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Response of plant community composition and productivity to warming and nitrogen deposition in a temperate meadow ecosystem

T. Zhang^{1,3}, R. Guo², S. Gao¹, J. X. Guo¹, and W. Sun¹

¹Institute of Grassland Science, Northeast Normal University, Key Laboratory of Vegetation Science, Ministry of Education, Changchun 130024, China

²Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Key Laboratory of Dryland Agriculture, Ministry of Agriculture, Beijing 100081, China

³State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences Urumqi 830011, China

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Correspondence to: J. X. Guo (gjixun@nenu.edu.cn) and W. Sun (sunwei@nenu.edu.cn)

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Abstract

Climate change has profound influences on plant community composition and ecosystem functions. However, its effects on plant community composition and net primary productivity are not well understood. A field experiment was conducted to examine the effects of warming, nitrogen (N) addition, and their interactions on plant community composition and productivity in a temperate meadow ecosystem in northeast China. Experimental warming significantly increased species richness, evenness and diversity, by contrast, N addition highly reduced species richness, evenness and diversity. Warming reduced the importance value of gramineous species but increased in forbs, N addition had the opposite effect. Warming had a significant positive effect on belowground productivity, but had a negative effect on aboveground biomass. The influences of warming on aboveground productivity were dependent on precipitation. Experimental warming had little effect on aboveground productivity in the years with higher precipitation, but significantly suppressed the growth of aboveground in dry years. Our results suggest that warming had indirect effects on plant productivity via altering water availability. Nitrogen addition significantly increased above- and belowground productivity, suggesting that N is one of the most important limiting factors which determine plant productivity in the studied meadow steppe. Significant interactive effects of warming plus N addition on belowground productivity were also detected. Our observations revealed that climate changes (warming and N deposition) plays significant roles in regulating plant community composition and productivity in temperate meadow steppe.

1 Introduction

The mechanisms that determine plant diversity and community composition are the key issues in ecological studies. Results from previous studies have indicated that sustaining ecosystems productivity, stability and multi-functionality in grassland communities requires higher biodiversity (Tilman et al., 2006; Hector and Bagchi, 2007; Zavaleta

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et al., 2010; Cardinale et al., 2012). Plant diversity and community composition are determined by biotic and abiotic factors, such as, herbivores, soil microbes and soil available nutrients (De Deyn et al., 2004; Van Der Heijden et al., 2008; Burns et al., 2009). Importantly, an increasing number of studies reported that climate change can alter plant community composition and diversity (Klanderud, 2005; Kardol et al., 2010).

Global surface temperature has increased at a rate of 0.2 °C per decade over the past 30 years due to rising greenhouse gas emissions (Hansen et al., 2006), and global warming is expected to increase continually in the next 100 years (IPCC, 2007), severely affecting terrestrial ecosystems. Several consequences of global warming on terrestrial plant ecosystem stability includes significant decreased in species richness and diversity (Rull and Vegas-Vilarrúbia, 2006; Fonty et al., 2009; Yang et al., 2011). Studies found that different functional groups have differential response to warming (Fay et al., 2011) as well as its profound influence on plant productivity (Hutchings and de Kroon, 1994; Natali et al., 2012). However, some studies through non-intrusive field experiments showed that plant responses to warming are those ecosystems dependent, with plants in cold-wet northern sites more sensitive to warming (Penuelas et al., 2004), while warming in other ecosystems decreased productivity of both above- and belowground biomass (Ciais et al., 2005; De Boeck et al., 2008).

