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Grassland species respond differently to altered precipitation amount and pattern

Bin Zhang[a,b,1], Jianjun Zhu[a,1], Qingmin Pan[a,*], Yanshu Liu[c], Shiping Chen[a], Dima Chen[a], Yue Yan[a], Shande Dou[a], Xingguo Han[a]

[a] State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, China
[b] College of Ecology and Environmental Science, Inner Mongolia Agricultural University, Huhhot 010018, China
[c] Institute of Desertification Studies, Chinese Academy of Forestry, Beijing 100091, China

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ABSTRACT

An increase in precipitation amount with prolonged inter-rainfall intervals is predicted to occur in the Inner Mongolia grassland in the future. However, how the native species respond to such alterations remains poorly understood. We collected the seeds of eight species from a natural community and raised their seedlings by pot culture. The responses of these species to manipulated precipitation amount and inter-rainfall intervals were examined by rainout shelters. The biomass production in seven out of eight species was enhanced by increased precipitation amount. However, the impacts of prolonged inter-rainfall interval differed substantially among species, with one being promoted, two suppressed and five not affected. For most species, biomass allocations among vegetative organs were neither affect by precipitation amount nor by inter-rainfall intervals. In contrast, the impacts on species' reproductive allocation were highly species-dependent. Soil moisture, soil temperature and soil inorganic nitrogen played important roles in affecting species' biomass production but the pathways, directions (positive or negative) and magnitudes were species-dependent. Given that these eight species jointly represent about 80% of community biomass production, the impact of altered precipitation pattern on grassland ecosystems may be more difficult to predict than that of altered amount.

1. Introduction

Human-induced global warming has greatly changed the global hydrological cycles, resulting in alterations in both the amounts and patterns of precipitation (Easterling et al., 2000; Groisman et al., 2005). In the Inner Mongolia grassland for example, the annual precipitation amount is predicted to increase in the future as global warming causes a northwestward migration of the eastern Asia monsoon rain belt (Yang et al., 2015). At the same time, the frequency of heavy precipitation events with longer inter-rainfall intervals (prolonged drought period) is predicted to increase in this area (IPCC, 2013). These changes may have profound impacts on the growth, biomass allocation and reproduction of these grassland species, as water is a primary limiting factor for biomass production in arid and semiarid ecosystems (Easterling et al., 2000; Weltzin et al., 2003; Reynolds et al., 2004; Schwinning et al., 2004).

Previous studies have shown that alterations in precipitation amount and pattern may greatly affect the structure and functioning of natural ecosystems (Fang et al., 2005; Heisler-White et al., 2008; Knapp et al., 2002; Yang et al., 2011; Robertson et al., 2009; Wilcox et al., 2015). However, the direction (positive or negative) and magnitude of these impacts were highly context-dependent and the underlying mechanisms remain poorly understood. In fact, the community level change is an integrative outcome of all changes at the species level, therefore examining species-level responses to altered precipitation regimes can help us better understand and predict the community-level changes (Gutschick and BassiriRad, 2003; Nippert et al., 2009; Robertson et al., 2009). For example, Robertson et al. (2009) have found that three Chihuahuan species respond to precipitation timing and magnitude in different ways, resulting in different community-level changes between wet years and dry years. By contrast, the

* Corresponding author.
E-mail addresses: zhangbin_158@163.com (B. Zhang), zhujianjun@ibcas.ac.cn (J. Zhu), pqm@ibcas.ac.cn (Q. Pan), liuyanshu@caf.ac.cn (Y. Liu), spchen@ibcas.ac.cn (S. Chen), chendima@ibcas.ac.cn (D. Chen), yanyue@ibcas.ac.cn (Y. Yan), doushande@ibcas.ac.cn (S. Dou), xghan@ibcas.ac.cn (X. Han).
[1] These authors contributed equally to this work.

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Inner Mongolian grassland ecosystem can maintain strong stability of community primary productivity for 24 years mainly due to the compensatory responses of species to precipitation variations (Bai et al., 2004), implying that the co-occurring species respond differently to precipitation variations. However, our knowledge about how species from the same community differ in their responses to changes in precipitation amount and pattern remains poorly understood.

Biomass allocation in plants plays a central role in response to unpredictable environmental changes (Bazzaz and Grace, 1997). According to optimal partitioning theory, plants allocate biomass to the organs that acquire the most limiting resource (Mccarthy and Enquist, 2007). In consistence with this theory, it has been demonstrated that under water deficient scenarios plants can increase biomass allocation to roots to maximize acquisition of water and nutrients from soils (Mokany et al., 2006) or reduce biomass allocation to shoots to minimize water loss (Wang and Gao, 2003). Moreover, species adapted to desert and Mediterranean environments may display different plasticity in reproductive allocations under conditions of water stress (Aronson et al., 1993). These results highlight the role of allocation strategy in plant performance under conditions of varying water supply. However, to what extent plant species in the Inner Mongolian grassland may adjust their allocation patterns to adapt the alterations in amount and inter-rainfall interval of precipitation remains largely unknown.

Alterations in precipitation amount and pattern not only alter the availability of soil moisture but also modify other edaphic factors such as soil temperature and soil nitrogen availability. Different species may differ in their response to these feedbacks. For example, in the Chihuahuan desert ecosystem, the above-ground net primary productivity (ANPP) of *Dasylirion leiophyllum* was primarily affected by N availability in wet years and by water availability in dry years (Robertson et al., 2009). This is explained by the fact that *Dasylirion* is a shrub with both deep and shallow roots making its ANPP more dependent on overall levels of resource availability (Fay 2009). In contrast, the ANPP for *Opuntia phaeacantha* was primarily regulated by precipitation seasonality and pattern rather than by soil variables (Robertson et al., 2009), because *Opuntia* is a succulent with shallow root system. Thus its growth was sensitive to precipitation seasonality and pattern (Fay, 2009).

To examine the responses of grassland species to altered precipitation amount and pattern, we collected the seeds of eight species from a mature natural community and raised their seedlings by pot culture. These species covered a spectrum of dominant, subdominant and minor species and represent the major plant life forms in this community. After two years, the seedlings of each species were subjected to manipulated precipitation amount and inter-rainfall interval during growing season in rainout shelters. We address the following three specific questions: 1) how do changes in precipitation amount and inter-rainfall interval affect the biomass production of these species? 2) How do changes of precipitation amount and inter-rainfall interval affect species' biomass allocation patterns between above- and belowground parts, between leaves and stems, and between vegetative and reproductive organs? 3) What are the relative roles of soil moisture, soil temperature and soil inorganic nitrogen in affecting the biomass production of eight species?

