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Effect of soil moisture and atmospheric humidity on both plant productivity and diversity of native grasslands across the Loess Plateau, China

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ABSTRACT

Water is a key element in building and maintaining regional ecosystems functions, particularly in arid and semi-arid regions, in which ecosystem productivity, surface energy balance, and water availability are closely interconnected. However, the effects of differences in soil moisture levels at different depths and humidity index involved MAT and MAP on plant diversity have received only scant attention. To determine effects of soil moisture and humidity index on both plant productivity and diversity of native grasslands on the Loess Plateau, China, a gradient analysis of soil moisture and above- and below-ground properties of plant communities showed that vegetation cover and above- and below-ground biomass were significantly and positively correlated to the levels of soil moisture. More specifically, the below-ground biomass was significantly and positively correlated to moisture in the top 10 cm layer of soil, whereas plant height, litter biomass, and root-to-shoot ratio were unrelated to the level of soil moisture. Plant diversity (richness index and the Shannon–Wiener diversity index) was significantly and positively correlated to a greater degree with moisture in the topsoil (0–5 cm layer) than in the subsoil, and was also closely correlated to the humidity index. Overall, changes in plant diversity in arid and semi-arid grassland ecosystems are closely determined by soil moisture and atmospheric humidity, and that higher moisture content in soil and higher atmospheric humidity favour greater plant diversity.

1. Introduction

Water is fundamental to the biophysical processes that sustain ecosystem functions, particularly in the arid and semi-arid regions where tight coupling exists between ecosystem productivity, surface energy balance, and water source availability (Potts et al., 2006; Heisler-White et al., 2008; Yang et al., 2014). Water availability is the primary constraint to plant communities in many terrestrial ecosystems (Weltzin et al., 2003; Zhou and Shangguan, 2007). Soil water controls plant canopy cover, leaf area, transpiration, and community composition particularly in arid and semi-arid regions (Cooper et al., 2006; Huang et al., 2013; Wu et al., 2016), The water stored in different soil layers is recognized as an important driver of productivity and sustainability of arid and semi-arid terrestrial ecosystems (Deng et al., 2016), because vegetation strongly affects the water cycle, soil erosion, and run-off, and interactions between vegetation and soil water are fundamental to ecological processes in arid and semi-arid regions.

The productivity and diversity of plant species within grassland communities in arid and semi-arid regions have most often been related to climatic, geographic and edaphic heterogeneity factors (Enright et al., 2005; Chen et al., 2007; Vásquez-Méndez et al., 2010; Sanchez-Mejia et al., 2014; Wu et al., 2014a, b; Zhang et al., 2016). Regional climate (precipitation and temperature) and soil moisture can play decisive roles in shaping community structure and large scale species distributions (Peters et al., 2012). The availability of soil moisture may affect species richness and distributions, as only a few species are adapted to extremely water poor conditions

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(Wu et al., 2016). Moreover, soil water is the primary constraint to plant communities (Heisler-White et al., 2008), and influences the uptake of water by plants and species succession in a plant community. Variation in soil water can also influence grassland plant communities and soil properties directly and indirectly (Wu et al., 2013). Recent studies have focused mainly on the effects of soil moisture on soil nutrients (Wu et al., 2013), soil carbon storage (Deng et al., 2014), and soil microbial structure (Bell et al., 2014; Zhang et al., 2014a). Some researchers have also worked on soil moisture (Wu et al., 2016), but studies on its effect on plant productivity and plant diversity have been somewhat limited (Kardol et al., 2010), especially in large-scale regions (Wu et al., 2014a). In addition, among the factors influencing species distributions, precipitation may be an especially important limiting factor in the arid and semi-arid regions; hence, changes in precipitation regimes may lead to substantial alterations in community composition and ecosystem structure (Adler and Levine, 2007).

