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## Soil Water Availability Drives Changes in Community Traits Along a Hydrothermal Gradient in Loess Plateau Grasslands<sup>☆</sup>

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### ABSTRACT

Plant functional traits can be used to predict ecosystem responses to climate gradients, yet precipitation explains very little variation for most traits. Soil water availability directly influences plant water uptake and thus may assist with the improvement of plant trait–water relationships. However, this promise remains poorly realized due to rare tests. Here, we provide the first study that attempts to link climate factors, vertical soil water availability, and community composition at a regional scale. Our study paired field-measured vertical soil available water (0–300 cm) and community functional composition at 46 herbaceous grassland sites along a steep hydrothermal gradient in the Loess Plateau of Central China. Community functional composition was expressed via community-weighted means of eight traits. Structural equation modeling was employed to evaluate the role of vertical soil available water content, controlled by precipitation and air temperature, in affecting plant community-weighted traits. We found that soil available water content at depths of 20–100 cm was typically responsible for mediating the effects of precipitation and air temperature on plant community composition. This emerged as the predominant factor to explain variations in grassland response traits, including leaf area, specific leaf area, and leaf dry matter content. These traits exhibited clear drought-induced shifts along soil desiccation gradients and responded to drier conditions by reducing leaf area/specific leaf area and increasing leaf dry matter content. Our findings rehighlighted soil water availability as the core driver that needs to be considered in the restoration and management of dryland ecosystems.

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### Introduction

The determination of how plant communities respond to hydrothermal (precipitation and temperature) gradients is a major challenge in dryland ecosystems (Suding et al. 2008). Precipitation and temperature have been two of the most commonly considered drivers of plant form and function at the global and regional scales (Moles et al. 2014). They affect plant growth and reproduction, such as leaf energy balance and plant growth rate. In particular,

concurrent changes in precipitation and temperature at both spatial and temporal scales potentially trigger complex interactive effects on ecosystem structure and functioning in many ways (Luo et al. 2008), with change in water availability as one of the primary mechanisms (Griffin-Nolan et al. 2018). For example, these changes in water availability will alter plant community assembly (Schellenberger Costa et al. 2017), soil and water conservation (Fu et al. 2016), carbon sequestration (Taylor et al. 2017), and other ecosystem properties. Indeed, the sensitivity of ecological responses to changes in water availability may vary between ecosystems; however, the underlying mechanism of this variability remains fragmented (Griffin-Nolan et al. 2018).

A functional trait–based approach has been proposed to characterize the consequences to ecosystems in response to environmental changes (Valencia et al. 2015). This approach categorizes any adaptations, via the morphologic and physiologic characteristics of plants to changes in environmental conditions as “response traits” (Suding et al. 2008), such as leaf size conveying different

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water and heat balances. Response traits influence the capacity of species to colonize or thrive in a given habitat and to persist in the face of environmental changes (Díaz et al. 2013). In terms of water availability, plant traits associated with the acquisition and use of water are the primary response traits. A wealth of literature has described trait variation along water availability gradients by only considering intraspecific or interspecific variations at species level (Choat et al. 2007; Fauset et al. 2012; Gleason et al. 2013). However, most commonly measured plant traits do not align well with water availability gradients (Moles et al. 2014). In contrast, community-level traits that can explain community shifts are usually masked along environmental gradients due to both intraspecific and interspecific variations (Schellenberger Costa et al. 2017). Thus, community-level traits often capture more variation than species-level traits. Siefert et al. (2015), for example, found that intraspecific trait variation only accounted for 32% of the total trait variation among communities on average by conducting a global meta-analysis. Therefore, scaling trait data to the community level (community functional traits) helps to enhance trait-water relationships (Suding et al. 2008). However, few studies (4%, according to Griffin-Nolan et al. 2018) have endeavored to assess plant traits at the community level, due to inherent requirement of extra time and effort. For all these reasons, community weighting deserves more attention toward the forecasting of ecosystem responses to water availability gradients.

Plant traits have long been observed and measured by ecologists along precipitation gradients to identify the response traits to water availability. However, precipitation explains little in the way of global and regional variations in commonly measured plant traits (Griffin-Nolan et al. 2018). For example, mean annual precipitation (MAP) captured only 0.1% of the variances in specific leaf area on a global scale (Moles et al. 2014) and, further, was not strongly associated with specific leaf area in the Mediterranean grasslands of Central Spain (Rota et al. 2017). These weak correlations revealed that mean annual precipitation was a poor proxy of water availability, because precipitation is not intrinsically linked to water access for plants (Moles et al. 2014). In contrast, soil available water is a key proxy of water availability that is employed in many ecological studies (Collins et al. 2018; Minasny and McBratney 2018). It is controlled by precipitation and temperature (Reich et al. 2018) and also influenced by either localized or global variations in textural composition, soil structure, organic matter content, and other factors (Dymond et al. 2017). Consequently, soil available water is widely recognized as a direct water resource that affects vegetation structure and organization (Minasny and McBratney 2018). Despite its promise for linking hydrothermal gradients and plant community composition, no tests have yet been conducted to evaluate the contribution of soil available water at different depths, to the relationships between hydrothermal gradients and plant traits.

