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Inconsistent changes of biomass and species richness along a precipitation gradient in temperate steppe

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ABSTRACT

Biomass and species richness are two important indicators of ecosystem stability. The relationship between biomass and species richness along precipitation gradient in semi-arid regions is significant for prediction of ecosystem stability under the estimated climatic drying in the future. In this study, we investigated species richness, aboveground biomass and cover of temperate steppe along a mean annual precipitation (MAP) gradient in central Inner Mongolian of China. We also measured water use efficiency (WUE) of selected species and overall communities. Our results showed that biomass almost remained unchanged in the moist half of the gradient, but species richness decreased markedly with decreasing MAP. Species richness further showed a negligible decrease, whereas a much sharper drop was detected in biomass towards the arid end with decreasing MAP. Vegetation cover shared a similar pattern with biomass and dropped sharply towards the arid end, which may create a strong light and low competition environment favoring C_4 plants. The increment of C_4 species richness could prevent a more intensive decline of species richness under severe arid conditions by raising overall community water use efficiency. Thus, plant communities experiencing water deficiency could also maintain species richness with the occurrence of C_4 plants.

1. Introduction

Relationships between plant biomass and species richness of grasslands have interested ecologists for decades (Bai et al., 2007). A considerable amount of research has led to the hypothesis that species richness, as one of the most important ecosystem traits, has a positive relationship with plant biomass (Cardinale et al., 2006; Tilman et al., 2006; Van Ruijven and Berendse, 2010). For example, research has indicated that changed biomass may be stabilized by high species richness under severe environmental conditions (Hughes and Roughgarden, 2000). However, the above hypothesis has not yet been fully tested by field investigations and experiments (Bai et al., 2007; Gonzalez and Loreau, 2009; Campbell et al., 2011; Crawford and Rudgers, 2012). In addition, in natural environments, various stresses, such as soil moisture, may change the relationship between plant biomass and species richness (Fridley, 2002; Steudel et al., 2012).

Water availability is the most important limiting factor for grassland plants in arid and semiarid regions (Namgail et al., 2012). Plants may enhance their water use efficiency (WUE) as well as change the morphological features of organs to survive in harsh environmental conditions (Wang et al., 2013). A multitude of studies have demonstrated that both plant biomass and species richness decrease with an increase in drought (Rolim et al., 2005; Bai et al., 2008; Wang et al., 2013). However, ecosystems could still remain stable under drought stress because different functional groups have varied competitive abilities and can compensate for each other (Tilman et al., 2006; Gross et al., 2007; Volaire et al., 2009; Cadotte, 2011; McLaren and Turkington, 2011). Hence, focusing on the adaptive strategies that different plant functional groups display in response to drought may be the key to explain the relationships between plant biomass and species richness in grassland communities. Previous studies have found that water availability has a marked impact on plant functional groups as well as plant functional group traits in grasslands (Maseda and Fernández, 2006; Bai et al., 2008; Letts et al., 2010), but their results are widely disparate, and the underlying mechanism for the plant biomass–species richness relationship remains unclear.

C_3 and C_4 plants are two main functional groups with different photosynthetic pathways. C_4 carbon fixation improves photosynthetic efficiency under habitats of drought, strong light, high temperatures, and low atmospheric CO_2 (Buchmann et al., 1997;

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Spriggs et al., 2014). C_4 plants possess high photosynthetic efficiency, which leads to high WUE relative to C_3 plants under water stress (Ghannoum, 2009; Way et al., 2014). Thus to distinguish C_3 and C_4 photosynthetic functional groups in plant community could contribute to a better understanding of the plant biomass-species richness relationship (Qi and Redmann, 1993; Ward et al., 1999). We hypothesize that grassland community can maintain species richness under water stress through increase in richness of the C_4 plants with high WUE.

In order to explain the variance of community biomass and species richness, we analyzed the distribution patterns of C_3 and C_4 plants as well as their physiological traits along a precipitation gradient in the Inner Mongolian steppe of China. Particularly, we focused on: 1) detailing the different effects of drought on stand-level plant biomass (stand biomass) and species richness, and 2) explaining the effects through the distribution of C_3 and C_4 plants.

