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Effects of Changing Precipitation and Warming on Functional Traits of Zonal *Stipa* Plants from Inner Mongolian Grassland

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ABSTRACT

The mechanisms driving changes in dominant plant species are the key for understanding how grassland ecosystems respond to climate change. In this study, we examined plant functional traits (morphological characteristics: plant height, leaf area, and leaf number; biomasses: aboveground, belowground, and total; and growth indices: root-to-shoot ratio, specific leaf area, and leaf mass ratio) of four zonal *Stipa* species (*S. baicalensis, S. bungeana, S. grandis,* and *S. breviflora*) from Inner Mongolian grassland in response to warming (control, +1.5, +2.0, +4.0, and +6.0°C), changing precipitation (–30%, –15%, control, +15%, and +30%), and their combined effects via climate control chambers. The results showed that warming and changing precipitation had significant interactive effects, different from the accumulation of single-factor effects, on functional traits of *Stipa* species. The correlation and sensitivity of different plant functional traits to temperature and precipitation differed. Among the four species, the accumulation and variability of functional traits had greater partial correlation with precipitation than temperature, except for leaf number, leaf area, and specific leaf area, in *S. breviflora, S. bungeana*, and *S. grandis*. For *S. baicalensis*, the accumulation and variability of plant height, aboveground biomass, and root-to-shoot ratio only had significant partial correlation with precipitation. However, the variability of morphological characteristics, biomasses, and some growth indices, was more sensitive to temperature than precipitation in *S. bungeana, S. grandis*, and *S. breviflora*—except for aboveground biomass and plant height. These results reveal that precipitation is the key factor determining the growth and changes in plant functional traits in *Stipa* species, and that temperature mainly influences the quantitative fluctuations of the changes in functional traits.

Key words: precipitation change, warming, functional traits, *Stipa* species, Inner Mongolian grassland

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1. Introduction

Global warming caused by increased concentrations of carbon dioxide and other greenhouse gases is widely believed to be currently occurring. According to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), the average surface temperature over land and sea globally has linearly increased by 0.85°C from approximately 1880 to 2012 (IPCC, 2013). The corresponding effects have enhanced the heterogeneity of precipitation, which has in turn resulted in inevitable effects on plant growth in terrestrial ecosystems (Parmesan and Yohe, 2003; IPCC, 2013; Chang et al., 2015; Zhang et al., 2015). Previous studies have found that climate change has seriously affected the relationship between vegetation and climate. Significant changes in global and local vegetation have occurred as a result (Zhou et al., 2001;

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Pettorelli et al., 2005; Gao et al., 2013), and these changes have significantly reshaped the response patterns of plants to climate factors (Cleland et al., 2013; Xie et al., 2014; Liu et al., 2015; Zhu and Meng, 2015). Vegetation is regarded as a comprehensive indicator of ecological environmental change in terrestrial ecosystems. Therefore, unveiling the mechanisms driving changes in dominant plant species in the context of climate change has become a critical focus for global change studies.

In recent years, many studies have been conducted on the responses of plant function to climate change, including the impacts of climate change on plant traits (Naudts et al., 2013; Sapeta et al., 2013; Flanagan and Farquhar, 2014; Xu G. et al., 2014); the relationship between vegetation composition, geographical patterns, and climatic factors (Wang Dawei et al., 2013; Li and Yang, 2014); and the responses of plant diversity and ecosystem productivity to climate change (Wang Z. et al., 2013; Cowling et al., 2015). These studies have largely been conducted by using growth chambers, open-top chambers, and field observations (Zavalloni et al., 2012; Xu et al., 2013; Xu Z. Z. et al., 2014). Plant functional traits, including morphological characteristics, biomass characteristics, and growth indices, are main performance adapting to the interaction between plants and environment. Furthermore, plant functional traits can objectively express the adaptability and sensitivity of plant function to its external environment (Lundholm et al., 2015; Sakschewski et al., 2015). Although the effects of climate change on plant function have been elucidated in these studies, knowledge on how plant functional traits of dominant species from different ecosystems across a broad region respond to climate change is still lacking.

Owing to differences in regional climate change, dominant plants normally respond differently to climate factors at functional levels in different areas. For example, on the global scale, Wright et al. (2004) synthesized leaf trait data spanning 2548 species at 175 sites, and found that leaf mass per area was actually more strongly and positively correlated with mean annual temperature than with mean annual precipitation. In central New Mexico, Eurasia, and semi-arid tropical Africa, the changes in normalized difference vegetation index (NDVI) tend to be closely related to precipitation (Weiss et al., 2004; Camberlin et al., 2007; Piao et al., 2011); however, NDVI has been found to be more influenced by temperature in North America (Wang et al., 2011), based on direct field observation. Recently, Wertin et al. (2015) studied plant growth in a cool desert on the Colorado Plateau via a long-term climate controlled experiment. Their results showed that photosynthesis and growth of C_3 and C_4 grasses were negatively affected by increased temperature, but were not affected by increased summer precipitation for many plant species.

