



# Plant-soil interactions in grasslands of the Mongolian Plateau under global change

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The Mongolian Plateau (MP) is one of the largest contiguous global drylands, stretching about 2.75 million km<sup>2</sup> from western Mongolia to the eastern part of the Inner Mongolian Autonomous Region in China, and is famous for its extensive grasslands. As an indispensable component of Eurasian steppes, grasslands of the MP play important roles in animal husbandry, biodiversity conservation, carbon sequestration and ecological barriers (Kang et al. 2007). The grasslands are characterized by perennial herbaceous forbs and grasses with great adaptation to the

arid and semi-arid climates. Soils of the grasslands in MP are mainly chestnut with neutral to alkaline pH and are distinguished by low availability of mineral nutrients such as nitrogen (N), phosphorus (P) and iron (Fe), while the soil is rich in calcium and potassium (Hou 1982). Plant species in these grasslands have evolved a diverse range of strategies to adapt to the climatic and edaphic environments. The grasslands in MP, particularly in Inner Mongolia, have degraded severely since 1980's due to global change (e.g., atmospheric N deposition, changes in patterns of precipitation, and global warming) and human activities (e.g., grazing, mowing and reclamation), as evidenced by reduced aboveground biomass and plant biodiversity, soil desertification and salinization (Zhou et al. 2014; Batunacun et al. 2018; Li et al. 2000). Therefore, restoration of the degraded grasslands in this region is a great challenge to maintain biodiversity and productivity of grasslands under the scenarios of global change.

The number of papers indexed in the Web of Science (Clarivate) with topics of Inner Mongolia and grasslands has increased sharply in the past three decades. For example, less than 10 papers were published annually before 2001, and the number of papers has increased from 12 in 2002 to 323 in 2022 (Fig. 1A). The published papers belong to 111 research fields categorized by the Web of Science as Environmental Sciences, Ecology, Soil Science, Plant Sciences and Geosciences Multidisciplinary the top five research fields (Fig. 1B). The papers were published in 592

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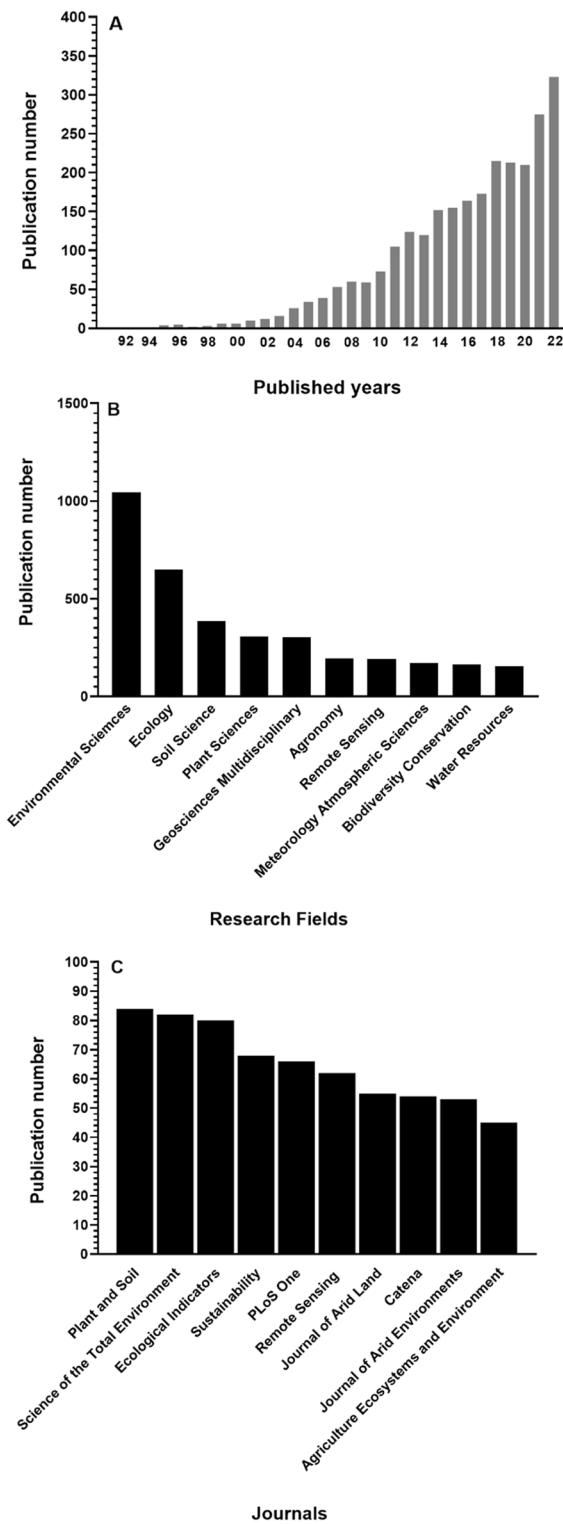
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**Fig. 1** Number of papers indexed in Web of Science (Clarivate) with topics of Inner Mongolia and grasslands between 1991 and 2022 (A), the top 10 research fields of the published papers (B) and the top 10 journals of the papers published (C)