2. Study area

Our study area is located in the mid-east portion of the Inner Mongolia plateau, China (40°–50°N, 107°–125°E), with mean annual precipitation (MAP) of approximately 150 mm–450 mm. And mean annual temperature (MAT) of this area ranges from 0.1 °C to 4.9 °C. Following the MAP gradient, vegetation types change from meadow steppe, through typical steppe, to desert steppe. Steppe chestnuts soil is widely distributed in the study area and sandy soil also exists. The Palmer Drought Severity Index (PDSI) in this region has increased continuously during the last 70 years, especially after 1990s (Dai et al., 2004; Dai, 2011), and this trend could seriously threaten local ecosystems.

3. Methods

3.1. Data collection

We collected data on mean monthly temperature and mean monthly precipitation since the 1950s with 1 km × 1 km resolution data from the WorldCLIM dataset (http://www.worldclim.com/). MAT and MAP were calculated on the basis of monthly data over the past 50 years.

We systematically sampled 120 plots with different rainfall regimes in July and August, when vegetation growth is the most vigorous (Fig. 1). Size of each plot is 2 × 2 m^2. We firstly defined randomly sampling area along a rainfall gradient, then randomly set sampling sites on the mature grassland. We recorded the latitude, longitude, and altitude of plots. We also recorded plant species, as well as cover, abundance, and height of each species in each plot. Visual measurement was used for stands canopy coverage proportionally, and the aboveground biomass was harvested and weighed after 48 h storage in a consistent 65 °C drying oven. The mean dry mass of the harvested plants was used to estimate annual biomass production. For functional groups biomass, C_3 and C_4 plants were harvested and weighted respectively. For isotopic measurements, leaves of dominant species were sampled and kept in bags with silica-gel desiccant. A single 30 cm deep transect was sampled at each site and soil samples were collected every 10 cm. We used surface soil to measure total organic carbon (TOC) and total nitrogen (TN) using the Elementar Vario EL (Germany).

In the field investigations, we only picked mature and healthy leaves on 13 selected widespread species to find changes and tendency along the rainfall gradient. These species are dominant of each stands at temperate grassland in Inner Mongolia. Their cover accounts for 25% or more of total cover in 62.1% plots and 50% or more of total cover in 36.2% plots. Thus they are expected to play a central role in ecosystem functioning (Grime, 1998). In the lab, leaf samples had been dried under 48 °C for 70 h, then grinded into powder until they can through the 80-mesh sieve, and packaged into special tinfoil. The carbon isotope values of pretreated samples were measured by the CM-CRDS Isotopic Carbon Analyzer, produced by Picarro Inc (USA).