The increase of atmospheric nitrogen (N) deposition induced by human activities has been recognized as another important threat to terrestrial ecosystem that causes the shifts in plant community structure in terrestrial plant community structure (Duprè et al., 2010). A large number of studies found that N deposition in soil highly reduced plant diversity and species richness (Zavaleta et al., 2003; Clark and Tilman, 2008; Song et al., 2011). Some studies, however, demonstrated that N deposition do not actually changes species richness of the vegetation (Goldberg and Miller, 1990; Huberty et al., 1998), instead, increases plant diversity (Bowman et al., 2006). Moreover, the ecological impacts of even relatively small N deposition on plant species interactions at species level are still not well understood (Payne et al., 2013). Hence, nitrogen availability play a more important role in limiting plant primary productivity than other soil

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available nutrients elements, and nitrogen deficiency is globally distributed (LeBauer and Treseder, 2008; Norby et al., 2010). In general, the response of grassland productivity to N deposition is determined whether the soil has reached N saturation or not. Small amounts N deposition can improve plant productivity before soil N reaching saturation point (Hutchings and de Kroon, 1994; LeBauer and Treseder, 2008), while N deposition can also reduce plant productivity when the soil had reached N saturation point (Magill et al., 2000).

It is predicted that the temperature will elevate by 2.8–7.5 °C in the next 100 years in Songnen grassland in northeast China (IPCC, 2007). Although, some previous studies focused on the effects of warming on plant competitive hierarchy (Niu and Wan, 2008) and soil N cycling (Ma et al., 2011) in temperate grassland ecosystem in northern China, the influence of warming on plant community composition and productivity remains unclear. Liu et al. (2011, 2013) reported that N deposition significantly increased in China in the last three decades, which had affected agriculture and grassland ecosystems. Studying the mechanisms that N deposition alter plant community composition, especially the effects of interactions between N deposition and other global change factors are still not well understood. In order to ascertain the potential effects of climate warming and increased in N deposition on plant community composition and productivity, we conducted a field experiment with manipulated warming and N addition. In this experiment, we aim to answer the following questions: (1) how does warming and N addition affects plant community composition and productivity in temperate meadow ecosystem? (2) The influences of abiotic (e.g. soil moisture) and biotic factors (plant interspecific interactions) on plant community and productivity under climate warming and N addition conditions.

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2 Materials and methods

2.1 Study site

The experiment was conducted at the Songnen Grassland Ecological Research Station (44°45' N, 123°45' E), Northeast Normal University, Jilin Province, northeastern China. The grassland is situated at the eastern edge of the Eurasian steppe and is characterized as Eurasian continental meadow steppe. Mean annual precipitation is approximately 400 mm with 90 % occurs from May to October. Annual average air temperature is 4.9 °C, and annual average land surface temperature is 6.2 °C. The soil in the studied area is a soda-saline type, and has pH of 8.2, with 3–4 % organic matter in the surface layer. Vegetation in the experimental site is dominated by *Leymus chinensis*, *Kalimeris integrifolia*, *Carex duriuscula* and *Rhizoma phragmitis*.

2.2 Experimental design

We used a complete randomized block factorial experimental design with two factors: warming and N addition. There were four treatments: control (C), warming (W), N addition (N), and warming plus N addition (W + N), and replicated 6 times. The size of each plot was 2 m × 3 m. All the warmed plots were heated continuously by infrared radiators (MSR-2420, Kalglo Electronics Inc. Bethlehem, PA, USA) suspended in 2.25 m over the plot center. In each control or N addition plots, one “dummy” heater with the same shape and size was installed to mimic the shading effects of the infrared radiator. All the heaters under the warming treatments were set at a radiation output of approximately 1700 W. It is estimated that anthropogenic N deposition is up to 80–90 g m⁻² yr⁻¹ and even higher N deposition would occur in the future owing to land-use change and activities (He et al., 2007; Liu et al., 2013). In the northern temperate grassland ecosystem the community saturation of N deposition rates was approximately 10.5 g m⁻² yr⁻¹ (Bai et al., 2010), though atmospheric N deposition was only 2.7 g m⁻² yr⁻¹ in the last decade in this area (Zhang et al., 2008). Thus, in the N addition treatments plots, am-

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monium nitrate (10 g m⁻² yr⁻¹) was added as a pulse of aqueous on the first day in May every year. In the control and warming plots, the same amount of water (without N) as the N addition treatment was added to account for N addition induced differences in water availability. The experiment started in May 2006 and finished in September 2009.

