Plant traits in influencing soil moisture in semiarid grasslands of the Loess Plateau, China☆

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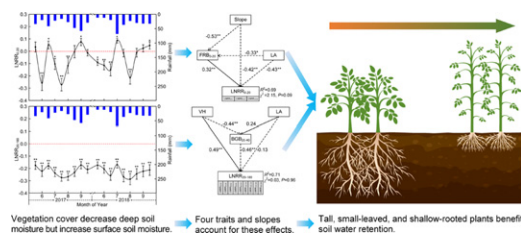[c] Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA
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HIGHLIGHTS

- Vegetation effects on soil moisture were quantified via a grass removal experiment.
- Vegetation cover decrease deep soil moisture but increase surface soil moisture.
- Four plant traits and slope gradients account for these vegetation effects.
- Tall, small-leaved, and shallow-rooted plants benefit soil water retention.
- Terracing further enhances these beneficial effects on soil moisture.

GRAPHICAL ABSTRACT

Vegetation cover decrease deep soil moisture but increase surface soil moisture. → Four traits and slopes account for these effects. → Tall, small-leaved, and shallow-rooted plants benefit soil water retention.

ABSTRACT

Large-scale vegetation restoration projects pose threats to water resource security in water-limited regions. Thus, the quantification of how vegetation cover affects soil moisture is of key importance to support effective restoration schemes in drylands. However, the current understanding of such effects remains poor. For this study, an in-situ vegetation-removal experiment was conducted at 36 herbaceous grassland sites having different community compositions and topographical conditions in two adjacent loess watersheds of the Loess Plateau, China. The effects of vegetation cover (vegetation effects) on soil moisture were analyzed across soil profiles (0–180 cm) and two growing seasons. Overall, 13 plant traits and 7 topographic and soil properties were employed to evaluate how community compositions modulated vegetation effects on soil moisture. The results showed that vegetation cover increased soil moisture in the surface layer (0–20 cm) by 6.81% during wet periods (semi-monthly rainfall >30 mm) relative to an in-situ unvegetated control, but primarily induced a decline of soil moisture in the deep soil layer (20–180 cm) by 19.44% across two growing seasons. Redundancy analysis (RDA) and structural equation modeling (SEM) suggested that these vegetation effects on soil moisture were significantly correlated with vegetative height, leaf area, shallow root allocation, and slope gradient. Our study revealed that tall, small-leaved, and shallow-rooted plants on flat topographies were beneficial to soil water retention and replenishment. This implied that current restoration strategies may be significantly improved through the development of optimal communities and diverse terracing measures. Our findings are anticipated to provide effective guidance for soil water conservation, as well as ecosystem rehabilitation in dry and degraded regions.

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1. Introduction

Soil moisture is a critical component that controls many terrestrial hydrological, geomorphic, and biogeochemical processes (Su and Shangguan, 2019; Yang et al., 2012). Thus, it plays a pivotal role in determining the ecosystem compositions and function, particularly in dry and degraded ecosystems (Fu et al., 2016; Yan et al., 2015). However, large-scale vegetation restoration projects have exacerbated soil water scarcity in these regions, resulting in severe ecosystem degradation, as well as conflicts between vegetation productivity and anthropogenic demands for water (Feng et al., 2016; Reich et al., 2018). Nevertheless, the effects of vegetation cover (vegetation effects hereafter) on soil moisture has been considered a critical issue in the sustainability of water-limited terrestrial ecosystems (Gross et al., 2008; Wang et al., 2016b; Wang et al., 2018). Therefore, an elucidation of the vegetation effects on soil moisture is of key importance to balance ecosystem restoration and water conservation in drylands.