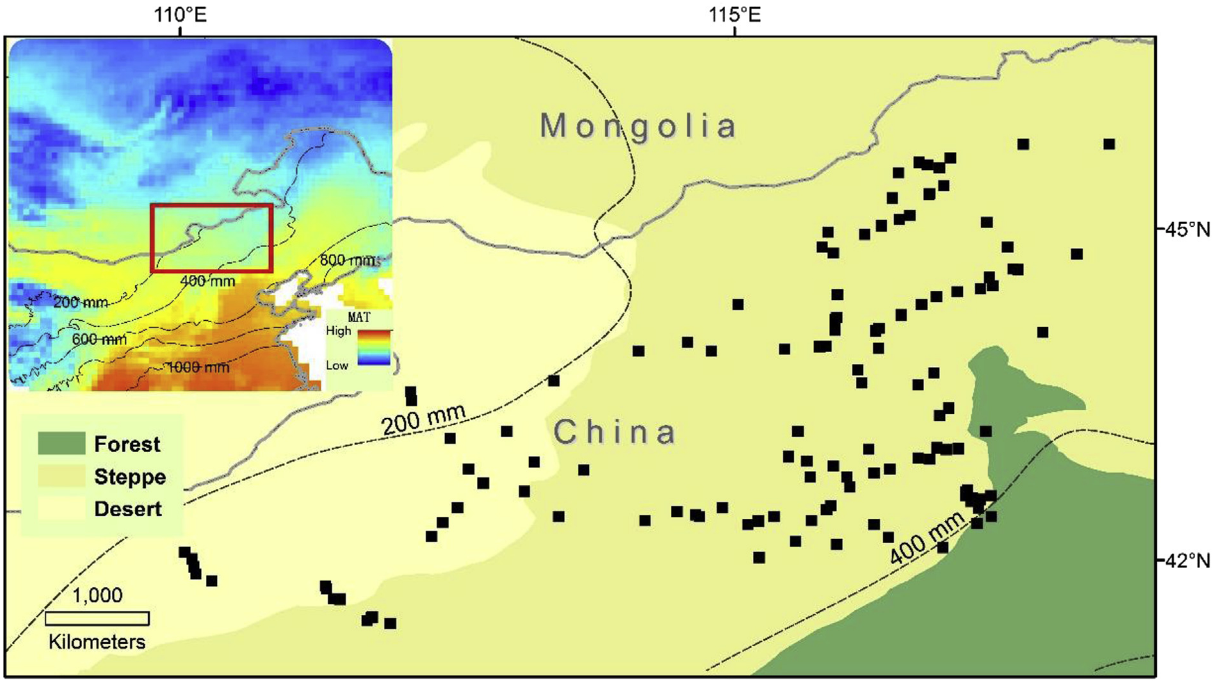

Fig. 1. Location of study area with sampling sites and vegetation types. Filled squares indicate sample sites. Light dark lines denote isohyets.

