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Divergent responses of plant biomass and diversity to short-term nitrogen and phosphorus addition in three types of steppe in Inner Mongolia, China

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Abstract

Background: Understanding the response of the plant community to increasing nitrogen (N) and phosphorus (P) inputs is helpful for managing and protecting grassland ecosystems in semiarid areas. However, information about different types of steppe responses to N and P availability in semiarid grasslands is limited. In 2017–2018, two field experiments were conducted with six levels of N (from 5 to 30 g N m^{-2} yr^{-1}) and P (from 2.5 g to 15 g P m^{-2} yr^{-1}) additions in three different temperate steppes, including meadow steppe (MS), typical steppe (TS), and desert steppe (DS), in northern China to study the effects of these addition rates on community biomass and diversity.

Results: Our results showed that plant biomass and diversity in the three steppe types in Inner Mongolia responded differently to elevated N and P inputs. Increasing P promoted aboveground and belowground biomass more than increasing N in the three temperate steppes. Short-term N and P additions reduced plant diversity to some extent, with the most pronounced decreases in MS and DS. It is noteworthy that there were response thresholds for plant diversity and biomass in response to N and P inputs in different steppe types (e.g., 10 g P m^{-2} yr^{-1}). Furthermore, redundancy analysis and stepwise regression analysis revealed that changes in soil properties induced by nutrient addition and climate conditions jointly regulated changes in vegetation biomass and diversity.

Conclusions: The plant biomass and diversity of three steppe types in Inner Mongolia respond divergently to elevated N and P inputs. Our results indicate that regional differences in climate and soil substrate conditions may jointly contribute to the divergent responses of plant biomass and diversity to short-term N and P addition. Our analyses provide new insights into managing and protecting grassland ecosystems. Considering that the effects of nutrient addition on plant diversity and productivity may have increasing effects over time, studies on long-term in situ nutrient addition are necessary.

Keywords: Steppe type, Nitrogen (N) addition, Phosphorus (P) addition, Plant diversity, Biomass, Inner Mongolia

Introduction

Grassland covers ~ 40% of the world's land and is one of the most important components of terrestrial ecosystems (Hufkens et al. 2016). Grasslands play an important role in providing vital ecosystem services, such as regulating global climate change, sequestering carbon, and soil and water conservation (Scurlock et al. 2002). Plant productivity and diversity of grassland communities, which

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is significantly influenced by anthropogenic activities and environmental changes, are critical parameters for understanding the community dynamics, stability, and ecosystem services (Hovenden et al. 2019).

In recent years, nitrogen (N) and phosphorus (P) inputs to terrestrial ecosystems have increased dramatically due to intensified human activities, such as agricultural practices and fossil fuel combustion (Galloway et al. 2008; Pan et al. 2021). Currently, China has become the third-largest region subjected to N deposition in the world, with a mean increase in atmospheric N deposition of 59% since the 1960s (Lu and Tian 2014). In addition, the deposition of P has also been increasing in some regions in the last two decades (Pan et al. 2021). In the semiarid regions of northern China, the total N deposition rate may be greater than 1.5 g N m^{-2} yr^{-1} (Xu et al. 2015) and will continue to increase in the future (Liu et al. 2013). This enrichment can alter ecosystem biogeochemistry, productivity, species richness, and species composition (Seabloom et al. 2021). For example, enhanced N and P inputs would strongly affect vegetation diversity and productivity and would further affect the structure, function, and stability of grassland ecosystems (Bai et al. 2010; Cui et al. 2020; Huang et al. 2018; Li et al. 2019; Lu et al. 2011; Wang et al. 2019a; Xia and Wan 2008). Thus, understanding the effects of different N and P additions on both species diversity and biomass in semiarid ecosystems is of fundamental importance and could provide new insights into managing and protecting grassland ecosystems (He et al. 2016).

Numerous studies in grassland ecosystems have illustrated that the addition of limiting mineral nutrients, such as N and P, generally increases productivity and reduces plant diversity, although its impacts vary among ecosystems (He et al. 2016; Isbell et al. 2013; Jaramillo and Detling 1992; Li et al. 2010; Wang et al. 2019a; Zhang et al. 2014). Because of the positive effect of diversity on productivity, the loss of biodiversity induced by nutrient addition may reduce the effect of nutrients on productivity over time (Isbell et al. 2013). Notably, there existed a threshold for the N and P requirements of grassland communities, beyond which there may be negative effects on community productivity (Li et al. 2009; Zhang et al. 2016). Currently, there are four possible mechanisms regarding the saturation response of ecosystem productivity to nutrient addition: light limitation, biodiversity loss, soil acidification, and ammonium toxicity (Ma et al. 2020). For example, acidification and ammonium toxicity induced by excessive N input may cause species loss (Zhang et al. 2014), possibly accompanied by a decline in community productivity (He et al. 2016; Isbell et al. 2013; Wang et al. 2019a). In contrast, P addition had little effect on biomass and species diversity, as most terrestrial ecosystems were significantly limited by N (Avolio et al. 2014; Gao et al. 2016). Elevated P deposition tended to promote an increase in belowground biomass, but the effect depended on the limitation status of the ecosystems (Yang et al. 2014).

Previous studies have examined the effects of environmental factors (climate conditions, soil properties, anthropogenic interference) on plant diversity and biomass (Chiarucci and Maccherini 2007; Hufkens et al. 2016; Hovenden et al. 2019; Wang et al. 2019b). However, the dominant environmental factors driving diversity and biomass differences among community types in temperate steppe are still unclear (Bai et al. 2021). Temperate grasslands are an indispensable ecological protection screen in northern China, providing unique ecosystem services, such as climate regulation, plant production, and sequestering carbon. Across the east to the west precipitation gradient in Inner Mongolia, three distinct grassland types are formed, including meadow steppe (MS), typical steppe (TS), and desert steppe (DS). How plant diversity and biomass respond to multilevel nutrient additions may vary in contrasting grassland ecosystems due to differences in hydrothermal and soil conditions. It is unclear, however, to what extent the changes in plant species and biomass of different grassland communities depend on nutrient additions.