China is located in the East Asian monsoon region and features complex climate types and abundant vegetation types. Therefore, plants also respond in various ways to climate factors at the functional level in China (Piao et al., 2006; Zhao et al., 2011). For instance, a recent study showed that vegetation growth in summer exhibited a decreasing tendency with increased temperature and decreased precipitation in northeastern China from 1982 to 2009, but this decreasing tendency was more affected by temperature (Mao et al., 2012). Yang et al. (2010) investigated aboveground biomass in China's grasslands, and reported that aboveground biomass in temperate and alpine grasslands significantly increased with mean annual precipitation, but did not show any significant trend with mean annual temperature, based on long-term field observation. Similar patterns were also reported from a 24-yr field study of Inner Mongolian grassland (Bai et al., 2004).

Most of the previous studies mentioned above were conducted on the relationship between plant function and climate factors at the plant community level. It is well-known that different plant species respond differently to climate change. In other words, the responses of different species to environmental changes differ, so the degree of response of dominant species on the species scale might differ from the degree of response of vegetation on the community scale, in view of the compensatory effects occurring among the species (Tilman et al., 1997; Bai et al., 2004). Moreover, numerous studies have also indicated that grasslands in northern China and their dominant plant species have faced degradation in recent years (Yang and Wang, 2013; Zheng et al., 2015). Xu Z. Z. et al. (2014) examined the effects of main climate factors on plant growth in dominant species from temperate grassland via environmentally controlled phytotrons, and their results indicated that species-specific responses could play a vital role in plant adaptation to future climate change. There is an increasing awareness that a better understanding of how dominant species respond to climate change could provide new insights into the adaptation of dominant species to a changing world. As a consequence, only a limited suite of countermeasures are available to manage the adaptation of dominant plant species and regional biodiversity to climate change.

Inner Mongolia is the principal location of temperate grassland in China. The Inner Mongolian grassland occupies approximately 67% of its area and represent more than 20% of the total national grassland area. This region has more xeric and harsh natural conditions than any other region in China, so it has already been documented as a more sensitive and fragile region in response to climate change (Qian et al., 2007; Sui et al., 2013), and predicted to experience some of the strongest and earliest effects of climate change (IPCC, 2013). *Stipa* species are the dominant constituent of grassland communities in Inner Mongolia and zonally present an alternating ecological distribution along a changing precipitation gradient from east to west (Lu and Wu, 1996; Wan et al., 1997). This distribution is a reflection of plant-environment interactions that implicate the various adaptabilities of *Stipa* species to environmental changes on a long evolutionary timescale. Four typical *Stipa* species in different areas of Inner Mongolia were studied in the present reported work. Among these species, *S. baicalensis*, a perennial bunchgrass, is a dominant species in meadow steppe (semi-arid area and sub-humid area), and is distributed in eastern Inner Mongolia. *S. bungeana*, a constructive species, is distributed widely in warm-temperate typical steppe (semi-arid area). *S. grandis* and *S. breviflora* are dominant species in typical steppe (semi-arid area) and desert steppe (arid and semi-arid area), respectively (Lu and Wu, 1996; Wan et al., 1997).

As the structure and function of grassland ecosystems are more susceptible to the response of dominant plants to climate change (Hooper et al., 2005), the primary goal of this study is to examine the responses of four dominant *Stipa* species (*S. baicalensis, S. bungeana, S. grandis,* and *S. breviflora*) in the Inner Mongolian grassland to warming and changing precipitation by using climate control chambers. Specifically, the objectives of this work are to: (1) quantify the different influences of changes in temperature and precipitation on plant functional traits (morphological characteristics, biomass, and growth indices) of the four *Stipa* species; (2) investigate the species-specific responses of functional traits to changes in temperature and precipitation; and (3) explore the mechanisms driving the changes of functional traits of *Stipa* species in response to altered temperature and precipitation regimes.

2. Materials and methods

2.1 Plant culture

The experiment was conducted by using the seedlings of *Stipa* plants to investigate their plant functional traits in response to anticipated climate change during 2011–2012. Seeds of the *Stipa* plants were collected from local steppe habitats the year prior to the experiment from local steppes in Inner Mongolia, China. Seeds of *S. baicalensis*, *S. grandis*, *S. breviflora*, and *S. bungeana* were collected from a natural meadow steppe in Hulun Buir (49°13′N, 119°45′E), a typical steppe in Xilinhot (43°38′N, 116°42′E), a desert steppe in Siziwang Banner (41°43′N, 111°52′E), and a sandy grassland in Ordos (39°50′N, 109°59′E), respectively (Fig. 1). Each *Stipa* plant was the dominant species of each site. Seeds from each species were sterilized in a 5% potassium permanganate solution for 8 min, and then rinsed before sowing. Sowing was performed in plastic pots (10.9 cm in diameter, 9.5 cm in height, and 0.71 L in volume) with plastic film on the bottom as a seepage control measure. Each plastic pot was filled with 0.58 kg of air-dried soil that was retrieved from the local surface soil (0–30 cm) for the four corresponding plants. After the sowing on 23 February 2011, all pots were initially placed in a naturally illuminated glasshouse (day/night temperature of 26–28°C/18–20°C, maximum photosynthetic photon flux density of 1000 mol m^{-2} s^{-1}) until the third leaf emergence (3 weeks after sowing), and then transferred into the climate control chambers (RXZ-500D, Southeast Instruments Inc., Ningbo, China). In the chambers, all plants were subjected to 3-month warming and changing precipitation treatments, which simulated the temperature and precipitation from June to August during the growing season of the four *Stipa* species. Precipitation was added to the pot at the surface of the soil with a sprayer at approximately 1700 BT every 3 days, following our similar previous experiments (Xu and Zhou, 2006; Xu Z. Z. et al., 2014). The four *Stipa* species were each sown and cultured for one month, followed by the climate control chamber experiment for three months, meaning that the experiment ended on 20 March 2012.