We hypothesize that these co-occurring species may differ substantially in biomass production in monoculture under altered precipitation amounts and patterns but such a change may not affect their biomass allocation patterns as species' allocation strategy is shaped by long-term evolutionary processes and relatively stable. The effects of altered precipitation amounts and patterns on soil moisture, soil temperature and soil inorganic nitrogen may be highly species-specific as plants have strong feedback regulations on these environmental factors.

2. Materials and methods

2.1. Study site and species selection

This experiment was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS), the Chinese Academy of Sciences from 2007 to 2009. This station is located in the central part of the Inner Mongolia Autonomous Region of China (116°40′40″ E, 43°32′45″ N, 1250–1280 m a.s.l.). Climatically, this area belongs to middle temperate and semiarid zone, characterized by the alteration of dry and cold winters and relatively wet and warm summers. The mean annual precipitation and mean annual temperature (1982–2008) is 337 mm and 0.92 °C, respectively, with about 75% of precipitation events occurring during the period from June to September.

Communities in this area usually consist of about 20 vascular plant species. Eight species were selected based on their abundance and life form in a natural community. These species were *L. chinensis*, *S. grandis*, *Achnatherum sibiricum*, *Agropyron michnoi*, *Cleistogenes squarrosa*, *Setaria viridis*, *Artemisia frigida* and *Kochia prostrate*. *L. chinensis* (a rhizomatous grass) and *S. grandis* (a bunchgrass) were two dominant species. Three bunchgrasses, *A. sibiricum*, *A. michnoi*, and *C. squarrosa* were subdominant species while two semi-shrubs, *A. frigida* and *K. prostrata*, and an annual, *S. viridis*, were minor species. Thus our selection included species from dominants to subdominants and minors and represented major plant life forms in this community. Based on the monitoring data of Inner Mongolia Grassland Ecosystem Research Station (2008–2012), these species together constituted 71.7–95.1% of the aboveground biomass and 72.6–92.7% of vegetation cover of this plant community.

2.2. Seedlings preparation

For each species, we collected their seeds from a natural community in 2007. These seeds were sown in a seedbed on May 2 of 2008 and covered with a plastic film. Seedlings were carefully nursed for 40 d and then acclimatized for 10 d by removing the plastic film. Uniform seedlings were selected and transplanted to pots (28 cm diameter by 26 cm depth) with a density of 3 plants per pot at middle June of 2008. For each species, 100 pots were transplanted and buried into the soil (24 cm in depth) in a field. Then these seedlings received natural rainfalls in 2008. The seeds of *S. viridis* (an annual species) were collected on August 28 of 2008 and were sown again on May 2 of 2009.

2.3. Rainout shelter

We constructed four rainout shelters with steel frames, each covering an area of 90 m^2 (6 m × 15 m) (Fig. S1). Each shelter had a slanting roof made of waterproof cloth that can be removed by a steel roller fixed on the top of each shelter. The height of the south and north sides of the frame were 50 cm and 90 cm, respectively. On fine days, the waterproof cloth was wound to the roller and placed on the top of north side, thus leading to the removal of the roof from the shelter. The cloth was wound off the roller to form the roof for the shelter prior to the onset of rainfall. After rain, the cloth was wound back on the roller again. As the roof was only formed during rain events, there is no significant difference within and outside the shelter in air temperature, air moisture and light, which are important factors for rainout shelter design (Beier et al., 2012).

2.4. Experiment design and field manipulation

We used a two-way factorial design to manipulate the amount and pattern (interval between rainfall events) of precipitation from June 1 to September 30 in 2009. Two levels of precipitation amount were used. Level 1 (W1) was 249 mm, which was consistent with the long-term average amount of precipitation (1982–2008) during the period from June 1 to September 30. Level 2 (W2) was 373 mm, representing a 50% increase relative to long-term average. Two levels of inter-rainfall interval, three-day and fifteen-day, were used. Three-day interval (D3) is the most frequent interval between rainfall events (1982–2008) during the period from June 1 to September 30, while a fifteen-day interval (D15) represented extreme drought events in this area. The events with daily precipitation greater than or equal to 2 mm were regarded as biological effective events (Heisler-White et al., 2008). Moreover, the cases of >3 days of consecutive precipitation were divided into two events and the date receiving the greatest daily precipitation were assigned an event date (Heisler-White et al., 2008).

For each species, 60 pots with similar plant size were selected and buried into the soil with the upper 2 cm edge above soil surface in the rainout shelters on May 22 of 2009. Four precipitation treatments were arranged in each shelter. Specifically, four pots of each species for each treatment were placed in three shelters and three pots of each species for each treatment were laid in the other shelter. In total, we used 480 pots for the current experiment. The pots were placed 1 m away from the edge of each side to prevent exposure of ambient rainfall (Yahdjian and Sala, 2002; Beier et al., 2012). The aisles between treatments were 0.4 m. The patterns of water application to simulate rainfall events for the four treatments were shown in Fig. S2. During the experimental period, treatment D3 and D15 were watered 40 and 9 times, respectively. The water used in this experiment came from a nearby well with its concentrations of nitrogen, phosphors, and potassium below detectable levels. The soil used for pot culture is collected from the site where the plant seeds were collected. It belongs to chestnut (Calcic Chernozems according to the IUSS Working Group WRB, 2006) with a loamy-sand texture. The pH, soil organic matter and total nitrogen for the soil were 7.5, 2.7%, and 1.73 mg g^{-1}, respectively. To mimic the natural conditions, each pot has three 1cm-dimeter holes that allows infiltration out of the pots at the bottom. We did not allow for runoff by controlling the water flux when watering the plants.

2.5. Soil measurements and plant sampling

For each pot, soil moisture (volume water content) at a depth of 10 cm was measured by a Time-Domain Reflectometry (TDR, CS620 Hydrosense, Campbell Scientific, Logan, Utah) at 8:00–9:00 every 3, 7, and 14 d of a 15-d treatment round (Fig. S2). At the same time, soil temperature at 10 cm depth was recorded by a digital thermometer. Soil cores (3 cm diameter) of two layers (0–10 cm and 10–20 cm) from each pot were collected on September 28 in 2009. After removal of roots, soil samples at the same layer from three pots were gently mixed and passed through a 2-mm-mesh sieve as one sample replicate to determine soil moisture and concentrations of soil NO_3-N and NH_4-N. A 20-g subsample of fresh soil was oven-dried at 105 °C for 24 h to determine soil moisture for calculating dry weight-based soil nitrogen concentration. NH_4-N and NO_3-N concentrations were determined by extracting inorganic N at 100 rpm for 2 h from subsamples with 100 ml of 2 M KCl before and after incubation. The extract was subjected to colorimetric determination on a 2300 Kjeltec Analyzer Unit (FOSS, Höganäs, Sweden).