In the Loess Plateau in north-western China, with lower mean annual precipitation and higher evaporation, availability of soil moisture is generally low (Shangguan, 2007); water stored at different depths is critical to plant growth and serves as a key source of water for sustaining ecosystems in this region (Yang et al., 2014). In addition, lower soil moisture content also leads to land degradation and loss of plant diversity. Vegetation is important in regulating hydrological processes in arid and semi-arid areas (Zhang et al., 2014b; Zhou and Shangguan, 2006). It is therefore necessary to study the relationship between soil moisture and plant community on the Loess Plateau. In addition, precipitation and climate can affect the spatial heterogeneity of soil moisture (Longobardi, 2008), which, in turn, affects plant diversity in ecosystems (Knapp et al., 2002; O'connor et al., 2001). Therefore, understanding how soil water heterogeneity and atmospheric humidity (climatic humidity index, a bioclimatic index developed by Yang et al., 2007) affect plant community structure in arid and semi-arid regions has several major implications for both the scientific community and for decision makers (Wu et al., 2014a).

The present study covered 81 sites dominated by natural grasslands across the Loess Plateau to test the hypothesis that soil moisture and atmospheric humidity are the main factors that influence plant productivity and plant diversity in arid and semi-arid grasslands. The study sought answers to the following questions: (1) What is the relationship between soil moisture and properties of the above- or below-ground structures of plant communities? (2) How does soil water heterogeneity affect plant diversity? (3) How does the humidity index affect plant diversity in natural grasslands of the arid and semi-arid regions on the Loess Plateau?

2. Materials and methods

2.1. Characteristics of the study area

The Loess Plateau covers approximately 0.64 million square kilometres. The region is a transition zone between sub-humid and semi-arid to arid climate, characterized by a large south–north precipitation gradient. The mean annual temperature ranges from 3 °C to 12 °C; mean annual precipitation, from 100 mm to 800 mm; and elevation, from 500 m to 2500 m. Except for the most humid south-eastern part, which is dominated by forests, over 80% of the Loess Plateau is covered by arid and semi-arid grassland ecosystems. The main grassland species include *Agropyron cristatum* (Linn.) Gaertn., *Agriophyllum squarrosum* (L.) Moq., *Artemisia giraldii* Pamp., *Artemisia ordosica* Krasch., *Artemisia sacrorum* Ledeb., *Bothriochloa ischaemum* (L.) Keng, *Cleistogenes songorica*, *Lespedeza davurica* (Laxm.) Schindl., *Stipa bungeana* Trin. and *Stipa grandis* P. Smirn.

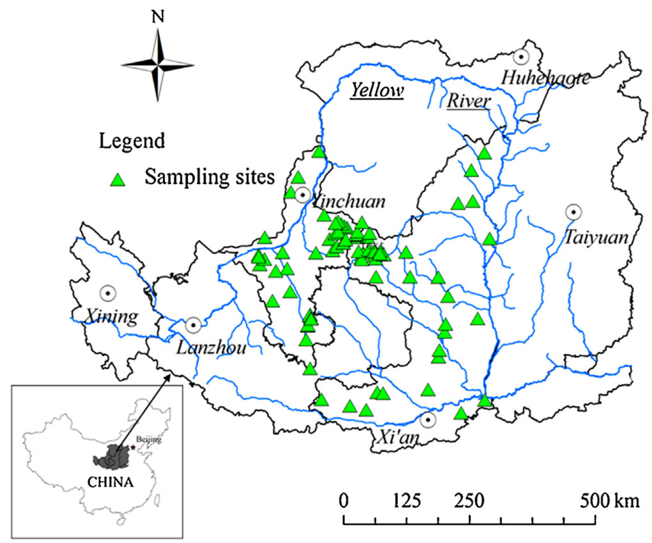

Fig. 1. Location of sampling sites used in this study.

2.2. Arrangement of plots

In the summer (July–August) of 2011, when plant biomass had reached its peak, we sampled 81 grassland sites across the Loess Plateau (Fig. 1). To elucidate the relationship between grassland biomass and climate, along with other natural factors, we investigated and sampled natural grasslands that had been free from any human interference. At each site, 10 plots (1 m × 1 m), or quadrants, were established along a 100–200 m long linear transect for surveying the plant community. The quadrants were numbered, and the following observations were recorded for the odd-numbered quadrants: canopy coverage and height, species composition and height, abundance (number of individuals per plot), and the above-ground biomass of individual species. In the even-numbered quadrants, canopy coverage and height, and above- and below-ground biomass in the 0–30 cm soil profile, were recorded. Plant height was measured with a steel tape. Each survey plot of 1 m × 1 m was divided into 100 small quadrants (0.1 m × 0.1 m), and canopy cover of the plant community within the larger quadrants was estimated by extrapolating the data from the smaller quadrants, retaining the proportions of different species.