journals, with *Plant and Soil*, *Science of the Total Environment*, *Ecological Indicators*, *Sustainability* and *PLoS ONE* as the top five journals for the published papers (Fig. 1C). More papers on grasslands of the Mongolian Plateau are expected to appear in high-impact journals.

Several studies have addressed how the grasslands in Inner Mongolia respond to N enrichment (Zhang et al. 2014; Diao et al. 2022), changes in precipitation (Zhang et al. 2017), mowing and grazing (Bai et al. 2015; Guo et al. 2021; Zhang et al. 2023a, b) at species, functional group and community level by in situ field experiments across different steppe types in the last two decades. Previous studies mainly focused on aboveground communities of grasslands (Bai et al. 2010b). Belowground processes in general and plant-soil interaction in grassland ecosystems in particular have drawn significant attention in recent years (Tian et al. 2021, 2022). Given the importance of plant-soil interactions in grassland ecosystems, it is necessary to evaluate the roles of plant-soil interactions in response of grasslands in MP to global change and human activities. To highlight the current status of plant-soil interactions of temperate grasslands in Inner Mongolia under scenarios of global change, we organized this special issue of “Plant-soil interactions in grasslands on the Mongolian Plateau”. The special issue includes 16 papers covering a wide range of topics of plant-soil interactions of Inner Mongolian grasslands in response to N enrichment, changes in precipitation, mowing and grazing. Among the 16 paper, six are related to the effect of N and sulfur (S) addition on different types of grasslands, six discuss the effects of variation in precipitation on grassland ecosystems, and four explore the response of grasslands to mowing and grazing.

### Effects of nitrogen enrichment on Inner Mongolia grasslands

Deposition of atmosphere N has increased substantially in China over the past decades, and this increase will continue to some degrees (Liu et al. 2013; Xu et al. 2015). The enhanced N deposition has great impacts on terrestrial ecosystems (Bobbink et al. 2010). Like other terrestrial ecosystems, the grasslands in Inner Mongolia are limited by N. Accordingly, many studies have investigated the effects of

N addition on grassland ecosystems in Inner Mongolia over the last 20 years, and found that N addition enhances aboveground biomass and reduces plant species richness (Bai et al. 2010b; Zhang et al. 2014; Tian et al. 2016), acidifies soil (Tian et al. 2016), affects root production and rhizosphere-mediated processes (Bai et al. 2010a; Tian et al. 2021, 2022), and alters soil bacterial and fungal communities (Liu et al. 2020). These findings suggest multiple effects of N enrichment on grassland ecosystems in Inner Mongolia.