On September 29 in 2009, the above-ground organs for each pot were harvested and separated into leaves, stems and fruiting spikes (grains + flowering stalks). Below-ground organs were gently washed from the soil and collected by a 1-mm-mesh sieve. All samples were oven-dried at 65 °C for 48 h and weighed. The seeds for each pot were collected and weighed.

2.6. Statistical analysis

We used two-way ANOVAs to assess effects of precipitation amount and inter-rainfalls interval on biomass production, root to shoot ratio, leaf to stem ratio and reproductive allocation (seed to total biomass ratio). Differences between treatments were compared by a Duncan' multiple range test. These statistical analyses were performed using SAS, version 9.3 (SAS Institute, Cary, NC, U.S.A.). Structural Equation Modeling (SEM) (Shipley, 2000; Grace, 2006) was used to estimate the relative roles of soil moisture (SM), soil temperature (ST), and soil inorganic nitrogen (ION) in influencing species' biomass production.

3. Results

3.1. Biomass production

Changes in precipitation amount had significant impacts on biomass production for all species except for *C. squarrosa* (Table 1, Fig. 1). With the increase of precipitation amount from 249 mm to 373 mm, the biomass production of *L. chinensis*, *S. grandis*, *A. sibiricum*, *A. michnoi*, *S. viridis*, *A. frigida*, and *K. prostrata* increased by 23.0%, 17.6%, 27.7%, 15.1%, 38.8%, 73.8%, and 43.4%, respectively (Fig. 1). Changes in inter-rainfall interval had significant impacts on the biomass production of *L. chinensis*, *A. sibiricum and C. squarrosa* but not on the other five species (Table 1, Fig. 1). With the increase of inter-rainfall interval from 3 d to 15 d, the biomass of *L. chinensis* and *C. squarrosa* decreased by 21% and 17%, respectively, while that of *A. sibiricum* increased by 18.5% (Fig. 1). In addition, changes in precipitation amount and pattern also exhibited significant interactive effects on biomass production of *S. grandis*, *A. sibiricum*, *S. viridis*, *A. frigida* and *K. prostrata* but not on the other three species (Table 1).

Table 1
Results (F-values) of two-way ANOVA of the effects of precipitation amount (W) and inter-rainfall interval (D), and their interaction (W*D) on biomass (B), root to shoot ratio (R/S), stem to leaf ratio (S/L) and reproductive allocation (RA) of eight species. *, ** and *** indicate significant effect at P = 0.05, 0.01 and 0.001 levels, respectively.

Species	Treatment	B	R/S	S/L	RA
L.chinesis	W	13.65**	14.81**	0.49	4.79
	D	16.69**	9.97*	1.52	2.7
	W*D	0.02	5.61*	0.01	2.6
S. grandis	W	9.23*	1.39	5.26	2.96
	D	0.44	14.67**	0.84	0
	W*D	6.58*	0	2.76	0.01
A. sibiricum	W	26.9***	0.11	0.01	2.93
	D	13.08**	2.37	1.55	0.22
	W*D	17.04**	0.13	0.2	0
A. michnoi	W	7.47*	0.27	0.05	14.88**
	D	2.8	0.51	6.59*	45.4***
	W*D	0	0.04	0	0.07
C. squarrosa	W	0.16	2.19	5.15	14.91**
	D	9.16*	0.61	6.24*	117.58***
	W*D	2.06	0.1	0.79	0.42
S. viridis	W	26.71***	0.1	16.17**	3.29
	D	0.08	2.52	0.48	12.21*
	W*D	9.19*	1.18	0.38	0.64
A. frigida	W	55.25**	0	0.11	0.73
	D	1.67	1.25	3.08	3.11
	W*D	11.07*	0.33	0.05	2.85
K. prostrata	W	35.47**	4.02	1.32	35.08**
	D	0.07	0.33	0.06	15.94**
	W*D	9.59*	1.78	0.05	7.6*

