


Legacy effects of historical grazing affect the response of vegetation dynamics to water and nitrogen addition in semi-arid steppe

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Abstract

Question: Climate change interacts with land use and introduces new pressures that trigger growing concerns about increasing vulnerability of the Eurasian steppes. However, it is not well known how increasing precipitation and atmospheric N deposition interact with the land use legacy to affect nutrient availability, plant species composition and therefore vegetation dynamics of the Mongolian Steppe.

Location: Steppe in Xilin River Basin, Inner Mongolia, China. The mean annual precipitation is 343 mm with 60%–80% of it occurring during the plant growing season.

Methods: We conducted a 6-years (2005–2010) field experiment to manipulate N and water availability on sites experiencing two different historical stocking rates. Species composition, above-ground biomass and plant N concentration were determined at both individual and community levels. Soil cumulative inorganic N and N mineralization rates were determined by laboratory incubation.

Results: (1) Supplementary irrigation increased soil cumulative inorganic N and N mineralization rate, plant community N uptake, and the abundance of perennial species for the site with high historical stocking rate. In contrast, long-term water addition decreased soil cumulative inorganic N and N mineralization rate, and did not change the plant community N uptake, but increased the abundance of *Cleistogenes squarrosa* as a species indicative of degradation for sites with moderate historic stocking rate. (2) Nitrogen addition increased soil cumulative inorganic N and N mineralization rate irrespective of grazing history under ambient precipitation, and resulted in a burst of annuals in moist years at both sites. Under supplementary irrigation, N addition increased soil cumulative inorganic N and N mineralization rate at the site with moderate historic stocking rate, but not at the site with high historical stocking rate, and increased the abundance of taller perennial species at both sites.

Conclusions: Legacy effects of grazing greatly affect plant composition responses to increasing water and N availability. The effectiveness of N application in restoring heavily degraded sites in the Mongolian steppe depends on precipitation availability. In the face of increasing precipitation and atmospheric N deposition, resource managers should be prepared to cope with the different vegetation succession and recovery trajectories as a result of historical land-use difference.

KEYWORDS

degraded grassland, grazing intensity, Inner Mongolia steppe, nitrogen availability, nitrogen mineralization, nitrogen uptake, plant species composition, water availability

1 | INTRODUCTION

Climate change interacts with land use and introduces new pressures that trigger growing concerns about increasing vulnerability of the Eurasian steppes (Angerer, Han, Fujisaki, & Havstad, 2008; Wesche & Treiber, 2012). Overgrazing has led to severe degradation of grasslands globally, and over 70% of the Inner Mongolian steppe, which is distributed in a relatively dry areas of the Eurasian steppe, has been degraded due to a protracted period of livestock grazing at a high stocking rate (Han et al., 2008; Peters, Havstad, Archer, & Sala, 2015; Tong, Wu, Yong, Yang, & Yong, 2004; Vanderpost, Ringrose, Matheson, & Arntzen, 2011). This long-term grazing practice had exerted unique legacy effects on plant community composition and soil properties (Han et al., 2014; Wang & Wesche, 2016). Livestock overgrazing can cause plant species composition to switch from a productive and desirable perennial grass-dominated state to one of several degraded states dominated by sub-shrubs, shrubs or annual plants in arid and semi-arid grasslands (Lohmann, Tietjen, Blaum, Joubert, & Jeltsch, 2012; Sasaki, Okayasu, Jamsran, & Takeuchi, 2008; Wang, Wang, & Wang, 2006). This change in plant species composition alters the nutrient cycling and reduces resilience of the steppe to environmental change (Chen et al., 2017; Wang et al., 2017), detrimentally affecting the socio-ecological services the steppe provides (Han, Owens, Wu, Wu, & Huang, 2009).

Intensive grazing also alters soil properties and causes deterioration in soil functions (Pulido, Schnabel, Contador, Lozano-Parra, & González, 2016; Sandhage-Hofmann et al., 2015). In Inner Mongolian grasslands, heavy grazing was found to increase soil sand content, decrease soil macroporosity and decrease soil water-holding capacity, consequently reducing plant available water and vegetation cover (Zhao et al., 2010). The decrease in vegetation cover was reported to accelerate soil water evaporation, loss of soil organic C and N, and loss of fine soil particles through aeolian transport (Steffens, Kolbl, Kai, & Kogel-Knabner, 2008). Thus, long-lasting effects of overgrazing may create conditions susceptible to water and N limitation for plant growth (Bagchi & Ritchie, 2010; Giese et al., 2013), and may lead to the abundance of species with high water and N use efficiency (Tilman, 1988; Wang, Wang, & Chen, 2003). However, some studies have reported that overgrazing accelerated soil N turnover and increased plant available soil N, plant N uptake and litter quality in grassland ecosystems, and created a positive feedback between grazing effect and soil available nutrients (Augustine & McNaughton, 2006; Bagchi & Ritchie, 2010; Chapman, Hart, Cobb, Whitham, & Koch, 2003; Xu, Li, Wang, Chen, & Cheng, 2007). Thus, it remains unresolved whether overgrazing will definitely result in N limitation for plant growth in the Inner Mongolian steppe where soil moisture is a frequent limiting factor in the growing season (Gong, Chen, Dittert, Taube, & Lin, 2011).

