Effects of Extreme Drought and Nitrogen Addition on Species Diversity, Leaf Traits, and Productivity in Semi-arid Sandy Grassland (Postprint)

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Abstract

Using the Horqin sandy grassland as the study system, we examined the effects of short-term extreme drought (60% precipitation reduction and 60-day drought) and nitrogen addition (20 g · m-2 · a-1) on plant community species diversity, leaf traits, and biomass. The results demonstrated that alterations in water and nitrogen availability changed the importance values of dominant species within the community, with the importance values of the dominant species Echinops gmelinii and Artemisia scoparia significantly increasing under short-term extreme drought and nitrogen addition treatments. Short-term extreme drought significantly affected plant height (Hight, H), leaf nitrogen content (Leaf Nitrogen Content, LNC), and aboveground biomass; specifically, 60% precipitation reduction decreased H but increased LNC, while biomass was significantly reduced under both 60% precipitation reduction and 60-day drought treatments. Species diversity, specific leaf area (Specific Leaf Area, SLA), leaf dry matter content (LeafDry Matter Content, LDMC), and leaf carbon content (Leaf Carbon Content, LCC) showed no significant differences across different drought treatments. Short-term nitrogen addition significantly influenced plant leaf traits and aboveground biomass; H, SLA, and LNC increased under nitrogen addition, whereas LDMC decreased, with no significant change in plant diversity. The interaction between extreme drought and nitrogen addition had no significant effects on species diversity, leaf traits, or biomass. Correlation and regression analyses revealed that species diversity, SLA, LDMC, LCC, and LNC were not significantly correlated with biomass, whereas H was significantly positively correlated with biomass. Annual plant-dominated communities in semi-arid sandy grasslands adapt to extreme drought and nitrogen deposition

by modifying key traits of dominant species, with H exerting a substantial influence on the maintenance of grassland productivity.

Full Text

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Abstract

We examined the effects of extreme drought (60% rainfall reduction) and nitrogen addition (20 g $\cdot$ m^{-2}) on plant community species diversity, leaf traits, and biomass in Horqin sandy grassland. Our results demonstrate that water and nitrogen alterations changed the important values of dominant species in the community. Specifically, the important values of *Echinops gmelini* and *Artemisia scoparia* increased significantly under short-term extreme drought and nitrogen addition treatments. Short-term extreme drought significantly affected plant height (H), leaf nitrogen content (LNC), and aboveground biomass. Rainfall reduction by 60% decreased H while increasing LNC, and aboveground biomass declined under both drought treatments. However, species diversity, specific leaf area (SLA), leaf dry matter content (LDMC), and leaf carbon content (LCC) showed no significant differences among drought treatments. Short-term nitrogen addition significantly influenced plant leaf traits and aboveground biomass, increasing SLA and LNC while decreasing LDMC, though plant diversity remained unchanged. The interaction between extreme drought and nitrogen addition had no significant effects on species diversity, leaf traits, or biomass. Correlation and regression analyses revealed no significant relationships between species diversity indices and biomass, whereas H showed a significant positive correlation with biomass. Annual-dominated plant communities in semi-arid sandy grasslands adapt to extreme drought and nitrogen deposition by altering key traits of dominant species, with H having a particularly strong influence on grassland productivity maintenance.

Keywords: extreme drought; nitrogen addition; species diversity; leaf functional trait; productivity

Introduction

Grasslands constitute a vital component of terrestrial ecosystems, covering approximately 40% of global land area and contributing about 33% of total terrestrial net primary productivity. Over recent decades, grassland ecosystems have experienced severe degradation due to human activities and global change, with extreme drought and nitrogen deposition representing key factors affecting grassland productivity and ecosystem stability. Precipitation patterns and rainfall regimes influence grassland plant community composition, functional traits, phenology, and productivity, particularly in arid and semi-arid ecosystems. Statistics indicate that drought-related losses account for half of all climate disaster damages in China. The Inner Mongolia region serves as a crucial base for green agricultural and livestock products and ranks among China's major grain production areas, but drought frequency has been increasing, with profound implications for socioeconomic development. Concurrently, nitrogen accumulation from fertilizer use, fossil fuel combustion, and biological nitrogen fixation alters nutrient limitation and affects global nitrogen cycling and ecosystem processes.