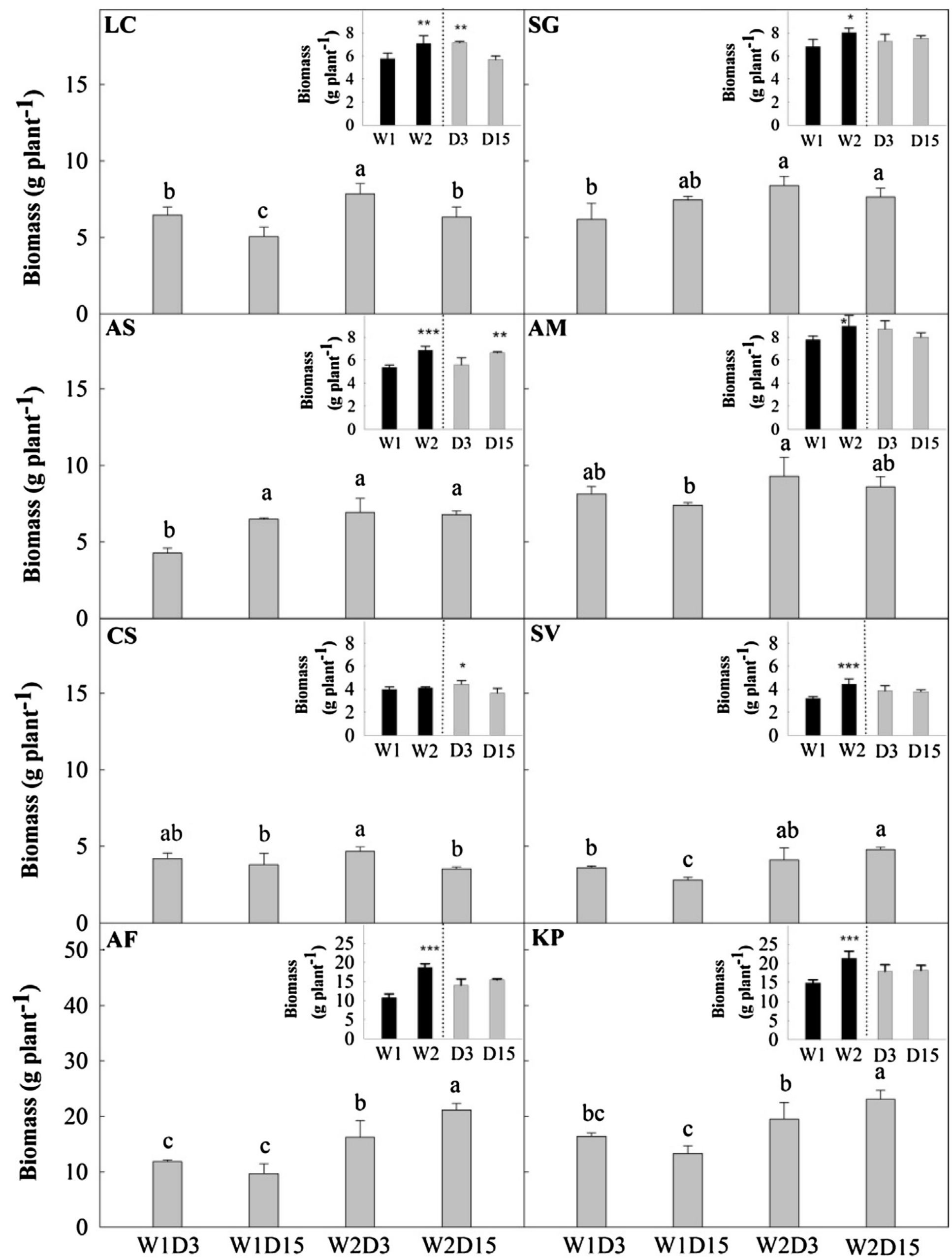

Fig. 1. Effects of seasonal precipitation amount (W) and inter-rainfall interval (D) on biomass production of eight species. Species were *L. chinensis* (LC), *S. grandis* (SG), *A. sibiricum* (AS), *A. michnoi* (AM), *C. squarrosa* (CS), *S. viridis* (SV), *A.frigida* (AF) and *K. prostrata* (KP). W1 and W2 represented 249 mm and 373 mm precipitation, respectively, during the period from June 1 to September 30. D3 and D15 represented inter-rainfall intervals were 3 d and 15 d, respectively. Values are means ± SE. Different letters indicate significant differences between treatments at $P = 0.05$. The average effects of precipitation amount and inter-rainfall interval were shown as an inset figure for each species. *, ** and *** indicate significant difference between treatment levels at $P = 0.05$, 0.01 and 0.001 levels, respectively.

3.2. Root to shoot ratio

Changes in precipitation amount, inter-rainfall interval and their interaction had significant effects on root to shoot ratio (R/S ratio) of *L chinensis*, the dominant rhizomatous species, however, this did not hold true for all subdominant and minor species (Table 1). *L. chinensis* consistently displayed a significant decline in R/S ratio with the increase in precipitation amount and the increase in inter-rainfall interval (Fig. 2). In addition, the dominant bunchgrass, *S. grandis*, decreased its R/S ratio with the increase of interval between precipitation events from 3 d to 15 d (Table 1, Fig. 2).

3.3. Stem to leaf ratio

Changes in precipitation amount had no significant effect on stem to leaf ratio (S/L ratio) for all species examined, except for *S. viridis* that displayed a significant increase in S/L ratio with the increase in precipitation amount from 249 mm to 373 mm (Table 1, Fig. 3). Similarly, changes in inter-rainfall interval had no significant effect on S/L ratio for all species, except for *A. michnoi* and *C. squarrosa* that exhibited a declining trend in S/L ratio with increasing interval from 3 d to 15 d (Table 1, Fig. 3). Also, the interactive effects of precipitation amount and inter-rainfall

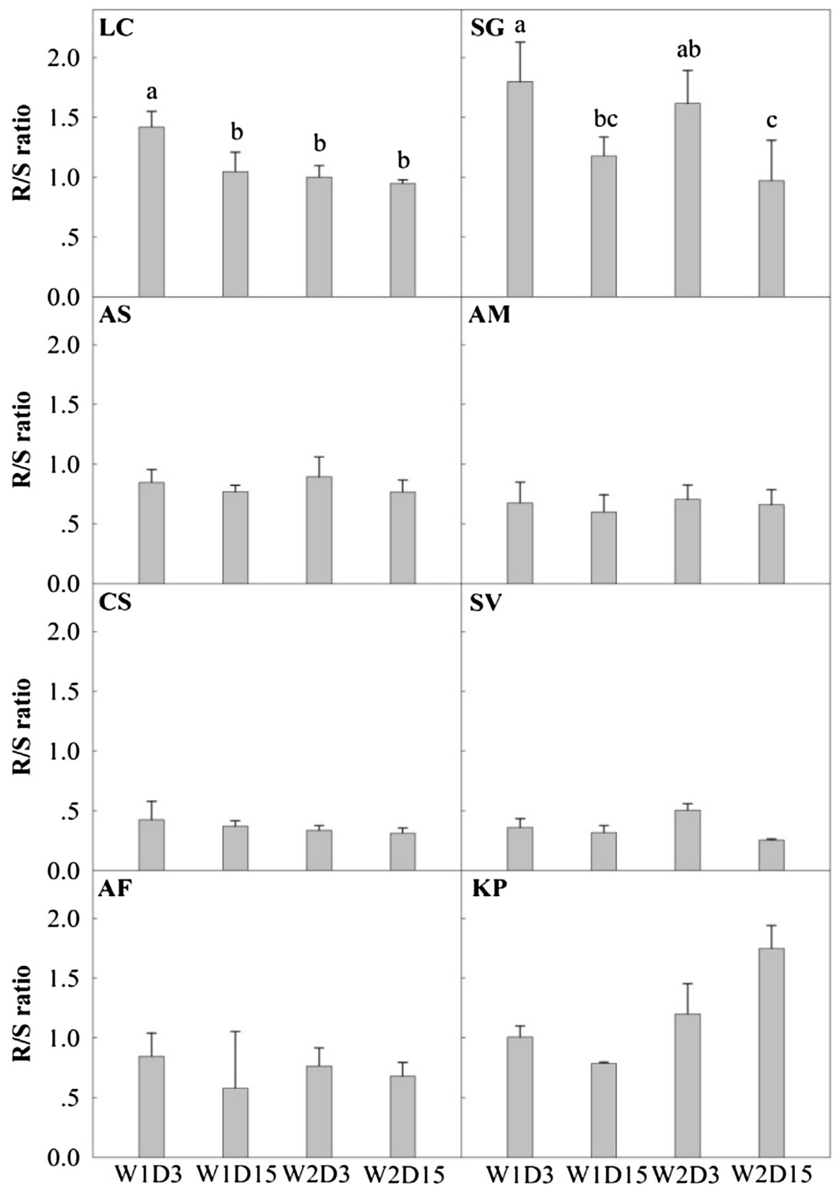

Fig. 2. Effects of seasonal precipitation amount (W) and inter-rainfall interval (D) on root to shoot ratios (R/S ratios) of eight species. Values are means ± SE. Different letters indicate significant differences between treatments at $P = 0.05$. Abbreviations for species and treatments are explained in Fig. 1.

interval on S/L ratios were consistently insignificant for all species (Table 1).