A trait-based strategy has been proposed to characterize the ecosystem-level consequences of localized modifications in plant communities (Cortois et al., 2016; Valencia et al., 2015). This approach categorizes any changes in community composition that partially impacts ecosystem functioning as "effect traits" (Funk et al., 2017). Previous studies have confirmed that several specific traits might facilitate the determination of different aspects of ecosystem functioning, such as drought resistance (Anderegg et al., 2018), decomposition rate (Zirbel et al., 2017), and ecosystem multifunctionality (Gross et al., 2017). However, little is known in regard to vegetation effects on soil moisture via plant functional traits (Gross et al., 2008). The vegetation effects on soil moisture involve the complex and multiscale dynamics of hydrologic partitioning and circulation. In general, the most likely candidate effect traits on soil moisture are those continuous traits that are related to the capacities for accessing, transporting, and transpiring soil moisture, which encompass leaf-, root-, and biomass-related traits (Jian et al., 2015). For example, leaf area and thickness are key indicators of plant water-use strategies (Vendramini et al., 2002). Under identical conditions, vegetation with small and thick leaves tends to consume less soil moisture than that having large and thin leaves (Díaz et al., 2015). Thus, leaf area and thickness may be considered as effect traits on soil moisture. However, it has been argued that some traits remain highly paradoxical, leading to uncertainties in correlations with soil moisture (Pérez-Harguindeguy et al., 2013). For instance, tall vegetation is considered to have a more acquisitive water-use strategy than the converse, while it is likely to reduce soil evaporation due to a thick boundary layer and high albedo (Suleiman and Ritchie, 2003). Similarly, there may be complex feedback loops between biomass and soil moisture. In practice, these relationships are variably negative (Yang et al., 2015) and positive (Ren et al., 2015). These inconsistent findings imply that our current understanding of vegetation effects on soil moisture remains fragmented. Furthermore, previous studies have demonstrated that topographic and soil properties affect soil moisture patterns, particularly at the watershed scale (Korres et al., 2015; Yang et al., 2015). However, diverse topographic and soil conditions with different community compositions increase the uncertainties and complexities of soil resident water status (Wei et al., 2019; Yu et al., 2019; Yu et al., 2017). It is therefore crucial to explore how vegetation cover affects soil moisture via plant traits under diverse topographic and soil conditions in water-limited areas such as the Chinese Loess Plateau.

Grassland ecosystems in the Loess Plateau are characterized by a remarkable diversity of community compositions, as well as variable topographic and soil properties (Yang et al., 2018). For this study, we conducted an in-situ vegetation-removal experiment in the semiarid grasslands of the Loess Plateau, China. We hypothesized that vegetation cover induces significant changes in soil moisture, and that vegetation effect on soil moisture is related to plant traits. To test these hypotheses, 36 herbaceous grassland sites were established, which possessed different species compositions and topographical conditions in two adjacent loess watersheds. We investigated soil moisture content at depths of 0–180 cm over two growing seasons, including plant traits, as well as topographic and soil properties. Our objectives were to: (1) elucidate the vertical and temporal changes in the vegetation effects on soil moisture across various grassland sites, (2) identify plant effect traits on soil moisture, and (3) develop trait-based recommendations to improve future restoration schemes in water-limited regions.

2. Materials and methods

2.1. Study area

This study was carried out in the Lijiawan and Jianzicha watersheds (35°43′–35°45′, 104°29′–104°31′), which are adjacently located in the western region of the Chinese Loess Plateau (Fig. 1a). These watersheds have altitudes that range from 1900 m to 2150 m, with areas of 0.94 km^2 and 0.30 km^2, respectively. The climate is typically semiarid with a strong continental influence. The mean annual temperature is 6.8 °C, whereas the mean annual precipitation is 386 mm, most of which falls from July to September (Yang et al., 2014a). The mean annual potential evaporation is ~1649 mm. According to the FAO-WRB classification (IUSS Working Group WRB, 2015), the local soil belongs to the Calcic Cambisol group with low organic matter (ca. 0.2–2.9%), a loose soil structure, and high silt content (ca. 81%). Thus, local ecosystems are vulnerable to soil erosion during torrential rainstorms. The volumetric field capacity is 21–28%, and the wilting point is ~6.3% (Yang et al., 2018). The zonal vegetation is a typical steppe, while the current vegetation types in these two watersheds consist of replanted forests, grasslands (including restored and native grasslands), and farmlands. The replanted forests are dominated by Siberian apricot (*Armeniaca sibirica* (L.) Lam.), korshinsk peashrub (*Caragana korshinskii* Kom.), and Chinese arborvitae (*Platycladus orientalis* (L.) Franco). The grasslands are primarily dominated by bunge needlegrass (*Stipa bungeana* Trin.), common leymus (*Leymus secalinus* (Georgi) Tzvel.), Russian wormwood (*Artemisia sacrorum* Ledeb.), capillary wormwood (*Artemisia capillaris* Thunb.), alfalfa (*Medicago sativa* Linn.), and others. Alfalfa was the introduced grass, which was formerly mown annually for hay. Due to rural depopulation, alfalfa grassland has been increasingly abandoned in recent years, which has resulted in different restoration stages. Farmlands are planted with annual crops such as potatoes and corns. For the same reason as the alfalfa grassland, farmlands located far from the village were left abandoned since 2002, which are currently dominated by several native grass species as described above.