2.2 Experimental design

The experiment was conducted by using climate control chambers at the campus of the Institute of Botany, Chinese Academy Sciences, Beijing, China. The 30-yr (1978–2007) monthly average temperature and precipitation of the growing season (June, July, and August) for the four *Stipa* plants were used as baselines (Fig. 2). Based on future climate change scenarios, the experiment was designed to encompass variants of two factors: five temperature patterns, including T0 (normal temperature, local monthly average temperature), T1.5 (increase by 1.5°C), T2.0 (increase by 2°C), T4.0 (increase by 4°C), and T6.0 (increase by 6°C); and five precipitation patterns, including W0 (normal precipitation, local monthly average precipitation), W–30 (–30% relative to local average precipitation), W–15 (–15% relative to local average precipitation), W+15 (15% relative to local average precipitation), and W+30 (+30% relative to local average precipitation). For each species, five climate control chambers were used for the five warming treatments, and with the separate precipitation treatments within each chamber as a split plot. There were six replicates per treatment (pot/treatment) for each species. The pots were randomly placed into each chamber, and moved again randomly within each layer (exchanging pot positions from center to edge, and vice versa) every 3 days and between two layers every week to minimize any difference between the growth chambers, except for the desired warming and water regimes (Qaderi et al., 2012; Xu Z. Z. et al., 2014).

2.3 Plant harvest

At the end of the experimental treatments for each species, plant height and leaf numbers of each plant were recorded prior to harvest. Plant height per plant was measured with a ruler, and leaf numbers were counted with respect to all leaves per plant. Harvested plants were further separated into stems, roots, and leaves. Leaf area per plant was measured with a WinFOLIA system for root/leaf analysis (WinRhizo, Régent Instruments, Quebec, Canada). Separated items were then oven-dried to a constant weight to obtain the biomass at 80°C, and then the biomasses of the separated items were measured with an analytical balance. The aboveground biomass was summed from the biomasses of stems and leaves, and added to the root biomass to obtain the total biomass. Based on the reports of Poorter (1999), plant growth indices were calculated as follows: specific leaf area (SLA; m^2 kg^{-1})

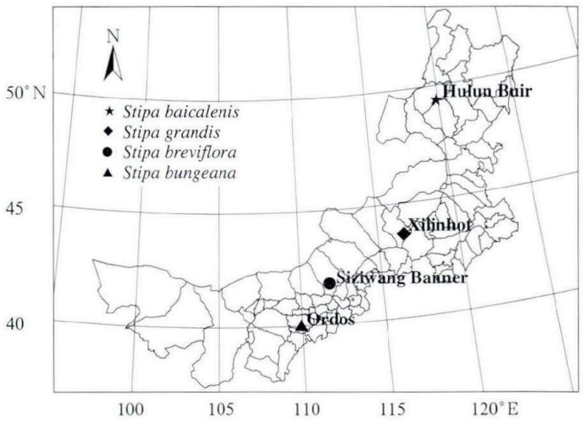

Fig. 1. Geographical distribution of seed collection for the four *Stipa* plants in Inner Mongolia.