2.3. Sampling and measurements

In the odd-numbered plots, the above-ground parts of plants, including both live biomass and standing dead biomass produced in the current year, were cut, sorted by species, labelled, and placed into envelopes. The majority of plant species were identified in the field; the unidentified specimens were dried in a plant press and were later identified by plant taxonomists. In the even-numbered plots, all the above-ground green plants were cut, collected, labelled, and put into envelops. In addition, all litter was also collected and put into envelopes and labelled. To measure the below-ground biomass, 3–5 soil samples were collected from four layers in each plot, namely 0–5 cm, 5–10 cm, 10–20 cm, and 20–30 cm, with a root corer 9 cm in diameter. Most of the roots from the soil samples could be separated by using a 2 mm sieve. The remaining finer roots were separated by spreading the samples in shallow trays, filling them with water, and allowing the overflow to pass through a 0.5 mm sieve. No attempt was made to distinguish between living and dead roots. All the roots thus collected were oven-dried at 65 °C and weighed to within 0.01 g. The origi-

Table 1
One-way ANOVA analysis of grassland community characteristics and soil properties among the sampling sites across the Loess Plateau. **indicates significant difference.

Community characteristics /soil properties	Mean	SE	95%CI		F	Df	Sig. (P)
			Lower Bound	Upper Bound			
Coverage (%)	42.90	1.19	40.57	45.24	59.91	80	<0.0001**
Height (cm)	39.29	2.14	35.08	43.49	3.32	80	<0.0001**
Above-ground biomass ($g\,m^{-2}$)	167.00	6.43	155.07	180.33	25.57	80	<0.0001**
Litter ($g\,m^{-2}$)	115.29	6.88	101.78	128.79	14.74	80	<0.0001**
Below-ground biomass ($g\,m^{-2}$)	415.52	27.57	361.33	469.71	3.32	80	<0.0001**
Total biomass ($g\,m^{-2}$)	582.52	34.00	516.40	650.04	16.43	80	<0.0001**
Root/Shoot ratio	2.49	3.78	2.33	3.60	4.56	80	<0.0001**
Richness index (*R*)	7.45	0.18	7.09	7.82	15.45	80	<0.0001**
Shannon-Wiener diversity index (*H*)	1.60	0.03	1.55	1.65	11.44	80	<0.0001**
Evenness index (*E*)	0.84	0.01	0.82	0.86	2.27	80	<0.0001**
0–30 cm soil water content (%)	7.64	0.35	6.94	8.33	16.55	80	<0.0001**
0–30 cm soil bulk density ($g\,cm^{-3}$)	1.29	0.01	1.26	1.30	14.04	80	<0.0001**
0–30 cm soil water storage (mm)	26.61	1.16	24.32	28.90	13.40	80	<0.0001**

Table 2
Pearson correlation analysis of the relationships between the characteristics of plant community and soil water storage at different soil layers/depths. $n = 81$. Soil depths is cumulative soil layers from top (0–5 cm) to sub-soils (5–10, 10–20 and 20–30 cm, respectively).

Plant community characteristics	Soil water storage in four soil layers (cm)			
	0–5	5–10	10–20	20–30
Coverage (%)	0.280*	0.460**	0.414**	0.423**
Height (cm)	0.038	−0.087	−0.089	−0.004
Above-ground biomass ($g\,m^{-2}$)	0.286**	0.269**	0.179	0.225*
Litter ($g\,m^{-2}$)	0.201	0.102	−0.016	−0.002
Below-ground biomass ($g\,m^{-2}$)	0.316**	0.279*	0.162	0.198
Total biomass ($g\,m^{-2}$)	0.358**	0.322**	0.194	0.239*
Root/Shoot ratio	0.078	0.081	−0.014	−0.011

Plant community characteristics	Soil water storage in four soil depths (cm)		
	0–10	0–20	0–30
Coverage (%)	0.407**	0.426**	0.439**
Height (cm)	−0.031	−0.061	−0.044
Above-ground biomass ($g\,m^{-2}$)	0.300**	0.249*	0.246*
Litter ($g\,m^{-2}$)	0.161	0.075	0.046
Below-ground biomass ($g\,m^{-2}$)	0.321**	0.252**	0.236*
Total biomass ($g\,m^{-2}$)	0.367**	0.292**	0.278*
Root/Shoot ratio	0.086	0.039	0.018