In this study, we investigated the responses of aboveground and belowground biomass and species diversity to multilevel N and P additions in three steppe types. The objectives of our study were to (1) compare the differences in plant diversity and biomass response to multiple levels of N and P addition in different steppe types; (2) determine the nutrient addition threshold for different steppe communities; and (3) explore the dominant environmental factors driving plant biomass and diversity differences among steppe types in temperate grasslands at the regional scale under N and P addition.

Materials and methods

Field site

Three steppe sites ranging from east to west were selected in this study in Inner Mongolia, China, spanning three steppe types (MG, TD, and DG) (Table 1 and Fig. 1). The first site is a meadow steppe in Ewenki Autonomous Banner (48°55′ N, 119° 11′ E), with a mid-temperate continental climate. The annual mean precipitation is 362 mm, and the mean annual temperature (MAT) is − 0.84 °C (from 1998 to 2018). The dominant plant species were *Leymus chinensis* and *Carex duriuscula,* and the soil was calcic chernozems (FAO taxonomy). The second site, with a mid-temperate semiarid continental climate, is a typical steppe in Xilinhot Autonomous Banner (43° 94′ N, 115° 86′ E). The MAP is 256 mm, and the MAT is

Table 1 Location and basic characteristics of the three steppe sites of Inner Mongolia, China

Site	Location	MAT (℃)	MAP (mm)	Vegetation type	Dominant species	Soil type	pH	SOC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})
MG	48° 55′ N, 119° 11′ E	− 0.84	362	Meadow steppe	*Leymus chinensis, Carex duriuscula*	Calcic Chernozems	6.60	21.79	2.09	0.44
TG	43° 94′ N, 115° 86′ E	2.28	256	Typical steppe	*Stipa krylovii, Convolvulus ammannii*	Haplic Kastanozems	8.34	19.77	2.09	0.38
DG	41° 70′ N, 110° 10′ E	7.09	284	Desert steppe	*Stipa krylovii, Heteropappus altaicus, Convolvulus ammannii*	Calcic Kastanozems	8.90	6.93	0.70	0.38

Climatic variables, including mean annual temperature (MAT) and mean annual precipitation (MAP) (1998–2018) for each site, were derived from the China Meteorological Data Service Centre (http://data.cma.cn)

SOC soil organic carbon, *TN* soil total nitrogen, *TP* soil total phosphorus

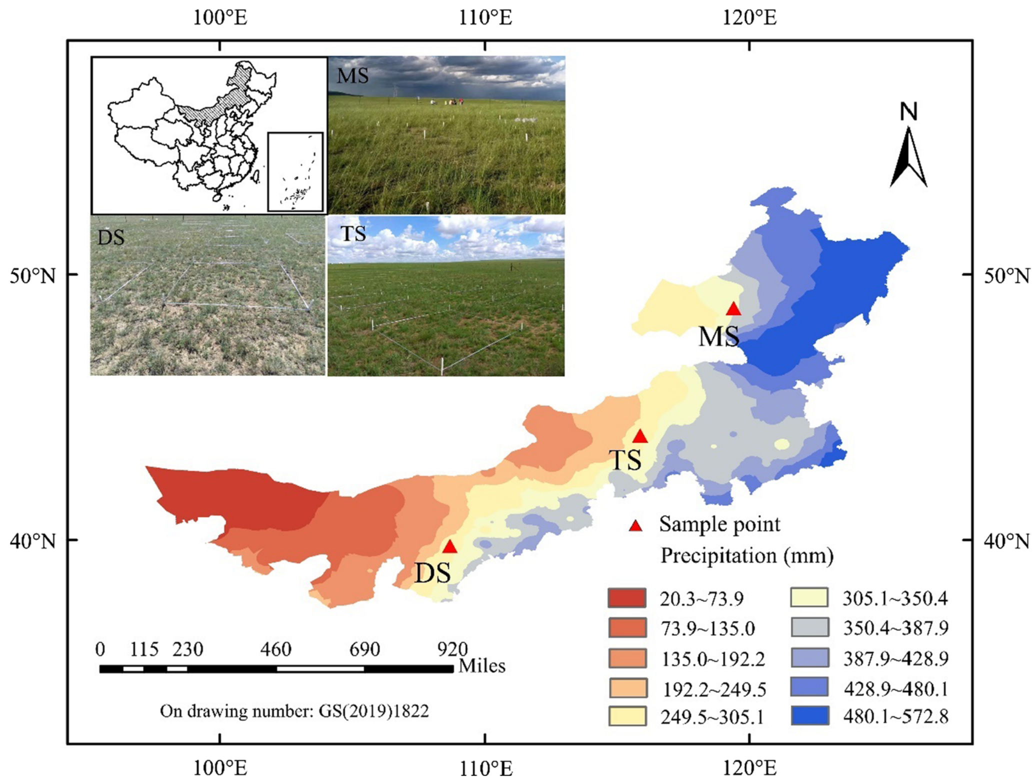

Fig. 1 Locations and landscapes of the three steppe types in Inner Mongolia. MS, TS and DS represent meadow steppe, typical steppe and desert steppe, respectively

2.28 °C. The area of the plant community is dominated by *Stipa krylovii* and *Convolvulus ammannii*, and the soil is Haplic Kastanozems. The third site is a desert steppe in Hangjin Banner (41° 70′ N, 110° 10′ E). The climate here is a mid-temperate semiarid continental climate with an MAT of 7.09 °C and an MAP of 284 mm. The grassland community is dominated by *Stipa krylovii*, *Heteropappus altaicus*, and *Convolvulus ammannii,* and the soil is Calcic Kastanozems. A more detailed site description can be found in a recent report by Yan et al. (2021).