2.2. Experiment design and field measurements

2.2.1. Experimental sites

In the early spring of 2016, 36 herbaceous grassland sites (6 m × 20 m) were selected for the monitoring of soil moisture, surveying of vegetation, and sampling of plant traits (Fig. 1a). These sites were established according to different species compositions and topographical conditions. We focused on native and abandoned grasslands, including abandoned alfalfa grasslands and farmlands. To span the widest possible range of topographic and soil properties, 33 sites were scattered across 20 hillslopes, which were covered with grasses on at least one slope position (upper, upper-middle, middle, middle-bottom, and bottom). On each position consisting of a homogeneous community and topography, one separate experimental site was located in the center. Moreover, 3 extra sites were selected from three upper slopes, due to the great spatial heterogeneity in species composition for each upper slope. A total of 36 sites were spaced ~50 m apart from each other. The dominant species, as well as the topographic and soil properties for each site are shown in Table S1.

Two circular plots (Ø 4.0 m) up to 3 m apart were established to monitor soil moisture at each site (Fig. 1b, c). According to the trait-based response-and-effect framework (Suding et al., 2008), plant
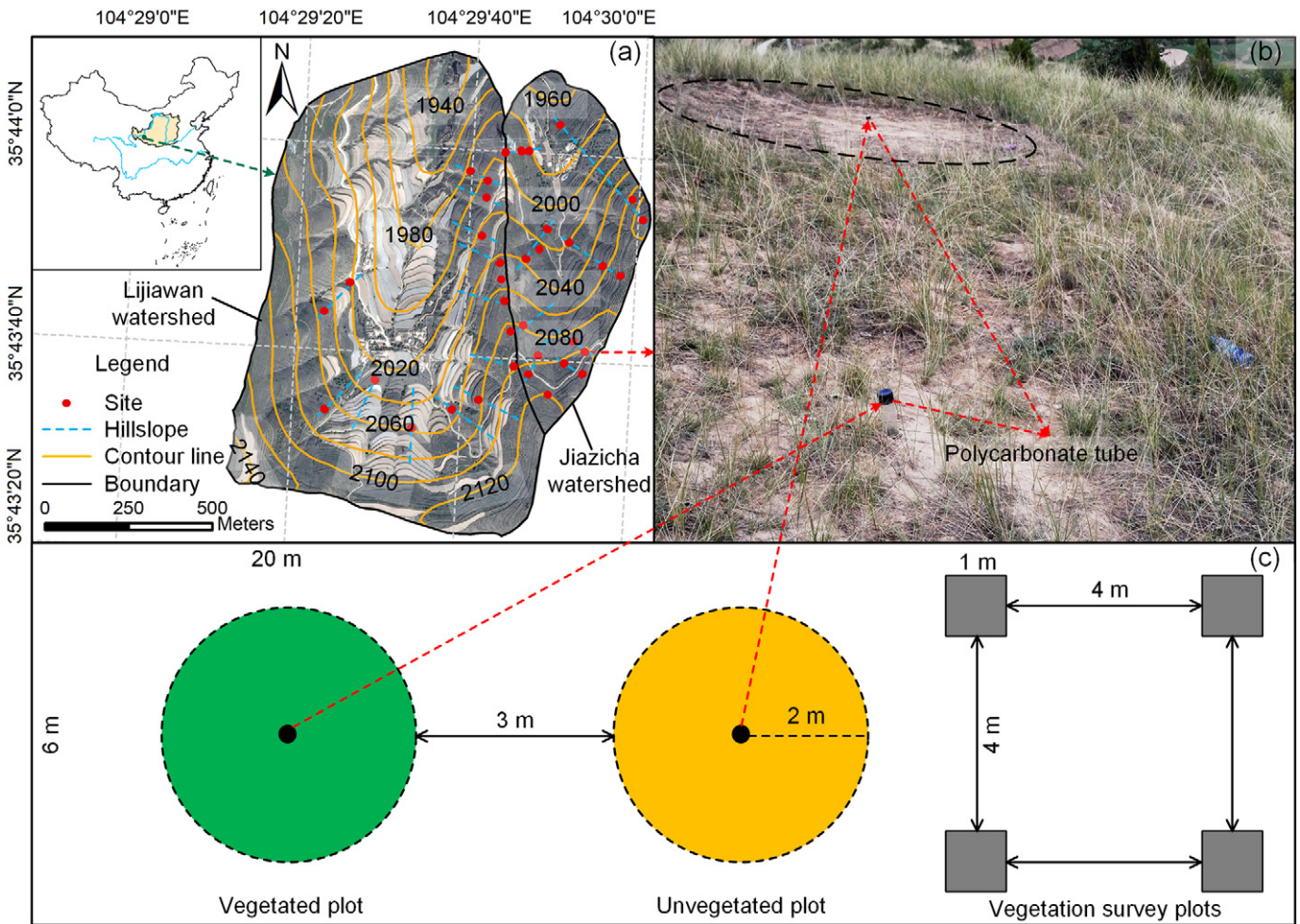
Fig. 1. Location of the grassland sites in two watersheds of the Loess Plateau (a), photograph of in-situ vegetation-removal experimental site (b, c).

