum* (18.5%). Under N10 treatment, the three species with highest relative coverage were *Geranium pylzowianum* (34%), *Elymus nutans* (22.3%), and *Festuca sinensis* (21.5%). Under N15 treatment, grasses gradually became dominant, with the three highest relative coverage species being *Scirpus pumilus* (30%), *Thalictrum alpinum* (22%), and *Geranium pylzowianum* (12%). Under P10 treatment, the three highest relative coverage species were *Geranium* *pylzowianum* (23%), *Comastoma pulmonarium* (22.6%), and *Festuca sinensis* (16.7%). Under P15 treatment, the three highest relative coverage species were *Festuca sinensis* (21.3%), *Geranium pylzowianum* (15.3%), and *Daucus carota* (12.3%).

In N+P combined addition communities, grasses gradually occupied absolute dominance with increasing nutrient addition. In N5P5, the three highest relative coverage species were *Geranium pylzowianum* (22%), *Thalictrum alpinum* (15.7%), and *Daucus carota* (12.7%). In N10P10, the three highest were *Geranium pylzowianum* (22.6%), *Poa crymophila* (22%), and *Daucus carota* (22%). In N15P15, the three highest were *Festuca sinensis* (56%), *Elymus nutans* (26.6%), and *Pedicularis kansuensis* (9.6%). The increase of grasses in N+P combined addition communities was more responsive than in single N addition treatments.

2 Effects of Nitrogen and Phosphorus Addition on Plant Community Similarity

Ordination analysis revealed that different nutrient additions and different addition levels of the same nutrient significantly affected vegetation community composition. The stress coefficient from the NMDS ordination was 0.152, indicating that the ordination results adequately explained differences in plant community composition among nutrient addition treatments. The two-dimensional ordination diagram showed that plant communities from the same treatment clustered together. Under single nutrient addition conditions, vegetation with different addition levels diverged, while vegetation with the same addition level converged. Under N+P addition, vegetation from the three addition levels showed overall convergence.

3 Responses of Different Plant Growth Forms to Nitrogen and Phosphorus Addition

Regardless of stem growth type or root growth type, species richness of all groups decreased with increasing nutrient addition, with greater declines under combined N+P addition. Among all communities and stem growth types, erect-type species had the highest richness. In root growth types, the proportions of species among groups were relatively uniform. P addition did not significantly affect species richness of various growth forms in the community ($P > 0.05$).

Changes in relative coverage of different growth forms differed from changes in richness. For all communities, erect-type plants had significantly higher relative coverage than other stem growth type plants. In root growth types, taproot groups had higher coverage than rhizome and fibrous root groups. For stem growth types, under N and N+P addition conditions, relative coverage of rosette and branching plants in the community decreased to varying degrees with increasing element addition, while tufted plants increased to varying degrees. Erect-type plants under N10P10 treatment were significantly higher than the control. For root growth types, under N and N+P addition conditions, the relative coverage proportions of rhizome and fibrous root species were higher than taproot plants. Under N15P15 treatment, the proportions of rhizome and taproot plants were significantly lower than fibrous root plants, with the community dominated by fibrous root growth forms. Under maximum combined addition, the community was dominated by rhizome-type plants. P addition did not significantly affect relative coverage of various growth forms in the community ($P > 0.05$).

4 Effects of Plant Growth Form Characteristics and Community Species Richness on Community Species Abundance Distribution

Plant growth form characteristics and element addition treatments explained 56.97% of the total variation in community species abundance distribution. In the RDA ordination diagram, species with high central aggregation were common species in the sample area, while scattered species at the edge positions held absolute dominance in their nearest quadrats and determined the position of that quadrat in the ordination diagram. Species richness showed the highest correlation with the first axis. Among growth forms, tufted and fibrous root species showed the highest correlation with the first axis, while erect and rosette types showed the highest correlation with the second axis. All growth forms showed the highest correlation between erect and rosette types and rhizome types. Tufted and fibrous root types showed significant positive correlation with species richness, while erect and rosette types showed significant negative correlation with species richness. Tufted and fibrous root species had high correlation with quadrats under N10P10 and N15P15 treatments, while erect and rosette species had close relationships with control and N5P5 treatment quadrats. Tufted grasses with fibrous roots, such as *Elymus nutans* and *Festuca sinensis*, held absolute dominance under N10P10 and N15P15 treatments, forming typical single-dominant communities.

3 Discussion

In this sample plot, vegetation community productivity increased and species richness decreased under fertilization treatments, possibly due to differences in habitat and soil physicochemical properties. With increasing N addition, plant community species richness gradually decreased, consistent with numerous studies on nutrient enrichment effects across ecosystems from terrestrial to freshwater systems. The mechanism closely related to aboveground biomass is light resource limitation, which is a primary explanation for species diversity loss after N enrichment. Our results confirm this viewpoint.

The sensitivity of plant community species richness decline to combined N+P addition was greater than to N addition alone, suggesting that both nutrient elements may co-limit productivity and species composition in Qinghai-Tibet subalpine meadows. As N addition gradually reduces N limitation, it may increase limitation of other nutrients. This aligns with the niche dimension hypothesis, which suggests that as the number of added resources increases, environmental niche dimensions decrease, leading to increased community biomass and decreased species diversity. Under N enrichment conditions, multiple nutrients jointly regulate community productivity and diversity.

With increasing N addition, plant community SAD curves shifted from gentle to steep, and community evenness decreased. These results contradict traditional forward succession trajectories. During early forward succession, species composition is simple, with intermediate-type species occupying most of the community and showing obvious dominance. As succession proceeds, the system becomes increasingly complex. However, nutrient enrichment processes, especially during productivity increases, cause communities to become dominated by a few species because high N environments favor different species than low N environments, potentially increasing toxic effects.

Combined N+P addition significantly improved the dominance of tufted grasses with fibrous roots in the community, especially under high N addition treatments where the dominance of grasses became particularly significant. In subalpine meadow ecosystems, grasses have competitive advantages for water and light due to their height and fibrous root characteristics, making them dominant constructive species. Plant growth form characteristics and differences in species richness among communities caused by element addition methods and amounts contributed decisively to community species abundance distribution and similarity patterns. Different growth form species showed different sensitivities to N and P addition. Rhizome species were only highly correlated with low N addition communities. As the proportion of nutrients available for direct plant uptake changed in the soil environment, the proportion of species adapted to low N environments decreased or disappeared, while species with tufted growth forms and fibrous roots adapted to high N environments increased in proportion, leading to turnover of dominant and rare species and changes in community structure.

Our results also found that communities receiving different amounts of N diverged in species composition, while those receiving the same amount of N showed increased similarity. Communities with P addition alone also showed some differentiation in ordination space. P addition can supplement N and improve N use efficiency, but as N content increases, the limiting factor for the community shifts to P differences. The initial species composition differences and varying sensitivities of different plants to N enrichment determine changes in community similarity across N addition gradients.

Conclusion

In the subalpine meadow region of the Qinghai-Tibet Plateau, N is the main limiting factor. With increasing N addition, plant community species richness is gradually lost, SAD curves become steeper, and community similarity increases. P addition can supplement single N addition, improving N use efficiency. The effects of combined N+P addition on community changes are more significant than single N addition. The differentiation of growth form characteristics among species and changes in species richness caused by N and P addition explain up to 56.97% of the variation in plant community species abundance distribution patterns, including species turnover and loss, and changes in dominant species and their relative abundances. Single P addition does not significantly affect plant community structure.

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Note: Figure translations are in progress. See original paper for figures.