The Loess Plateau of China was considered to be an ideal region for examining water availability controlling trait variability along a strong hydrothermal gradient. This area lies within the Asian continental monsoon region. Due to its great geographical magnitude, the average annual precipitation varies from 798 mm in the southeast to 123 mm in the northwest, with average annual temperatures that range from 14.8°C to 3.0°C (1981–2010). These regional climate variabilities result in the significant spatial heterogeneity of water availability (Wang et al. 2016). In addition, low precipitation coupled with inappropriate land use and poor management makes local ecosystems extremely vulnerable and susceptible to water scarcity (Wang et al. 2010). Therefore, water availability appears to be a key limiting factor for the sustainability of ecosystems (Feng et al. 2016). For this study, we sampled 46 herbaceous grassland sites along a southeast to northwest transect

in the Loess Plateau to examine how variations in precipitation and air temperature affect soil available water in the vertical soil profile and how that further affects community functional traits. We thus endeavored to address the following three questions: 1) In what ways does soil available water in the vertical soil profile affect community functional traits? 2) How do community response traits change in response to environmental gradients? and 3) How does soil available water mediate the relationships among precipitation, air temperature, and community response traits?

## Materials and Methods

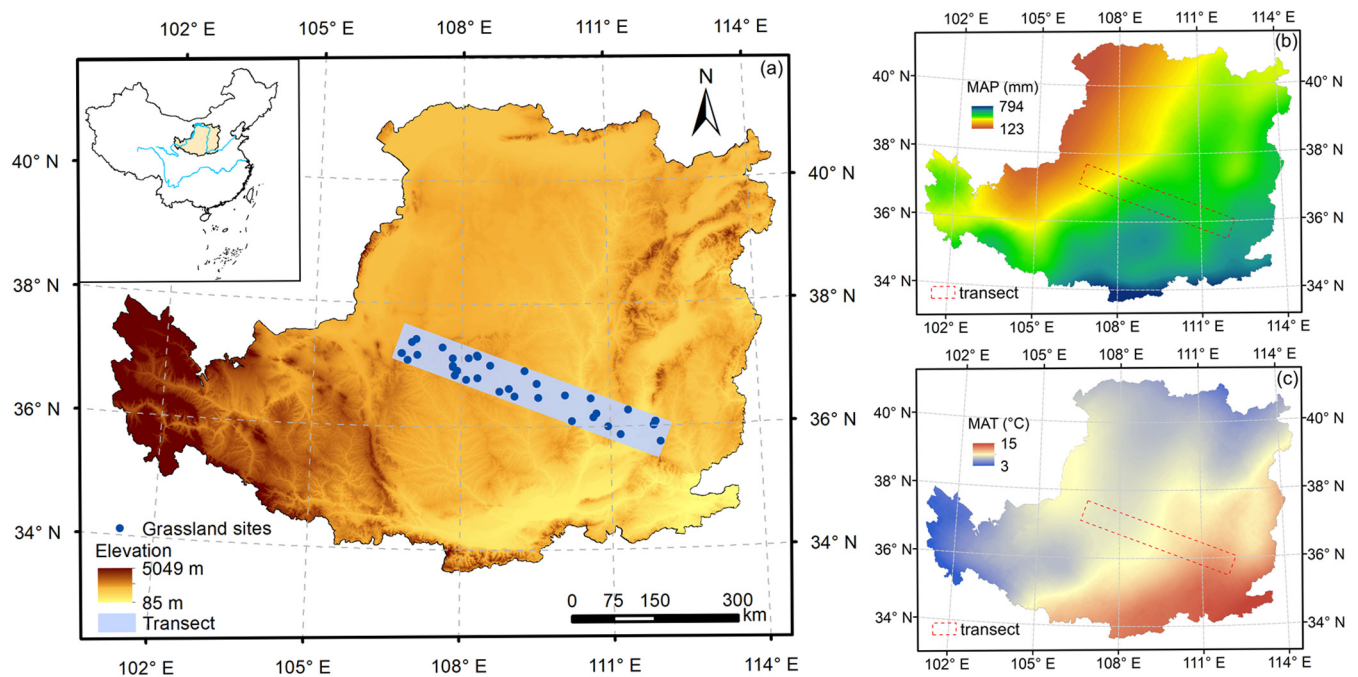
### Study Area

A regional scale transect along a hydrothermal gradient was selected from southeast to northwest across the Loess Plateau (Fig. 1). The transect is located at 35.08–37.95°N and 103.12–112.47°E, with elevations between 400 m and 2 800 m. The main soil type is loessal soil, and soil thickness varies from 30 m to 80 m (Wang et al. 2011). The mean annual precipitation ranges from 550 mm in the southeast to 250 mm in the northwest (see Fig. 1b), where ~80% of the precipitation was concentrated during the growing season, from May to August. The mean annual temperature (MAT) ranges from 13°C in the southeast to 6°C in the northwest (see Fig. 1c). The transect is about 520 km long and covers three major grassland types from southeast to northwest: forest-steppe, typical steppe, and desert steppe.