2.3 Meteorological data collection

The monthly mean temperature and precipitation from 2006 to 2009 were recorded using an eddy covariance system installed 200 m apart from the experimental site. One probe of EM50/R (Decagon Ltd, Pullman WA, USA) was buried 0–15 cm from the soil surface in each experimental plots, measuring soil temperature (ST) and soil moisture (SM) one hour interval.

2.4 Plant diversity and productivity

During the growing season, we sampled abundance, height, frequency, and cover of all plant species found within 1 m × 1 m subplot in each plots. The number of plant species present in the quadrat was recorded as the species richness. Plant numbers per species were also used to calculate importance value (IV), species richness, diversity (Shannon–Wiener index H) and evenness value (Pielou index E).

$$\text{Shannon–Wiener index (H): } H = - \sum_{i=1}^S P_i \ln P_i \quad (1)$$

$$\text{Pielou index (E): } E = \frac{H}{\ln S} \quad (2)$$

Where S is the total number of species, and P_i is the proportion of species i in total species. Importance values per species were calculated using the following formula.

$$\text{Importance value: (IV) = (RC + RF + RD)/3} \quad (3)$$

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3.3 Importance value

During the four experimental years, the importance value (IV) of gramineous ($P < 0.01$) and forbs ($P < 0.01$) showed significant interannual variation (Table 2). N addition significantly decreased IV of gramineous by 18.1% ($P < 0.01$) in 2006 and enhanced it by 19.2% in 2007, whereas N addition had no effect on IV of gramineous in 2008 and 2009. Compared to the control treatment, IV of forbs in N addition plots increased by 34.1% ($P < 0.05$) and 11.1% in 2006 and 2007, respectively; however it was reduced by 11.5% in 2009 ($P < 0.05$). Despite warming had no effects on IV of gramineous in 2006 and 2007, it caused a reduction in IV by 11.8% ($P < 0.05$) and 17.4% ($P < 0.05$) in 2008 and 2009, respectively. The IV of forbs in warming plots improved 13.6% ($P < 0.05$) compared to control treatment in 2007 (Fig. 4). In warming plus N addition treatment, IV of gramineous species improved by 11.5% ($P < 0.05$) compared with control treatment in 2008. There were main effects of experimental years, N addition, and interactive effects of warming plus N addition on IV of gramineous species ($P < 0.01$) (Table 2). Interactive effects of years \times N addition, warming \times N addition on IV of forbs were observed ($P < 0.05$) (Table 2). The IV of gramineous species were higher than forbs across the four treatments from 2006 to 2008; however the IV of forbs was greater than gramineous in 2009 (Fig. 3).

3.4 Aboveground and belowground biomass

Aboveground biomass showed apparent interannual variation, with the highest (394.8 g m^{-2}) and lowest (270.2 g m^{-2}) values in 2006 and 2007, respectively (Fig. 4a). On average, N addition increased aboveground biomass by 20% ($P < 0.01$) compared to the control plots from 2006 to 2009. Warming decreased aboveground biomass by 9.2% ($P < 0.05$) and 16.6% ($P < 0.05$) in 2006 and 2009, respectively; but it increased aboveground biomass by 20.8% ($P < 0.05$) in 2008. Interactive effects between warming and N addition on aboveground biomass ($P < 0.05$) were only observed in 2006.

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There were interactive effects between experimental year and N addition on aboveground biomass ($P < 0.01$).

Mean belowground biomass across the four treatments in 2006 was much higher than the other three experimental years (Fig. 4b). From 2006 to 2009, N addition increased the belowground biomass by 6.1% ($P < 0.05$) on average. Warming treatment showed no effects on belowground biomass in 2006; however it increased the belowground biomass by 11.2% ($P < 0.05$) in 2007, 2008 and 2009. Warming plus N addition enhanced the belowground biomass by 50.7% ($P < 0.05$) across the four experimental years. There were significant effects of year, N addition and interactive effects between warming and N addition on belowground biomass (Table 2).