3.4. Reproductive allocation

Changes in precipitation amount, inter-rainfall interval and their interaction had no effect on reproductive allocations of two dominant species, *L. chinensis* and *S. grandis*, a subdominant species, *A. sibiricum* and a minor species, *A. frigida* (Table 1, Fig. 4). The other species (*A. michnoi*, *C. squarrosa*, *S. viridis* and *K. prostrata*) were significantly affected by changes in inter-rainfall interval but their direction and magnitude differed substantially (Table 1, Fig. 4). With the increase of inter-rainfall interval from 3 d to 15 d, the reproductive allocation of *C. squarrosa* significantly decreased under both levels of precipitation amount while that of *A. michnoi* decreased only under the 373 mm precipitation level and that of *K. prostrata* decreased only under the 249 mm precipitation level (Fig. 4). Increase in precipitation amount significantly increased the reproductive allocation of *C. squarrosa* but decreased the reproductive allocation of *A. michnoi* under the scenario of 15-day interval between rainfall events. By contrast, *S. viridis* increased its reproductive allocation significantly when precipitation amount increased from 249 mm to 373 mm and the inter-rainfall interval increased from 3 d to 15 d (Fig. 4).

3.5. Relative roles of soil variables on species' biomass production

Structure equation modeling (SEM) analysis indicated that changes in soil moisture, soil temperature and soil inorganic nitrogen (NH_4-N and NO_3-N) ensuing from the alterations in precipitation amount and inter-rainfall interval affected the biomass production of eight species in different ways (Fig. 5). In general, soil moisture exhibited positive (for six species) or no effect (for two species) on biomass production while soil temperature exhibited negative (for five species) or no effect (for three species). Soil inorganic nitrogen displayed positive effect for five species, negative effect for two species and no effect for one species (Fig. 5).

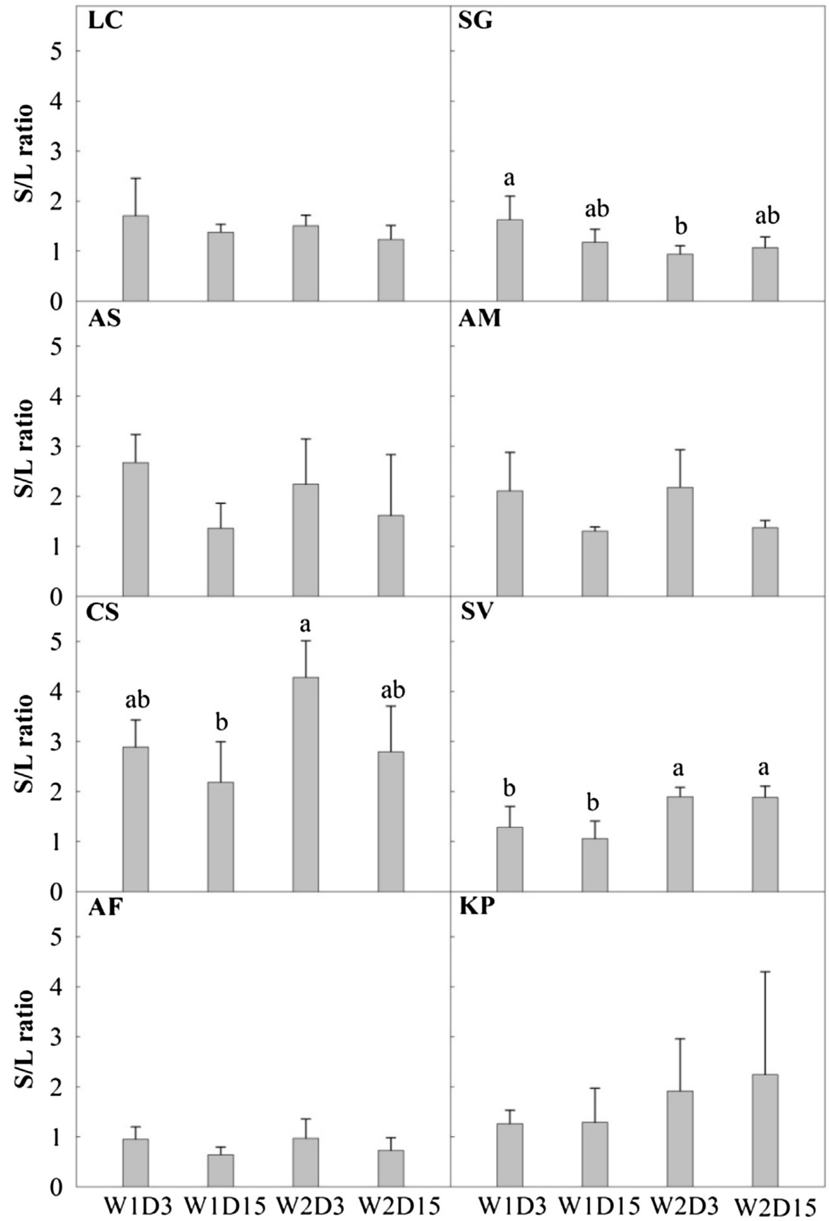

Fig. 3. Effects of seasonal precipitation amount (W) and inter-rainfall interval (D) on stem to leaf ratios (S/L ratios) of eight species. Values are means ± SE. Different letters indicate significant differences between treatments at $P = 0.05$. Abbreviations for species and treatments are explained in Fig. 1.

For the two dominant species, *L. chinensis* and *S. grandis,* the biomass production was enhanced by soil moisture and soil inorganic nitrogen. However, *L. chinensis* is greater controlled by soil inorganic nitrogen relative to soil moisture while *S. grandis* was equally regulated by the two feedbacks (Fig. 5).

For the three subdominant species, the biomass production of *A. sibiricum* was enhanced by increased soil moisture and depressed by elevated soil temperature. By contrast, the biomass production of *A. michnoi* and *C. squarrosa* was not affected by soil moisture but negatively affected by soil inorganic nitrogen (Fig. 5).