### Field Sampling and Measurements

Overall, 46 herbaceous grassland sites along the transect were investigated in July and August 2016, which corresponded to the annual peak in standing biomass (Valencia et al. 2015). One 20 × 20 m site was established with similar topographic characteristics: south-facing, gentle slope (1–24°), and upper slope. Each site was divided into four 10 × 10 m plots, within which one 1 × 1 m subplot in the center were surveyed. For each site, the species composition and coverage of plant species within four 1 × 1 m subplots were recorded, separately.

At each site, we collected the trait data of herbaceous species ( $n \geq 6$ ), which accounted for at least 80% of the total subplot coverage. The most common species were *Stipa* spp., *Artemisia* spp., *Potentilla* spp., and others. Ten individuals per plant species/site were randomly selected to ensure that intraspecific trait variability was considered in our sampling. Eight traits (Table 1) related to water acquisition and use (Fonseca et al. 2000; Maharjan et al. 2011; Niinemets 2001) were measured after standardized protocols (Cornelissen et al. 2003). Vegetative height was measured as the distance between the ground and highest photosynthetic structure. Stem-specific density was calculated as the dry mass of stem samples divided by volume. The volume was determined by the water replacement method: Totally immerse the fresh stem sample in water for 5 sec in a volumetric flask and measure the increase in volume (Cornelissen et al. 2003). The dry mass was weighed after being dried in the oven at 60°C for 72 h. If the plant exhibited no recognizable stems, the stem density was recorded as zero. Leaf length, leaf width, and the leaf length/width ratio were measured via a digital caliper, whereas the leaf area was calculated on the basis of scanned photographs by Image J 1.49 (National Institute for Mental Health, Bethesda, MD). The specific leaf area and leaf dry matter content was quantified by weighing fresh material that consisted of 10 to several hundred leaves depending on the leaf size, and cumulative leaf area was also calculated. Subsequently, the leaf samples were dried for 24 h at 80°C and then reweighed. The specific leaf area was calculated as the cumulative leaf area divided



**Figure 1.** Locations of the grassland sites across the southeast-northwest transect (a) and spatial distribution of mean annual precipitation (MAP, b) and mean annual air temperature (MAT, c) in the Loess Plateau

by dry mass (Smart et al. 2017). The leaf dry matter content was calculated as the leaf dry mass divided by fresh mass. To each species we assigned the average value of the individuals measured within the sites. The mean trait values at each site indicated the average response of species to environmental variables, given that habitat filtering takes place at the site level (Ackerly and Cornwell 2007). In cases where the species had no local trait values due to small relative coverage (< 3%), the average trait values of the two closest sites were used. Altogether 93 herbaceous species were recorded, and 67.8%, 40.9%, and 18.3% species appeared in more than 2, 5, and 10 sites, respectively.

#### Soil Sampling and Water Availability

Soil samples at depths of 0–300 cm were taken using a drill (Ø5 cm) at 20-cm intervals. No rainfall occurred a week before sampling or during the sampling periods at each site. One soil profile from each site was selected to represent the overall condition of each site. Soil samples were collected for each profile. Soil moisture content (g/g) was measured by the oven-dry method: Soil samples were immediately sealed in airtight aluminum cylinders and weighed for the first time and then transported to the laboratory for 24-h drying at 105°C using the oven-dry method, after which the samples were weighed again. The soil texture was determined

using a laser diffraction instrument (Mastersizer 2000, Malvern Instruments Ltd., Malvern, UK). Subsequently, three proportions of sand (> 0.02 mm), silt (0.002–0.02 mm), and clay (< 0.002 mm) contents were calculated. The soil organic matter content was analyzed by the dichromate oxidation method. Undisturbed soil cores were collected to measure soil bulk density using a stainless-steel cutting ring (volume 100 mm<sup>3</sup>). On the basis of these data, wilting point was estimated from the Soil-Plant-Air-Water (SPAW) model (Saxton and Rawls 2006). The soil characteristics across the transect are shown in Table 2. Finally, soil available water content (AWC, g/g) at each site was determined by subtracting wilting point from soil moisture content.

#### Climate Data

Mean annual precipitation and air temperature from 1981 to 2010 were derived separately from precipitation and temperature maps based on 273 meteorological stations across the entire Loess Plateau (Climate Database, National Meteorological Information Center of China), interpolated with ordinary kriging by ArcGIS (Esri, Redlands, CA) (Lü et al. 2012). Across the grassland sites, both mean annual precipitation (273–540 mm) and mean annual temperature (8.4–12.4°C) decreased from southeast to northwest (see Fig. 1b, c).