4 Discussion

4.1 Effects of experimental warming and N addition on plant community composition

In the present study, the plant community composition was altered significantly after four years' of warming and N addition treatments. Warming induced a significant increase in species richness in the studied meadow steppe community, which is in accordance with the results observed in temperate grasslands (Harmens et al., 2004; Yang et al., 2011) and annual grassland (Zavaleta et al., 2003); however, it was inconsistent with the results of some other researches where warming was associated with larger species loss (Klein et al., 2004; Gedan and Bertness, 2009). We found that warming significantly increased species number of forbs, which might be related to warming induced by changes in soil moisture. Warming aggravated evapotranspiration and reduced soil moisture, which are likely caused gramineous species to allocate more biomass to belowground (Wang et al., 2010), and subsequently suppress the growth of aboveground biomass, so that the competition ability of gramineous species declined and the increased the competition ability of forbs species.

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In contrast to the significant enhancement effects of warming on species richness at the community level, N addition reduces species richness. This observed reduction in species richness under the N addition treatment is in agreement with the results obtained in a prairie grasslands (Clark and Tilman, 2008), a California annual grassland (Zavaleta et al., 2003), in European acidic grasslands (Stevens et al., 2004; Duprè et al., 2010), and a savannah grassland (Isbell et al., 2013). In the studied temperate steppe (dominated by a perennial grass *L. chinensis*), productivity is often limited by N availability (Bai et al., 2010). In general, gramineous species are sensitive to N (Foster and Gross, 1998); therefore N addition significantly improved the growth and cover of gramineous species and suppresses the growth of other species (e.g. Leguminosae, Compositae, etc.).

Current empirical and theoretical ecological results suggest that many species could be at risk and plant diversity would decline with the continuation of global warming (Botkin et al., 2007). The experimental warming associated with loss of plant diversity were detected in many ecosystems, such as in moist tussock tundra (Chapin III et al., 1995), and in New England salt marshes (Gedan and Bertness, 2009). However, there are some other studies reported that plant diversity was not significantly affected by warming (Harmens et al., 2004; Yang et al., 2011). In our study, although warming did not affect plant diversity from 2006 to 2008, the diversity increased dramatically in the warming plots in the fourth experimental year (Fig. 4). These results may be partly ascribed to the reduction of competitive dominant species *L. chinensis* and improved the survival of other species (such as, Compositae, Leguminosae). This can be explained based from similar previous results that climate change indirectly affects co-existing species via affecting dominant species (Engel et al., 2009; Kardol et al., 2010). While no significant effects of N addition on plant diversity was observed during the first two experimental years, and subsequently found significant effects in 2008 and 2009, which are in agreement with the results of previous observations in many terrestrial ecosystems (Pennings et al., 2005; Bobbink et al., 2010). N addition improved the growth condition of *L. chinensis*, which subsequently reduced the survival space of other co-

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existing species. Furthermore, no decline of species richness, evenness and diversity under N addition at the early two experimental years, which might be related to the soil N availability, in Songnen meadow steppe with total N (2 g kg^{-1}) and available N (40 mg kg^{-1}) is much lower, which limited the survival of annual forbs. A small quantity or short-term of N deposition can not affect plant diversity, but long-term N deposition might significantly reduce plant diversity and ecosystems stability. In the present study, significant decline of plant diversity in warming plus N addition treatment in 2008 and 2009 was observed. The result might suggest that the changes of plant diversity are determined by the effects of many global changes. The influence of long-term integrated environmental factors on plant diversity should be further investigated.

Changes in importance values (IV) of species can reflect the variation of plant community composition. We found that the IV of gramineous species were much higher than forbs from 2006 to 2008, but the IV of forbs species were greater than gramineous species in 2009. N addition highly improved the IV of gramineous species, while warming decreased it and increased importance value of forbs (Table 2). The significant influence of experimental years, N addition, interaction between years and N addition on importance of gramineous and forbs species ($P < 0.05$) might be due to the improved growth of *L. chinensis* and *Phragmites australis*, and reduced the proportion of forbs, whereas warming restrained the growth of gramineous species. These observations in this study highlights that climate changes have the potential to alter species interactions. However, many studies have demonstrated that climate change can also influence the composition of insects and soil microorganisms (Liu et al., 2009; Potts et al., 2010), which subsequently can also alter plant species interactions (Bidart-Bouzat and Imeh-Nathaniel, 2008; Singh et al., 2010). Up to now, climate changes associated with interactions between soil microorganisms and plant species, and the influence of interactions of belowground and aboveground on plant community composition are remained to be studied.