Species diversity serves as a fundamental indicator of ecosystem function, elucidating developmental stages and stability characteristics of plant community structure. Grassland ecosystem stability and productivity maintenance depend heavily on species diversity. Numerous studies have investigated water and nitrogen effects on terrestrial ecosystem species diversity, community structure, and productivity. Simulated extreme drought experiments have shown that drought reduces plant community productivity, coverage, and diversity, while long-term simulated nitrogen deposition significantly decreases species richness but increases leaf size, plant height, and community productivity. Water-nitrogen coupling effects on plant growth show compensatory mechanisms, though some studies found no significant effects of extreme drought and nitrogen addition on ecosystem productivity and diversity, likely due to differences in study duration, methodology, and research area.

Plant functional traits bridge the connection between plants and their environment. Through plant-environment interactions during development, plants have evolved morphological and physiological adaptation strategies to reduce damage from adverse conditions. Regional environmental factors act as filters selecting for specific traits, particularly precipitation and soil nutrients. Species with different functional traits may respond differently to environmental changes, thereby affecting ecosystem processes. Research suggests ecosystem stability depends not only on species diversity but also on plant traits such as specific leaf area, leaf dry matter content, and plant height, which help maintain community stability under climate warming. Under global change, extreme drought can reduce leaf area while increasing specific leaf area, whereas nitrogen addition increases plant height, specific leaf area, and leaf nitrogen content while decreasing leaf dry matter content. Interactive effects of extreme drought and nitrogen addition can affect photosynthesis, significantly increasing specific leaf area while decreasing leaf nitrogen content per unit area. Therefore, studying functional traits under global change enhances understanding of ecosystem stability mechanisms.

The Horqin Sandy Land, located in China's northern semi-arid agro-pastoral ecotone, is highly sensitive to global change and experiences frequent human activity and severe soil erosion, resulting in severe vegetation degradation. Most research has focused separately on global change and human activity effects on grassland ecosystem composition and structure, with relatively few comprehensive studies examining interactive effects of extreme drought and nitrogen deposition on species diversity, leaf traits, and productivity in semi-arid sandy grasslands. This study investigates responses of Horqin semi-arid sandy grassland plant communities to extreme drought and nitrogen addition through field control experiments, aiming to reveal adaptation mechanisms to extreme climate and nitrogen deposition and provide theoretical foundations for degraded vegetation restoration and sustainable management.

1. Materials and Methods

1.1 Study Area The study was conducted in Naiman Banner, Tongliao City, Inner Mongolia (42°55 –42°57 N, 120°40 –120°43 E), in the central-southern Horqin Sandy Land. The region experiences a temperate continental semi-arid monsoon climate with a mean annual temperature of 6.4°C (ranging from -13.1°C to 23.7°C) and a frost-free period of 150 days. The accumulated temperature $\geq$ 10°C is 3000°C. Mean annual precipitation is approximately 360 mm, with 70% concentrated in June–August, while mean annual evaporation reaches about 2000 mm. The mean annual wind speed is 3.2–4.1 $m \cdot s^{-1}$, with northwesterly winds prevailing in spring and winter and southwesterly winds in summer and autumn. The research area features alternating distributions of mobile, semi-fixed, and fixed dunes as well as interdune lowlands, with aeolian sandy soil and sandy chestnut soil as the main soil types. Dominant plant species include *Cleistogenes squarrosa*, *Pennisetum centrasiaticum*, *Artemisia scoparia*, *Echinops gmelini*, *Chenopodium acuminatum*, and *Setaria viridis*.

1.2 Experimental Design This study was based at the Naiman Desertification Research Station of the Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences. To minimize effects of spatial heterogeneity and disturbances from livestock and human activities, we fenced a relatively flat and homogeneous sandy grassland area in early May 2018. Within the fenced area, we established 24 plots and implemented four treatments: natural rainfall (control), 60% rainfall reduction (extreme drought), nitrogen addition (20 $g \cdot m^{-2}$), and combined extreme drought plus nitrogen addition. Each treatment had six replicates arranged in a completely randomized block design.