Precipitation and N availability are the primary limitations to productivity, affecting plant species composition in grassland ecosystems (Hooper & Johnson, 1999). The interactive effects of N and water availability on plant growth were investigated in grasslands such as desert steppe, temperate steppe (Chen, Hooper, & Lin, 2011; Ren et al., 2017; Ronnenberg & Wesche, 2011) and tallgrass prairie (Smith, Schuster, & Dukes, 2016). Both significant interactions (Smith et al., 2016; Xia & Wan, 2008; Yang et al., 2011) and non-significant interactions (Ronnenberg & Wesche, 2011; Wesche & Ronnenberg, 2010) between N addition and water availability have been reported. N addition and water availability alter plant community structure and composition due to differences in N and water use strategies among species, and their interaction with abiotic conditions (Xia & Wan, 2008; Yang et al., 2011). Various studies have shown that cover of perennial grasses is sensitive to water availability in semi-arid grasslands (Guo, Lohmann, Ratzmann, & Tietjen, 2016; Orr & O'Reagain, 2011). Some experiments suggested that N addition favours a few species adapted to rapid exploitation of available resources, such as annual and biennial species having high potential growth rates (Bobbink et al., 2010; Chen et al., 2011; Xia & Wan, 2008), and therefore the recovery of primary productivity response to N addition may not necessarily result in a desirable community composition (Chen et al., 2017). However, other studies reported that nutrient addition increases success of good quality tall perennial species in the competition for light (Bai et al., 2010; Ronnenberg & Wesche, 2011; Yang et al., 2011). The different N responses of plant species were potentially derived from interactions with other ecosystem drivers such as precipitation regime, grazing history, plant species composition and the amount of N addition (Xia & Wan, 2008). For instance, N addition benefited perennial rhizomatous grasses at a heavily grazed site, but benefited annuals at an ungrazed site, especially at levels of $>10.5 \text{ g N/m}^2$ in Inner Mongolian grasslands (Bai et al., 2010).

Overgrazing increased the sensitivity of plant species composition and nutrient cycling to a change in abiotic conditions (Moreno-Jiménez, Peñalosa, Esteban, & Bernal, 2012). The interactive effects of grazing history and abiotic factors on above-ground biomass, plant cover, richness and species composition have been reported in several studies (Cumming, Bradfield, & Newman, 2014; Klein, Harte, & Zhao, 2008). For example, the impact of grazing on plant cover was reported to depend on water availability in Tibetan grasslands (Wang & Wesche, 2016; Wang et al., 2017). The mechanisms underlying the interaction of abiotic conditions (such as N and precipitation) and grazing history on plant species composition are not well understood (Overbeck, 2014), yet this knowledge is fundamentally important for predicting vegetation dynamics of grasslands with different grazing histories under climate change (Wu et al., 2011; Zhou, Wen, Xu, Song, & Zhang, 2014).

The overall goal of this study was to understand the interactive effects of grazing history, N addition and water availability on plant–soil N status and vegetation dynamics in the semi-arid grasslands of Inner Mongolia. We asked:

1. How does grazing history affect soil N mineralization and plant N status responses to supplementary water and N addition? We hypothesized that a site with a history of intensive grazing would be more responsive to both supplementary water and N addition compared to a site with a moderate grazing history. Removal of either or both limitations of water and N in an intensively grazed site would result in rapid increases in soil N mineralization and plant N uptake, approaching the level in the moderately grazed site.
2. Does supplementary water have different effects on plant species composition in the moderately and heavily grazed grasslands? We hypothesized that supplementary water would reduce water stress and promote plant growth regardless of grazing history. Supplementary water would increase the abundance of perennial grasses irrespective of the grazing history.
3. How does N addition affect plant species composition with and without supplementary water in the moderately and heavily grazed grasslands? We hypothesized that N addition would benefit annual and biennial species without supplementary water at the heavily grazed grassland. With supplementary water and N addition, the species-specific competition will centre on light competition, benefiting taller, perennial grass species at both sites.

2 | METHODS

2.1 | Site description

This study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS) in the Xilin River Basin (43°26′–44°29′ N, 115°32′–117°12′ E, 1,270 m a.s.l.), Inner Mongolia, China. The steppe in Xilin River Basin covers about 10,000 km² in the area and over 70% of the basin is considered degraded (Tong et al., 2004). The Inner Mongolian steppe is part of the world's largest grassland—the Eurasia steppe. Based on the long-term data from 1982 to 2003, the mean annual precipitation is 343 mm, with 60%–80% of it occurring during the plant growing season from May to late August (Chen et al., 2011). Mean annual temperature is 0.7°C, with the highest monthly average of 19.0°C in Jul, and lowest monthly average of –21.1°C in Jan. The annual precipitation during the experimental period (2005–2010) was 249 mm, substantially less than the mean precipitation of 343 mm during the 22 years before this study (1992–2003; Appendix S1: Table S1). Based on ambient precipitation and soil moisture availability, 2005, 2006, 2009 and 2010 were classified as dry years, and 2007 and 2008 as moist years (Chen et al., 2011, 2017).