* Correlation is significant at the 0.05 level (P < 0.05) (2-tailed).
** Correlation is significant at the 0.01 level (P < 0.01) (2-tailed).

nal volume of each soil core and its dry mass after oven-drying at 105 °C were measured. The moisture content of the soil samples was determined gravimetrically and expressed as a percentage of the dry weight of soil. Soil bulk density ($g\,cm^{-3}$) of the four soil layers was measured (3 replicates) using a soil bulk sampler, in the form of a stainless steel cutting ring 5 cm in diameter and 5 cm tall, at points adjacent to soil sampling points in each plot.

2.4. Soil water storage

Soil water storage (SW*s*) was calculated using the following formula:

$$SW_s = BD \times (1 - f_c(\%)) \times SW \times D/10 \quad (1)$$

where SW_s is the soil water storage (mm); BD is soil bulk density ($g\,cm^{-3}$); fc is the coarse fraction (particles larger than 2 mm) in the soil; SW is the soil moisture content (%); and D is soil thickness (cm).

2.5. Species diversity

Species richness is a measure of the number of species in each plot. The richness index (*R*) and Shannon–Wiener diversity index (*H*) were calculated as follows:

$$\text{Richness index (R)}: R = S \quad (2)$$

$$\text{Shannon – Wiener diversity index } (H): H = -\sum_{i=1}^{s}(Pi \ln Pi) \quad (3)$$

$$\text{Evenness index } (E): E = \frac{H}{\ln S} \quad (4)$$

where *S* is the total number of species in the grassland community; *H* is the Shannon–Wiener diversity index; and *Pi* is the density proportion of *i* species

$$P_i = \frac{RH_i + RA_i + RB_i}{3} \quad (5)$$

where RH_i, RA_i, and RB_i are the relative height, relative abundance, and relative biomass of *i* species in each plot.

2.6. Humidity index

Because of the significant correlation between mean annual temperature and mean annual precipitation ($P < 0.05$) in China, we used the humidity index (HI) (Yang et al., 2007) as a bioclimatic index to explore the relationship between plant community structure (plant biomass and diversity) and climate.

$$HI = \frac{MAP}{MAT + 10} \quad (6)$$

where MAT and MAP are the mean annual temperature and mean annual precipitation, respectively, for 40 years (1970–2010), calculated from the data obtained from the China Meteorological Data Sharing Service System.

2.7. Data analysis

One-way analysis of variance (ANOVA) was used for identifying the differences among the sites in terms of grassland community biomass (above-ground biomass, below-ground biomass, litter biomass, and total biomass), vegetation cover, height, richness index, Shannon–Wiener diversity index, and evenness index. Linear regression analysis was used for identifying correlations between plant diversity and soil water storage or humidity index. The level of significance was 0.05 unless otherwise stated, and SPSS ver. 16.0 (SPSS, Chicago, Illinois, USA) was used for the ANOVA.

3. Results

Sites across the Loess Plateau differed significantly ($P < 0.0001$) in terms of vegetation cover, plant height, biomass of various kind, root-to-shoot ratio, plant diversity (all the three indices), soil moisture, and bulk density (Table 1).

Overall, the relationships between vegetation cover, above- or below-ground biomass, and soil water storage were stronger in the two upper layers (0–5 cm and 5–10 cm) than in the two deeper layers (10–20 cm and 20–30 cm) (Table 2). Vegetation cover and above- and below-ground biomass were significantly and positively correlated with soil water storage in the top layer (0–30 cm) ($P < 0.05$, Table 2) but none of the other parameters (plant height, litter, and root-to-shoot ratio) showed any correlation with soil water storage in the top layer ($P > 0.05$, Table 2).

Plant diversity was significantly influenced by the differences in soil water storage in the top layer (0–5 cm) but not in the deeper layers (Fig. 2): plant richness index and Shannon–Wiener diversity index showed very strong and significant correlation ($P < 0.01$) with soil water storage in the top layer but not in the other layers (Fig. 2) but the evenness index showed no such correlation ($P > 0.05$, Fig. 2). Richness index and Shannon–Wiener diversity index were significantly and positively correlated with soil water storage in the 0–30 cm layer as well ($P < 0.05$) (Fig. 3), whereas the evenness index was not ($P > 0.05$, Fig. 3), although it was correlated with soil water storage in the 0–20 cm layer ($P < 0.05$, Fig. 3). The first two indices were closely correlated also with the humidity index (Fig. 4).