Experimental design and treatment description

Early November 2016, we selected 50 m × 50 m homogeneous flatlands in each grassland site for enclosure treatment. In May 2017, multifactorial field experiments were established at these three steppe sites, with N and P addition levels as two nutrient factors. A total of 14 treatments were performed, including seven addition levels for N (0–30 g N m^{-2} yr^{-1}) and P (0–15 g P m^{-2} yr^{-1}). Seven N addition rates of 0 (CK), 5 (N1), 10 (N2), 15 (N3), 20 (N4), 25 (N5) and 30 g N m^{-2} yr^{-1} (N6) of urea and seven P addition rates of 0 (CK), 2.5 (P1), 5 (P2), 7.5 (P3), 9 (P4), 12.5 (P5) and 15 g P m^{-2} yr^{-1} (P6) of KH_2PO_4 were applied. The amount of fertilizer in our study was set according to previous studies in Inner Mongolia (Bai et al. 2010). Each experimental site was laid out in an identical Latin square design with three replicate plots that were 2 m × 2 m in size, as well as a 2 m buffer zone to prevent movement of fertilizer between the adjacent plots. The fertilizer was applied to each plot in early May and early August 2017. The fertilizer particles were spreading evenly on the soil surface on rainy or cloudy days.

Plant and soil sampling and soil microenvironment

In late August 2017 and 2018, we laid out a subplot (0.75 m × 0.75 m) for sampling and community investigation within each plot at the three grassland sites. The coverage, abundance, frequency and height of each species were accurately recorded in each subplot, and all aboveground plants in the subplots were clipped with sheep shears. Clipped plants were oven dried to constant weight (65 °C for 48 h) and weighed as aboveground biomass (AGB). After that, soil and root samples were collected in each plot by extracting two soil cores (7-cm diameter) from 0 to 30 cm topsoil, which was separated using a 2-mm sieve. Soil samples were air-dried in the laboratory for further nutrient analysis. Root samples were carefully washed and then oven-dried to constant weight to determine belowground biomass (BGB). In addition, the mean annual temperature (MAT) and mean annual precipitation (MAP) (1998–2018) for each site were derived from the China Meteorological Data Service Centre (http://data.cma.cn).

Laboratory analysis

In the laboratory, soil pH was measured using an acidity meter (at a soil/water ratio of 1:2.5). Soil total C (SOC), soil total N (TN) and soil total P contents (TP) were determined by the Walkley–Black method (Nelson and Sommers 1996), Kjeldahl method (Bremner and Mulvaney 1996) and molybdenum antimony anti-colorimetric method (Olsen and Sommers 1982), respectively. The soil available nitrogen, including NH_4^+–N and NO_3^-–N, was analyzed using a continuous analytical system (Liu et al. 2019). The soil available phosphorus (AP) was measured by the molybdenum antimony colorimetry method (Olsen and Sommers 1982).

Calculation of plant community diversity

The indices of plant community diversity were calculated using the following formulas (Wang et al. 2019b):

$$\text{Margalef richness index}(M_a) : M_a = (S - 1)/\ln N \tag{1}$$

$$\text{Shannon} - \text{Wiener index}(H) : H = -\sum_{i=1}^{s} P_i \ln P_i \tag{2}$$

where S refers to the number of species and N stands for the sum of the number of individuals of all species in each subplot. P_i refers to the relative importance value of species i, and species relative importance value = (relative coverage + relative abundance + relative frequency)/3.

Statistical analysis

For each site, statistical significance was determined using one-way ANOVA with Duncan's test for comparisons between multiple nutrient levels. Further analyses were performed to test the main and interactive effects of nutrient additions, steppe type, and year on AGB, BGB, H and M_a using three-way ANOVA. When necessary, log-transformation of our data was used to satisfy the normality and homogeneity of variance criteria (Legendre and Gallagher 2001). Redundancy analysis (RDA) was performed to identify the role of environmental variables in shaping community biomass and diversity. Further analyses were conducted to determine the critical factors influencing them using a stepwise regression (SRA). Data are presented as the means ± standard error (SE), and the significance level ($P < 0.05$) was employed for all analyses in our study.

Results

Effects of N addition on plant biomass and diversity in three steppe types

N addition altered the AGB and community diversity (H and M_a) in three temperate steppes varying with the steppe type and year but had no significant effects on BGB (Figs. 2 and 3). Specifically, the AGB in MS and DS gradually increased with increasing N inputs only in 2018 (Fig. 2a, c). In contrast, N addition reduced plant diversity (H and M_a) in all three steppe types (Fig. 3), most notably in MS and DS, while the M_a of TS only experienced a significant reduction under high N levels (N25 and N30) in 2018 (Fig. 3e). In addition, AGB, H and M_a were also affected by the interactions among treatment, year, and steppe type (Y × S, T × Y, and T × S, $P < 0.05$, Table 2).

Effects of P addition on herbaceous biomass and diversity in three steppe types

Obviously, P addition affected the community biomass and diversity of the three temperate steppes to a greater extent than N addition (Table 2). As shown in Fig. 4, the AGB and BGB of the three steppe types showed a trend of increasing and then decreasing with increasing inputs of P addition for 2017 and 2018. The occurrence of the inflection point was observed roughly around the P10 treatment, indicating that exceeding 10 g P m^{-2} yr^{-1} somewhat inhibited the increase in above- and belowground biomass. For the community diversity index, P addition notably decreased the H and M_a of MS and DS but not MG in 2017 and 2018 (Fig. 5). For example, the H and M_a of DS were significantly lower under high P inputs (P15) than those of the control in 2018. ANOVA results further revealed that treatment, year, steppe type, and their interactions (Y × S, T × Y, and T × S) had significant effects on AGB and BGB ($P < 0.05$, Table 2) but not on diversity (H and M_a).