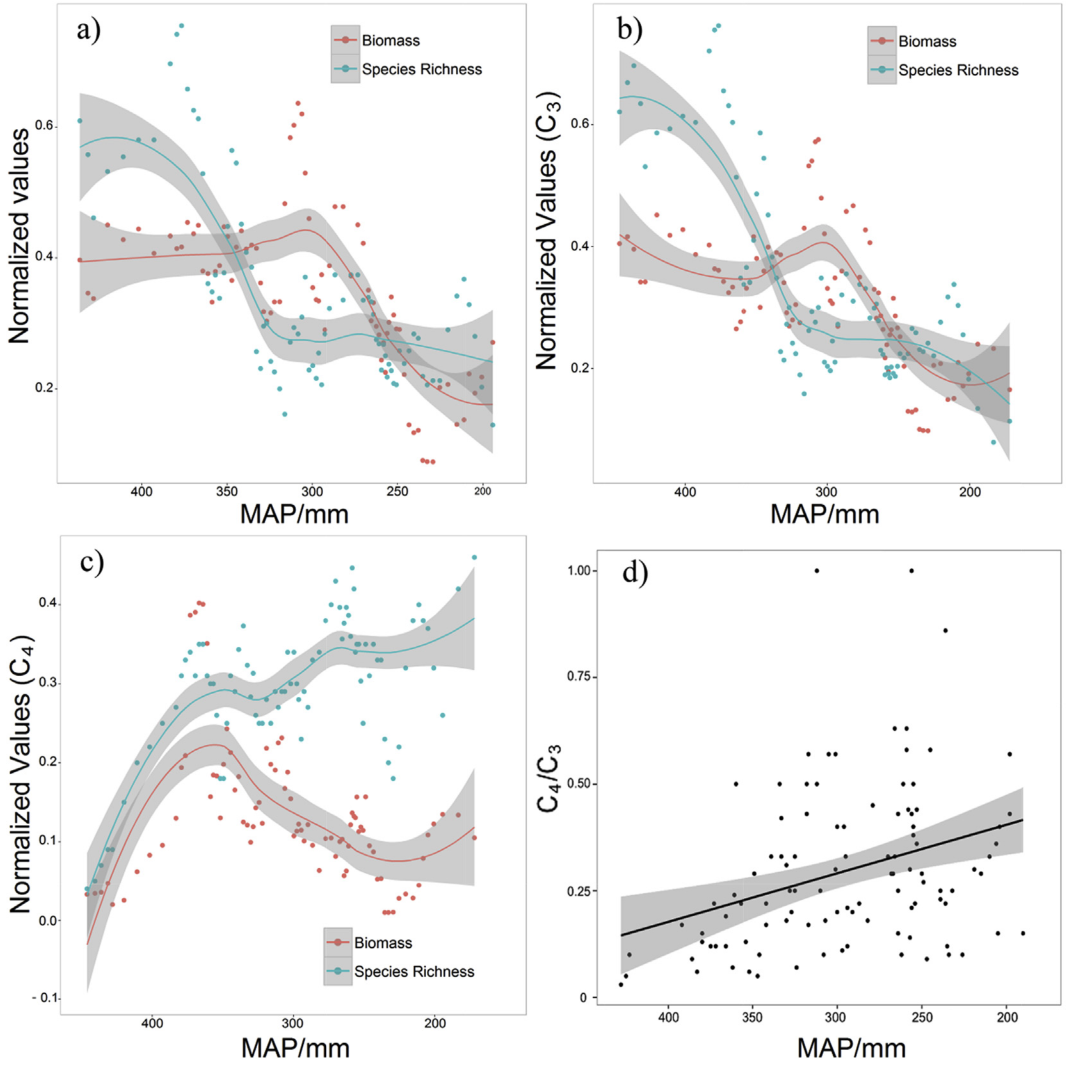

Fig. 2. Changes of normalized biomass and species richness of a) all species, b) C_3 plants, and c) C_4 plants along the MAP gradient. The red points and line represent the distribution and trend of aboveground biomass, while the blue points and line represent the distribution and trend of plant species richness. d) Linear regression of C_4/C_3 species richness ratio along the MAP gradient ($y = -0.00112x + 0.62435$, $R^2 = 0.128$, $P = 0.0001$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Data treatment

3.2.1. Importance value (IV)

In each plot, the importance value (IV) of each species was calculated by:

$$IV = (RD + RC + RH)/3 \tag{1}$$

In which RD is the relative abundance, RC the relative cover, and RH the relative height of each species (ter Braak, 1986). IV was used as a weight of each species when estimating the comprehensive index of communities.

3.2.2. Water use efficiency (WUE)

A great number of studies have demonstrated that plant water use efficiency (WUE) has a significant positive correlation with the $\delta^{13}C$ isotope (Farquhar et al., 1982; Farquhar and Richards, 1984; Seibt et al., 2008). Plants with different photosynthetic pathways (C_3, C_4, and CAM) have clearly different $\delta^{13}C$ isotope values. Consequently, the $\delta^{13}C$ isotope can be an effective index of plant water use efficiency (Hubick and Farquhar, 1987; Johnson et al., 1990; Arslan et al., 1999). In this paper, $\delta^{13}C$ isotope data were analyzed by redundancy analysis (RDA) in CANOCO 5.0 to illustrate the distribution of C_3 and C_4 group traits with environmental factors. The formula of $\delta^{13}C$ isotope is shown as the following:

$$\delta^{13}C(‰) = \{[{}^{13}C/{}^{12}C(\text{sample}) - {}^{13}C/{}^{12}C(\text{standard})]/[{}^{13}C/{}^{12}C(\text{standard})]\} \times 1000 \tag{2}$$

In which ${}^{13}C/{}^{12}C$ (sample) means the ${}^{13}C/{}^{12}C$ ratio of leaf samples. ${}^{13}C/{}^{12}C$ (standard) is the ${}^{13}C/{}^{12}C$ ratio of international standard material Pee Dee Belemnite (PDB). The measuring error is $0.45‰ \pm 0.08‰$.

3.2.3. Community-weighted mean water use efficiency

In order to clarify the relationship between the functional trait and community structure, and make the pattern of water-use trait along the MAP gradient more clearly, it is necessary to estimate the integrative WUE of stands (Wang et al., 2010). Previous studies have quantified the integrative WUE of plant communities through net primary production divided by actual evapotranspiration (Hu et al., 2008). Eddy covariance techniques can provide high-precision

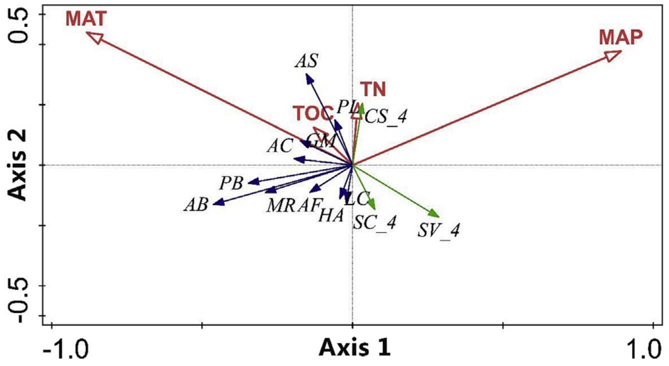

Fig. 3. RDA of leaf $\delta^{13}C$ isotope and environmental factors for 13 widespread grassland species. The blue arrows represent ten C_3 species. PL: *Potentilla longifolia*. AS: *Astragalus scaberrimus*. GM: *Gueldenstaedtia multiflora*. PB: *Potentilla bifurca* var. *major.* AB: *Allium bidentatum*. MR: *Medicago ruthenica*. AC: *Agropyron cristatum*. AF: *Artemisia frigida*. HA: *Heteropappus altaicus*. LC: *Leymus chinensis*. The green arrows represent three C_4 species. CS_4: *Cleistogenes squarrosa*. SC_4: *Salsola collina*. SV_4: *Setaria viridis*. The red arrows represent environmental factors. MAP: mean annual precipitation. MAT: mean annual temperature. TOC: soil total organic carbon. TN: soil total nitrogen. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