For the three minor species, the biomass production was enhanced by soil moisture and soil inorganic nitrogen but depressed by soil temperature. However, *S. viridis* was stronger controlled by soil inorganic nitrogen relative to soil moisture while *K. prostrata* was greater affected by soil moisture rather than soil inorganic nitrogen. However, *A. frigida* was equally regulated by the two resource feedbacks (Fig. 5).

4. Discussion

4.1. Effects of precipitation amount and inter-rainfall interval on species' biomass production

This experiment provides robust evidence that increased precipitation amount of growing season facilitates the growth of most grassland species. This is consistent with previous findings that increasing the total amount of precipitation led to increase in biomass for multiple plant species (Didiano et al., 2016). These results suggest that future increase in precipitation may potentially improve community biomass production in this area, as suggested by a remote sensing study (Fang et al., 2005) and a large-scale transect investigation (Ni, 2003). Moreover, we found that the magnitudes of biomass increases differed greatly among eight species. The semi-shrubs (*A. frigida* and *K. prostrata*) and the annuals (*S. viridis*) exhibited larger increases than perennial

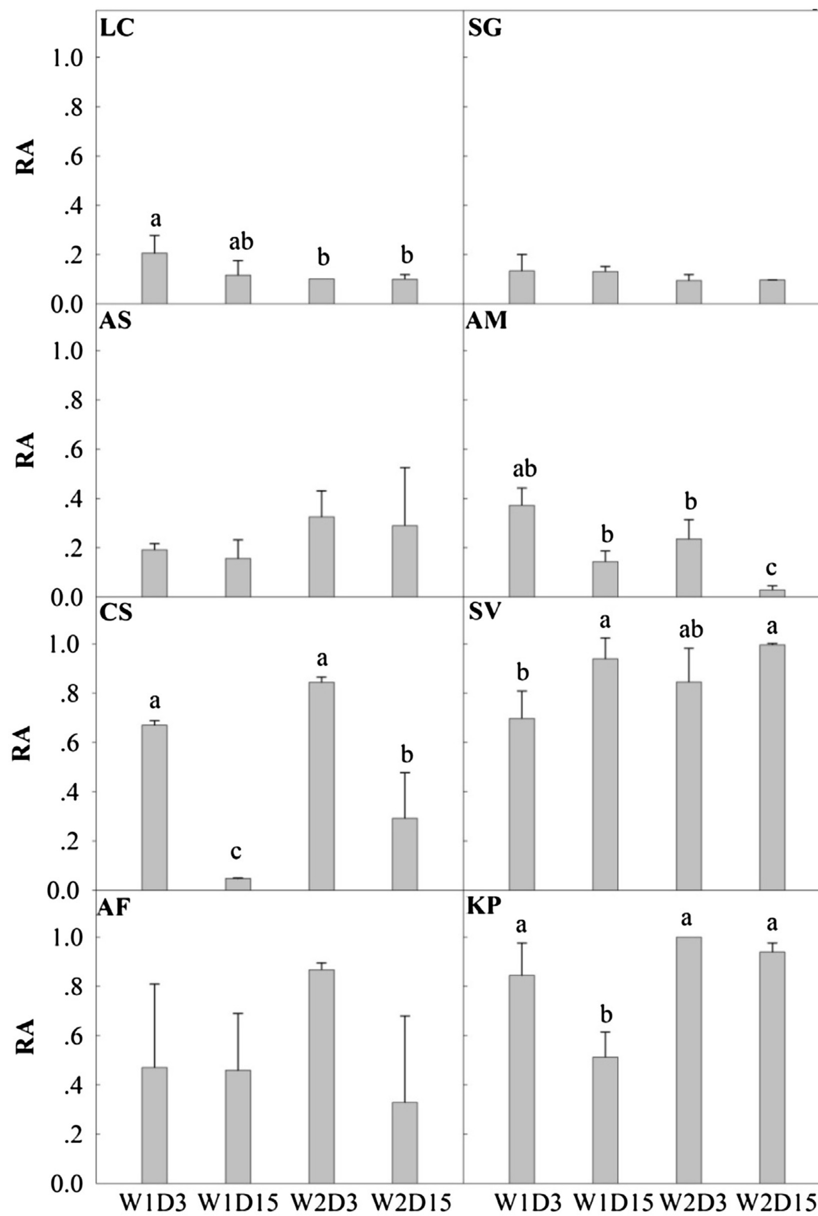

Fig. 4. Effects of seasonal precipitation amount (W) and inter-rainfall interval (D) on the reproductive allocations (RA) of eight species. Values are means ± SE. Different letters indicate significant differences between treatments at $P = 0.05$. Abbreviations for species and treatments are explained in Fig. 1.

grasses (*L. chinensis*, *S. grandis*, *A. sibiricum and A. michnoi*), suggesting that future increase in precipitation amount in this area may facilitate the growth of the semi-shrubs and the annuals. In contrast, the biomass production of *C. squarrosa* was not affected by increased precipitation amount. This may be due to the fact that *C. squarrosa* is a C_4 grass, and C_4 perennial plants are more sensitive to variation in seasonal temperature and seasonal distribution of rainfalls (Auerswald et al., 2012) rather than precipitation amount.

Unlike the consistent and positive impacts of precipitation amount, the effects of inter-rainfall interval on biomass production differed substantially among eight species. Five species (*S.grandis*, *A. michnoi*, *A. frigida*, *K. prostrata* and *S. viridis*) sensitive to changed precipitation amount had no response to changes in inter-rainfall interval, suggesting that these species are more sensitive to changes in precipitation amount relative to pattern. By contrast, prolonged inter-rainfall interval greatly reduced the biomass of two species (*L. chinensis* and *C. squarrosa*), especially when the seasonal precipitation amount increased by 50%, which is consistent with previous findings (Liu et al., 2012). For these species, the positive effect of increased precipitation amount can be suppressed by the negative effect of prolonged inter-rainfall intervals. Moreover, the biomass of *C. squarrosa* significantly declined under the combination of prolonged inter-rainfall interval (15d) and increased precipitation amount (373 mm), implying that the abundance of this C_4 species is likely to decrease in the current community if the precipitation amount increases and the inter-rainfall interval prolongs in the future.