Factors driving plant biomass and diversity under N addition

RDA showed that plant diversity (M_a and H) and biomass (AGB and BGB) were determined by climate factors and soil properties under N addition (Fig. 6a, c). The first two axes explained 78.78% of the environmental data (adjusted $R^2 = 74.9\%$, $P < 0.05$), with axis 1 explaining 54.32% of the variance and axis 2 explaining another 24.46% (Fig. 6a). M_a and H were strongly positively correlated with MAT and pH, AGB was positively correlated with MAP and TP, and BGB was positively correlated with NH_4^+ and SOC. However, AGB, M_a, and H were strongly negatively correlated with TN, and BGB was strongly negatively correlated with MAT and pH. In

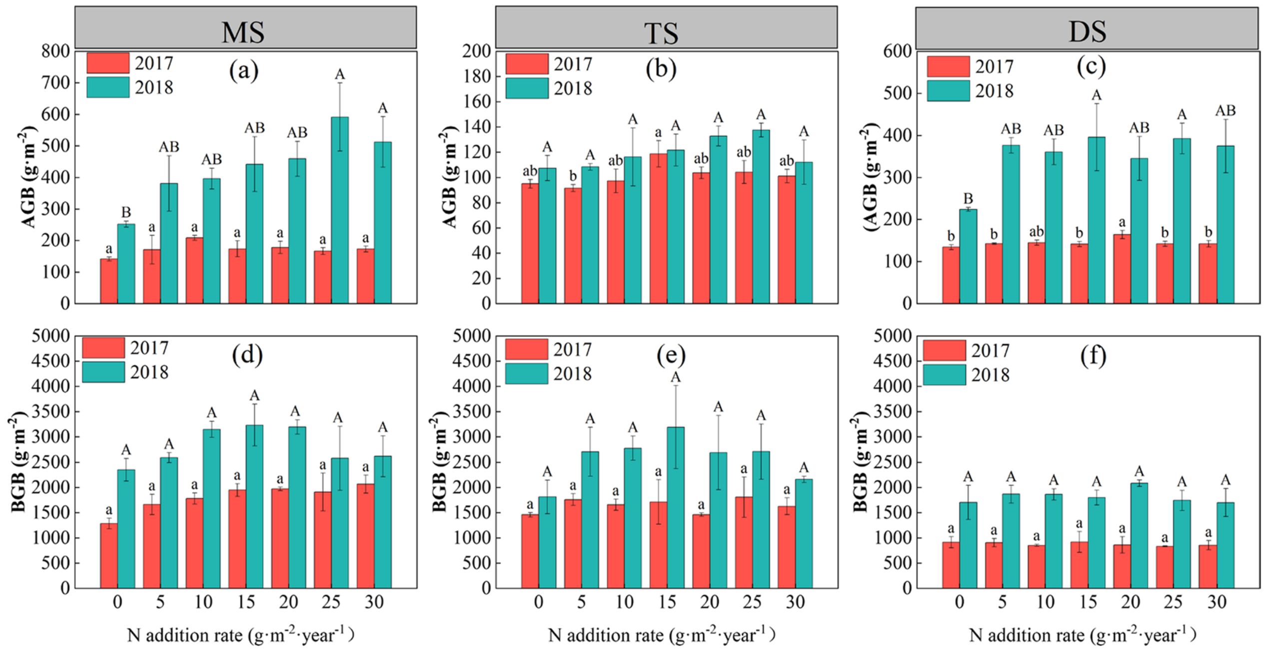

Fig. 2 Effect of experimental N addition on above- ((**a**) MS, (**b**) TS, (**c**) DS) and below-ground biomass ((**d**) MS, (**e**) TS, (**f**) DS) of three temperate steppes from 2017 to 2018. Lowercase letters represent significant differences among different treatments in 2017 at the 0.05 level, while uppercase letters represent significant differences among treatments in 2018 at the 0.05 level. Data show the mean ± standard error ($n = 3$) (same as below)