Two sites that differed in stocking rate over the past 30 years were selected for the study: (1) site with a history of moderate grazing (MG site, 2 sheep/ha), and (2) site with a history of heavy grazing (HG site,

4 sheep/ha). These stocking rates are typical of the Inner Mongolian steppe. The two sites were 3 km apart and the soil is calcic chernozems (Steffens et al., 2008). The soil texture of the MG site is sandy loam (71% sand, 22% silt, 7% clay), and the soil texture of the HG site is loamy sand (81% sand, 15% silt, 4% clay). At the MG site, the total N and C concentrations in the topsoil (0–30 cm) were 1.2 and 12 g/kg, respectively, which were relatively higher than 0.8 and 9 g/kg at the HG site (Gong et al., 2011). The soil moisture content at the MG site was usually higher than that in the HG site, particularly for the 30–50 cm soil layer during growing seasons (Zhao et al., 2010). The climax community of grassland in the study area is dominated by the perennial rhizomatous grass *Leymus chinensis* and the perennial bunchgrass *Stipa grandis*. In this study, the MG site was dominated by the perennial grasses *S. grandis*, *L. chinensis* and *Cleistogenes squarrosa*, and the HG site was dominated by the sub-shrub *Artemisia frigida*, the annual and biennial species *Artemisia scoparia*, the perennial graminoid *Carex korshinskyi* and the perennial forb *Potentilla tanacetifolia*. No fertilizers had been applied in the past. The primary limiting factors for plant growth were water and N, but not P at this site (Gong et al., 2011). In May 2005, an area of 45 m × 55 m was fenced at both sites, and the vegetation was mown to 3 cm for experiment treatments.

2.2 | Experimental design

The experiment was laid out as a split-plot factorial design, combined over sites and years. Within each of the two sites (MG and HG), the main plots were two water treatments— P_a (ambient precipitation) and P_w (simulated wet year precipitation). Within each water treatment, there were randomly assigned subplots with three levels of N addition (0, 25 and 50 kg N ha⁻¹ year⁻¹), each replicated four times. The 12 subplots were 5 m × 8 m separated by walkways of 0.8 m in width (Chen et al., 2017).

Simulated wet year precipitation treatment was achieved by adding water through irrigation and also called supplementary irrigation treatment (P_w treatment). Water was piped to the plots from a water retention pond constructed for this project. The ambient precipitation and supplementary irrigation plots were separated by buffer strips of 3 m in width. The amount of supplementary irrigation in the P_w treatment for a given year was calculated by analysing the long-term precipitation data from 1982 to 2003 at the IMGERS. The annual precipitation for those 22 years was sorted from the lowest to the highest and classified into three groups: dry years (<300 mm, 6 years), moderate years (300–400 mm, 10 years) and wet years (>400 mm, 6 years). The average rainfall from May through August for the dry and wet years was calculated at 10-day intervals. In the P_w treatment, when the preceding 10-day precipitation was less than the wet year average of the same period, supplementary irrigation was triggered, which was achieved using a few discrete irrigation events over a few days. The amount of supplementary water for each discrete irrigation event was limited to 20 mm. The irrigation water was hauled from the Xilin River and stored in a pond near the experimental plots. Water grab samples were taken from the pond at each irrigation event to measure ammonium (NH₄⁺) and nitrate (NO₃⁻) content using Continuous

Flow Analysis (Auto analyzer TRAACS Model 2000; Bran and Luebbe, Germany). The content of NH_4^+ was usually <0.5 mg/L and the content of NO_3^- was usually <0.05 mg/L, and total available N input from irrigation water was negligible. N addition was applied using granular urea mixed with sieved dry soil (<2 mm, the ratio of urea to soil is 1:10 by weight) for even spreading by hand on 15 May every year.

2.3 | Plant and soil sampling

Each year, three $0.25 \text{ m} \times 1.00 \text{ m}$ quadrats from each subplot were randomly selected for plant sampling on 15–16 Aug, the time of peak biomass. All plant material within the three quadrats was manually clipped to 0.5 cm above the soil surface and mixed as one composite plant sample. Clipped plant material was sorted by species first, then by green vegetation, standing dead tissue and litter for the same species. Samples were oven-dried (75°C , 48 hr), then weighed to obtain biomass of individual components. Dried green plant samples were first milled in a micro hammer mill (Culatti, Zurich, Switzerland) and then with a ball mixer mill (MM400, Retsch, Haan, Germany) in preparation for determination of above-ground plant N concentration with an elemental analyzer (EA1108, Carlo Erba, Torino, Italy). Plant above-ground N uptake was calculated as the product of above-ground biomass and above-ground plant N concentration. At the end of Aug, vegetation in all plots was cut to 3 cm in height and removed from the site.

Soil samples for the incubation experiment were collected after plants and litter were removed on 25 Aug. To minimize the impact on experimental plots, we only took undisturbed soil samples in the 0 and $50 \text{ kg N ha}^{-1} \text{ year}^{-1}$ N treatment plots. PVC cylinders (17 cm in length, 5 cm in diameter), with one side sharpened, were hammered 15 cm into the soil to take undisturbed soil cores from each of the two sites for the incubation experiment to measure the N mineralization rate. Six soil cores were taken in each subplot at the same time. The PVC cores were covered with Parafilm to reduce water loss but allow gas exchange during transport. These soil cores were incubated at a constant temperature of 25°C and soil moisture of $10 \text{ g H}_2\text{O}/100 \text{ g}$ in the laboratory using the method of Raison, Connell, and Khanna (1987) with four replications. Constant soil moisture was maintained by adding water based on the weighing method every 3 days. The six soil cores from the same subplot were randomly assigned to one of six different incubation periods of 3, 7, 14, 28, 56, 112 days. The total incubation samples were 192 (2 water levels \times 2 N levels \times 4 replications \times 6 incubation periods \times 2 sites). After incubation, the soil cores were removed from the incubator and sieved through a 2-mm mesh. Sieved soils were extracted with 100 ml 0.01 M CaCl_2 . The extracts were analysed for ammonium (NH_4^+) and nitrate (NO_3^-) using Continuous Flow Analysis (Auto Analyzer 3, Nordstadt, Germany). Soil moisture was measured with the oven-dry method (48 hr at 105°C).