The below-ground biomass decreased with depth (Fig. 5), whereas soil water storage increased with depth (Fig. 5). Correlations between below-ground biomass and soil water storage varied, depending on the depth (Fig. 5): the two were positively and significantly ($P < 0.01$) correlated only in the top two layers (0–5 cm and 5–10 cm, Fig. 5).

4. Discussion

More extensive vegetation cover can protect the soil better against erosion due to rainfall and increase the absorption of water by the soil (Vásquez-Méndez et al., 2010). Our results showed

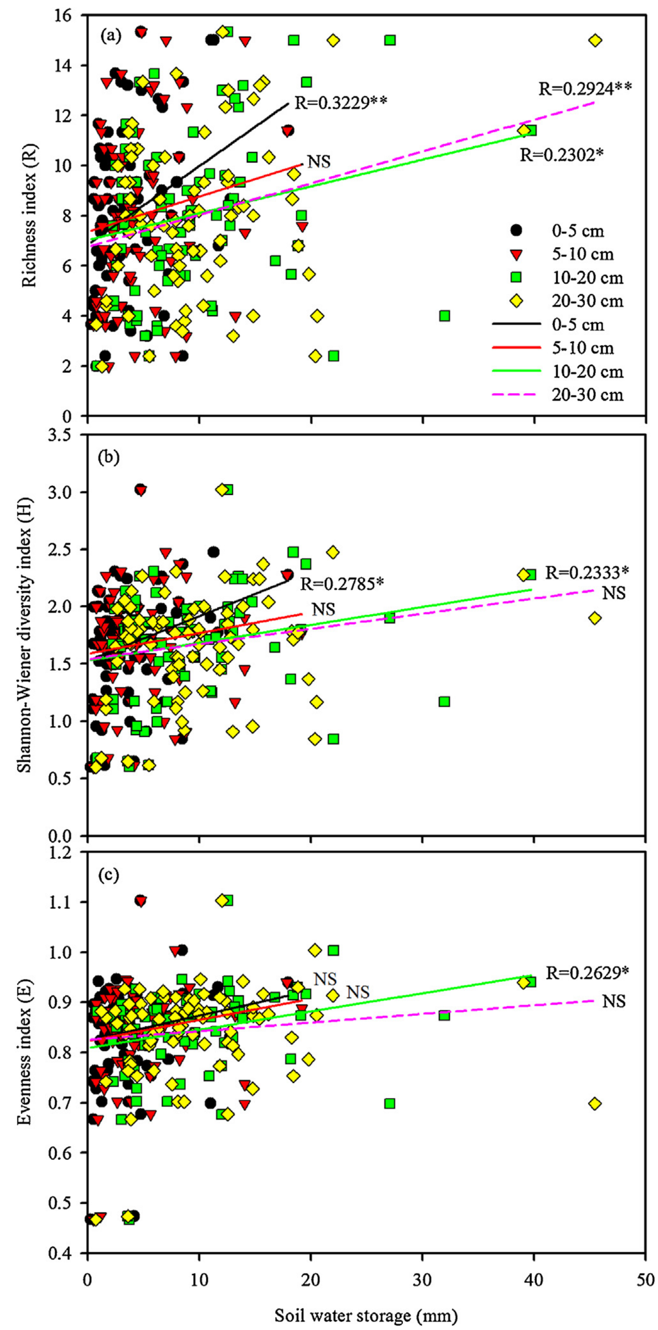

Fig. 2. The linear regression analysis relationships between plant diversity (Shannon–Winner index, evenness index, richness index) and soil water storage at different soil layers. Note: R is correlation coefficient; **indicate $P < 0.01$, *indicate $P < 0.05$, NS indicates no significant correlation ($P > 0.05$).