In this special issue, Song et al. (2023) compared different frequencies of N addition on grassland communities, and found that N addition-induced increase in plant community production was reduced with increasing frequency of N addition in a temperate grassland of Inner Mongolia. They further demonstrated that the high plant production under low frequency of N addition was related to soil nitrate concentration. These findings highlight the necessity to use a high frequency of N addition in field experiments to simulate atmospheric N deposition. Increased atmospheric N deposition and altered precipitation regimes are two important global-change factors influencing grassland communities by changing soil nutrient availability and acquisition by plants. Cai et al. (2023) investigated the effects of N addition and irrigation on leaf nutrient concentrations of a temperate steppe. They found that the monocots and dicots differed in their responses to N addition in terms of foliar mineral concentrations, and that irrigation can mitigate the N-induced increase in foliar manganese (Mn) and decrease in foliar Fe concentrations, as well as N-induced changes in foliar calcium (Ca) and potassium (K) concentrations. These findings may have important implications for grassland management under the scenarios of enhanced N deposition and altered precipitation patterns.

Hu et al. (2023) assessed the effects of N addition on ecosystem multifunctionality in a desert steppe of Inner Mongolia, and discovered that N addition increased plant functional diversity, but not species and phylogenetic diversity. They further showed that functional diversity was positively correlated with ecosystem multifunctionality, and that N addition increased ecosystem multifunctionality both directly and by increasing functional diversity. In addition to atmospheric N deposition, there is an increase in S deposition due to human activities in China

(Zhou et al. 2023). Like N deposition, S deposition can acidify soil, thus affecting grassland ecosystem. However, few studies have specifically focused on the effects of S deposition on grassland ecosystems. Feng et al. (2023) investigated the effects of S addition on foliar N, P and S concentrations as well as nutrient-resorption efficiency of a grass and a sedge in a meadow steppe of Inner Mongolia. They found that N, P and S concentrations in senescent leaves were increased by S addition, while N and P concentrations in green leaves of the grass were relatively constant in response to S addition. Leaf nutrient-resorption efficiency decreased with S addition driven by increasing soil N, P and S availability. More studies focusing on the effects of S enrichment on plant-soil interaction of grassland ecosystems may shed light on the responses of Inner Mongolian grasslands to S deposition. The implementation of stringent emission policies in some developed countries has led to a decline in regional N deposition across the globe. For example, N deposition has decreased over the last two decades in Europe based on the long-term monitoring (EEA 2011). Therefore, how the grasslands respond to the reduced N input following long-term N enrichment has been addressed (Clark and Tilman 2010; Street et al. 2015; Tilman and Isbell 2015). In this special issue, two papers evaluated the response of Inner Mongolian grasslands to cessation of N input after N addition. Kang et al. (2023) investigated the changes in mineral nutrition (K, Ca and magnesium (Mg)) in response to cessation of N addition after six years of N addition in a temperate steppe. They found that soil  $K/(Ca + Mg)$  ratio was increased by historical N addition across the three years. Plant mineral concentrations and  $K/(Ca + Mg)$  ratio at the plant community level showed no variation with increasing historical N addition rates across the three years. These results highlight the critical role of stoichiometric homeostasis in maintaining forage non-N mineral nutrition of grasslands in response to variation of mineral nutrients in soil. Meng et al. (2023) examined the legacy effects of N deposition and increased precipitation on plant productivity in a semi-arid steppe of Inner Mongolia after the cessation of 13 years of N and water addition. They found that historical N and water addition generally had positive effects on plant productivity, even after the treatments were ceased. Although N availability decreased rapidly, the positive effect of historical N input persisted after

two years of cessation due largely to the maintenance of the enhanced community plant stature through the increased stature of all functional groups. These findings highlight the importance of plant traits and community compositions in the short-term legacy effects of historical N and water input on community productivity.