2.4 | Statistics and data analysis

Statistical analyses were conducted in Proc Mixed ANOVA using SAS 8.0 (SAS Institute, Cary, NC, USA). For the incubation experiment, the

treatment effects for soil cumulative inorganic N, soil net N mineralization rate at each incubation time were fitted to the model for a split-plot design where grazing history (site), water availability (water) and N addition (nitrogen) were fixed effects and block \times water was a random effect. For the field experiment, the treatment effects for above-ground plant N uptake and N concentration were analysed with Proc Mixed ANOVA; repeated measures was used for effects of year, where site, water, N and year were considered as fixed effects and 'block \times water' as random effect. Akaike's Information Criterion (AIC) was used to select the most suitable covariance structure.

Because the dominant plant species differ between the heavily grazed site and the moderately grazed site, treatment effects on the above-ground biomass of dominant plant species were analysed for each site independently. A repeated measures analysis was conducted to test the effects of year, where water, N and year were considered as fixed effects and block \times water as the random effect. AIC was used to select the most suitable covariance structure. Analyses were run separately for each dominant species.

Multiple and pairwise comparisons of means for all parameters were done with the Bonferroni test (Steel & Torrie, 1980) with Bonferroni adjustment. All statistical significances were tested at 0.05 level of probability. Block had no significant effect on all measured variables and thus is not reported in the results.

3 | RESULTS

3.1 | Cumulative soil inorganic N and N mineralization rates

Supplementary irrigation increased the cumulative inorganic N in the soil for the HG site but decreased the cumulative inorganic N for the MG site (Figure 1a; Appendix S2: Table S2, significant site and water interaction). Supplementary irrigation significantly increased N mineralization rate at day 14 for the HG site but decreased N mineralization rate at day 7 for the MG site (Figure 1b). N addition significantly increased soil cumulative inorganic N and N mineralization rates at both sites under ambient precipitation (Figure 1c,d). Under supplementary irrigation, N addition significantly increased soil cumulative inorganic N and N mineralization rates at the MG but not at the HG site (Figure 1e,f).

3.2 | Plant N uptake and N concentration

Supplemental irrigation resulted in an increase of plant N uptake at the HG site but not at the MG site (Figure 2a; Appendix S2: Table S3). Plant N uptake was not significantly different between the MG site and the HG site across all three N addition levels without supplemental irrigation, but significantly higher at the HG site than at the MG site with supplemental irrigation (Figure 2b). N addition significantly increased plant N uptake at both MG and HG sites (Figure 2b). At the individual species level, supplementary irrigation resulted in a significant decrease in plant N concentration at the MG site (Figure 3a–e); however, the plant N concentrations of *L. chinensis* and *Agropyron cristatum* did not show