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4.2 Effects of experimental warming and N addition on plant community productivity

Nitrogen is one of the most essential elements for the development of plant species, N limit often determines terrestrial ecosystem net primary productivity (Elser et al., 2007; LeBauer and Treseder, 2008). Several published papers documented that N input increased aboveground productivity, such as in a high plateau near Julier Pass in the central Alps (Bassin et al., 2007), a temperate old field in Canada (Hutchison and Henry, 2010). Our results showed that N addition significantly increased the aboveground net primary productivity, which is consistent with the results of previous studies. Plant species can quickly respond to nutrient availability, especially for N (Hutchings and de Kroon, 1994). When soil available N increased, growth of plants will greatly improve and improve the total aboveground biomass in this area. Furthermore, the effect of N deposition on plant productivity is influenced by soil moisture. Model simulation results suggest that N addition improved ecosystem productivity when soil moisture were high, whereas it has no effects on ecosystem productivity when soil moisture was lower in semiarid ecosystem (Asner et al., 2001). In fact, we observed that the effects of N addition on aboveground biomass in the years of abundant rain were much higher than other years.

Significant decline in aboveground biomass induced by experimental warming was detected in semiarid ecosystem in Songnen meadow steppe except in 2008. Our observations is in accordance with the results of some studies from annual grasslands (Zavaleta et al., 2003), an old field site (Hutchison and Henry, 2010), in Europe wide (Ciais et al., 2005). These results may be partly ascribed to thermal damage by warming in summer (June to August) (Wang et al., 2010). In general, the hydrothermal condition in summer is good for plant growth, but high temperature beyond plant capacity will severely affect the growth of plant species (Wan et al., 2005). No significant effects of warming on the belowground biomass were observed, which was consistent with the previous results (Sebastiá et al., 2004). Despite warming plus N addition treatment

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enhanced the aboveground and belowground productivity, no significant interactions on productivity between N addition and warming were detected (Table 2), similar result from an old field study (Hutchison and Henry, 2010).

5 Conclusions and implications

In Songnen meadow ecosystem, experimental warming and N addition altered plant community composition and productivity. Species richness, evenness and diversity had contrasting responses to experimental warming and N addition, where warming significantly increased species richness and evenness, while N addition highly decreased the species richness and evenness. Long-term and vast N deposition is harmful to plant diversity, therefore, we must consider measures to reduce the influence of N deposition on plant diversity. Although the species richness and diversity in this steppe ecosystem will be altered in the future by climate change as predicted increases N deposition and temperature elevation, the interactions among different species under climate change condition needs long-term studies. Warming suppressed the growth of aboveground biomass, but improved the growth of belowground biomass. N addition highly enhanced both aboveground and belowground productivity. The positive interactions of warming and N addition on productivity were also detected. Our results highlighted that soil moisture and N nutrients play crucial roles in determining plant community productivity in this meadow ecosystem. These observations in the current study further improved our understanding of community composition and productivity response to the simultaneous climate change in temperate meadow ecosystems.

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Table 1. List of species within the experiment quadrats (1 m × 1 m) from 2006 to 2009. C, control; W, warming treatment; N, nitrogen addition treatment; W + N, warming plus N addition treatment.