that vegetation cover, above-ground biomass, and below-ground biomass were significantly and positively correlated with water storage in the top layer of the soil—results that are consistent with those obtained in other areas such as the Qinghai-Tibetan Plateau in China (Wu et al., 2013) and Oak Ridge in USA (Kardol et al., 2010). These results point to positive interaction effects between vegetation cover and soil water storage in the grasslands of arid and semi-arid regions. Deng et al. (2014) reported that the grassland with higher retention of water by soil had more extensive vegetation cover and productivity compared to the grassland community with lower soil water condition. The present study found that soil water storage influenced not only the quantity of plant biomass but also the distribution of below-ground biomass (Fig. 5), an obser-

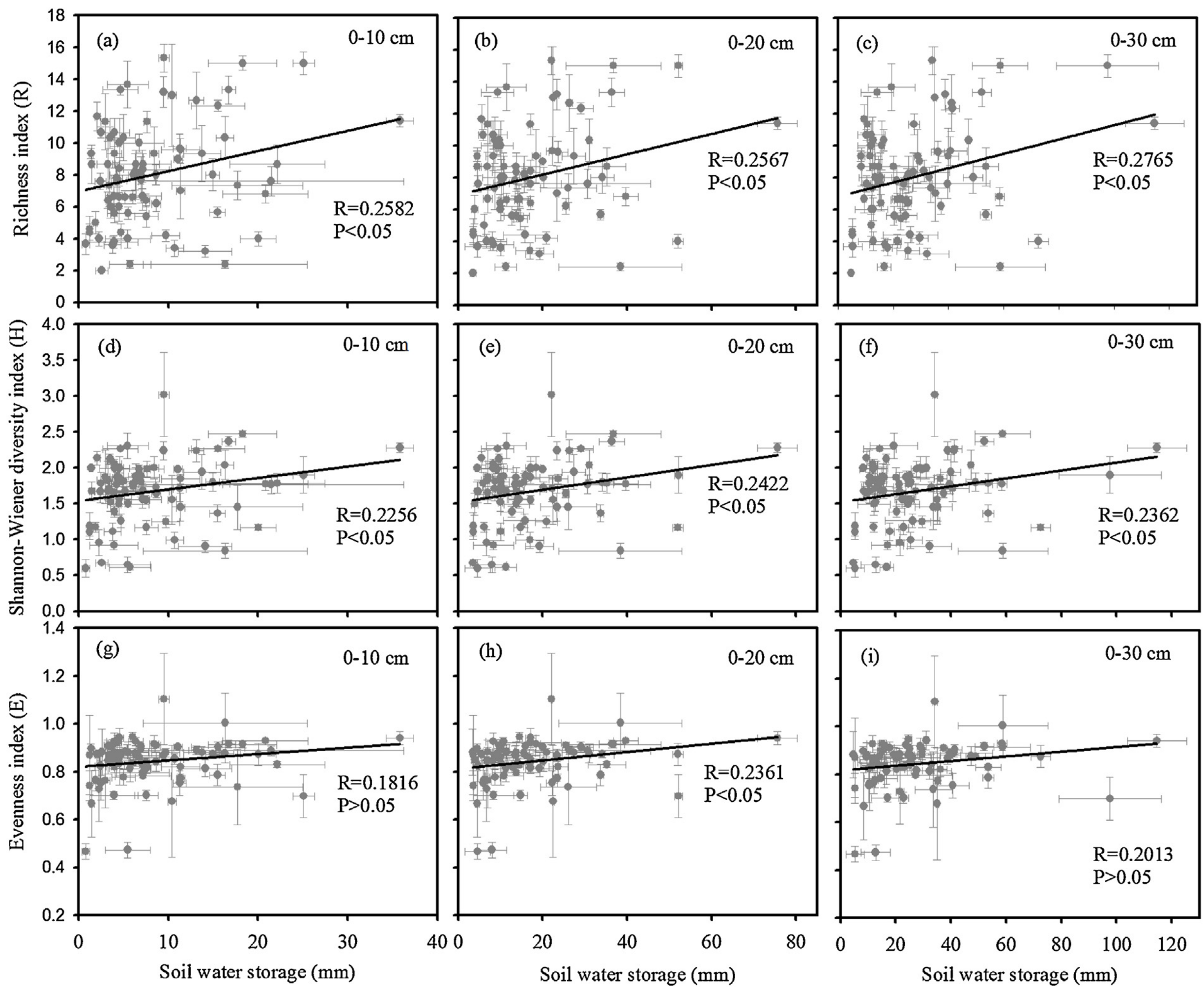

Fig. 3. The linear regression analysis relationships between plant diversity (Shannon–Winner index, evenness index, richness index) and soil water storage at different soil depths. Note: R is correlation coefficient; P > 0.05 indicates no significant correlation.