### Effect of changes in precipitation on Inner Mongolia grasslands

In addition to enhanced atmosphere N deposition, the Mongolian plateau has also experienced alterations in precipitation regimes (Piao et al. 2010). Therefore, understanding the response of Inner Mongolian grasslands to changes in precipitation can contribute to development of sustainable grassland management. Qin et al. (2023) investigated the responses of soil organic carbon (SOC) decomposition and accumulation to precipitation in an Inner Mongolian grassland. They found that SOC decomposition significantly increased and decreased under wet and dry treatments, respectively. SOC accumulation was enhanced by wet treatment via the increase of mineral-associated organic carbon, and vice versa for the dry treatment. Precipitation may affect soil microbial biomass and activities by plant derived carbon input, thus leading to changes in SOC dynamics. Zhang et al. (2023a) explored the impacts of altered precipitation on soil respiration and its autotrophic (Ra) and heterotrophic (Rh) components in an Inner Mongolian grassland. They found that reduced and increased precipitation decreased and increased Rs, Ra and Rh, respectively. Their results also showed that grazing and mowing had relatively small effects on Rs, while precipitation and land-use interactively impacted abiotic and biotic drivers and Rs.

Liu et al. (2023) reported that water supply significantly affected plant C:N and N:P ratios, and these effects differed among plant species of Inner Mongolian grasslands. Specifically, they found that C: N for the forb species *Artemisia frigida* and *Potentilla acaulis* was not responsive to water supply, while C:N for the grass species *Leymus chinensis* and *Stipa grandis* increased with increasing precipitation. In addition, above- and belowground N:P exhibited similar trends with changing water supply, suggesting

plant stoichiometry between above- and belowground parts follow an allometric pattern.

The natural abundances of stable carbon (C) and N isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) have been used widely to indicate the C and N biogeochemical cycles in terrestrial ecosystems (Han et al. 2020). To dissect the spatial patterns of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in plant-soil systems of grasslands in northern China and their main driving factors across an annual precipitation gradient (from 152 to 502 mm), Wu et al. (2023) measured plant and soil  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  composition as well as their associated environmental factors across a 2000-km climatic gradient in grasslands of northern China. They found that soil  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in surface soil were lower than those in subsurface soil for a typical steppe, but showed no significant differences for a meadow steppe and a desert steppe. Soil  $\delta^{13}\text{C}$  values were related to soil organic carbon and mean annual temperature, while  $\delta^{15}\text{N}$  values in soil and plant were negatively correlated with mean annual temperature and mean annual precipitation. These findings indicate the spatial patterns and different influencing factors on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values along the climatic gradient in grasslands of northern China. Given the dominance of clonal plants in temperate grasslands (Zheng et al. 2019), Tian et al. (2023) addressed how clonal integration affects plant productivity and nutrient uptake in a heterogeneous water environment by a microcosm experiment in a greenhouse using the dominant clonal grass *Leymus chinensis* and the non-clonal grass *Stipa grandis* grown under two soil moisture conditions (homogeneous water content vs heterogeneous water content) and two root connections (connected or severed *L. chinensis*). Their results reveal that plant biomass and N uptake are enhanced and suppressed by clonal integration in heterogeneous and homogeneous environments, respectively. They also highlight that clonal plants rely on the clonal integration of clonal roots and arbuscular mycorrhizal fungal networks to acquire N from soil.

Xie et al. (2023) tested whether the positive effect of shrubs on herbaceous communities is mediated by modifying soil biotic and abiotic properties in a desert steppe with limited precipitation (mean annual precipitation of 110 mm) of Inner Mongolia by comparing herbaceous plant communities and soil properties underneath and outside shrubs of five *Caragana* species. They found that the *Caragana* shrubs facilitated their associated herbaceous communities by

accumulating more soil resources and soil organisms and conserving more rainwater at shallow soil layers beneath than outside their canopies. Their findings reveal that shrub-mediated horizontal and vertical distributions of soil resources and soil organisms underpin the facilitation effects of shrubs on the associated herbaceous communities in desert steppes.