We used rainout shelters to simulate extreme drought, with shelter frames covered by high-transparency polycarbonate panels (85% light transmittance). Each shelter covered a 6 m × 6 m plot, with 1 m buffer zones between adjacent plots; panels were removed after the growing season. Shelters remained open on all sides to ensure air circulation. For nitrogen addition, we applied urea at 20 $g \cdot m^{-2}$ (based on internationally common nitrogen addition levels), split into two applications of 10 $g \cdot m^{-2}$ each in June and July. Nitrogen amounts were calculated based on plot area and urea nitrogen content (46%). We selected June–July for treatment because most rainfall in Inner Mongolia occurs during these months, having the greatest impact on community productivity. To minimize lateral water and nitrogen interference, we installed metal barriers wrapped in plastic sheeting around each plot perimeter.

1.3 Survey Methods We conducted surveys during the August biomass peak. To avoid edge effects, sampling points were at least 1 m from plot boundaries. Within each plot, we randomly established three 1 m × 1 m quadrats to investigate community species composition, plant height (H), coverage, and density. Aboveground biomass was harvested by species using ground-level clipping, and litter was collected simultaneously and oven-dried to constant weight. For dominant species in each quadrat, we measured specific leaf area (SLA) and leaf dry matter content (LDMC) following Cornelissen's *Handbook of Protocols for Standardised and Easy Measurement of Plant Functional Traits*. Leaf carbon content (LCC) and leaf nitrogen content (LNC) were determined using a Costech ECS 4010 elemental analyzer. Calculations were as follows:

$$\text{SLA}\ (\text{m}^2 \cdot \text{g}^{-1}) = \frac{\text{leaf area}}{\text{leaf dry mass}}$$

$$\text{LDMC}\ (\text{g} \cdot \text{g}^{-1}) = \frac{\text{leaf dry mass}}{\text{leaf saturated mass}}$$

$$\text{LCC}\ (\%) = \frac{\text{leaf carbon mass}}{\text{leaf dry mass}} \times 100$$

$$\text{LNC}\ (\%) = \frac{\text{leaf nitrogen mass}}{\text{leaf dry mass}} \times 100$$

Community-level leaf trait values were calculated as community-weighted means (CWM):

$$\text{CWM} = \sum_i P_i \times \text{trait}_i$$

where P_i is the relative biomass of species i in the community and trait_i is the trait value of species i.

1.4 Species Diversity Measurement We measured species diversity using species richness index (S), Simpson dominance index (D), Shannon-Wiener diversity index (H), and Pielou evenness index (J). Species richness was represented by the number of species in each quadrat. Other indices were calculated as:

Simpson dominance index (D):

$$D = \sum_i N_i^2$$

Shannon-Wiener diversity index (H):

$$H = -\sum_i N_i \ln N_i$$

Pielou evenness index (J):

$$J = \frac{H}{\ln S}$$

where N_i is the relative importance value of species i and S is the number of species in the community.

1.5 Data Processing Data organization, statistical analysis, and graphing were performed using SPSS 20.0, SigmaPlot 10.0, and Excel software. Two-way ANOVA was used to compare effects of extreme drought, nitrogen addition, and their interactions on species diversity, leaf traits, and biomass in semi-arid sandy grassland. One-way ANOVA compared differences in species diversity, leaf traits, and biomass among drought treatments at the same nitrogen level. T-tests analyzed effects of nitrogen addition on these parameters under the same drought conditions. Pearson correlation and linear regression analyses examined relationships between plant height and aboveground biomass under different nitrogen treatments. The significance level was set at $P < 0.05$. All data are presented as means ± standard error.