observations of carbon flux and water evaporation (Scanlon and Albertson, 2004; Ponton et al., 2006); however, these techniques are unavailable for estimation of WUE for plant communities along environmental gradient. Therefore, we used species $\delta^{13}C$ isotope to calculate the integrative WUE for each stand. CWM (Community-Weighted Mean) is an integrative calculation method of community functional traits which is broadly used by researchers in recent years. CWM can be adequately used to summarize shifts in mean trait values within communities due to environmental selection for certain functional trait, and explain distribution patterns of some community traits (Ricotta and Moretti, 2011; Conti and Díaz, 2013). This measure for CWM is computed as:

$$\mathrm{CWM} = \sum_{i=1}^{S} P_i * X_i \tag{3}$$

where CWM is the community-weighted mean value of a given functional trait, P_i is the relative abundance of species i (i = 1,2, ..., S), and X_i is the trait value for species (Ricotta and Moretti, 2011). In order to measure different species more comprehensively and persuasively, we used the importance value (IV) as weight of each species to replace abundance of plant species that has been adopted in previous studies.

So in this paper, the community-weighted mean $\delta^{13}C$ isotope was calculated by:

$$\mathrm{CWM\_}\delta^{13}\mathrm{C} = \sum_{i=1}^{S} IV_i * \delta^{13}C_i \tag{4}$$

In which $\delta^{13}C_i$ is referred to as the $\delta^{13}C$ of plant species i, IV_i is the importance value of plant species i, and S is the total number f species in each stand. CWM_^{13}C is a proxy community WUE index.

3.3. Data analysis

We normalized aboveground biomass and species richness for comparison. Moving average method was used to fit the curve of aboveground biomass and species richness along the rainfall gradient with R software. C_3 and C_4 species were distinguished according to previous works based on $\delta^{13}C$ measurement (Tang and Liu, 2001; Su et al., 2011). The RDA (Redundancy Analysis) was used to explain variance of response variables and executed in CANOCO 5.0 software.

4. Results

4.1. Variance of biomass and species richness along a rainfall gradient

The moving average fitting curve showed different tendencies for the aboveground biomass and plant species richness along the rainfall gradient. Two segments can be distinguished at a visible turning point of approximate 300 mm MAP. From MAP of 450 mm–300 mm, the aboveground biomass showed no clear trend while the species richness decreased significantly with declined rainfall. From MAP of 300 mm–150 mm, the biomass started to drop more markedly than the species richness (Fig. 2a). The C_3 plants exhibited similar variance pattern with the whole community (Fig. 2b). Different from the C_3 plants, consistent

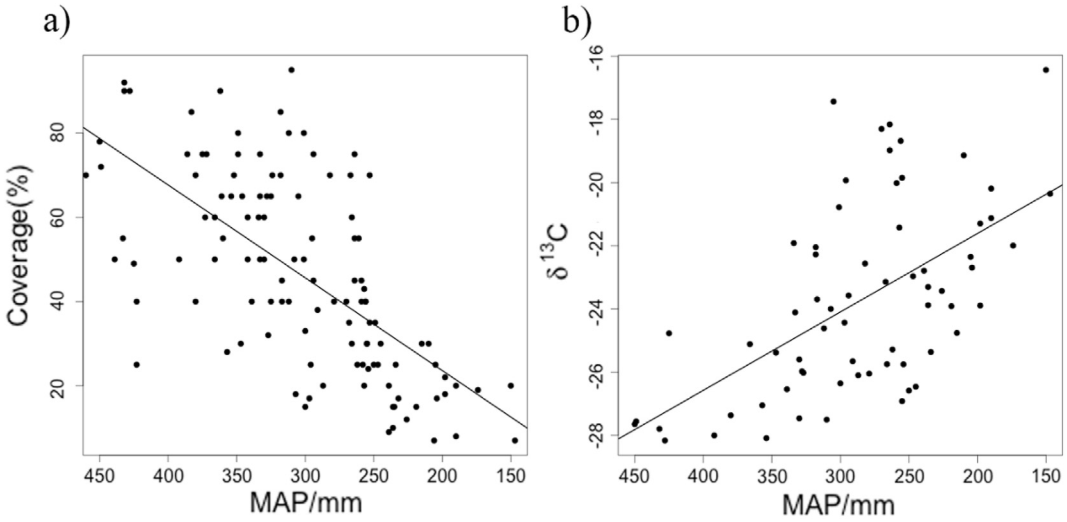

Fig. 4. Linear regression between a) vegetation cover (y = 0.2204x - 20.4817, $R^2 = 0.4336$, $P < 0.001$), and b) community-weighted mean $\delta^{13}C$ (y = −0.0248x−16.647, $R^2 = 0.3327$, P = 0.004) and MAP.