**Table 1**  
List of the functional traits measured in this study. A positive response to water is represented by a plus sign (+), and a negative response corresponds to a minus sign (–).

Trait	Abbr.	Unit	Functional role	Directional response to water
Vegetative height	VH	cm	Light capture, aboveground competition, and water-use efficiency	+
Stem specific density	SSD	mg/mm <sup>3</sup>	Physical resistance, water retention, and stress tolerance	–
Leaf length	LL	mm	Light capture, growth rate, and water stress tolerance	+
Leaf width	LW	mm	Light capture, growth rate, and water stress tolerance	+
Leaf length/width ratio	LL/W		Light capture, growth rate, and water stress tolerance	–
Leaf area	LA	mm <sup>2</sup>	Light capture, growth rate, and water stress tolerance	+
Specific leaf area	SLA	mm <sup>2</sup> /mg	Relative growth rate, light and carbon acquisition, and water use	+
Leaf dry matter content	LDMC	mg/g	Relative growth rate, carbon acquisition, and water use	–

**Table 2**  
Soil characteristics of grassland sites across the southeast-northwest transect in the Loess Plateau.

MAP gradient (mm)	<i>n</i>	Bulk density (g/cm <sup>3</sup> )	Clay (%)	Silt (%)	Sand (%)	Soil organic matter (g/kg)	Wilting point (g/g, %)
550–500	9	1.17 ± 0.06	4.74 ± 0.37	44.93 ± 1.67	49.96 ± 1.60	5.35 ± 0.90	6.87 ± 0.81
500–450	14	1.17 ± 0.05	3.94 ± 0.53	37.64 ± 2.80	58.06 ± 2.97	5.12 ± 0.28	6.07 ± 0.51
450–400	8	1.18 ± 0.05	4.03 ± 0.63	31.27 ± 2.87	64.71 ± 3.19	4.70 ± 0.25	5.87 ± 0.55
400–350	8	1.18 ± 0.05	3.80 ± 0.78	27.70 ± 3.16	68.51 ± 3.74	4.73 ± 0.65	5.87 ± 0.89
350–300	3	1.18 ± 0.06	3.50 ± 0.61	27.30 ± 3.12	69.21 ± 4.01	4.74 ± 0.52	5.85 ± 0.73
300–250	4	1.20 ± 0.06	3.40 ± 0.75	30.45 ± 2.03	66.16 ± 2.52	4.19 ± 0.49	4.83 ± 0.72

Note: *n* represents the number of grassland sites.

## Statistical Analyses

### Community Functional Traits

Before analysis, all trait data were conformed to satisfy the assumption of residual normality. We calculated the community-weighted mean (CWM) of each measured trait. The CWM corresponded to the mean trait value of a site weighted by the relative coverage of each species. It was calculated as follows (Garnier et al. 2004):

$$CWM_j = \sum_i^n p_{ij} T_{ij} \quad [1]$$

where  $p_{ij}$  is the relative coverage of the species  $i$  at the site  $j$ , and  $T_{ij}$  is the mean trait value of the species  $i$  at the site  $j$ .

### Identification of Vertical Soil Available Water in Relation to Traits

Simple linear regression was employed to quantify the potential relationships between community traits and soil available water content at each depth. As each trait may be associated with different soil available water layers, we selected the consistent depths (from top to bottom), which significantly explained most trait variations. The average depths of the selected soil available water content were used to indicate the soil water availability for subsequent analysis. It was calculated as follows:

$$AWC_j = \frac{1}{i} \sum_{i=1}^i AWC_i \quad [2]$$

where  $i$  is the number of selected layers at site  $j$  and  $AWC_i$  is the soil available water content in layer  $i$ .

### Identification of Response Traits

The statistical significance of single trait responses to the environmental variables (precipitation, air temperature, and soil water availability) was examined by creating a  $t$ -value biplot from the redundancy analysis (RDA). The  $t$ -value biplot can be used to approximate the  $t$ -values of regression coefficients, which would be obtained from a multiple regression, with a particular trait being the response variable and the environmental variables the predictors (Hiltbrunner et al. 2007; Braak et al. 2012). The  $t$ -value biplots with Van Dobben circles show graphically if an environmental variable contributes significantly to the multiple regression of a particular trait along the two first axes produced by the RDA. Plant traits were represented by a vector, while significant relationships with environmental variable were illustrated with Van Dobben circles to distinguish positive from negative relationships. If the vector of a particular trait fell within the circle, this trait could be considered as a response trait to the corresponding environmental variable. RDA and  $t$ -value biplots were conducted using CANOCO 5.0 (Braak et al. 2012).