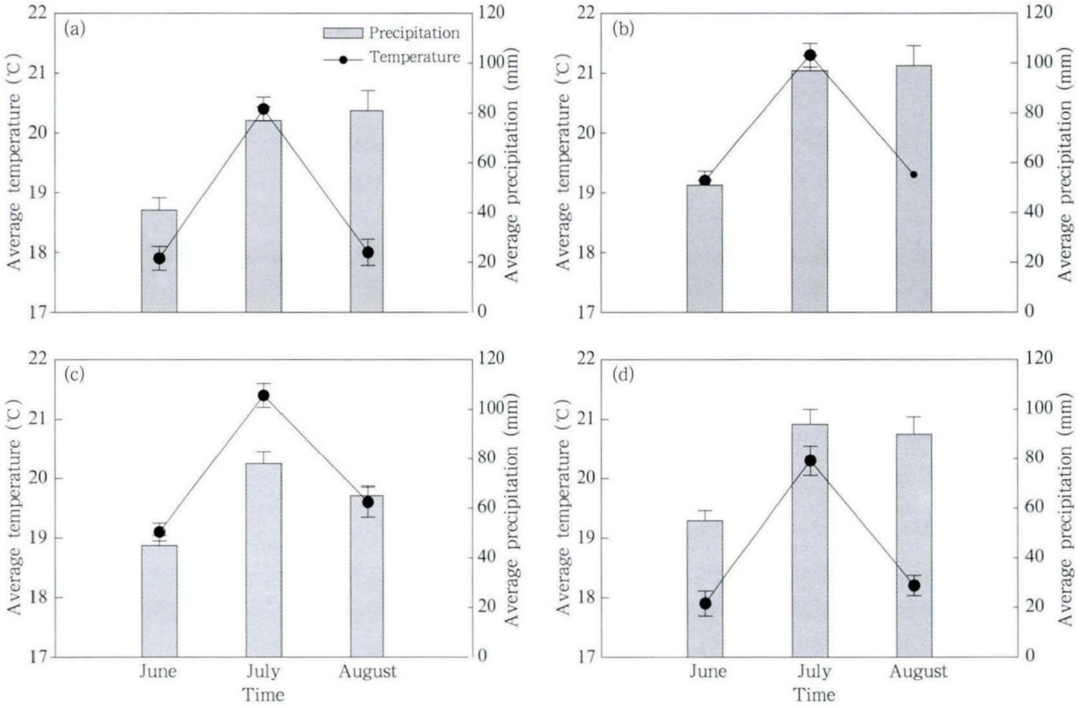

Fig. 2. The average temperature and precipitation of the growing season (June, July, and August) during 1978–2007 (30 yr) in the seed collecting regions of the four *Stipa* plants. Vertical bars represent mean ± SE ($n = 30$): (a) Siziwang Banner (*S. breviflora*), (b) Ordos (*S. bungeana*), (c) Xilinhot (*S. grandis*), and (d) Hulun Buir (*S. baicalensis*).

= leaf area/leaf mass; leaf mass ratio (LAR; $\mathrm{m^2\ kg^{-1}}$) = leaf area/plant total biomass; and root-to-shoot ratio (R/S) = root biomass/aboveground biomass. The soil relative water content (SRWC) was the ratio between the present soil moisture and the field capacity. The present soil moisture was measured by the difference between the dry soil and empty pot weight before the sowing in each pot, and the soil and empty pot weight at the end of the experimental treatments, with an analytical balance.

2.4 Data analysis

The values of plant morphological characteristics, biomass allocation, and growth index changes were subjected to an analysis of variance (ANOVA) with a general linear model–full factorial mode to test the main effects of warming, precipitation change, and their interaction.

Partial correlation analysis can be used to analyze only the degree of correlation between two other variables, eliminating the influence of the third variable in cases when the two variables are associated with the third variable at the same time. In this study, partial correlation analysis was selected to compare the partial correlation between functional traits and temperature and precipitation, and indicates the key factors of which influence regarding functional traits in the four *Stipa* plants. We selected the average temperature and precipitation data from June to August in the seed collection zones corresponding to the five levels of temperature and precipitation treatment in the four *Stipa* species as independent variables, and the data of every functional trait at the five levels of temperature and precipitation treatment as dependent variables. Then, we computed the partial correlation coefficient of every functional trait in the four plants with temperature as follows:

$$r_{xy\cdot z} = \frac{r_{xy} - r_{xz}r_{yz}}{\sqrt{(1 - r_{xz}^2)(1 - r_{yz}^2)}}, \quad (1)$$

$$r_{xy} = \frac{\sum_{i=1}^{n}(x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^{n}(x_i - \bar{x})^2 \sum_{i=1}^{n}(y_i - \bar{y})^2}}, \quad (2)$$

$$t = \frac{r_{xy}}{\sqrt{\frac{1-r_{xy}^2}{n-2}}}, \tag{3}$$

where x is the value of each functional trait; i represents the different treatments of temperature and precipitation; y is the temperature; z is the precipitation; $r_{xy\cdot z}$ is the partial correlation coefficient between the plant functional trait and temperature when precipitation is fixed; r_{xy}, r_{yz}, and r_{xz} are the correlation coefficients between the plant functional trait and temperature, between temperature and precipitation, and between the plant functional trait and precipitation, respectively, with values ranging from −1 to 1; $\bar{x}$ is the average value of each functional trait under all of the hydrothermal treatments; $\bar{y}$ is the average temperature in all temperature treatments; and t_a is the critical value at different significant levels, and can be calculated by using the t distribution table, where a significant correlation is indicated if $t > t_\mathrm{a}$, and a non-significant correlation is found if $t < t_\mathrm{a}$.

The partial correlation coefficients between plant functional traits and precipitation, between the variability of plant functional traits and temperature, and between the variability of plant functional traits and precipitation, are calculated similarly to above. Additionally, the variability of plant functional traits under different temperature and precipitation treatments compared to the control treatment are calculated as follows:

$$\Delta x_i = (x_i - x_\mathrm{ck})/x_\mathrm{ck}, \tag{4}$$

where Δx_i is the variability of the plant functional trait under the different treatments of temperature and precipitation i; x_i is the value of the functional trait; and x_ck is the value of the functional trait under the control treatment (T0W0).

The sensitivities of the *Stipa* plants to warming and precipitation changes were calculated by fitting a linear regression, and expressed by the regression coefficient a as follows:

$$Y = aX + b, \tag{5}$$

where Y is the value of the functional trait, X is either temperature or precipitation, a is the regression coefficient, and b is a constant.