Table 1
C_3 dominants (IV > 0.1) and their constancy indicated as percentage of plots with species occurrence within a certain MAP range.

450–350 mm		350–250 mm		250–150 mm	
Species name	Percentage /%	Species name	Percentage /%	Species name	Percentage /%
Leymus chinensis	37.04	*Stipa krylovii*	48.48	*Stipa krylovii*	79.17
Agropyron desertorum var. *pilosiusculum*	25.93	*Leymus chinensis*	39.39	*Festuca rubra*	29.17
Stipa baicalensis	18.52	*Stipa baicalensis*	12.12	*Agropyron desertorum* var. *pilosiusculum*	25
Carex korshinskyi	18.52	*Agropyron sibiricum*	10.61	*Artemisia frigida*	16.17
Calamagrostis epigeios	11.11	*Festuea rubra*	9.1	*Allium bidentatum*	12.5
Artemisia tanacetifolia	7.41	*Carex kobomugi*	7.58	*Calystegia hederacea*	8.3
Thalictrum petaloideum	3.7	*Allium bidentatum*	7.58	*Artemisia sacrorum*	8.3
Elymus nutans	3.7	*Artemisia frigida*	7.58	*Alhagi sparsifolia*	4.16
Radix sanguisorbae	3.7	*Calystegia hederacea*	7.58	*Peganum harmala*	4.16
Agrimonia pilosa	3.7	*Psammochloa villosa*	6.06	*Psammochloa villosa*	4.16
Artemisia mongolica	3.7	*Artemisia desterorum*	6.06		
Iris ventricosa	3.7	*Agropyron desertorum* var. *pilosiusculum*	6.06		
Carex kobomugi	3.7	*Carex korshinskyi*	4.55		
Potentilla longifolia	3.7	*Achnatherum splendens*	3.03		
Dontostemon micranthus	3.7	*Medicago ruthenica*	3.03		
Hemerocallis minor	3.7	*Allium ledebourianum*	1.51		
Potentilla acaulis	3.7	*Artemisia capillaries*	1.51		
Artemisia lavandulaefolia	3.7	*Potentilla longifolia*	1.51		
Carum carvi	3.7	*Artemisia sacrorum*	1.51		
Bromus ircutensis	3.7	*Melilotus suaveolens*	1.51		
Poa Sphondylodes	3.7	*Lappula myosotis*	1.51		
		Thlaspi arvense	1.51		
		Thalictrum minus var. *hypoleucum*	1.51		
		Lespedeza davurica	1.51		
		Neopallasia pectinata	1.51		
		Thymus mongolicus	1.51		

increase of the C_4 plant species richness along the rainfall gradient was found (Fig. 2c). The biomass of C_4 plant, however, showed an increase followed by a slight decrease with MAP decline (Fig. 2c). Scattered diagram of C_4/C_3 species richness showed a linear increment along the decline of MAP. The C_4 plants accounted for approximate one third of species richness at the lowest MAP in the study region (Fig. 2d).

4.2. Distribution of plant functional groups and functional traits with environmental factors

The $\delta^{13}C$ isotope of C_4 plants ranged between −11‰ and −14‰, and the C_3 plants had a larger distribution range of the $\delta^{13}C$ isotope (from about −24‰ to −30‰), which suggested that the C_3 plants had a low WUE and C_4 plants had the advantage of high WUE. In our study region, the C_3 plants enhanced their WUE in response to water shortage, and were mostly negatively related with MAP. *Astragalus membranaceus* and *Potentilla longifolia* have a neutral relationship with precipitation and were the exceptions to this pattern. However, Fig. 3 showed that the $\delta^{13}C$ isotope of C_4 species had a weak relationship with MAP (note the arrows were almost 90° apart), which meant that C_4 species kept the intrinsic higher WUE than C_3 species along the whole rainfall gradient.