### Direct and Indirect Effects of Environmental Variables

Structural equation modeling (SEM) was employed to determine direct and/or indirect pathways and test whether climate variables affected the response traits via soil water availability. SEM involves the use of a multiequational framework to develop and test theoretically based models in order to understand the direct and indirect effects of predictors in complex multivariate systems and determine the strength of each relationship clearly (Grace and Keeley 2006). The observed variables included three environmental variables and the trait variables, which were identified by the  $t$ -value biplots. We treat “response traits” as the latent variable, which was reflected by the trait variables (indicators). The related model of the latent variable was tested to assess the extent of goodness of fit represented by all indicators. The following hypothetical paths were developed in our initial path model. First, three environmental variables had direct effects on the response traits. Second, climate factors (precipitation and air temperature) indirectly affected the response traits via their effect on soil water availability. Finally, all significant correlation paths were retained in the frame. After arriving at the final acceptable model, we ensured that assumptions of residual normality and linearity were met. The model fit was assessed using a nonsignificant  $\chi^2$  test ( $P > 0.05$ ). No significant difference between observed and expected covariance matrices ( $\chi^2/df < 5$  and  $P > 0.05$ ) indicated good model fit. The SEM was performed using AMOS 17.0 (Amos Development, Crawfordville, FL).

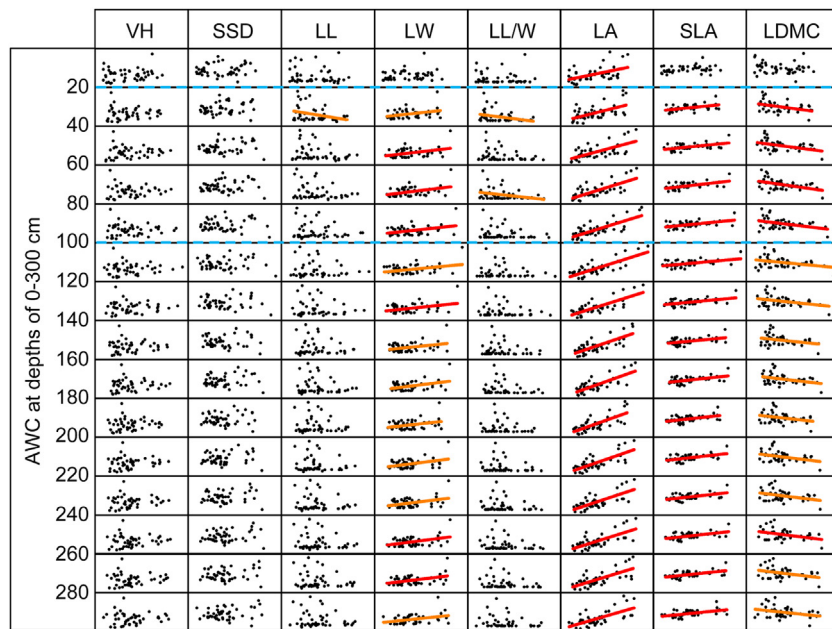
## Results

### Profile Distribution of Soil Available Water Associated with Traits

The variations of community traits along the soil available water content gradient at each depth are depicted in Figure 2. Linear correlation varied greatly within soil vertical profiles (see Fig. 2). The surface soil available water content (0–20 cm) had significant correlations with leaf area only. With increasing depth of soil vertical layers, the soil available water content was distinctly related to additional traits. However, these correlation coefficients decreased at depths of below 100 cm, particularly for leaf dry matter content. Finally, the soil available water content at depths of 20–100 cm had a closer relationship with most of the plant traits. We thus used  $AWC_{20-100}$  to represent the depth-averaged soil available water content at depths of 20–100 cm, serving as a proxy of soil water availability.

### Community Response Traits to Environmental Gradients

To identify which of these traits was responding to environmental variables,  $t$ -value biplots and Van Dobben circles were constructed, as shown in Figure 3. Leaf area and specific leaf area had positive responses to mean annual precipitation and  $AWC_{20-100}$ , while leaf dry matter content had a negative response (see Fig. 3a, c). Within our datasets, all measured traits failed to show any significant responses to mean annual temperature



**Figure 2.** Variations of community traits along soil available water content (AWC) gradient at each vertical soil depth. Abbreviations are explained in Table 1. Red trend line,  $P < 0.01$ ; yellow trend line,  $P < 0.05$ . Soil moisture at depths of 20–100 cm (between blue dashed lines) represents the selected depths of soil moisture to serve as an agent of soil water availability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(see Fig. 3b). As such, leaf area, specific leaf area, and leaf dry matter content could be considered as response traits to precipitation and soil water availability gradients.