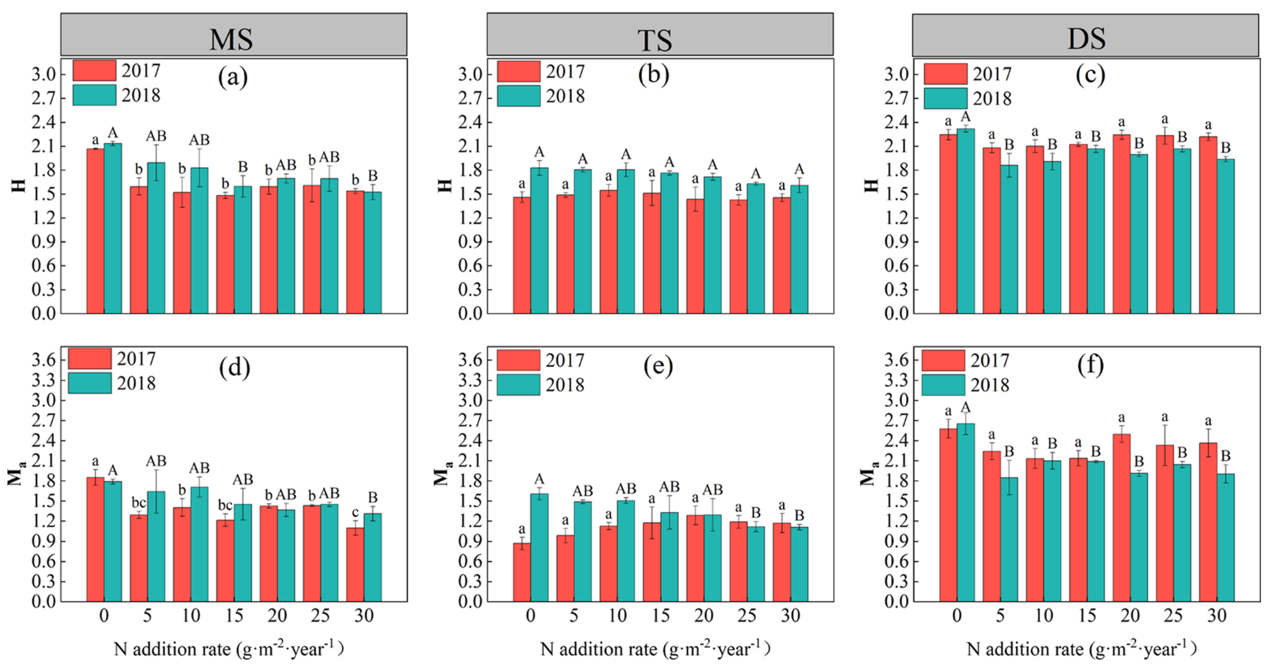

Fig. 3 Effects of experimental N addition on the Shannon-Wiener ((**a**) MS, (**b**) TS, (**c**) DS) and Margalef richness ((**d**) MS, (**e**) TS, (**f**) DS) of three temperate steppes from 2017 to 2018

Table 2 ANOVA results for the effects of treatment (T), steppe type (S), and year (Y) on community biomass and diversity in northern China

	Term	AGB		BGB		*H*		M_a	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
N addition	T	3.99	**0.001**	2.06	0.067	5.33	**0.000**	4.58	**0.000**
	Y	197.10	**0.000**	107.08	**0.000**	6.78	**0.011**	0.96	0.331
	S	99.16	**0.000**	39.33	**0.000**	94.96	**0.000**	172.72	**0.000**
	T × Y	2.78	**0.016**	0.95	0.462	0.78	0.589	2.43	**0.032**
	T × S	1.10	0.368	0.66	0.781	2.36	**0.012**	1.43	0.170
	Y × S	40.74	**0.000**	0.07	0.935	15.77	**0.000**	11.05	**0.000**
	T × Y × S	1.14	0.342	0.27	0.992	0.47	0.929	1.07	0.395
P addition	T	9.08	**0.000**	2.56	**0.025**	7.92	**0.000**	7.19	**0.000**
	Y	159.21	**0.000**	171.07	**0.000**	103.75	**0.000**	28.35	**0.000**
	S	159.47	**0.000**	64.16	**0.000**	100.42	**0.000**	258.51	**0.000**
	T × Y	2.54	**0.026**	2.49	**0.029**	1.06	0.392	1.04	0.407
	T × S	3.50	**0.000**	1.84	0.054	1.73	0.075	1.37	0.194
	Y × S	32.29	**0.000**	13.25	**0.000**	1.76	0.178	2.11	0.127
	T × Y × S	1.04	0.418	1.17	0.317	1.25	0.266	1.77	0.067

Bold font indicates a significant result ($P < 0.05$)

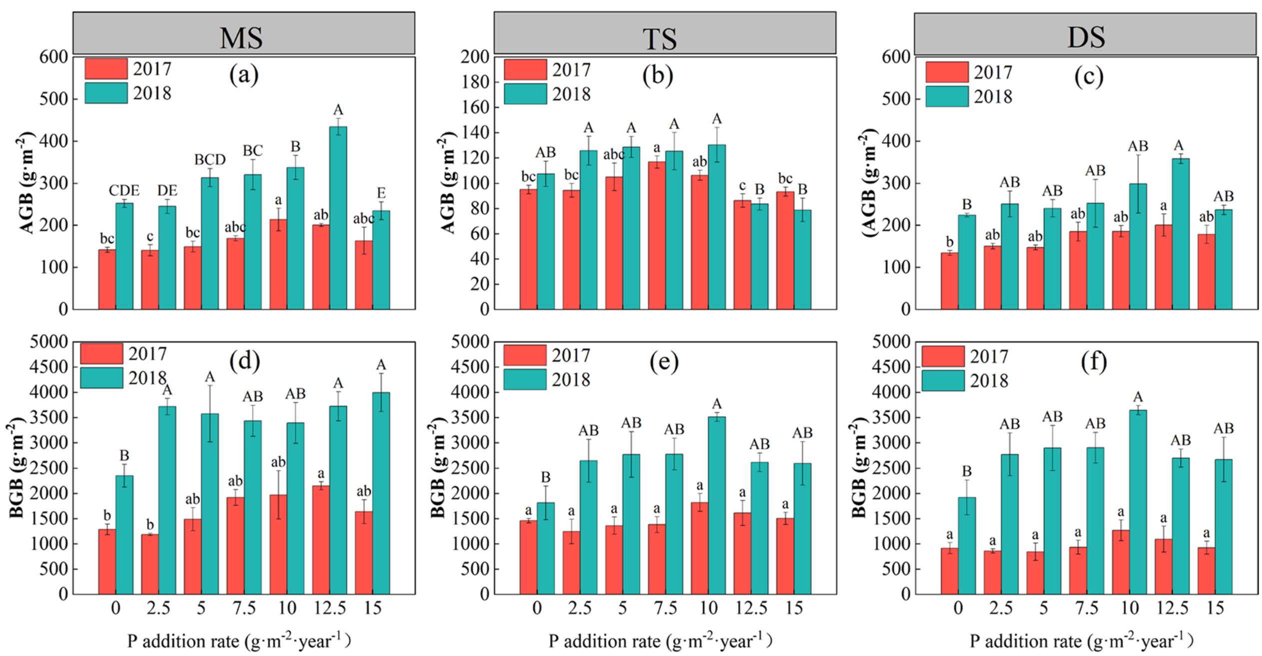

Fig. 4 Effect of experimental P addition on above- ((**a**) MS, (**b**) TS, (**c**) DS) and below-ground biomass ((**d**) MS, (**e**) TS, (**f**) DS) of three temperate steppes from 2017 to 2018

addition, SRA was run to detect the critical factors of soil properties and climatic conditions that affected plant biomass and diversity. Taken together, these results demonstrated that MAP, MAT, TP, TN, and NH_4^+ were the key driving factors of plant biomass and diversity (Table 3).