3. Results

3.1 Effect of temperature and precipitation changes on SRWC

Under the same temperature treatment, the changes in SRWC were associated with precipitation gradients in the four *Stipa* plants (Fig. 3). Under every temperature treatment, increased precipitation treatments (W+15 and W+30) were conducive to increasing SRWC, but decreased precipitation reduced SRWC. Likewise, the SRWC of the four species decreased with increased temperature under the same precipitation treatment (Fig. 3).

3.2 Effect of hydrothermal change on plant functional traits

Based on the two-way ANOVA, warming or changing precipitation alone significantly affected the morphological characteristics and biomass ($p < 0.05$), but did not significantly affect all of the growth indices, in the four *Stipa* species (Table 1). For *S. breviflora*, there were no significant ($p > 0.05$) interactive effects of temperature and precipitation on aboveground biomass, leaf number, and LAR. For *S. grandis* and *S. bungeana*, the interactive treatments of temperature and precipitation produced significant effects on all of the functional traits except leaf number and plant height. For *S. baicalensis*, the interactive effects of temperature and precipitation were only found in belowground biomass, total biomass, R/S, and LAR (Table 1).

3.3 Relationships of plant functional traits to hydrothermal factors

For *S. breviflora*, the partial correlations of morphological and biomass characteristics and precipitation were greater than temperature, except for leaf area ($p < 0.05$). LAR and R/S were only significantly correlated with precipitation, but SLA was significantly partially correlated with both temperature and precipitation (Table 2).

For *S. bungeana* and *S. grandis*, all functional tra-

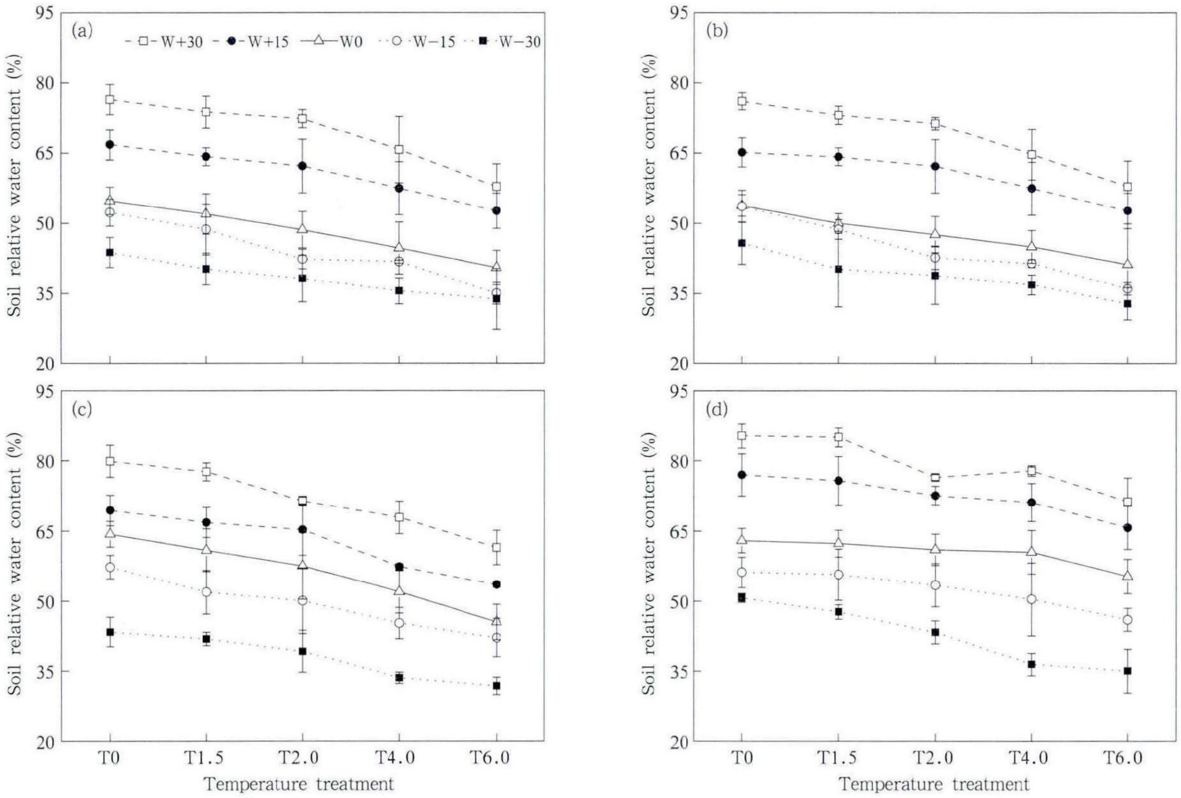

Fig. 3. Changes in the SRWC of the four *Stipa* plants under different temperature and precipitation treatments. Vertical bars represent the mean ± SE ($n = 6$): (a) *S. breviflora*, (b) *S. bungeana*, (c) *S. grandis*, and (d) *S. baicalensis*.