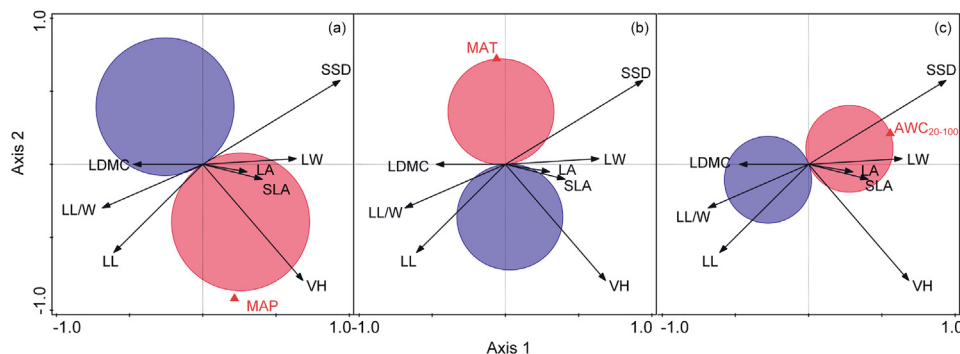
#### Direct and Indirect Pathways of Variation in Response Traits

The SEM in Figure 4 demonstrated causal relationships between response traits and their influencing factors. Three response trait (leaf area, specific leaf area, and leaf dry matter content) loadings for the indicators on the latent variable were significant ( $P < 0.05$ , see Fig. 4a). The SEM explained 42% of the variation of community response traits in the Loess Plateau grasslands (see Fig. 4b). Precipitation had a direct effect on response traits and also joined with temperature to indirectly alter the response traits, via its effects on the  $AWC_{20-100}$  pathway. In addition, a significant positive interaction between precipitation and temperature was observed. This indicated that the co-occurrence of less rain and cold at the same sites led to lower soil water availability (see Fig. 4b) and by extension to drought-tolerant traits characterized by small leaves, low specific leaf area, and high leaf dry matter content (see Fig. 4a).

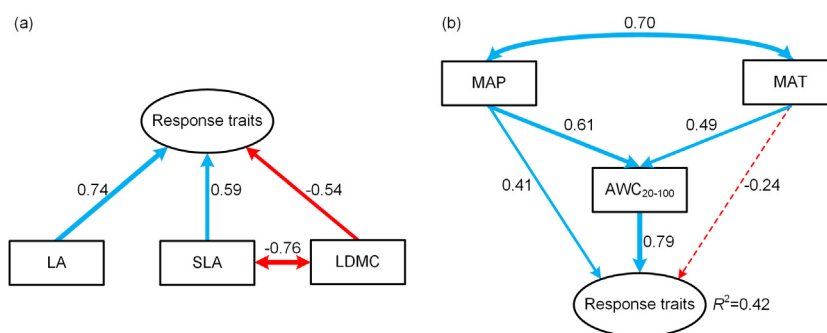
Overall, the SEM standardized path coefficients revealed that  $AWC_{20-100}$  was the most important factor that affected community response traits in the Loess Plateau herbaceous grasslands.

#### Discussion

Understanding and predicting ecological processes from community functional traits convey more generalized outcomes (Zirbel et al. 2017), and thus, trait-based ecology has been considered a powerful approach to explain and predict highly complex systems (Funk et al. 2017). Here, we integrated both community traits and vertical soil available water to provide an empirical approach for linking climate gradients and plant community responses. This study is among the first to assess the role of vertical soil water availability controlled by climate factors in affecting the plant community composition at a regional scale. We found that the community means of leaf area, specific leaf area, and leaf dry matter content were more responsive to changes in soil available water at depths of 20–100 cm than precipitation and air temperature along the hydrothermal gradient in the Loess Plateau grasslands. This was



**Figure 3.** T-value biplots with van Dobben circles showing the relationships between community traits and environmental variables: (a) mean annual precipitation (MAP), (b) mean annual temperature (MAT) and (c)  $AWC_{20-100}$ . Abbreviations are explained in Table 1. Traits that fall within the Van Dobben circles are significantly correlated ( $P < 0.05$ ) to the corresponding environmental variable, either positively (red circles) or negatively (blue circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Figure 4.** Latent variable with its indicators considered in the path analysis (a). Path analysis results of the direct and indirect effects of mean annual precipitation (MAP), mean annual temperature (MAT), and  $AWC_{20-100}$  on the response traits ( $\chi^2/df = 0.56, P = 0.79$ ) (b). Abbreviations are explained in Table 1. Number next to the latent variable is the explained variance. Values next to the arrows are the standardized path coefficients. Red and blue arrows indicate negative and positive relationships, respectively, and arrow width is proportional to the strength of the relationship. Solid and dashed arrows represent significant and non-significant effects, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in agreement with the finding that plant community composition is highly limited by soil water availability in dryland ecosystems (Ames et al. 2015; Grossiord et al. 2017).