Species	Life history traits	2006				2007				2008				2009			
		C	W	N	W+N	C	W	N	W+N	C	W	N	W+N	C	W	N	W+N
<i>Leymus chinensis</i>	P	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Thalictrum simplex</i>	A	+				+	+	+		+	+	+		+	+	+	
<i>Setaria viridis</i>	A								+				+				+
<i>Limonium bicolor</i>	P																+
<i>Phragmites australis</i>	P	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Kalimeris integrifolia</i>	P	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Carex durluscula</i>	P	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Artemisia mongolica</i>	P	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Artemisia anethifolia</i>	AB	+				+	+	+	+	+	+	+	+	+	+	+	+
<i>Artemisia scoparia</i>	AB									+	+		+	+	+	+	+
<i>Inula japonica</i>	P					+	+	+	+					+	+	+	+
<i>Potentilla flagellaris</i>	P	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+
<i>Polygonum sibiricum</i>	P		+	+	+					+	+	+	+	+	+	+	+
<i>Pocockia ruthenica</i>	P				+									+	+	+	
<i>Xanthium strumarium</i>	A				+						+	+	+				
<i>Lespedeza davurica</i>	P									+	+	+		+	+	+	+
<i>Cynanchum chinense</i>	P												+				
<i>Saussurea amara</i>	P				+								+	+	+		+
<i>Taraxacum mongolicum</i>	P				+			+	+					+			

A, annual plants; P, perennial plants; AB, annual and biennial.
 +: plants were present in samples.

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Table 2. Results of three-way factorial ANOVA on the effects of year (Y), warming (W), N addition (N), and their interactions on importance value of gramineous (IVG), importance value of forbs (IVF); richness (R); evenness (E); diversity (H), aboveground net primary productivity (ANPP), belowground net primary productivity (BNPP).

Source of variation	IVG	IVF	R	E	H	ANPP	BNPP
Y	**	**	ns	*	**	**	**
W	ns	ns	ns	ns	ns	ns	ns
N	**	*	*	ns	**	**	**
Y × W	ns	ns	*	ns	ns	ns	ns
Y × N	ns	*	ns	ns	ns	**	ns
W × N	*	**	ns	ns	ns	ns	**
Y × W × N	ns	ns	ns	ns	ns	ns	ns

*: $P < 0.05$, **: $P < 0.01$, "ns" indicated differences are not significant.

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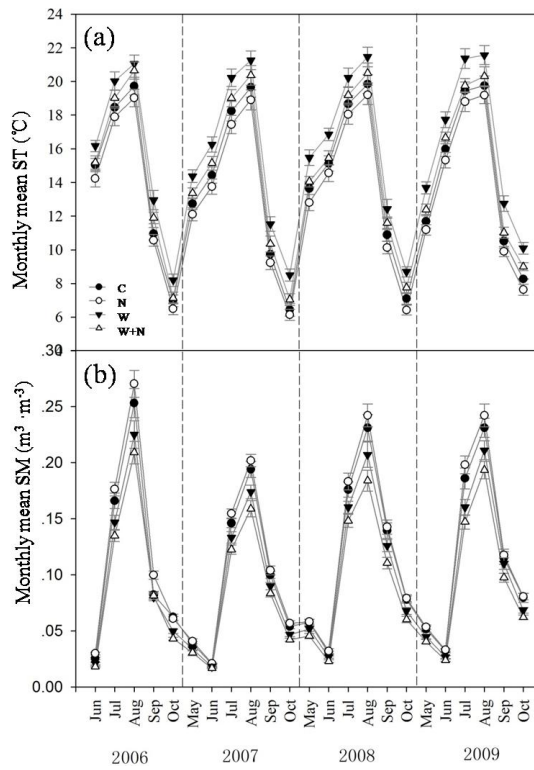


Fig. 1. Effects of warming and N addition treatments on the seasonal and interannual variation in monthly surface layer (0–15 cm) soil mean temperature (a) and soil moisture (b) during the growing season from 2006 to 2009. Data are reported as means \pm SE ($n = 6$).