functional traits can be considered in terms of their response to environmental factors ('response traits'), or from their impacts on ecosystem properties ('effect traits'). As interactive effects between plant communities and soil moisture are dynamic, an in-situ vegetation removal experiment should be possible to isolate vegetation effects/effect traits on soil moisture (Gross et al., 2008). Thus, we cleared all plants using a sickle in a randomly selected plot at each site in the early spring of 2016 (Fig. 1c). Subsequently, a non-selective herbicide (Glyphosate, Shanghai Hulian Inc., Shanghai, China) was sprayed to kill residual, or newly sprouting plants, in April, June, and August, respectively. The dead plants were removed from the unvegetated plot, and the plant roots around each plot edge were severed with a spade at depths of 0–25 cm. To avoid different responses of surface runoff between the vegetated and unvegetated plots within each site, the two plots were adjacently located at the same level on the site slope. Polycarbonate access tubes with uniform lengths (200 cm) were inserted at the centers of each plot so as to avoid edge effects. To minimize the influences of other measurements on the monitoring of soil moisture, vegetation surveying and environmental variable measuring were conducted externally to the monitoring plots within each site (Fig. 1c).

2.2.2. Soil moisture and rainfall data

Soil moisture within each plot was directly monitored using a portable time-domain reflectometer (TDR, Trime-FM, IMKO, Ettlingen, Germany) at the depths of 0–180 cm. The TDR probe was lowered to a desired depth of the cylindrical tube to acquire data from different soil layers. We measured soil moisture semi-monthly (the transition and middle of each month) across the growing season (from May to

September in 2017 and 2018). In total, nine soil moisture measurements were conducted at the 36 sites each year. Rainfall data was collected at the nearby Chankou Forestry Station, which is located 2.2 km from the watersheds. Owing to the relatively small total area ($1.94 km^2$), we assumed that rainfall did not vary between these sites.

2.2.3. Community functional traits

Vegetation surveying and plant sampling were conducted in August 2017, which corresponded to the annual peak in standing biomass (Valencia et al., 2015). Four 1 × 1 m plots were established at four corners of remaining area for each site (Fig. 1c). All plots were located at a similar distance from the site edge. For each plot, the species composition and coverage of plant species were recorded separately. Overall, 74 herbaceous species (Table S2) were recorded, with the most common species being *Stipa* spp., *Leymus* spp., *Artemisia* spp., *Potentilla* spp., alfalfa, and others.

2.2.3.1. Community aboveground traits. At each site, we collected the aboveground trait data of the species that were present, which accounted for at least 80% of the total biomass, in a decreasing order of relative coverage. Ten individuals per species/per site were randomly selected to ensure that intraspecific trait variability was considered in our sampling. Seven aboveground traits were measured following standardized protocols (Cornelissen et al., 2003). Vegetative height (VH, cm) was measured as the distance between the ground and highest photosynthetic structure. Leaf length (LL, mm), leaf width (LW, mm), and leaf thickness (LT, mm) were measured via a digital caliper, whereas leaf area (LA, mm^2) was calculated based on scanned

photographs using an Image J 1.49 (National Institute for Mental Health, Bethesda, USA). Specific leaf area (SLA, mg/mm^2) and leaf dry matter content (LDMC, mg/g) were quantified by weighing fresh material, which consisted of from 10 to several hundred leaves, contingent on the leaf size, and the cumulative leaf area was also calculated. Subsequently, the leaf samples were oven-dried for 48 h at 80 °C and then reweighed. The specific leaf area and leaf dry matter content were calculated as follows:

$$SLA = CLA/LDM \tag{1}$$

$$LDMC = LDM/LFM \tag{2}$$

where CLA is the cumulative leaf area (mm^2), LDM and LFM are the leaf dry mass (mg) and fresh mass (g), respectively.