#### Effect of Climate Factors and Soil Available Water on Plant Community Traits

Our results illustrated that three environmental variables (precipitation, air temperature, and  $AWC_{20-100}$ ) explained 42% of the overall variation in community response traits. In fact, there may be two explanations for the moderate variance explained by the hydrothermal gradient. Firstly, plants in dryland ecosystems are also nutrient limited (Ndagurwa et al. 2015). Wang et al. (2017) found that carbon and nitrogen availability drives distinct spatial variations along the hydrothermal gradient in this region. However, this study focused on plant community response to water availability, thereby revealing only the explained variations in response traits by measured hydrothermal variables. Secondly, the community-weighted mean of traits would be better for capturing the signals of the habitat filtering process (Keddy 1992), rather than other community assembly processes, such as niche differentiation, neutrality-based stochastic processes, and evolutionary history (Muscarella et al. 2016). For instance, habitat filtering and niche differentiation often jointly determine plant species responses to their environments; however, they lead to different predictions (Maire et al. 2012). Habitat filtering forces plants to converge toward a suitable trait value to cope with local environmental stress and thereby exhibits similar traits. In contrast, niche differentiation requires plants to diverge from suitable trait values to avoid competitive exclusion and thus have dissimilar traits. However, the strongest patterns of trait convergence are expected in harsh conditions, due to forceful habitat filtering (Bernard-Verdier et al. 2012). For this study, clear shifts in community response traits provided strong support for the existence of habitat filtering along the hydrothermal gradient.

We also recognized that water availability had a relatively strong constraining effect on community composition in contrast to temperature (see Figs. 3 and 4). One potential explanation was that plant responses may indeed depend on which stress initially occurs, and on the degree to which the plant has acclimated to this first stress factor (Grossiord et al. 2017). Since dryland ecosystems are generally water limited, community functional traits always change considerably with water availability (Marksteijn and Poorter 2009). Furthermore, we found that precipitation and air temperature gradients shifted  $AWC_{20-100}$  (see Fig. 4) and finally altered plant community composition. In fact, the crucial role of soil available water is widely recognized in hydrology, agriculture, and

meteorology (Dumedah et al. 2015). However, our work provided new insights into the role of soil water availability.

Our research revealed that  $AWC_{20-100}$  mediated the effects of precipitation and air temperature on the composition of grassland communities. This may be explained in terms of the hydrothermal gradient conveying significant differences in soil available water and, thus, strong gradients in intraspecific variation and species turnover (Huston 2012). Precipitation infiltration is the only source of soil moisture in the Loess Plateau, and precipitation revealed considerable spatial variability (Wang et al. 2016). In terms of the standardized path coefficient, precipitation (0.61) rather than temperature (0.49) primarily determined the changes in  $AWC_{20-100}$  across the transect (see Fig. 4). Furthermore, we noted that temperature altered response traits by its effects on soil available water pathways. A possible explanation for this finding was that temperature change influenced plant communities in dryland ecosystems primarily by altering soil available water, rather than thermal effects (Reich et al. 2018). Consequently,  $AWC_{20-100}$  was lower along the southeast to northwest transect, due to changes in precipitation and temperature, thereby inducing shifts in plant response traits. In short,  $AWC_{20-100}$  provided an important correlation between hydrothermal gradients and plant community responses.

We also found that  $AWC_{20-100}$  had the most significant impact on grassland community composition. This was likely due to the combined roles of less rainfall and cold, which led to drier soils, in contrast to either less rain or cold alone. Further,  $AWC_{20-100}$  may also mediate the effects of other factors, including topographic features, soil properties, and vegetation cover. In addition, these factors also varied greatly across the entire Loess Plateau (Wang et al. 2016). The effects of these factors on soil water availability would improve their explanatory power (Moles et al. 2014). For the current study,  $AWC_{20-100}$  had a strongest direct effect (0.79) on the response traits in comparison with precipitation (0.41) and air temperature (-0.42). Briefly,  $AWC_{20-100}$  appeared to be the primary factor in determining grassland community composition across the entire Loess Plateau.

#### Vertical Features of Soil Available Water Associated with Community Functional Traits

For this study, correlations between soil available water content and community traits initially increased with further depth and then decreased (see Fig. 2). However, surface soil available water content (0–20 cm) exhibited weak relationships with most of the traits. One potential explanation was that surface soil available water always revealed greater variations in comparison with other layers (Wang et al. 2016). Previous studies indicated that surface

soil available water content was more prone to be affected by precipitation, land evaporation, and vegetation transpiration in shallow-rooted systems (Teuling and Troch 2005). During rainfall events, plants with shallow-rooted systems consumed surface resident soil water (Yang et al. 2012). However, relatively low soil water between different rainfall events was expected due to high evapotranspiration in the surface layers (Schwinning and Sala 2004). Since surface soil available water demonstrated obvious temporal variations, it did not seem to be suitable as a proxy of soil water availability. Therefore, weak correlation relationships were captured between community traits and surface soil available water.

Compared with surface soil available water,  $AWC_{20-100}$  was more distinctly related to plant traits (see Fig. 2). The key reason is that water uptake is dependent on soil water availability and root distribution. As noted earlier, precipitation infiltration is the only source of soil available water in the Loess Plateau and the infiltration depth is generally < 100 cm (Yang et al. 2018). More importantly, most of the fine roots in grasslands are mainly distributed within the upper 100 cm (Yang et al. 2014). Previous studies found that plant fine root indices were significantly correlated with soil moisture content within the profiles (Wang et al. 2011). Accordingly, grassland community traits were well correlated with  $AWC_{20-100}$  because of their root systems. In this study,  $AWC_{20-100}$  presented statistically significant relationships with three response traits (see Figs. 3 and 4). Finally, grasslands consume minimal water from deep soil layers. Thus, it is reasonable that the relationship between soil available water content below 100 cm and community traits revealed a consistent decreasing trend.