Table 1. ANOVA for plant functional traits of the four *Stipa* plants under different temperature and precipitation treatments

Stipa species		Morphological characteristics			Biomass			Growth index		
		PH	LN	LA	AB	BB	TB	R/S	SLA	LAR
	T	10.03**	6.54**	7.31**	8.25**	9.86**	9.73**	11.39**	4.30**	0.51
S. breviflora	P	18.12**	9.52**	3.75**	20.29**	10.65**	18.91**	1.84	5.45**	4.39**
	$T \times P$	2.43**	1.35	4.45**	1.29	3.15**	3.20**	3.02**	2.57**	1.31
	T	5.93**	20.34**	18.68**	4.41**	17.40**	14.05**	13.48**	2.41	3.38*
S. bungeana	P	14.74**	17.51**	30.89**	46.50**	11.51**	32.02**	5.36**	9.25**	3.63*
	$T \times P$	1.25	1.54	7.15**	4.67**	8.29**	9.69**	4.36**	3.04**	4.91**
	T	8.73**	3.08*	28.96**	40.78**	29.83**	54.42**	1.77	2.55*	3.87**
S. grandis	P	4.54**	9.21**	11.20**	21.00**	36.43**	51.35**	4.29**	0.74	3.56*
	$T \times P$	4.27**	2.02**	4.18**	7.18**	4.03**	6.32**	2.82**	2.73**	3.47**
	T	4.19**	4.15**	1.38	1.46	2.73*	3.75**	1.09	4.63**	6.17**
S. baicalensis	P	2.45*	0.72	3.57**	10.64**	11.22**	16.25**	4.46**	1.44	6.52**
	$T \times P$	1.57	1.21	1.20	1.66	6.73**	8.27**	3.23**	1.47	6.22**

Notes: T, temperature; P, precipitation; PH, plant height; LN, leaf number; LA, leaf area; AB, aboveground biomass; BB, belowground biomass; TB, total biomass; R/S, root-to-shoot ratio; SLA, specific leaf area; LAR, leaf mass ratio. * Significance value: $p < 0.05$; ** significance value: $p < 0.01$.

its had greater partial correlations with precipitation than temperature, except for leaf number and SLA ($p < 0.05$; Table 2).

For *S. baicalensis*, plant height, leaf area, aboveground biomass, and R/S were significantly partially correlated with precipitation, rather than temperature, but the other functional traits did not have significant partial correlations with temperature or precipitation ($p > 0.05$; Table 2).

3.4 Sensitivity of plant functional traits to hydrothermal changes

For the accumulation and variability of morphological characteristics, *S. breviflora*, *S. bungeana*, and *S. grandis* were more sensitive to temperature than precipitation, except for leaf number, based on linear regression analysis ($p < 0.05$; Tables 3 and 4). However, only plant height demonstrated significant linear regression with precipitation rather than temperature in *S. baicalensis* (Tables 3 and 4).

As for the accumulation and variability of biomass, *Stipa* plants showed larger sensitivity to temperature than precipitation, except *S. baicalensis.* In addition, based on the sensitivity of total biomass to temperature and precipitation, the sensitivity of the four *Stipa* species was *S. breviflora* > *S. grandis* > *S. bungeana* > *S. baicalensis* (Tables 3 and 4).

For growth indices, only SLA, R/S, and LAR, in

Table 2. Partial correlation analyses for the accumulation of plant functional traits with temperature and precipitation in the four *Stipa* plants

Stipa species		Morphological characteristics				Biomass		Growth index		
		PH	LN	LA	AB	BB	TB	R/S	SLA	LAR
S. breviflora	T	0.210*	0.015	0.258**	0.335**	0.237*	0.306**	0.006	–0.244*	0.031
	P	0.520**	0.411**	0.213*	0.668**	0.375**	0.525**	–0.090*	–0.331**	–0.315**
S. bungeana	T	0.365**	–0.557**	0.263**	0.022	0.316**	0.294*	0.257*	–0.106	–0.093
	P	0.463**	0.523**	0.366**	0.751**	0.346**	0.563**	–0.291*	–0.412**	–0.077
S. grandis	T	–0.081**	–0.262**	–0.319**	–0.576**	–0.555**	–0.616**	0.125	0.194	0.316**
	P	0.154**	0.347**	0.347**	0.693**	0.687**	0.685**	0.262*	–0.110	–0.324**
S. baicalensis	T	–0.159	0.069	0.064	–0.013	–0.056	–0.055	–0.055	–0.127	–0.063
	P	0.194**	0.022	0.182*	0.333**	–0.117	–0.044	–0.247*	–0.182	0.194

Note: Abbreviations and symbols as in Table 1.

Table 3. Linear regression analyses for the accumulation of plant functional traits with temperature and precipitation in the four *Stipa* plants

Stipa species		Morphological characteristics				Biomass		Growth index		
		PH	LN	LA	AB	BB	TB	R/S	SLA	LAR
S. breviflora	T	0.442**	0.032	0.369**	0.003**	0.009**	0.013**	0.002	–3.872*	0.108
	P	0.039**	0.034**	0.010*	0.000**	0.001**	0.001**	–0.001	–0.215*	–0.047**
S. bungeana	T	0.317**	–3.518**	0.429**	0.000	0.011**	0.011**	0.075*	–1.754	–0.426
	P	0.017**	0.128**	0.023**	0.001**	0.000**	0.001**	–0.003*	–0.297**	–0.014
S. grandis	T	–0.154	–0.447**	–0.195**	–0.004**	–0.008**	–0.012**	0.035	3.069	1.082**
	P	0.018	0.032**	0.010**	0.000**	0.001**	0.001**	0.004*	–0.090	–0.055**
S. baicalensis	T	–0.173	0.212	0.031	–0.002	–0.001	–0.002	–0.018	–1.023	–0.221
	P	0.010*	–0.003	0.004*	8.44E–5**	0.000	0.000	–0.004*	–0.067	0.032

Note: Abbreviations and symbols as in Table 1.