The community-weighted mean (CWM) and functional diversity (FD) of each aboveground trait were calculated as follows:

$$CWM_j = \sum_i^n p_{ij} T_{ij} \tag{3}$$

$$FD_j = \sum_i^n p_{ij} \left(\frac{|T_{ij} - CWM_j|}{\sum_i^n |T_{ij} - CWM_j|} \right) \tag{4}$$

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. Community-weighted mean reflects the trait value of the most dominant plant species at a certain site and corresponds to the mass ratio process (Ackerly and Cornwell, 2007). Functional diversity quantifies the degree of trait dispersion at a site and suggests the niche complementary in the resources used (Valencia et al., 2015). The community aboveground traits at the 36 sampling sites are shown in Table S3.

2.2.3.2. Community fine root traits. For each site, fine roots were sampled using four soil cores (Ø 8 cm) at depths of 0–60 cm. As herb roots were primarily distributed at depths of 0–50 cm in this region (Yang et al., 2014b), we assumed that almost all of the fine roots in our samples were harvested. The soil cores were divided into three layers (0–20 cm, 20–40 cm, and 40–60 cm) from the surface. For each layer, soil samples from the four cores were blended together to represent a community level sample (Erktan et al., 2018). Fine roots (Ø < 2 mm) were extracted by washing, and then conserved in a 25% alcohol solution pending analysis. A random subsample of fine roots (>25% of root fresh weight) was scanned at a resolution of 600 dpi using a flatbed scanner (Epson Expression 10000XL, Seiko Epson Corp., Tokyo, Japan), and were analyzed using a WinRHIZO 2009b (Regent Instruments Inc., Quebec, Canada) to determine the root length and mean root diameter (RDIAM, mm). Subsequently, these roots were oven-dried at 80 °C to a constant mass and weighed to obtain their dry mass. Specific root length (SRL, m/g) was equal to the root length divided by the dry mass. Thereafter, the remaining fine roots were also oven-dried at 80 °C to a constant mass and weighed. The total root dry mass (DM, g) in each layer was the sum total of the fine roots, including the scanned roots and the remaining roots. The fine root biomass (FRB, g/m^2) and root length density (RLD, mm/cm^3) were calculated as follows:

$$FRB = RDM/SA \tag{5}$$

$$RLD = (SRL \times RDM)/AV \tag{6}$$

where RDM is the total root dry mass, SA and AV are the accumulated sectional areas and volume of the four soil cores, respectively, and SRL is the specific root length.

2.2.3.3. Community biomass. For each site, the aboveground biomass (AGB, g/m^2) and belowground biomass (BGB, g/m^2) were harvested from three randomly distributed 50 × 50 cm plots. The belowground biomass was harvested at depths of 0–60 cm and also divided into three layers (0–20 cm, 20–40 cm, and 40–60 cm) from the surface. The plant material was oven-dried at 80 °C to a constant mass and weighed. The community biomass and root traits for each site are shown in Table S4.

2.2.4. Topographic and soil properties

The slope gradients and aspects (clockwise from south) were determined for each site using a compass and were recorded in degrees. Slope aspects were expressed as cos (aspect), where greater values indicated sunnier and drier conditions (Zhang et al., 2019a). Slope positions were calculated as the ratios between the distances from the slope crests and total slope lengths, where smaller values indicated upper slopes. At each site, soil samples were collected from three randomly distributed points and then blended together to form a single sample. The soil particle sizes were measured via laser diffraction (Mastersizer 2000, Malvern Instruments Ltd., Worcestershire, UK). The contents of clay (<0.002 mm), silt (0.002–0.02 mm), and sand (>0.02 mm) were then calculated. The soil organic matter content (SOM) was determined using the dichromate oxidation method. Undisturbed soil cores were collected to measure the soil bulk density (BD) using a stainless-steel cutting ring (volume 100 mm^3).