#### Response Trait Variation Along Soil Water Availability Gradient

Our findings revealed that the leaf area, specific leaf area, and leaf dry matter content of grasslands were identified as response traits to soil water availability, as evidenced by the clear shifts in community-weighted mean values observed along the  $AWC_{20-100}$  gradient (see Fig. 4). More specifically, grasslands responded to drier soils by reducing leaf area, specific leaf area, and increasing leaf dry matter content. Leaf area and specific leaf area are often positively correlated with photosynthesis and transpiration rate (Gross et al. 2008). Plant species with small leaves are considered to reduce boundary layer resistance, while assisting with the maintenance of favorable leaf temperatures and higher photosynthetic water-use efficiencies under low water availability (Ackerly et al. 2002). Specific leaf area relates to growth rate and stress tolerance, with slower growing, and more stress-tolerant species having lower specific leaf area (Wright et al. 2004). Leaf dry matter content is also strongly correlated with resource availability and relative growth rate (Wilson et al. 1999). High leaf dry matter content might limit water losses and enable tolerance to tissue desiccation (Bernard-Verdier et al. 2012). Finally, drier soil forces species to converge toward a suitable trait syndrome to reduce transpiration and optimize water use efficiency.

We also found that leaf area, specific leaf area, and leaf dry matter content emerged as alternative markers to discriminate the ecological strategies that were able to persist under different soil available water conditions (see Fig. 4). Among them, leaf area was the better marker as its loading on the latent variable was highly significant (0.74, see Fig. 4a). These traits were typically correlated with resource acquisition and conservation trade-offs along the leaf economics spectrum (Bernard-Verdier et al. 2012). They revealed a gradual change in community ecological strategies, from the relatively acquisitive water-use communities in moist soils, to conservative water-use communities in drier soils. In moist soils, slow-growing less competitive plants with conservative water-use strategies were filtered out, whereas plants with high rates of tissue

turnover and acquisitive water-use strategies appeared to prevail, such as *Bothriochloa ischaemum*, *Artemisia dubia*, and *Rubus parvifolius*. As soils became drier, plants with conservative and drought-tolerant strategies, such as *Stipa caucasica* subsp. *Glareosa*, *Potentilla acaulis*, and *Artemisia frigida*, appeared to dominate. In sum, it was more evident that communities filtered plants with different ecological strategies at each end of the soil available water gradient.

Given that plant communities affect many ecosystem properties, ongoing soil desiccation may select plant communities with more slow-growing and water conservative strategies, thereby collectively affecting ecosystem functions and services. For example, soil desiccation can reduce gross primary production through habitat filtering, causing vegetation mortality and further exacerbating climate extremes due to land–atmosphere feedbacks (Anderegg et al. 2019; Green et al. 2019). As such, plant functional traits are key to understanding ecosystem responses to changing soil water availability. Furthermore, it is imperative to consider soil water availability in the restoration and management of dryland ecosystems, notably given the often strong anthropogenic and climatic impacts on soil moisture. Current large-scale restoration measures in water-restricted regions often attempt to introduce species that consume more water than the original vegetation types, aggravating local water scarcity and soil desiccation (Fu et al. 2016). Future sustainable restoration projects may need to select appropriate plant materials more suited to local precipitation conditions to balance water conservation and other ecological functions such as carbon sequestration, soil erosion, and sediment control (Yu et al. 2017; Zhang et al. 2019). In addition, diverse land preparation techniques (e.g., adversely graded tableland and fish-scale pits) are strongly advocated to improve the relative extractable water for plants, as they can increase soil moisture retention by creating many microcatchments (Wei et al. 2019). Finally, we recognized that on the basis of our results, plant response traits had a high significant relationship with soil available water. Consequently, plant response traits can be used as ecological indicators of soil available water condition. The most important aspect is that these traits are universal and easily measured in the field. Thus, these response traits hold great promise for monitoring soil water changes in water-limited regions. However, further studies are needed in the future to provide model simulations and empirical tests in dry and degraded ecosystems.

#### Conclusions

By adopting a trait-based approach, our study represents the first attempt to assess the relationship among climate factors, vertical soil available water, and plant community composition at a regional scale. It was clearly demonstrated that soil available water content at depths of 20–100 cm mediated the effects of precipitation and air temperature on grassland community composition along the hydrothermal gradient in the Loess Plateau. This appeared to be the primary factor in determining grassland community composition and thereby improved plant trait–water relationships. Grassland communities responded to drier soils by reducing leaf area and specific leaf area, as well as increasing leaf dry matter content. As plant communities affect many ecosystem properties, soil water availability should be considered the core driver in the restoration and management of dryland ecosystems.

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