Table 4. Linear regression analyses for the variability of functional traits with temperature and precipitation in the four *Stipa* plants

Stipa species		Morphological characteristics				Biomass		Growth index		
		ΔPH	ΔLN	ΔLA	ΔAB	ΔBB	ΔTB	$\Delta R/S$	ΔSLA	ΔLAR
S. breviflora	T	0.012**	0.004	0.035**	0.029**	0.036*	0.034*	0.001	–0.029*	0.004
	P	0.002**	0.001**	0.001*	0.003**	0.002**	0.003**	0.000	–0.002**	–0.002**
S. bungeana	T	0.646**	–0.042*	0.037**	0.002	0.098**	0.044**	0.092*	–0.009	–0.009
	P	0.035**	0.001**	0.002**	0.004**	0.004**	0.004**	–0.004*	–0.002**	0.000
S. grandis	T	–0.008	–0.019	–0.037**	–0.075**	–0.067**	–0.071**	0.016	0.026	0.038**
	P	0.001	0.002**	0.002**	0.003**	0.005*	0.004**	0.002*	0.000	–0.002**
S. baicalensis	T	–0.011	0.007	0.006	0.000	–0.010	–0.008	–0.010	–0.008	–0.007
	P	0.001*	0.000	0.001	0.001**	–0.001	0.000	–0.002*	0.000	0.001

Notes: Δ, variability compared to control treatment; abbreviations and symbols as in Table 1.

S. breviflora, S. bungeana, and *S. grandis*, respectively, demonstrated significant sensitivity to both temperature and precipitation, and their sensitivities to temperature were stronger than to precipitation ($p < 0.05$; Tables 3 and 4).

4. Discussion

4.1 Effect of hydrothermal change on plant functional traits

Changes in temperature and precipitation interactively affect plant growth (Albert et al., 2011; Naudts et al., 2013; Springate and Kover, 2014), but result in different effects on various plant functional traits (Poorter and Navas, 2003). Qaderi et al. (2012) reported that changes in water regimes—through a short-term simulation experiment—significantly affected the morphological characteristics, biomass allocation, and growth index of *Brassica napus*, but the effects of temperature on most functional traits were not observed. Naudts et al. (2013) examined two grassland species, i.e., *Lolium perenne* and *Plantago lanceolata*, in sunlit climate controlled chambers, and found that drought significantly inhibited their biomasses but not their R/S ratios; and warming did not significantly affect their growth indicators. Moreover, through long-term direct field observations, Mowll et al. (2015) concluded that the variation in growing season temperature was negatively related to total aboveground net primary production in western U.S. grasslands, but precipitation was a stronger predictor than temperature. Analogous response patterns were also reported from a 24-yr field study in the Inner Mongolian grassland (Bai et al., 2004). In the present study, the responses of plant functional traits to hydrothermal changes were different among the four zonally distinct *Stipa* species from the Inner Mongolian grassland (Table 1). The morphological characteristics and biomass were significantly affected by changing temperature or precipitation in *S. grandis, S. breviflora*, and *S. bungeana*. However, growth indices in the four *Stipa* plants were not all significantly affected by the precipitation changes (Table 1). This supports another recent experimental result and reflects the fact that the impacts of temperature and water on plant functional traits are strongly species-dependent (Xu Z. Z. et al., 2014). It is possible that these different responses of plant functional traits to temperature and precipitation are caused by plants' fundamental growth characteristics and specific ecological niche (Donovan et al., 2011; Xu et al., 2013).

We further found that the precipitation change alone significantly affected the R/S for *S. grandis*, and, while temperature alone showed a non-significant effect, their interactive effect was significant ($p < 0.05$; Table 1). A number of experimental studies have also shown similar results; for example, changes in temperature and water alone imposed significant effects on the R/S of *Abies fabri*, but an interactive effect of the two factors was not apparent (Yang et al., 2013). Additionally, the interactive effects of water and temperature on plant biomass were found to be significant in *Cleistogenes squarrosa*, but only the effect of water alone was significant (Xu Z. Z. et al., 2014). These results indicate that the interactive effects of environmental factors are dramatically different from the accumulative effects of single factors (Morison and Lawlor, 1999; Williams et al., 2007). Moreover, the effects of temperature on plant functional traits can be altered by precipitation changes, and vice versa (Xu and Zhou, 2006; Barnabás et al., 2008).