Factors driving plant biomass and diversity under P addition

According to the RDA results shown in Fig. 6, climate factors (MAT, MAP) and soil properties (TP,

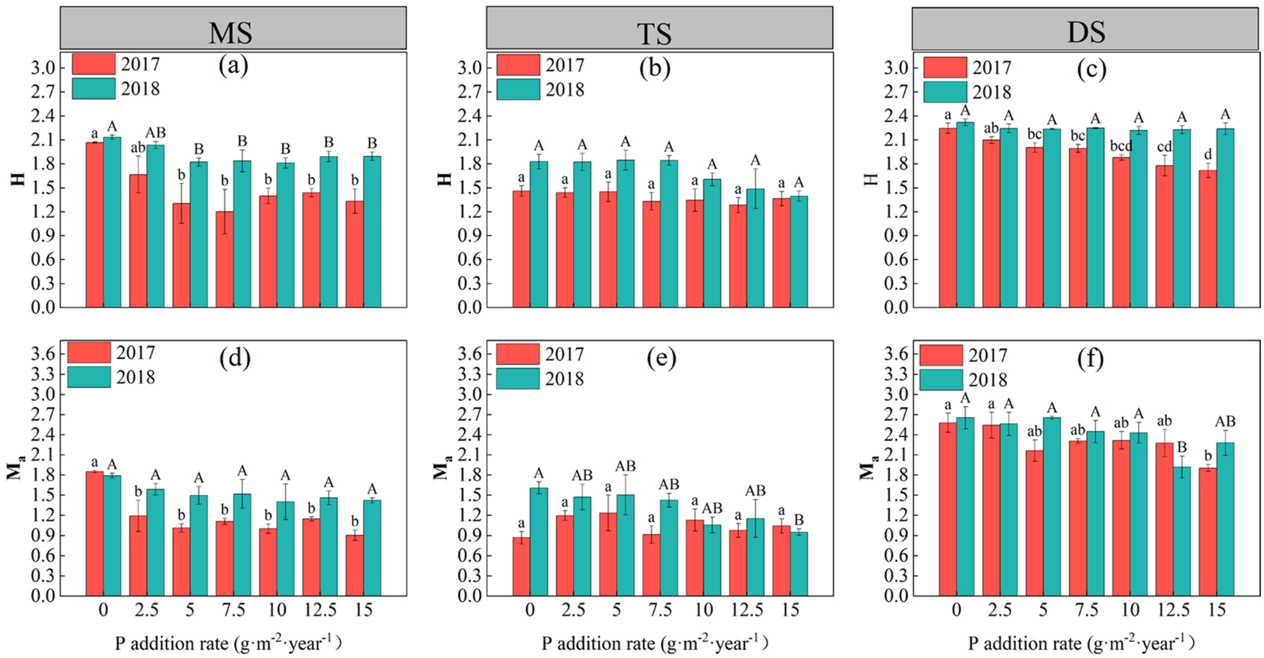

Fig. 5 Effects of experimental P addition on the Shannon-Wiener ((**a**) MS, (**b**) TS, (**c**) DS) and Margalef richness ((**d**) MS, (**e**) TS, (**f**) DS) of three temperate steppes from 2017 to 2018

NH_4^+, TN, NO_3^-, SOC, pH and AP) explained 79.5% of the total variability in the data (adjusted $R^2 = 79.5\%$, $P < 0.05$), with axes 1 and 2 explaining 45.53% and 34.81% of the total variation, respectively. AGB, M_a, and H were positively correlated with MAT, MAP, and TP but negatively correlated with TN and NO_3^-. BGB was positively correlated with NH_4^+, MAT and TP but strongly negatively correlated with MAT and pH. Furthermore, the SRA results showed that MAT, MAP, TN TP, AP, NH_4^+, NO_3^-, and pH together influenced community biomass and diversity under P addition (Table 3).

Discussion

Divergent response of community biomass to nutrient additions in three grassland types

Many studies have shown that nutrient addition alleviates the state of nutrient limitation by increasing the effective resources in the soil, thus greatly stimulating biomass increase (Song et al. 2012; Yang et al. 2014; Bai et al. 2010; Huang et al. 2018; Wang et al. 2019a). In our study, we found that N and P additions contributed differently to the increase in biomass in the three steppe types. Similar to other N experimental studies (Isbell et al. 2013; Niu et al. 2018; Stevens et al. 2004), N addition tended to

Table 3 Stepwise regression analysis (SRA) used to identify the critical factors of plant biomass and diversity