Table 3
Pearson correlation analysis of the relationships between the humidity index (HI) and soil water storage at different soil layers/depths. $n = 81$.

	Soil layers (cm)				Soil depths (cm)		
	0–5	5–10	10–20	20–30	0–10	0–20	0–30
HI	0.504**	0.415**	0.349**	0.456**	0.494**	0.436**	0.459**

** Correlation is significant at the 0.01 level (P < 0.01) (2-tailed).

vation that agrees with that of Zhou and Shangguan (2007), who found that soil water was a key factor in the distribution of fine roots in the Loess Plateau. However, our study also found that it is mainly the moisture in the top layer (0–10 cm) that had a positive impact on below-ground biomass (P < 0.01), probably because the vegetation cover influenced the moisture content of surface soil (P < 0.05). Although we do not have data to test this hypothesis explicitly, earlier reports indicate that plant cover regulates run-off (Vásquez-Méndez et al., 2010) and that canopy coverage alters such parameters of the micro-environment as the bulk density of soil, soil infiltration rate, soil porosity, and oxygen concentration (Wu et al., 2010), which, in turn, increase the amount of water available to plants and thus biomass production (Bever, 2003).

Species richness or diversity is an essential characteristic of communities and plays an important role in regulating the structure and function of an ecosystem (Howard and Lee, 2003). Although one study reported a negative correlation between soil moisture and plant diversity (species richness) in an alpine wetland (Wu et al., 2013), our results show the opposite results in the arid and semi-arid regions of the Loess Plateau and are consistent with those obtained by Wu et al. (2014a, b). The difference may be attributed to differences in the threshold value of soil moisture content. From the results reported by Wu et al. (2013), we estimate that the average soil moisture content in the 0–20 cm layer at the 15 sites in the alpine wetland ecosystem on the Qinghai-Tibetan Plateau was 55%. In the present study, it was 7.64% in the 0–30 cm layer (Table 1). Soil moisture alters the growth and relative superiority of dominating species (Wu et al., 2013): in the alpine wetland ecosystem, because species density was high, competition decreased plant diversity; in the arid and semi-arid grassland ecosystem, species density was low, and competition was therefore limited (Wu et al., 2014a, b). Thus, plant diversity increased with increasing levels of soil water storage in the arid and semi-arid grasslands (Figs. 2 and 3), revealing a positive correlation between species diversity and soil water storage in arid or semi-arid regions with lower soil water content but a negative correlation between