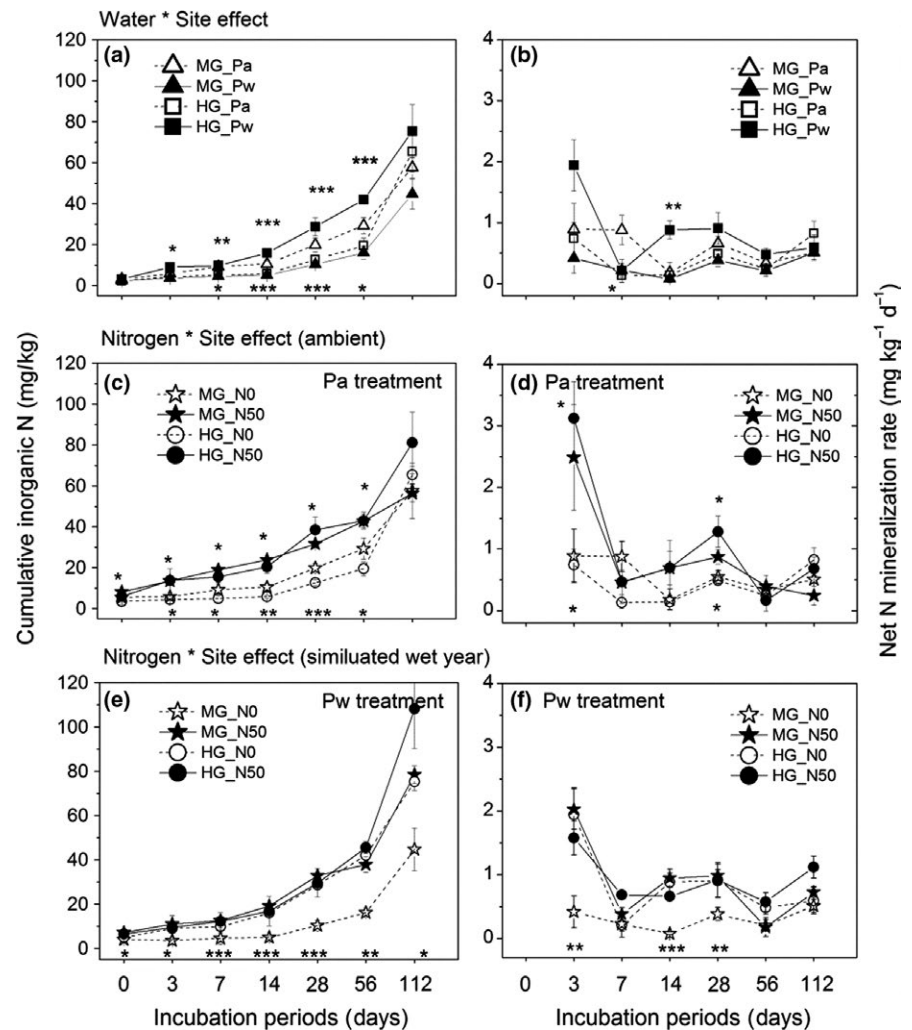


FIGURE 1 Soil cumulative inorganic N and net N mineralization rate (mean \pm SE, $n = 4$) as affected by supplementary water (P_a and P_w), sites with different grazing histories (MG and HG) and N addition. The cumulative inorganic N (a) and average net N mineralization rate (b) after specified incubation periods as affected by supplementary water treatment and site. Cumulative inorganic N (c, e) and net N mineralization rate (d, f) after specified incubation periods as affected by N addition and site under P_a (c, d) and P_w (e, f) treatment. P_a , ambient precipitation; P_w , simulated wet year precipitation; N0, and N50 represent 0 and 50 kg N/ha addition, respectively. ANOVA results are available in Appendix S2: Table S2. Treatment effects at a given incubation time are indicated above the data for the HG site and below the data for the MG site as: *** $p < .001$, ** $p < .01$, * $p < .05$, no sign $p > .05$

a pronounced decrease after irrigation at the HG site (Figure 3a,b). Plant community N concentration decreased significantly (21%) at the MG site, but did not decrease significantly at the HG site (Figure 3e; Appendix S2: Table S3, significant site and water interaction).

Plant N concentrations at the species and community levels were not significantly different between the HG site and the MG site for all three N addition levels under ambient precipitation (Figure 3f–j). However, with supplementary irrigation, the plant N concentration was significantly higher at the HG site than at the MG site under N0 and N25 treatments but not significantly different under N50 treatment (Figure 3f–j). N addition significantly increased the plant community N concentration at the MG site but not at the HG site under both ambient and wet year precipitation treatments (Figure 3j; Appendix S2: Table S3, significant site and N interaction).

3.3 | Responses of plant species composition to supplementary irrigation and N addition

The plant species composition had different responses to supplementary irrigation at the MG and the HG sites (Figure 4; Appendix S2: Tables S4, S5). With supplementary irrigation, the above-ground biomass and the relative abundance of the perennial grass *C. squarrosa*

increased significantly and became the dominant species at the MG site (Figure 4; Appendix S2: Table S4). In contrast, supplementary irrigation increased the above-ground biomass and relative abundance of the perennial species *Artemisia frigida* and *Agropyron cristatum*, while the abundance of annuals *Salsola collina* and *Chenopodium glaucum* decreased at the HG site (Figure 4; Appendix S2: Table S5).

Under ambient precipitation, N addition resulted in a rapid increase of the annual species *S. collina* in the two moist years (2007 and 2008) at both MG and HG sites (Figure 4). Under supplementary irrigation and N addition, the abundance of the perennial species *S. grandis* increased at the MG site (Figure 4), while at the HG site the abundance of the sub-shrub *Artemisia frigida* rapidly increased initially and was subsequently replaced by the perennial grass *Agropyron cristatum* (Figure 4; Appendix S2: Tables S4, S5).

4 | DISCUSSION

4.1 | Plant–soil N status responses to water addition and legacy effects of grazing

Supplementary irrigation resulted in larger increases in above-ground plant N uptake at the site with a history of heavy grazing

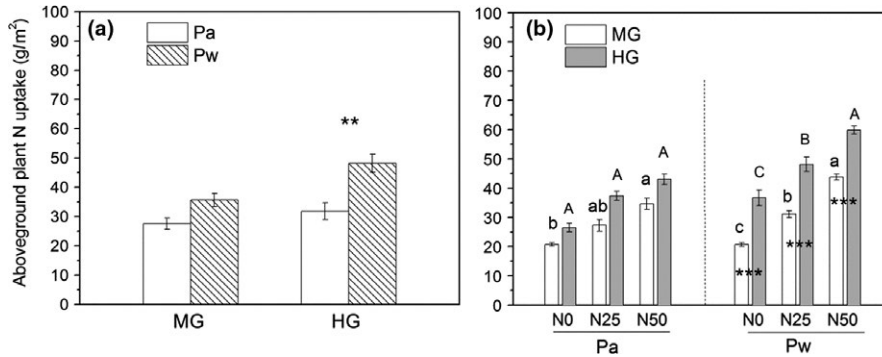


FIGURE 2 Above-ground plant N uptake (mean ± SE) as influenced by grazing history, N addition and supplementary water across years. Plant N uptake (kg N/ha) as affected by the interaction of sites with moderate grazing history (MG) and heavy grazing history (HG) and supplementary water, with data pooled over all N treatments and years (a, n = 72). Plant N uptake (kg N/ha) as affected by the interaction of site, water and N, with data pooled over all years (b, n = 24). (a) Effect of water at the same site are indicated with: ***p* < .01, no sign *p* > .05. (b) Effect of site in the same water and N treatment are indicated with: ****p* < .001, no sign *p* > .05. Bars labelled with the same lowercase and capital letter are not significantly different between N treatments within the same water treatment at *p* < .05 at the MG site and HG site, respectively. ANOVA results are available in Appendix S2: Table S3