The pattern of vegetation cover with rainfall gradient was similar as that of the aboveground biomass (Fig. 4a). From moist to arid, the CWM $\delta^{13}C$ had an obvious increment along the MAP gradient with a linear relationship (Fig. 4b), indicating that communities under lower rainfall have higher integrative water use efficiency despite reduction in vegetation cover.

Along the MAP gradient, the C_3 plants had a sharp species substitution (Table 1). For the widely distributed *Stipa* species, *Stipa krylovii* replaced *Stipa baicalensis* and became dominant at almost half of the whole stands. There are more dominants with IV value more than 0.1 under intermediate than relatively moist and

Table 2
C_4 dominants (IV > 0.1) and their constancy indicated as percentage of plots with species occurrence within a certain MAP range.

450–350 mm		350–250 mm		250–150 mm	
Species name	Percentage /%	Species name	Percentage /%	Species name	Percentage /%
Cleistogenes squarrosa	55.56	*Cleistogenes squarrosa*	83.33	*Cleistogenes squarrosa*	87.5
Salsola collina	40.74	*Salsola collina*	66.67	*Salsola collina*	66.67
Setaira viridis	22.22	*Chenopodium acuminatum*	54.55	*Tribulus terrestris*	33.33
Chenopodium acuminatum	18.52	*Setaira viridis*	39.39	*Chloris virgata*	25
Artemisia sieversiana	14.81	*Bassia dasyphylla*	18.18	*Bassia dasyphylla*	25
Bassia dasyphylla	14.81	*Kochia prostrata*	7.58	*Setaira viridis*	20.83
Chloris virgata	11.11	*Tribulus terrestris*	7.58	*Suaeda przewalskii*	8.33
Tephroseris kirilowii	7.41	*Chloris virgata*	4.55	*Suaeda heteroptera*	8.33
Agriophyllum squarrosum	3.7	*Agriophyllum squarrosum*	3.03	*Chenopodium acuminatum*	8.33
		Suaeda heteroptera	3.03	*Atriplex sibirica*	8.33
		Artemisia sieversiana	3.03	*Salsola passerina*	4.17
				Agriophyllum squarrosum	4.17
				Suaeda dendroides	4.17
				Atriplex centralasiatica	4.17
				Artemisia sieversiana	4.17

relatively arid climate. The C_4 plants exhibited species increment instead of species substitution along the rainfall gradient (Table 2). Widely distributed species, such as *Cleistogenes squarrosa* and *Salsola collina*, appeared in most plots, whereas drought-adapted species, such as *Suaeda przewalskii* and *Salsola passerine*, were limited to relative arid climate.

At the plant functional group level, the aboveground biomass and plant species richness of C_3 plants had similar variation tendencies as the entire community (Fig. 5). This would result in more C_3 plants in humid and cool areas, contributing to most of grassland cover. Fig. 5 also showed that the C_4 plant species richness had an almost inverse relationship with MAP (note the arrows are almost 180° apart), indicating that C_4 species can tolerate arid environments. A negative relationship between the aboveground biomass of C_4 plants and MAT can be found (Fig. 5).

5. Discussion

Our results showed that due to the different distributions and functional traits of C_3 and C_4 plants, the aboveground biomass and plant species richness of grassland changed inconsistently with the decline of MAP. As MAP has a negative correlation with MAT and high temperature enhances evaporation, both high MAT and low MAP can bring drought stress to plants in the study region (Fig. 3). In fact the aboveground biomass changed inconspicuously at the moist half of the gradient and followed by a sharp decline towards the arid end, while the plant species richness decreased sharply followed by a much weaker decrease along a rainfall gradient from the moist end to the arid end (Fig. 2a). A linear decrease of vegetation cover with the MAP was also found (Fig. 4a). Previous study had verified that the intensified competition for light along the increased vegetation cover could reduce species richness (Borer et al., 2014). Thus a sharp decrease in aboveground biomass as well as vegetation cover can lead to a decline of interspecific competition which may favor C_4 species and thus maintain plant species richness to some extent. The investigated grassland communities also change the plant species composition with more C_4 species and less C_3 species under dryer climate (Table 2). C_4 plants cannot take advantage of the high photosynthesis efficiency because of the shortage of light under high vegetation cover (Kromdijk et al., 2008; Bellasio and Griffiths, 2014). Drought creates a strong light environment through reducing vegetation cover, thus C_4 plants can survive and compensate for the disappearance of C_3 plants. As a result of the increased plant photosynthetic rate associated with a decrease in MAP, WUE also increases (Feng et al., 2011).