An interesting result from this experiment is that the biomass of *A. sibiricum* significantly increased with prolonged intervals between rainfall events under average precipitation amount, which is markedly different from the other species. This may be due to its unique symbiotic relationship with endophytes as the inflection rate of endophytes for this species is higher than 86% in this area (Wei et al., 2006). Endophytes can help plants resist drought stress (Elmi and West, 1995; Latch et al., 1985). Such a response of *A. sibiricum* to prolonged inter-rainfall interval implies

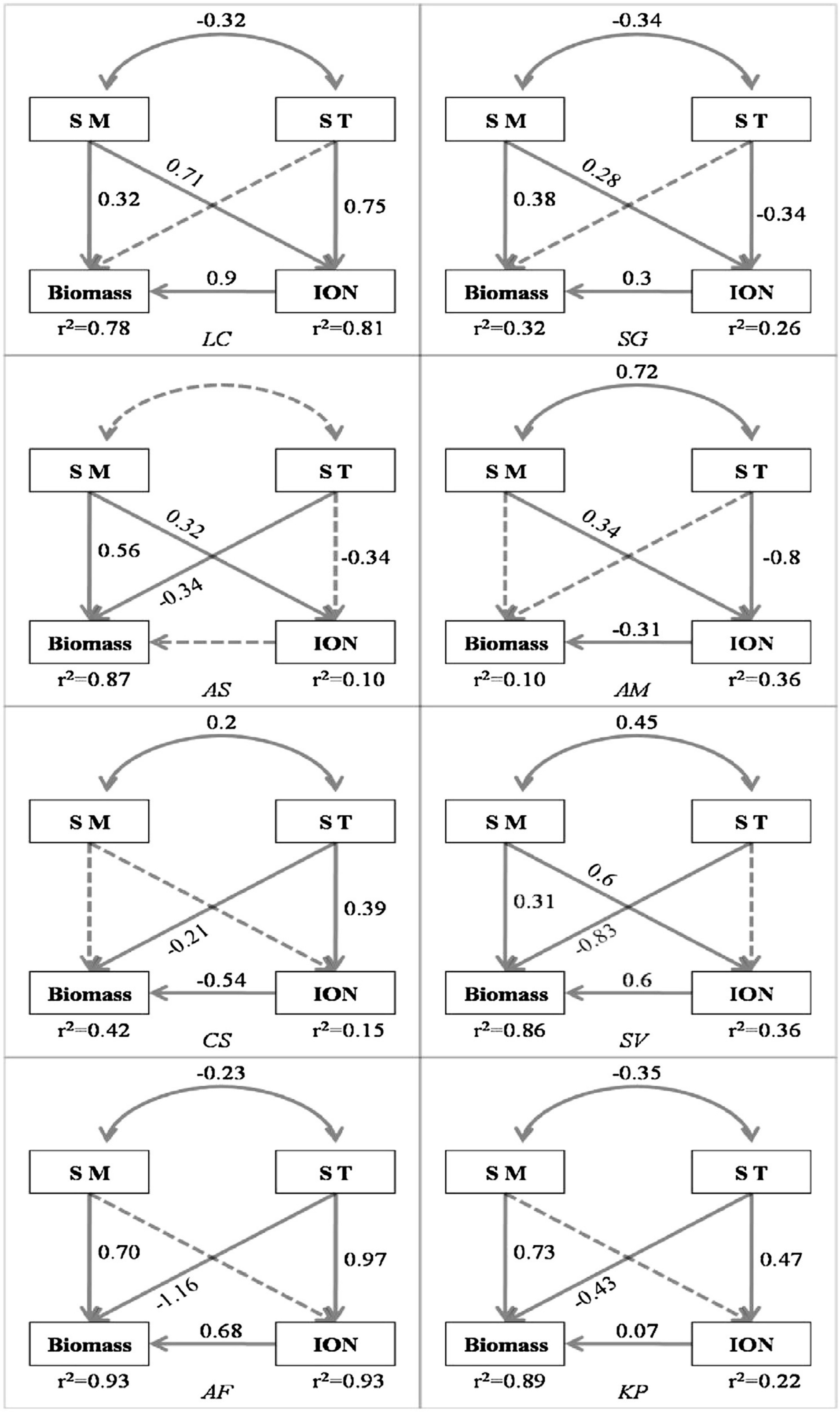

Fig. 5. Results of structure equation modeling on the effects of soil moisture (SM), soil temperature (ST) and soil inorganic nitrogen (ION) on species' biomass. Solid and dashed arrows indicate significant ($P < 0.05$) and non-significant effects ($P > 0.05$), respectively. r^2 values associated with response variables indicate the proportion of variation explained by relationships with other variables. Values associated with solid arrows represent standardized path coefficients. Positive and negative values represent positive and negative effects. Abbreviations for species are explained in Fig. 1.

that this sub-dominant species may increase its biomass when facing some drought events and thus stabilize the overall biomass production at the community level. This is supported by the long-term monitoring results of the Inner Mongolia Grassland Ecosystem Research Station. On average, the aboveground biomass of *A. sibiricum* from 1982 to 2010 is 16.4 g m^{-2}, contributing 10.4% to community aboveground biomass. However, in 2005, an extreme drought year with an annual precipitation of 131.5 mm, much lower than the mean annual precipitation (292.7 mm) from 1982 to 2010, the biomass of *A. sibiricum* reached a peak value of 53.7 g m^{-2}, contributing 34.3% to community level aboveground biomass (Fig. S3).

In contrasting to previous findings that fewer but larger rainfall events can increase biomass production at the community level (Heisler-White et al., 2008), this study indicated that different species from the same community responded differently to increased inter-rainfall intervals. Under the long-term mean precipitation treatment (249 mm), increased inter-rainfall interval led to biomass increase for 1 species (*A. sibiricum*), decrease for 2 species (*L. chinensis and S. viridis*), and no significant alteration for other five species. By contrast, under the 50% increased precipitation treatment (373 mm), prolonged inter-rainfall interval caused biomass increase for 2 species (*L. chinensis and C. squarrosa*), decrease for 2 species (*A.frigida and K. prostrate*) and no significant change for the other four species. Compared with the treatment of long-term mean precipitation amount and inter-rainfall interval, increased amount and prolonged interval resulted in biomass increase for 4 species and no marked change for the other 4 species.

Taken together, our results suggest that species from the same community may respond differently to altered precipitation amounts and patterns. The overall effects of changed precipitation regimes on community biomass production depend on the balance between different responses of species. Generally, future increases in precipitation amount and interval may improve community-level biomass production, as no species displayed decrease in biomass under such a scenario.