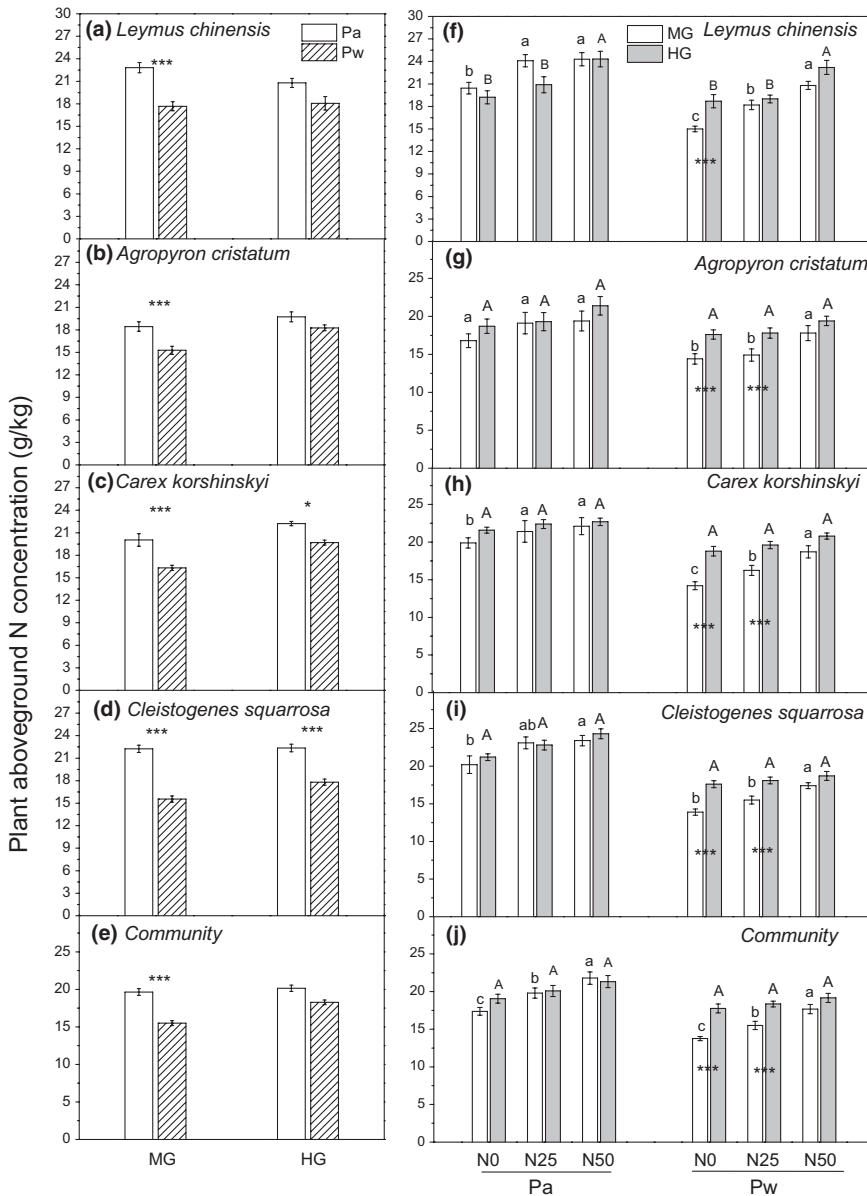


FIGURE 3 Plant above-ground N concentration (mean ± SE, g/kg) of common species and community as influenced by grazing history, supplementary water and N addition across years. Plant above-ground N concentration as affected by the interaction of site and supplementary water, with data pooled over all N treatments and years (a–e, n = 72). Plant above-ground N concentration as affected by the interaction of site, water and N, with data pooled over all years (f–j, n = 24). (a–e) Effect of water at the same site is indicated with: ****p* < .001, **p* < .05, no sign *p* > .05. (f–j) Effect of site under the same water and N treatment is indicated with: ****p* < .001, no sign *p* > .05. Bars labelled with the same lowercase and capital letter are not significantly different from N treatment under the same water treatment at *p* < .05 at the MG site and the HG site, respectively. ANOVA results are available in Appendix S2: Table S4