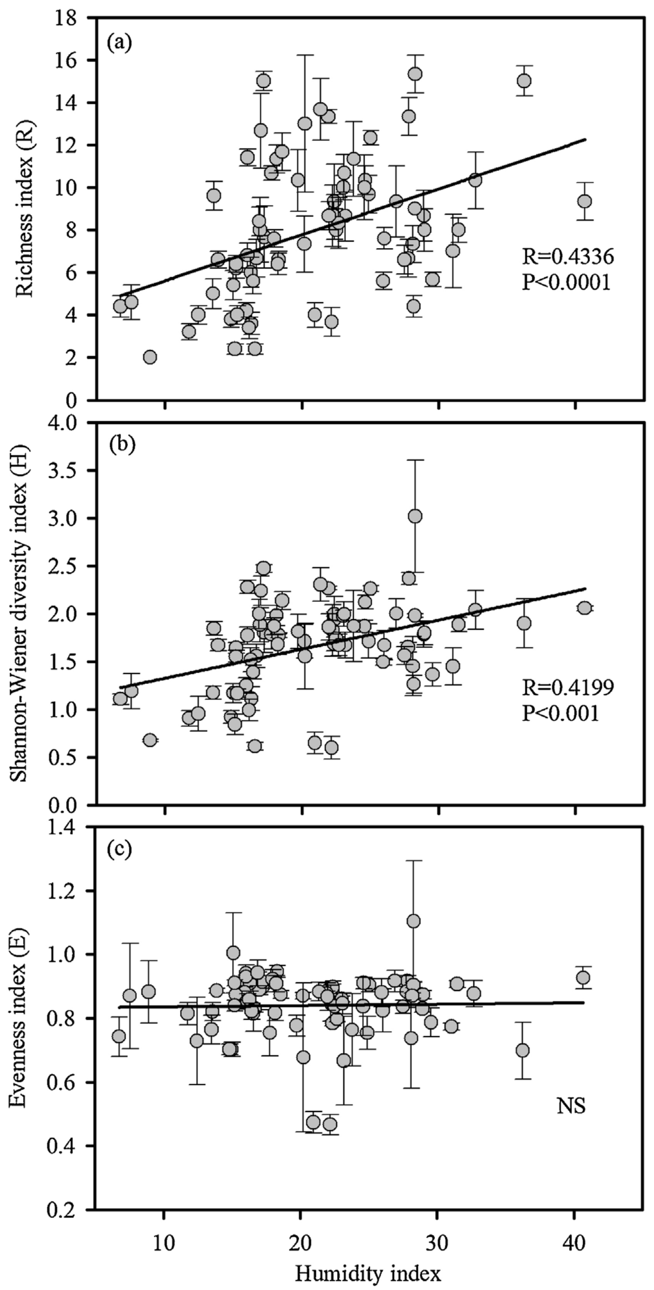

Fig. 4. The linear regression analysis relationships between plant diversity (Shannon–Winner index, evenness index, richness index) and humidity index. Note: ns, no significant correlation. Note: R is correlation coefficient; **P < 0.01; *P < 0.05; NS, no significant correlation.

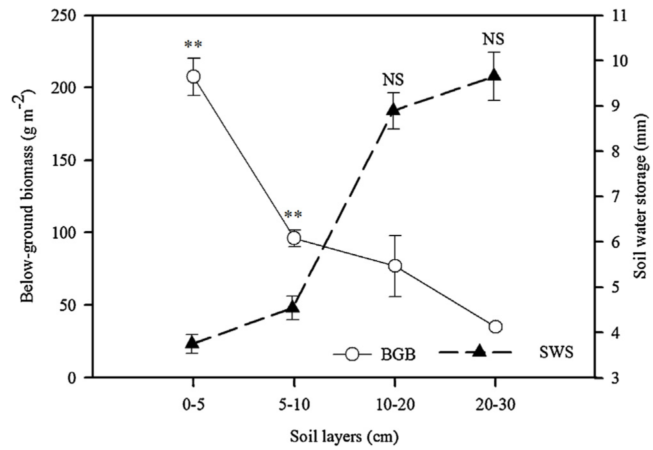

Fig. 5. The vertical distribution of BGB (below-ground biomass) and SWS (soil water storage). The values are mean ± SE. Significant correlation between BGB and SWS indicated by symbols, **P < 0.01; NS, no significant correlation.

the two in humid or semi-humid areas with higher soil water content. Soil water thus plays an important role in regulating plant productivity and plant diversity in semi-arid grassland ecosystems and generally, plant–soil feedback effects can alter the structure of a plant community and soil properties (Bezemer et al., 2006).

Moreover, plant diversity (richness index and Shannon–Wiener diversity index) was also closely and positively correlated with humidity index (Fig. 4), which, in turn, is closely and positively related to mean annual precipitation. So far, many studies have found that changes in precipitation as a result of climate change were among the factors that alter plant composition (Kardol et al., 2010; Klanderud et al., 2015). Xi et al. (2015) found that the amount of precipitation during the growing season plays a limited role in shaping the structure of the grassland community; Giladi et al. (2011) reported that species richness was affected mainly by the precipitation gradient; and Fry et al. (2014) observed that decreased rainfall lowers species richness in semi-arid grasslands. In fact, precipitation influences plant diversity by changing the soil water content as a result of infiltration, and soil water storage is closely and positively related to the humidity index (Table 3).

5. Conclusions

Vegetation cover had a positive effect on the moisture content of surface soil, and species diversity and productivity of plant communities can be influenced by soil moisture. In particular, species diversity in the present study was greatly influenced by soil moisture in the 0–10 cm layer. Changes in precipitation as a result of climate change were among the important factors that alter plant diversity. At the same time, it is soil moisture that affects the distribution of below-ground biomass and significantly affects the quality of root biomass in the surface soil layers. Soil moisture plays an important role in regulating plant productivity and plant diversity in arid and semi-arid grassland ecosystems.

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