	Item	Equations	R^2	Sig	*n*
N addition	AGB	$AGB = -476.32 + 747.32TP + 1.504MAP$	0.827	0.000***	42
	BGB	$BGB = 1367.7 + 34.1NH_4^+ - 145.69MAT + 2513.50TP$	0.840	0.000***	42
	H	$H = 2.317 - 0.309TN$	0.832	0.000***	42
	M_a	$M_a = 2.545 - 0.547TN$	0.849	0.000***	42
P addition	AGB	$AGB = -341.51 + 231.86TP + 1.30MAP + 14.48MAT$	0.859	0.000***	42
	BGB	$BGB = 1118.3 + 69.20NH_4^+ - 125.55MAT + 2107.50TP$	0.904	0.000***	42
	H	$H = 2.12 - 0.276TN + 0.567TP - 0.005NO_3^-$	0.903	0.000***	42
	M_a	$M_a = 3.340 - 0.371TN - 0.021AP + 0.144MAT + 0.029NH_4^+ - 0.215pH$	0.957	0.000***	42

*** indicates level of significance: $P < 0.001$

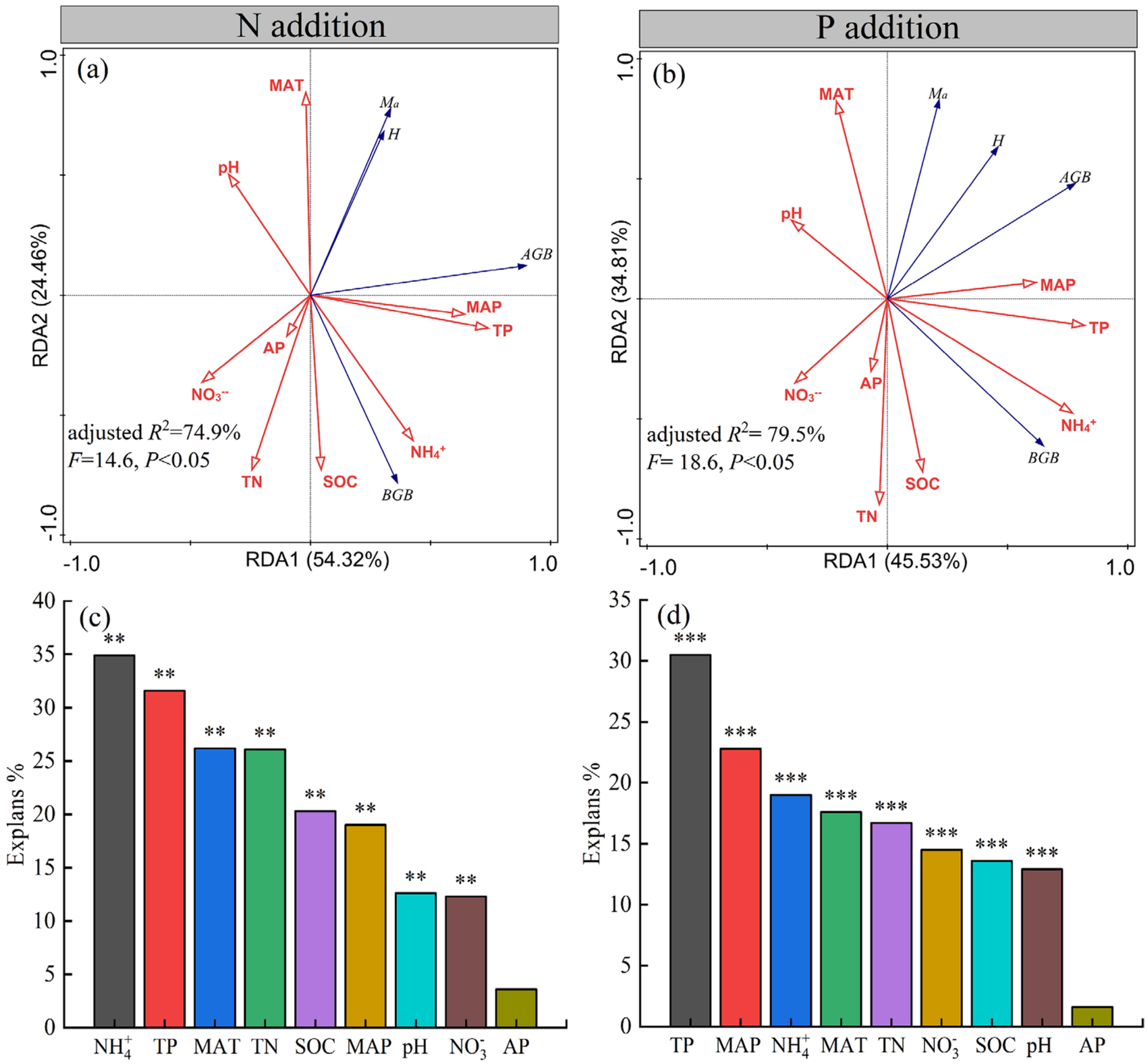

Fig. 6 Redundancy analysis (RDA) of community biomass and diversity (blue lines) in relation to environmental factors (red lines) under N or P addition. In Fig. 5a, RDA axes 1 and 2 explained 54.32% and 24.46% of the variation, respectively (adjusted $R^2 = 74.9\%$, $F = 14.6$, $P < 0.05$). In Fig. 5b, RDA axes 1 and 2 explained 45.53% and 34.81% of the variation, respectively (adjusted $R^2 = 79.5\%$, $F = 14.6$, $P < 0.05$)

increase AGB mainly, while it did not significantly affect BGB (Fig. 2 and Table 2). The different responses of AGB and BGB to N inputs support the theory of optimal partitioning, whereby N limitation in the belowground part of the plant is alleviated by nutrient addition, leading to increased competition for light in the aboveground part and prompting the plant to allocate more photosynthetic products to the aboveground part (Bai et al. 2010; Qi et al. 2019; Wan et al. 2008). In addition, RDA and SRA also found that AGB and BGB were more constrained by TP and MAP (Table 3). Therefore, TS with less precipitation had a weaker percentage increase in AGB than MS and DS (Table 1). The degree of response and sensitivity of grassland ecosystems to nutrient inputs, a key factor governing arid and semiarid grasslands, may also depend on ecosystem moisture conditions, with N inputs likely to positively affect community productivity only after moisture conditions reach a certain threshold (Hasi et al. 2021).