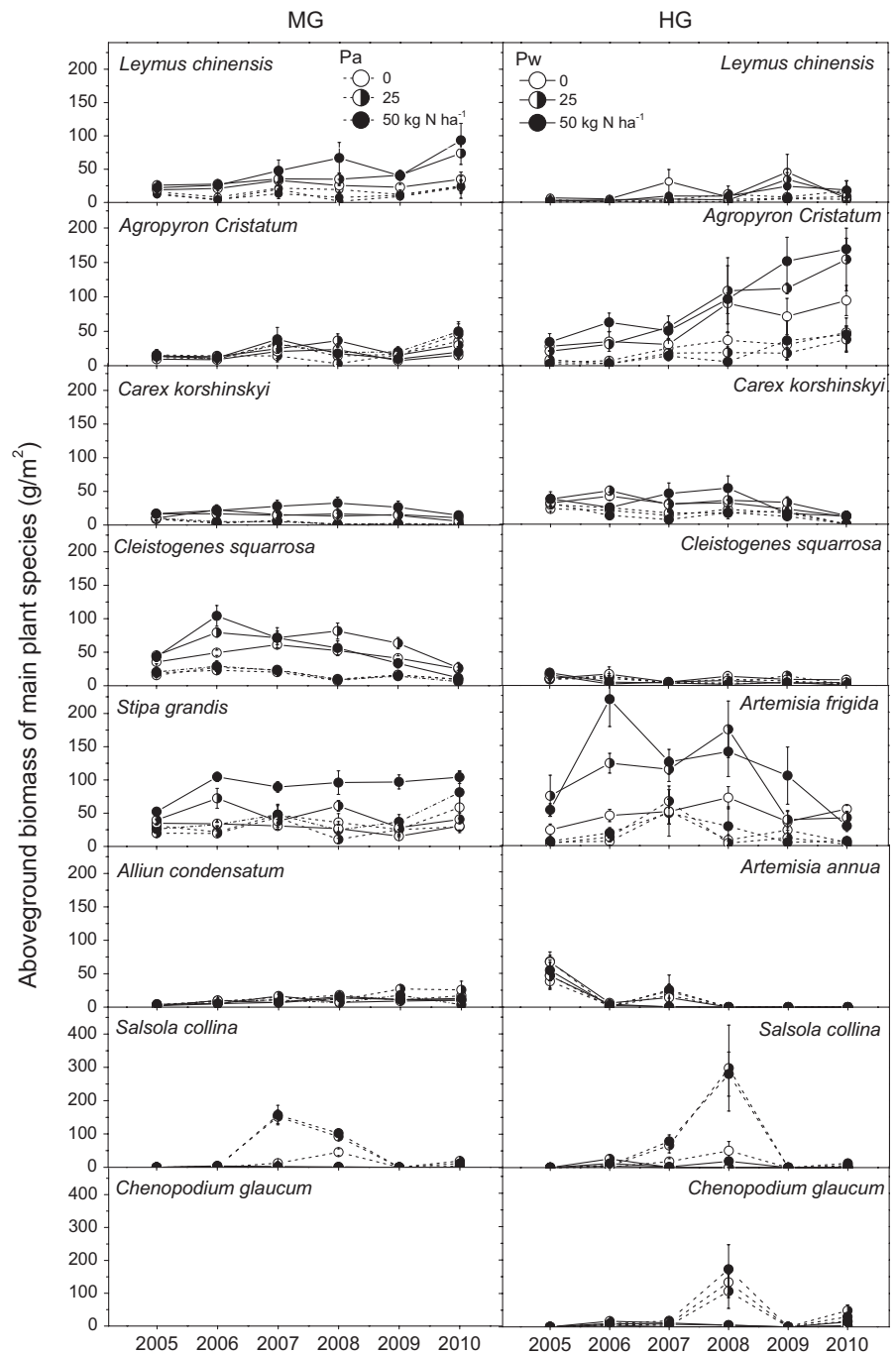


FIGURE 4 Changes of peak time above-ground biomass (mean \pm SE, g/m^2 , $n = 4$) of dominant species as affected by supplementary water and N addition over 6 years at the site with moderate grazing history (MG) and the site with heavy grazing (HG) history. ANOVA results are available in Appendix S2: Table S5

compared to the site with a history of moderate grazing (Figure 2). This is associated with faster soil N mineralization in soils with a heavily grazed history under high soil moisture availability. This faster N mineralization may be associated with decreased live root biomass, decreased soil fungi biomass and increased Gram-positive bacteria under high stocking rates (Augustine & McNaughton, 2006; Klumpp et al., 2009). After supplementary irrigation, the colour of plants became yellowish, a symptom of N deficiency for plant growth (Jones, 2012) at the moderately grazed site, but not at the heavily grazed site. These observations are consistent with our results that additional water input significantly decreased the soil

cumulative inorganic N, soil N mineralization rate (Figure 1a,b) and plant above-ground N concentration (Figure 3) with no increase in plant above-ground N uptake (Figure 2) at the moderately grazed site. This result supports our hypothesis that supplementary irrigation will enhance plant growth at the heavily stocked site more than at the moderately stocked site. Removal of water limitations in an intensively grazed site would result in rapid increases in soil N mineralization and plant N uptake. These results suggest that a long-term increase in precipitation may lead to more N limitation for plant growth at the moderately grazed site (Ren et al., 2017) than at the heavily grazed site.

4.2 | Plant species composition responses to water addition and legacy effects of grazing

With supplementary irrigation, the shallow-rooted (usually <15 cm) perennial grass *Cleistogenes squarrosa* increased quickly and became the dominant species at the MG site (Figure 4). *Cleistogenes squarrosa* is a C₄ grass, it has a competitive advantage over many other species in N and water-limited environments and is an indicator species of heavily grazed grassland (Li, Wang, Huang, Wang, & Wang, 2011; Wang & Wang, 2001; Wang et al., 2003). Increasing N limitation at the MG site could be the reason for the *C. squarrosa* increase after water addition. However, a grassland community dominated by shallow-rooted species could suffer a higher risk from wind erosion (McAlpine et al., 2009).