### Response of Inner Mongolian grasslands to mowing and grazing

Mowing and grazing are two common grassland management practices worldwide, and can have great impacts on the biodiversity, functioning and stability of grasslands (Yang et al. 2019; Moirardeau et al. 2018; Piseddu et al. 2021; Zhang et al. 2023b). In this special issue, Bai et al. (2023) investigated the long-term effect of mowing on plant and soil bacterial, fungal and protistan communities, and dissected the correlation between the soil bacterial community and plant/soil parameters in a temperate steppe. They found that the microbial community structures mainly correlated with those of plant parameters rather than with those of soil properties. They further demonstrated that  $\beta$ -diversity of the soil microbial communities was significantly affected by plant community  $\beta$ -diversity, and that mowing enhanced plant–microbe interactions in the networks. These findings indicate that changes in plant community attributes by long-term mowing rather than soil properties are more effective drivers in shaping soil microbial communities in grasslands. Mowing may also exert profound impacts on nutrient-acquisition strategies of herbaceous species due to removal of nutrients by the mown plants. Li et al. (2023) investigated the response of two nutrient-acquisition strategies: root traits and leaf nutrient resorption of perennial herbaceous species, and explored their correlations with long-term mowing in a temperate steppe. They found that root traits of tall and short plants had little response to long-term mowing, but mowing exerted opposite effects on leaf nutrient efficiency (NRE) of the two plant groups. They further showed that root absorption capacity was positively correlated with leaf nutrient-resorption efficiency for tall plants in control plots, but mowing eliminated this correlation. These results suggest that long-term mowing can alter the correlations between alternative

resource-acquisition strategies in perennial herbaceous species of Inner Mongolian grasslands.

Ning et al. (2023) focused on the interactive effect of mowing and N addition on soil microbial biomass in an Inner Mongolian grassland. They found that mowing increased soil inorganic N concentrations, available copper ( $\text{Cu}^{2+}$ ) concentrations, plant aboveground net primary production (ANPP), species richness, Shannon–Wiener biodiversity and ratio of fungal to bacterial biomass, and mitigated the N enrichment-induced increase in plant-available soil  $\text{Mn}^{2+}$  concentrations. They also showed that mowing did not affect the soil microbial biomass C (MBC), and that soil MBC was positively affected by plant species richness, but negatively by ANPP, soil inorganic N, available  $\text{Cu}^{2+}$  and  $\text{Mn}^{2+}$  concentrations in mown plots. These findings highlight that mowing cannot mitigate the negative effects of N enrichment on soil MBC, and that soil, plant and microbial properties play important roles in the response of soil MBC to mowing in N-enriched soil.

As a traditional grassland management practice in Inner Mongolia, grazing can affect plant communities (Talle et al. 2016) and soil microbial communities of grassland ecosystems (Rong et al. 2022). In this special issue, Wang et al. (2023) evaluated the effects of grazing intensity on soil microbial diversity and community composition in a desert steppe of Inner Mongolia. Their results show that grazing led to changes in soil bacterial and fungal community composition, such that heavy grazing significantly increased the relative abundances of Chloroflexi, Gemmatimonadetes, and Firmicutes bacteria, while light grazing significantly decreased the relative abundance of Actinobacteria. Further analysis revealed that the bacterial community responded to grazing via changes in the biomass of perennial plant species and SOC, whereas the SOC and soil pH altered the fungal community composition. These findings suggest that optimal grazing intensity can facilitate the recovery of primary productivity and ecosystem functions in a desert steppe.

In summary, the 16 papers in this special issue highlight the diverse roles of plant–soil interactions in responses of different types of grasslands in Inner Mongolia to nutrient enrichment, variation in precipitation, mowing and grazing at species, functional group and community levels. Future studies on the plant–soil interaction in grasslands on the Mongolian



Plateau at regional scales would contribute to our development of sustainable grassland management in this unique region under scenarios of global change.

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