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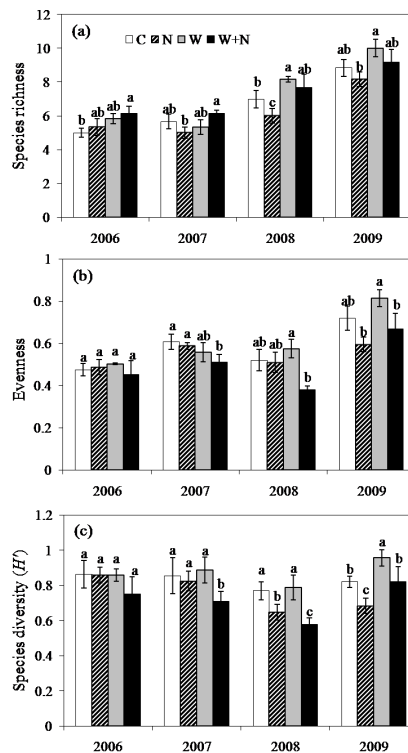


Fig. 2. Effects of warming and N addition on plant species richness (a), evenness (b) and diversity (c) from 2006 to 2009. C, control; N, N addition treatment; W, warming treatment; W + N, warming plus N addition treatment. Different lowercase letters on columns indicate significant difference ($P < 0.05$) among treatments every year. Data are reported as means \pm SE ($n = 6$).

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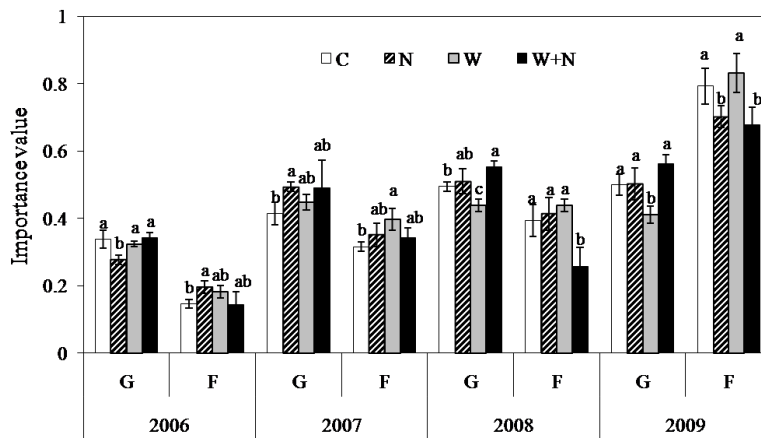


Fig. 3. Effects of experimental warming and N addition on importance values of gramineous (G) and forbs (F). C, control; N, N addition treatment; W, warming treatment, and W + N, warming plus N addition treatment. Different lowercase letters on columns indicate significant difference ($P < 0.05$) among treatments every year. Data are reported as means \pm SE ($n = 6$).

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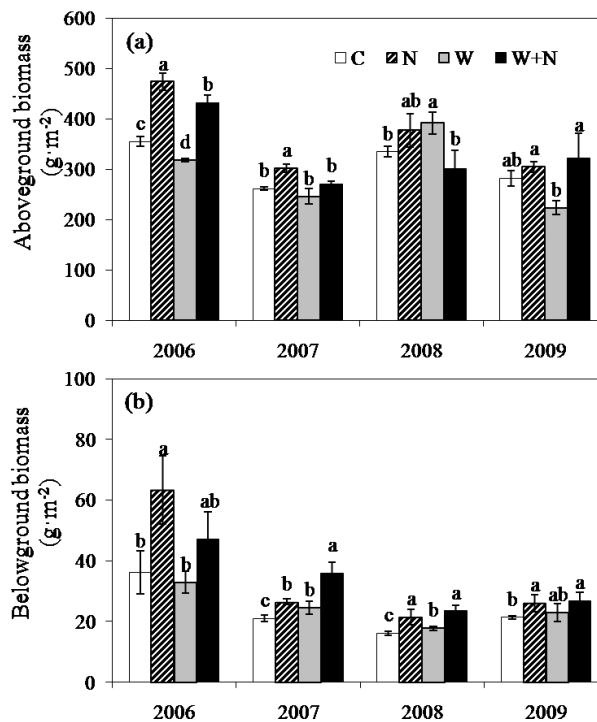


Fig. 4. Effects of warming and nitrogen addition on aboveground biomass (a) and belowground biomass (b) during 2006 to 2009. Different lowercase letters on columns indicate significant difference ($P < 0.05$) among treatments every year. Data are reported as means \pm SE ($n = 6$).

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