4.2 Hydrothermal driving mechanism in plant functional traits

Generally, grassland is mainly controlled by hydrothermal factors. An increase in temperature and precipitation could increase the availability of soil nutrients and moisture, thus accelerating the growth of grassland vegetation (Tilman et al., 1997; Xia and Wan, 2012). Wang et al. (2003) conducted a 9-yr field study and reported that the growth of terrestrial vegetation was more significantly affected by precipitation than temperature in the central Great Plains of the U.S. Our results also showed that the accumulation and variability of plant biomass were more closely related with precipitation than temperature in the four *Stipa* species (Table 2). These results are consistent with numerous previous studies in which the biomass of grassland species is mainly affected by precipitation in Inner Mongolia, because this region is located in arid and semi-arid zones and is more susceptible to precipitation (Bai et al., 2004; Xia and Wan, 2012; Xu et al., 2013).

However, owing to regional differences in hydrothermal factors, the degree of response of species-specific traits to hydrothermal factors is different in various grassland types (Yang et al., 2010; Zhao et al., 2011; Liu et al., 2015). For instance, in the desert steppe of North China, simulated warming resulted in an increase in C_4 grasses, while increased precipitation caused a decrease in the proportions of non-perennial C_3 plants and an increase in perennial C_4 plants (Hou et al., 2013). In the present study, precipitation was partially correlated with aboveground growth, but not significantly correlated with belowground growth, in *S. baicalensis* from meadow steppe (Table 2). The reason for this might be that the water supply is abundant in meadow steppe, and root growth is not restricted by water for *S. baicalensis*; but warming could promote plant leaf physiological and biochemical reactions, and then accelerate plants' aboveground growth (Bret-Harte et al., 2001). Moreover, the variability in leaf numbers was more sensitive to temperature than precipitation in *S. baicalensis* (Table 4), revealing that the seedlings mainly alter leaf numbers to ensure aboveground growth under hydrothermal changes. *S. bungeana* is a constructive species from warm-temperate typical steppe (Fig. 1) where precipitation is relatively scarce and the climate is warm, and it has a higher demand on the cooperative effects of hydrothermal factors (Lu and Wu, 1996). Therefore, the growth of *S. bungeana* was found to be most strongly correlated with precipitation, and most sensitive to temperature, among the four zonally distinct *Stipa* species (Tables 2 and 3). In short, the relative significance of hydrothermal changes was not identical to one another, compared to the climatic conditions in the habitats of the four *Stipa* species. Therefore, the response sensitivities of the four *Stipa* species to temperature and precipitation varied (Tables 3 and 4).

The distribution patterns of vegetation types and their changes along the Northeast China Transect and North–South Transect of eastern China were simulated under climate change by Zhang and Zhou (2008). Their results indicated that the major factors driving the changes in vegetation distribution patterns were water and heat, at the plant functional type level (Zhang et al., 2011; Xu G. et al., 2014). However, the responses of various vegetation types to water and heat factors were obviously different, in which water was the key factor determining the distribution of vegetation types but the vegetation changes were more sensitive to heat than water. In this study, we verified the findings of Zhang and Zhou (2008) through the results of a simulation experiment at the species level. In our study, the four *Stipa* plants presented an alternating ecological distribution along the changing precipitation gradient in the Inner Mongolian grassland (Wan et al., 1997). The results showed that biomasses, most of the morphological characteristics, and the growth indices were more partially correlated with precipitation than temperature, but their variabilities were more sensitive to temperature than precipitation, except for *S. baicalensis* (Tables 2 and 4). This reveals that precipitation is the key factor driving the type and growth of *Stipa* species, but temperature can only cause fluctuations in their functional traits.

Species diversity—representing the space of evolution and ecological adaptability to specific environments—is a main product of the evolution mechanism and a reflection of diversity for biological organisms (Giorgini et al., 2015; Pedro et al., 2015). As a consequence, the species level is considered the most direct, easily observable and suitable scale for studying biodiversity. Owing to the different responses of plant species to environmental changes, a certain level of biodiversity is determined by a variety of regional environments (Shen and Ma, 2014). In this study, we found that the four *Stipa* plants might be distributed in different steppe types because of their different plant functional trait responses and sensitivities to temperature and precipitation. Xu Z. Z. et al. (2014) stated that hydrothermal changes can alter species productivities and types in an ecosystem, and then further alter the biodiversity. Our present research explicitly examined whether the influences of temperature and precipitation were consistent. The results indicated that precipitation can result in essential changes in *Stipa* species, because the accumulation and variability in plant functional traits were more closely correlated with precipitation. Precipitation might then further alter interspecific relationships within the community and biodiversity. Increased temperature would increase *Stipa* plants' demand for water, but would only influence fluctuations in the changes in functional traits; it may not alter the biodiversity of *Stipa* species communities.

5. Conclusion

We conclude that most of the functional traits in the four *Stipa* plants studied here are significantly affected by changing temperature and precipitation. Conversely, the effects of temperature, precipitation and their interactions with specific functional traits differ. The changes in functional traits of *Stipa* species are driven by temperature and precipitation. However, the key factor determining the accumulation and variability of their functional traits is precipitation; temperature can only result in fluctuations in the changes of these traits. Based on the various responses and sensitivities of the dominant species to hydrothermal factors uncovered in this study, our results indicate that future climate change will most likely affect the structure and function of the Inner Mongolian grassland by altering the distribution and growth of these dominant species, through their greater reliance on precipitation change.

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