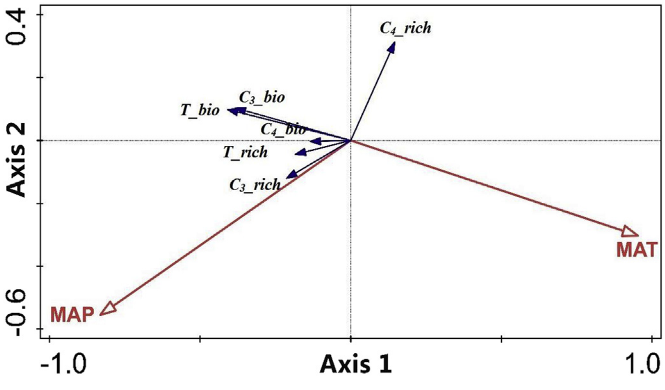

Fig. 5. RDA of grassland community traits and climate factors. The blue arrows represent community traits. T_bio: community total aboveground biomass. T_rich: community total species richness. C_3_bio: biomass of C_3 species. C_3_rich: species richness of C_3 species. C_4_bio: biomass of C_4 species. C_4_rich: species richness of C_4 species. The red arrows represent climate factors. MAP: mean annual precipitation. MAT: mean annual temperature. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

To survive in drought, plants may either use tolerance strategies, or actively enhance their WUE (Zhou et al., 2012). Different plant functional groups may use different strategies (Maseda and Fernández, 2006; Bai et al., 2008; Letts et al., 2010). C_4 plants can alleviate the contradiction between leaf transpiration and carbon absorption with separate locations for CO_2 absorption and photosynthesis under drought and intense light irradiation, because they have reduced stomatal conductance and increased WUE (Monson et al., 1986; Yu et al., 2004). Due to this physiological advantage, C_4 plants are distributed widely in arid regions, and this helps retain the species richness of plant communities. C_3 plants could slightly increase intrinsic WUE through the decrease of stomatal conductance and the ratio of intercellular CO_2 to ambient CO_2 concentrations under drought stress (Yu et al., 2004; Singh and Reddy, 2011; Ocheltree et al., 2014). Due to different drought responses, these two functional groups have discrepant changing tendency and they both constitute the complex community.

C_4 plants distributed more under lower rainfall regime (Fig. 2d). This indicated that they can compensate for the shortage of C_3 species and maintain species richness and make it possible for grassland communities to conserve their stability and resilience (Tilman et al., 2006; Volaire et al., 2009; Van Ruijven and Berendse, 2010). Hence, under the current rapid warming and intensifying drought conditions occurring in many arid regions, it is likely that C_4 plants may spread in temperate steppes. Species richness may respond less clearly to these changing conditions than stand biomass and plant functional group composition.

There was a great variation for species richness along rainfall gradient. This might have been caused by heterogeneities of landforms, soils, and microenvironments. For instance, Fig. 3 shows that the carbon isotopes of C_3 and C_4 plants had opposite relationships with MAP, but there were several species with significant positive relationships to soil organic carbon and total nitrogen instead of MAP or MAT, such as *Gueldenstaedtia multiflora*, *Potentilla longifolia*, *Astragalus scaberrimus* and *Cleistogenes squarrosa*. Finally, although we carefully avoided current overgrazing and cultivation, historical human activities and climate change may leave traces on the structure and species composition of the grassland sites in this region (Li and Xie, 2013).

Obviously, there were thresholds of precipitation (300 mm) for the nonlinear changes of biomass and species richness. Our data suggest that the decreased vegetation cover might favor C_4 plants; however, how 300 mm precipitation acting as a threshold remains a challenge and requires further investigation. We suggest that such topics as light environment under different vegetation covers and differences in light use between C_3 and C_4 plants should be the priority in future studies.

6. Conclusions

Through systematic study of grassland communities in the central Inner Mongolian steppe, we illustrated and explained the different rates of decrease between stand biomass and plant species richness along a precipitation gradient with a shift in functional group composition favoring C_4 plants. C_3 plants had declining biomass with declined rainfall, which led to an overall decrease of community biomass. Plant communities under low rainfall retain higher percentages of C_4 species and higher community-weighted mean WUE. Temperate grasslands are projected to develop more C_4 plants and enhance integrative WUE under anticipated future climatic drying.

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