In contrast, supplementary irrigation resulted in an increase of *Artemisia frigida* and *Agropyron cristatum* at the heavily grazed site (Figure 4). *Artemisia frigida* is a stoloniferous, perennial semi-shrub with high N competitiveness (Li, Li, & Ren, 2005). The grass *Agropyron cristatum*, native to Russia and Central Asia, is highly adapted to degraded rangelands and is often used to rehabilitate degraded rangelands (Blank, Morgan, & Allen, 2015). The positive response of *A. cristatum* to increased precipitation has been reported in other studies (Ren et al., 2017; Ronnenberg & Wesche, 2011). Under continuous water additions at the HG site, the *Artemisia*- + *Agropyron*-dominated stage changed to an *Agropyron*-dominated stage within 6 years (Figure 4). This trajectory of species composition change is similar to longer-term succession following the cessation of grazing in this ecosystem (Bai, Han, Wu, Chen, & Li, 2004; Wang, Liu, Hao, & Liang, 1996), with eventual dominance of *L. chinensis* and *S. grandis*.

4.3 | Plant species composition in response to N addition depends on water availability

The responses of plant species composition to N addition depended on water conditions at both sites (Figure 4). Under ambient precipitation, the annual species *S. collina* was very responsive to N addition in moist years following drought (2007 and 2008). However, with supplementary irrigation, the taller, perennial species *Stipa grandis* (at the MG site), and *Artemisia frigida* and *Agropyron cristatum* (at the HG site) were more responsive to N addition (Figure 4). The difference in N availability in the soil could be responsible for the difference in species response to N addition under ambient precipitation and supplementary irrigation. Previous studies reported N accumulation in soil from N addition during dry years under ambient precipitation, but not under supplementary irrigation (Chen et al., 2011). A combination of high precipitation after drought years and high N availability facilitated the explosive growth of the annual, *S. collina*, which dominated the plant community (Hwang & Lauenroth, 2008). Plant height plays an important role in affecting the responses of plant communities to N addition (Gough et al., 2012). N addition usually enhances canopy cover development and reduces incident radiation and shifts limiting resources from below-ground (water, mineral nutrients) to above-ground (light; Niu, Liu, & Wan, 2008; Hautier, Niklaus, & Hector, 2009).

Stipa grandis is a perennial bunch grass 80- to 100-cm tall and in our study site it was substantially taller than other plant species. The positive response of *S. grandis* (and the related *Stipa krylovii*), *Artemisia frigida* and *Agropyron cristatum* to N addition has been reported in other studies (Ronnenberg & Wesche, 2011). High grazing intensity in steppes favours *Artemisia* species (Li et al., 2011) as *L. chinensis* and *S. grandis* lose dominance. *Artemisia frigida* communities may form a relatively stable state that helps to prevent further progression to desertification in Inner Mongolian steppe (Li et al., 2005; Wang, Liang, Liu, & Hao, 1999), but could also constrain responses of the more palatable perennial grasses and forbs and inhibit grassland recovery (Wang et al., 1996). In contrast to some ecosystems (D'Odorico, Okin, & Bestelmeyer, 2012), dominance of the sub-shrub *Artemisia frigida* did not impede grassland recovery in our study system. In the last 2 years of our experiment (2009 and 2010), *Artemisia frigida* apparently decreased and was replaced by *Agropyron cristatum* (30–75 cm in height). This pattern suggests that *A. cristatum* is capable of recovering from dominance of *A. frigida*, although this recovery may take at least a decade (Schönbach et al., 2009; Wang et al., 1996, 1999). Other studies also showed that perennial grasses competed favourably with the sub-shrub *A. frigida* when grazers were removed for 18 years from steppes (Chen, Bai, Lin, Liang, & Han, 2005).

5 | CONCLUSIONS

The mechanistic understanding of interactive effects of water, N and land-use history on species composition and vegetation dynamics is fundamental for sustainable management of the Eurasian steppe. Through laboratory soil incubation and field manipulative experiments, we collected data that provide important insights on plant species composition change and soil N mineralization with concurrent alterations in N and water availability. First, the addition of N is not necessarily effective for plant species recovery in heavily grazed grasslands if supplementary water is not also provided. Second, supplementary water may promote the abundance of species associated with the degraded state in un-degraded grasslands but increase the abundance of species associated with the recovery state in heavily grazed grasslands. Third, our long-term study shows a combination of N addition and supplementary water result in the recovery of perennial species associated with the climax vegetation at both sites during our study period. Multi-decadal observations will be necessary for understanding the long-term effect of water and nutrient interactions for plant species recovery in the Eurasian steppe.

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CONFLICT OF INTEREST

No authors had a conflict of interest.

AUTHOR CONTRIBUTIONS

SL and QC designed the research, QC collected the data, QC, ZLW, CBZ, SL, YHF and DK did the statistics and wrote the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1 Total water input in ambient precipitation treatment and simulated wet year precipitation treatment

APPENDIX S2 Statistical results of treatment effects on the soil and plant parameters for Figs S1 to S4

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