2.3. Quantification of vegetation effects on soil moisture

Vegetation effects on soil moisture were determined using the log response ratio (LNRR) at each site (Gross et al., 2008).

$$LNRR = \ln(SMV/SMB) \tag{7}$$

where SMV is the soil moisture in the vegetated plot, and SMB is the soil moisture in the bare (unvegetated) plot. LNRR >0 signifies that the vegetation cover causes an increase in soil moisture and LNRR <0 denotes a negative effect on soil moisture.

2.4. Statistical analyses

To determine how to partition the data for soil profile and temporal analyses, linear mixed-effects models (LMMs) were performed separately to examine vegetated/unvegetated soil moisture content as a function of soil depths and measured times, which were considered as fixed effects; the site was also included as a random effect. LMMs were run using the *lmer* function in the *lmerTest* package (Schmid et al., 2017). The P values were calculated for fixed factors using Kenward–Roger's approximations.

All data were expressed as mean ± standard errors. Paired-sample t-tests were employed to detect the differences between the vegetated and unvegetated plots, while one sample t-tests were performed to detect whether LNRR was apparently different from 0 ($P < 0.05$). Initially, we calculated temporal-averaged soil moisture and LNRR, and then compared them across soil profiles (0–180 cm) between the vegetated and unvegetated plots ($n = 36$). The results suggested that the 20 cm soil depth was the threshold for distinguishing the degree of vegetation effects on soil moisture (Fig. 2). Accordingly, we divided the soil profile into two vertical layers for subsequent analysis: surface layer (0–20 cm) and deep layer (20–180 cm). Second, we calculated depth-averaged soil moisture and LNRR for the surface layer and deep layer at each measurement time, and then compared the differences between the vegetated and unvegetated plots ($n = 36$). The coefficient of variation (CV) of the average soil moisture was calculated to estimate the temporal stability of soil moisture content and LNRR across two growing seasons. Smaller CV values indicated a more stable temporal tendency. Third, redundancy analysis (RDA), which is a constrained ordination method, was conducted to quantify the relative contribution of explanatory variables to the variability of LNRR across the 36 sites. It should be
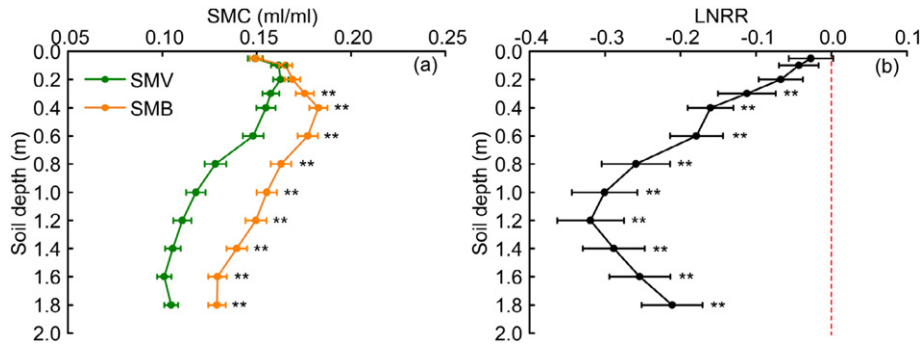
Fig. 2. Vertical changes in temporal-averaged SMC (a) and LNRR (b). Bars denote the standard errors of the mean ($n = 36$). Soil moisture content at depths of below 20 cm in the vegetated plots was obviously lower than that in the unvegetated plots (a), and the LNRR below 20 cm was significantly less than zero (b). Note: SMC represents soil moisture content; SMV represents soil moisture in the vegetated plots; SMB represents soil moisture in the bare (unvegetated) plots; LNRR represents the log response ratio.