2. Results

2.1 Effects of Short-term Water and Nitrogen Changes on Plant Important Values Under natural rainfall conditions, *Cleistogenes squarrosa*, *Echinops gmelini*, and *Artemisia scoparia* were dominant species with important values of 26.61%, 23.19%, and 20.11%, respectively, accounting for 69.91% of total important values. Under nitrogen addition alone, *Echinops gmelini*, *Pennisetum centrasiaticum*, and *C. squarrosa* ranked highest with important values of 26.59%, 23.08%, and 22.42%, respectively, totaling 72.09%. Under 60% rainfall reduction alone, *A. scoparia*, *E. gmelini*, and *C. squarrosa* were dominant (25.86%, 20.47%, and 15.72%, respectively), accounting for 62.05%. Under the combined treatment, dominant species were *E. gmelini*, *P. centrasiaticum*, and *A. scoparia* (22.43%, 21.73%, and 19.90%, respectively), totaling

64.06%. Under extreme drought (60% reduction + 60 days), *A. scoparia*, *E. gmelini*, and *P. centrasiaticum* were dominant (27.97%, 25.34%, and 16.81%, respectively), accounting for 68.68%. Under combined extreme drought and nitrogen addition, dominant species were *E. gmelini*, *A. scoparia*, and *P. centrasiaticum* (28.23%, 27.97%, and 15.48%, respectively), totaling 71.68%.

Extreme drought increased the important value of *A. scoparia* while decreasing that of *C. squarrosa*. Nitrogen addition increased the important values of *P. centrasiaticum* and *E. gmelini*. *Corispermum maorocarpum* appeared only under short-term extreme drought, while *Cannabis sativa* disappeared under this treatment. These results indicate that different species exhibit varying competitive abilities and response strategies to water and nitrogen resources, and that extreme drought and nitrogen addition significantly affect important values of dominant species and community composition in semi-arid sandy grasslands.

2.2 Effects of Short-term Water and Nitrogen Changes on Species Diversity and Productivity Species diversity and community productivity are important parameters of plant community structure. Two-way ANOVA showed that extreme drought, nitrogen addition, and their interactions had no significant effects on species richness, Simpson dominance index, Shannon-Wiener diversity index, or Pielou evenness index ($P > 0.05$). However, extreme drought significantly affected aboveground biomass and litter mass ($P < 0.01$). Compared with natural rainfall, extreme drought significantly reduced aboveground biomass ($P < 0.01$). Nitrogen addition significantly affected aboveground biomass ($P < 0.01$) but not litter mass ($P > 0.05$). The interaction had no significant effect on either aboveground biomass or litter mass ($P > 0.05$).

Under natural rainfall, nitrogen addition significantly increased aboveground biomass ($P < 0.05$), whereas under extreme drought, nitrogen addition had no significant effect ($P > 0.05$). At the same nitrogen level, extreme drought significantly reduced litter mass ($P < 0.05$), while nitrogen addition increased litter mass, though not significantly ($P > 0.05$). These findings suggest that short-term extreme drought and nitrogen addition have minimal effects on species diversity but substantial effects on community biomass.

[Figure 1: see original paper]
[Figure 2: see original paper]

2.3 Effects of Short-term Water and Nitrogen Changes on Leaf Traits Two-way ANOVA indicated that short-term extreme drought significantly affected plant height (H) and leaf nitrogen content (LNC) ($P < 0.05$). Specifically, at the same nitrogen level, extreme drought reduced H, with significant decreases under 60% rainfall reduction alone ($P < 0.05$). LNC increased significantly under extreme drought ($P < 0.05$). At the same rainfall level, nitrogen addition significantly increased H under 60% rainfall reduction ($P < 0.05$) but had no significant effect under extreme drought ($P > 0.05$). Nitrogen addition significantly increased LNC under natural rainfall and 60% rainfall reduction ($P < 0.05$) but not under extreme drought ($P > 0.05$).

For specific leaf area (SLA), extreme drought had no significant effect ($P > 0.05$), while nitrogen addition significantly increased SLA ($P < 0.01$). The interaction had no significant effect ($P > 0.05$). For leaf dry matter content (LDMC), extreme drought had no significant effect ($P > 0.05$), while nitrogen addition significantly decreased LDMC ($P < 0.01$). For leaf carbon content (LCC), neither extreme drought, nitrogen addition, nor their interaction had significant effects ($P > 0.05$). These results demonstrate that short-term extreme drought and nitrogen addition significantly affect key leaf traits of dominant species in semi-arid sandy grassland communities.