4.2. Effects of precipitation amount and inter-rainfall interval on species' biomass allocations

Our results demonstrated that seasonal precipitation amount, inter-rainfall interval and their interaction had no effect on biomass allocation between above- and belowground parts for six out of eight species, which is consistent with previous findings across China's grasslands that the R/S was not affected by precipitation (Yang et al., 2010). Moreover, we found that precipitation amount, inter-rainfall interval and their interaction had little impact on allocation patterns between stems and leaves for most examined species. Similarly, Perkins and Owens (2003) have found that the allocation patterns of grass and shrub seedlings in a semiarid savanna are not affected by changed precipitation regimes. These results suggest that it may be difficult for many grassland species to shift their allocation patterns rapidly to adapt to the changes in precipitation amount and/or pattern.

For reproductive allocations, we did not find consistent response patterns to the changes in precipitation amount and pattern across eight species, suggesting that the reproductive responses to altered precipitation regimes is highly species-dependent. A previous study also found that reproductive allocations differed substantially between desert and Mediterranean species under water stress scenarios (Aronson et al., 1993). These results suggest that the impacts of future changes in precipitation amount and pattern on species' reproduction may be very complex and such differentiation among co-occurring species may have profound impact on community structure or species composition. For example, some species, such as *C. squarrosa* and *A. michnoi*, in the current ecosystem, may face a risk of extinction if the frequency of prolonged inter-rainfall interval increases in this area in the future (IPCC, 2013), as their reproductive allocations decreased dramatically with prolonged inter-rainfall interval even under the scenario of enriched precipitation.

4.3. Relative role of soil moisture, soil temperature and soil inorganic nitrogen in affecting species' biomass production

Our experiment showed that different species may have developed different strategies to cope with variability in water supply, and each approach is likely related to species' life-history attributes. For example, *L. chinensis* is a dominant rhizomatous grass in the natural community. The developed rhizome system made it easier to acquire and store limiting resources and therefore its growth was mainly controlled by overall levels of resources. As indicated by our results, soil moisture and soil inorganic nitrogen jointly explained 78% of variation in its biomass production. This is consistent with previous results (Liu et al., 2012). However, Liu et al. (2012) used one-year-old seedlings and found that their biomass production was more affected by soil moisture than by soil inorganic nitrogen. In contrast, here we found that the biomass production of two-year-old seedlings of *L. chinensis* was more controlled by soil inorganic nitrogen than soil moisture. This indicates that the role of different resources in affecting biomass production of *L. chinensis* may shift and such shift may be age-dependent.

The other dominant species, *S. grandis*, is a bunchgrass. Although its biomass production was regulated by soil moisture and inorganic nitrogen, these two factors only explained 32% of variance of its biomass production, suggesting that factors other than soil moisture, temperature and inorganic nitrogen play more important roles in controlling its biomass production. A previous water and nitrogen addition experiment in this area have found that *S. grandis* has the lowest P concentration (0.9 mg g^{-1}) and the highest N:P ratio (17.8) among co-occurring species (Gong et al., 2011), implying that its growth may be relatively limited by the availability of phosphorus (Verhoeven et al., 1996). Moreover, arbuscular mycorrhizal fungi and soil phosphorus may interactively affect species' productivity (Yang et al., 2014).

A. frigida and *K. prostrata,* the two semi-shrubs, have both shallow and deep roots. Increased precipitation amount led to water infiltration into deep soils that these shrub species can access to but other species can not. Therefore, increased amount of precipitation greatly enhanced their biomass production but changed inter-rainfall interval had no impact. This is similar with the response of *Dasylirion leiophyllum*, a shrub in the Chihuahuan desert (Robertson et al., 2009), where its biomass production depended more on overall levels of resources than on variation of precipitation pattern. Also, we observed strong impact of soil temperature on these two shrubs. In total, 90% of variance in their biomass production can be jointly explained by the effects of soil moisture, soil inorganic nitrogen and soil temperature.

In addition, we found that the effects of soil moisture on soil inorganic nitrogen differed substantially among species, as positive for some species while negative for others. This may imply the difference in species-specific feedbacks of plants on their environments. In fact, the concentration of soil inorganic nitrogen is co-determined by many factors, such as soil temperature, soil moisture, microbial C:N ratio, and their interactions (Chapin et al., 2002). More importantly, the plants may have strong feedback regulations on soil inorganic nitrogen as plants continuously take up inorganic nitrogen from the soil by their roots and the uptake rates greatly depend on the growth of the plants. For example, with the turning green of plants in Inner Mongolian grassland, the concentration of soil inorganic notrogen declined greatly from ca. 3 g N m^{-2} on March 8 to ca. 1 g N m^{-2} on May 9 (Shan et al., 2011). Therefore, the effects of soil temperature on soil inorganic nitrogen may be positive or negative, to a great extent depending on the use of inorganic nitrogen by plants. This is further supported by previous findings that soil inorganic nitrogen was negatively correlated with soil temperature at the non-growing season, but positively correlated at the early growing season, while negatively correlated again at the peak growing season (Shan et al., 2011). Similarly, we found strong species-specific effects of soil temperature on soil moisture, with positive for some species but negative or have no effects for others. This may be also caused by the difference of feedbacks among species. A recent study indicated that the frequency of precipitation events greatly altered the stomatic conductance of plants (Didiano et al., 2016). Such an alteration may in turn affect the uptake of soil water and caused the change in soil temperature. These species-specific correlations between soil temperature, soil moisture and soil inorganic nitrogen highlight the role of feedback regulations by plants on their environments.

In summary, the pathways, directions (positive or negative) and magnitudes of the effects of three edaphic factors differed substantially among eight species. This suggests that species from the same community may cope with precipitation variability in different ways. Such species-level differentiation in their responses to precipitation regimes may greatly affect their abundance in a natural community. To illustrate this point, we reanalyzed the data of a precipitation addition experiment in the community we collected plant seeds (Zhang et al., 2015). We found that species' relative abundance in the community was consistently and positively correlated to their response ratio in terms of the biomass (Figs. S4 and S5). Therefore, we suggest that co-occurring plant species may respond differently to altered precipitation regimes and such difference is important for better understanding and/or predicting how precipitation alterations may affect community structure and functioning in a water limiting ecosystem. However, it should be mentioned that this is a short-term, monoculture and pot experiment, the responses of species to altered precipitation regimes may be affected greatly by the inter-specific interactions in a natural community. Moreover, species may exhibit different responses over longer term. Therefore, long-term field experiments with similar treatments are necessary for a mechanistic understanding of the impacts of changes in precipitation regime on plant growth from species to community levels.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.envexpbot.2017.02.006.

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