noted that we also initially included functional diversity (FD) of each aboveground trait as explanatory variables in our redundancy analysis. This, as niche complementary improves use of available soil water, lowers the interspecific competition for water in drylands (Yang et al., 2011). However, functional diversity and its joint effect with the community-weighted mean (CWM) of aboveground traits did not significantly improve the explained variance of LNRR based on a variance partitioning ($P > 0.05$, Table 1). Therefore, we removed FD indices as explanatory variables and retained CWM indices in the following analysis. In total, 13 community functional traits (Table S3, S4) and 7 topographic and soil properties (Table S1) composed 20 likely candidate explanatory variables for LNRR. Two separate RDAs were conducted for the surface layer and deep layer. Prior to the RDA, forward selection was also performed to identify the best subset of explanatory variables that significantly explained the variations in LNRR. The variation inflation factor for each selected variable was verified to ensure that it lay within acceptable limits (VIF < 3). In addition, a structural equation model (SEM) was employed to quantify the relationships between the selected explanatory variables and LNRR. RDA was conducted using CANOCO 5.0 (Microcomputer Power, Ithaca, NY, USA), while SEM was performed using AMOS 17.0 (Amos Development, Crawfordville, FL, USA).

3. Results

The linear mixed-effect models demonstrated that soil moisture in the vegetated and unvegetated plots was primarily affected by soil depths and time across 36 sites (Table 2, S5). Thus, the vertical and temporal changes in soil moisture and vegetation effects were analyzed as described in the following section.

3.1. Vegetation effects on vertical changes in soil moisture

On average, the vegetated plots (0.1275 ± 0.0007 ml/ml) had a lower soil moisture content than the control of unvegetated plots (0.1525 ± 0.0007 ml/ml; Fig. 2a). Significant differences in soil moisture were observed at depths of below 20 cm ($P < 0.01$), which was further confirmed by the vertical LNRR distributions. Overall, LNRR

(-0.1857 ± 0.0052) was below zero (Fig. 2b). Furthermore, the absolute LNRR values exhibited an increasing trend within the profiles, and then decreased at depths of below 120 cm. At depths of below 20 cm, the LNRR (-0.2453 ± 0.0060) was remarkably lower than zero ($P < 0.01$, Fig. 2b), and the soil moisture content of the vegetated plots was 19.44% lower than that of the unvegetated plots (Fig. 2a).

3.2. Vegetation effects on temporal changes in soil moisture

The temporal changes in rainfall, soil moisture content, and LNRR in the two layers are shown in Fig. 3. The cumulative rainfall during the 2017 and 2018 growing seasons was 292 and 263 mm, respectively, which represented normal rainfall levels. Soil moisture in the surface layer fluctuated synchronously with the trends in seasonal rainfall changes, and showed a relatively high temporal variation, whether for vegetated (CV = 0.299) or unvegetated plots (CV = 0.207). During the growing seasons, higher soil moisture was apparent following heavy or continuous rains (semimonthly rainfall >30 mm, wet periods hereafter, Fig. 3a). However, temporal changes in soil moisture in the deep soil layer were relatively stable over time (CV of SMV = 0.117, CV of SMB = 0.099; Fig. 3c).

The LNRR exhibited similar trends with soil moisture over the two layers (Fig. 3b, d). The LNRR in the deep layer was far below zero ($P < 0.01$) and more stable with rainfall than that in the surface layer, which also verified that vegetation cover primarily induced decreases in deep soil moisture over the entire growing season. Interestingly, the LNRR in the surface layer (0.0650 ± 0.0012) was obviously greater than zero in four instances (6/15/2017, 9/1/2017, 7/1/2018, and 9/15/2018) during the wet periods ($P < 0.01$; Fig. 3b), which indicated that vegetation cover increased soil moisture content in the surface layer by 6.82% following heavy, or continuous rains, in contrast to the control plots.

3.3. Relating vegetation effects on soil moisture to community traits

For this study, we focused on the soil surface layer during wet periods and the deep layer over the entire growing seasons, which might

Table 1
Variation partitioning analysis of LNRR explained by community-weighted mean (CWM) and functional diversity (FD) of aboveground traits.

Model	LNRR in the surface layer			LNRR in the deep layer		
	R^2 (%)	F	P	R^2 (%)	F	P
CWM	34.3	2.5	0.008	44.3	4.2	0.002
FD	15.3	1.2	0.318	15.8	1.5	0.138
Joint effect	13.1			8.6		

Notes: R^2 is variance decomposition analysis based on the sum of squares; the joint effect of CWM and FD was obtained by subtraction and could not be tested for significance.

Table 2
Results from linear mixed-effects models of soil moisture content predicted by soil depths and measured times.