[Figure 3: see original paper]

2.4 Effects of Species Diversity and Leaf Traits on Community Productivity Pearson correlation and linear regression analyses revealed no significant correlations between species diversity indices (richness, Simpson dominance, Shannon-Wiener diversity, Pielou evenness) and aboveground biomass. However, plant height (H) showed a significant positive relationship with aboveground biomass (Table 4). Without nitrogen addition, the correlation between H and aboveground biomass was not significant ($R^2 = 0.09$, $P > 0.05$), but with nitrogen addition, the relationship was significantly positive ($R^2 = 0.28$, $P < 0.05$). Overall, H and aboveground biomass were significantly positively correlated in semi-arid sandy grassland ($R^2 = 0.29$, $P < 0.01$). These results indicate that nitrogen addition increases plant height, enhances photosynthetic competitive ability, and promotes biomass accumulation.

[Figure 4: see original paper]

3. Discussion

Important value reflects a plant's dominant status and role in the community; higher values indicate greater importance. This study shows that water and nitrogen treatments affected important values of different plant species in semi-arid sandy grassland. Extreme drought reduced the important value of the perennial grass *Pennisetum centrasiaticum*, while nitrogen addition increased it. The combined treatment enhanced the dominance of the annual species *Echinops gmelini* and *Artemisia scoparia*. These findings suggest that water deficit hinders *P. centrasiaticum* growth, but nitrogen addition alleviates drought effects to some extent. The annual species *E. gmelini* and *A. scoparia* are also sensitive to nitrogen addition under extreme drought, indicating high nutrient use efficiency even with minimal rainfall, enabling rapid resource accumulation and life cycle completion. Consequently, these species show strong drought adaptation and nitrogen competition abilities.

Most studies report that extreme drought and nitrogen deposition significantly affect species diversity [14,34,35]. However, this study found no significant changes in species richness or diversity indices with short-term extreme drought and nitrogen addition. This may be because the relatively short treatment duration (less than one growing season) provided insufficient time for new species establishment, colonization, and reproduction. Additionally, different plant life forms exhibit distinct response strategies: annual plants have high water and nutrient use efficiency, enabling rapid germination and rooting under unfavorable conditions, while perennial plants have stricter germination requirements and lower competitive ability. Our study area is dominated by annuals with low proportions of perennials. Although short-term extreme drought and nitrogen addition reduced some perennials, they did not disappear completely, resulting in no significant diversity changes. Future research should investigate long-term effects of extreme climate change and nitrogen deposition on species diversity in semi-arid sandy grasslands.

Changes in plant functional traits represent important strategies for plant response and adaptation to environmental change. Leaf traits are particularly sensitive to environmental variation and effectively reflect plant responses and adaptations. Semi-arid sandy grasslands are typically co-limited by water and nutrients, and plants adjust morphological and physiological traits to cope with environmental changes. Plant height reflects light resource competition ability, and high specific leaf area (SLA) indicates a rapid resource-use strategy. Leaf dry matter content (LDMC) is important for drought adaptation. In this study, 60% rainfall reduction significantly decreased H without nitrogen addition, while nitrogen addition significantly increased H under 60% rainfall reduction. Extreme drought significantly increased LNC, and nitrogen addition significantly increased LNC under natural rainfall and 60% rainfall reduction. Both extreme drought and nitrogen addition significantly increased SLA, while nitrogen addition significantly decreased LDMC under natural rainfall and 60% rainfall reduction. Leaf carbon content showed no significant changes across water and nitrogen treatments. These trait changes enhance plant resource competition ability. Wright et al. [44] found that climate factors had non-significant effects on key leaf traits across global scales, contrasting with our results, possibly due to differences in research scale, as functional traits exhibit strong scale-dependence [45].

Community biomass is the most direct indicator of grassland ecosystem restoration. Climate conditions and soil resource status are important factors affecting community productivity [46], though study results on precipitation and nitrogen addition effects vary [47]. Regression analysis showed no significant relationship between H and aboveground biomass without nitrogen addition, but a significant positive correlation with nitrogen addition. Overall, H and aboveground biomass were significantly positively correlated because nitrogen addition increases soil nutrient content, alleviates nutrient limitation on sandy land plant growth, mitigates drought effects, promotes light resource competition [51,54], increases aboveground biomass accumulation, and indirectly enhances nitrogen use efficiency [55], maintaining high community productivity.

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