In contrast, P addition jointly significantly contributed to the increase in AGB and BGB in all three steppes (Fig. 4 and Table 2). The higher contribution of P addition to the biomass of the three steppes than N addition may be strongly related to the state of nutrient limitation of the temperate steppes in Inner Mongolia, in addition to the easy volatilization loss of N fertilizer, while the aridification trend in the study area somewhat limits the degree of biomass response to N input (Yan et al. 2021). Our analysis also found that the AGB and BGB of the three steppe types under P input were significantly influenced mainly by TP and climatic conditions (MAT and MAP). It is noteworthy that there were clear thresholds for the response of the three community biomasses to short-term P addition. For example, the proportion of AGB and BGB promotion in steppe communities was significantly lower under high P input (P15). Compared to most nutrient addition trials, the results of our short-term N and P addition (< 2 years) experiments may not be highly comparable and generalizable, and thus the nutrient addition thresholds for the three steppe types still need to be further determined and judged by long-term nutrient addition trials.

Divergent response of community diversity to nutrient additions in three steppe types

Most studies have shown that N deposition decreases species richness and leads to a decrease in community diversity, and even low N deposition affects species diversity (Bai et al. 2010; Clark and Tilman 2008; Seabloom et al. 2021; Zhang et al. 2014), while the effect of P addition on grassland species diversity has been relatively little studied (Chiarucci and Maccherini 2007). Our results showed that N and P additions somewhat reduced the diversity of the three communities, with the extent of the effect varying by steppe type and year (Table 2). For example, N addition significantly reduced MS community diversity (M_a and H) (Fig. 3a, d), while P addition significantly reduced MS and DS community diversity (M_a and H) in 2017 (Fig. 5a, c, d and f). According to the ecological niche compensation hypothesis, the dominance of different plants in the three steppe types leads to a sequential distribution of community resources between dominant and disadvantaged species (Silvertown 2004), and other studies have also shown that interspecific differences in species responses to nutrient addition (He et al. 2016) and competition for light resources among different species after nutrient addition are the main causes of community composition and diversity the main cause of changes (Avolio et al. 2014; DeMalach 2018; Ma et al. 2020). Due to significant differences in species composition among the three steppe types, in MS and DS, N and P additions caused asymmetric changes in the height of grasses and nongrasses, with grasses in the upper part of the community (e.g., *Leymus chinensis*, *Stipa krylovii*, etc.) shading nongrasses in the lower part of the community (e.g., *Potentilla acaulis*, *Carex duriuscula*, etc.), leading to a gradual loss of some species with weaker light competition, thus reducing species diversity. Unlike DS, where the dominant species are mainly low clumping species (*Allium ramosum*; *Stipa krylovii; Convolvulus ammannii*) due to sparse precipitation and simple vegetation species composition. There was no significant change in plant height asymmetry between functional groups under N and P input to produce shading, thus showing a significant decrease in diversity only at high N and P levels (Figs. 3c, f and 5c, f). This phenomenon may be related to the acidification and ammonium poisoning effects of excessive nutrient inputs. For the dominant influencing factors of community diversity, the results of RDA and SRA showed that TN was the key factor affecting diversity (M_a and H) under N addition, while community diversity under P addition was mainly related to TN, TP, available N and P, pH and MAT. Considering the short duration of nutrient addition in our study (< 2 years), it is difficult to reveal the nonlinear response pattern of ecosystems to long-term N and P inputs and their underlying mechanisms. Therefore, a long-term localized observational study for nutrient addition experiments is necessary, as well as close attention to ecosystem substrate conditions.

Conclusions

Our results showed that plant biomass and diversity in the three steppe types in Inner Mongolia responded differently to elevated N and P inputs. Increasing P promoted AGB and BGB more than increasing N in the three temperate steppes. N and P additions reduced plant diversity to some extent, with the most pronounced decreases in MS and DS. It is noteworthy that there are response thresholds for plant diversity and biomass in response to N and P inputs in different steppe types. RDA and SRA revealed that changes in soil properties induced by nutrient addition and climate conditions jointly regulated changes in vegetation biomass and diversity. Our results indicate that regional differences in climate and soil substrate conditions may jointly contribute to the divergent responses of plant biomass and diversity to short-term N and P addition. This study has limitations due to the short duration (< 2 years) of nutrient addition. Considering that the effects of nutrient addition on plant diversity and productivity may have increasing effects over time, studies on long-term in situ nutrient addition are necessary.

Abbreviations

N: Nitrogen; P: Phosphorus; RDA: Redundancy analysis; SRA: Stepwise regression analysis; MG: Meadow steppe; TG: Typical steppe; DG: Desert steppe; AGB: Aboveground biomass; BGB: Belowground biomass; MAT: Mean annual temperature; MAP: Mean annual precipitation; SOC: Soil total carbon; TN: Soil total nitrogen; TP: Soil total phosphorus; NH_4^+: Soil ammonium nitrogen; NO_3^-: Soil nitrate nitrogen; AP: Soil available phosphorus; M_a: Margalef richness index; *H*: Shannon–Wiener index.

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Authors' contributions
FJ designed the experiment. ZF and NG analyzed the data and wrote the draft. ZF, NG, XH and MX analyzed all soil and plant samples. FJ and ZF performed writing review and revision. All authors read and approved the final manuscript.

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Availability of data and materials
Data and materials can be obtained by contacting the corresponding authors if needed.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
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Competing interests
The authors declare that they have no competing interests.

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