Model	Source	SS	MS	Df	denDf	F	P
SMV	Soil depths	2.46	0.22	11	7709	319.51	<0.001
	Measured times	3.21	0.19	17	7709	270.08	<0.001
SMB	Soil depths	2.30	0.21	11	7709	259.64	<0.001
	Measured times	3.50	0.21	17	7709	255.64	<0.001

Notes: SMV, soil moisture in the vegetated plots; SMB, soil moisture in the bare (unvegetated) plots; SS, sum of squares; MS, mean squares; Df, degrees of freedom; denDf, denominator Df for the F value.
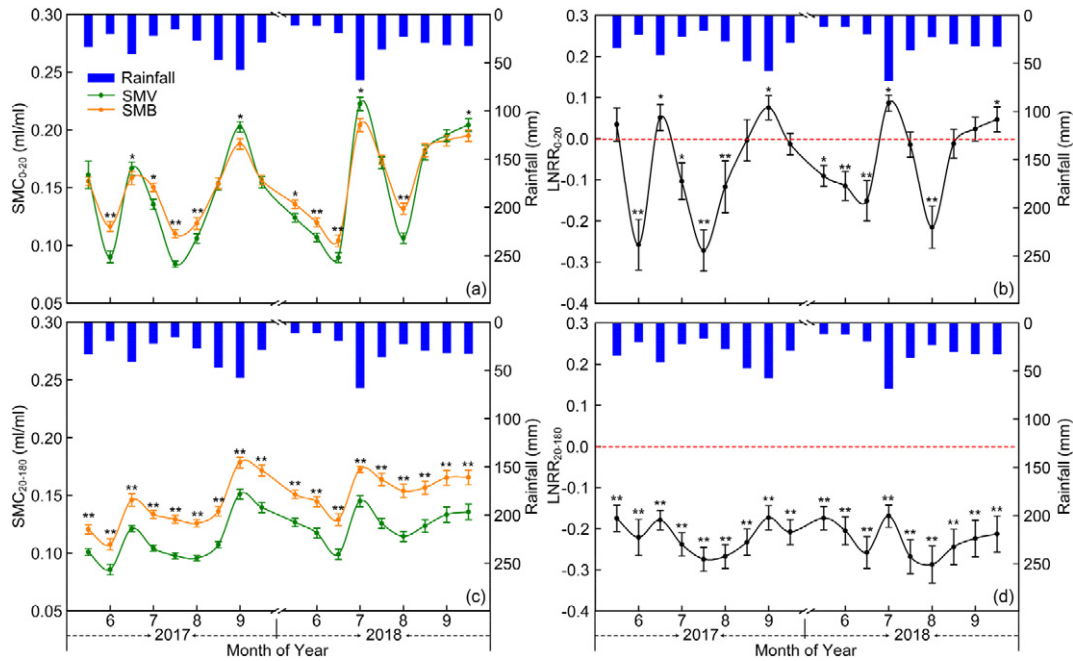
Fig. 3. Temporal changes in rainfall, soil moisture content, and LNRR from 2017 to 2018. Bars denote the standard errors of the mean ($n = 36$). Abbreviations are the same as in Fig. 2. Note: lower case numbers refer to soil depth (cm).

be employed to reflect the vegetation effects on soil moisture. As descriptive variables, RDA with a forward selection slope, leaf area, and fine root biomass at depths of 0–20 cm substantially explained variations of LNRR in the surface layer (Fig. 4a). For LNRR in the deep layer, leaf area, vegetative height, and belowground biomass at depths of 20–60 cm were identified as the explanatory variables (Fig. 4b). In the surface layer during wet periods, the LNRR was negatively related to leaf area and slope, and positively associated with fine root biomass at depths of 0–20 cm (Fig. 4a, Table S6). Further, the LNRR in the deep soil layer was more prone to correlation with vegetative height, leaf area and belowground biomass at depths of 20–60 cm (Fig. 4b, Table S7). Among the 13 candidate traits, four traits (vegetative height, leaf area,

fine root biomass, and belowground biomass) were significantly correlated with the LNRR; thus, they were identified as the effect traits on soil moisture.

SEM explained 69% of the variance of LNRR in the surface layer (Fig. 5a). Leaf area and slope had direct negative effects on LNRR, whereas fine root biomass at depths of 0–20 cm had direct positive effects. Moreover, slope and leaf area exerted strong indirect effects on LNRR through their negative correlations with fine root biomass at depths of 0–20 cm. Similarly, the model for three traits (vegetative height, leaf area, and belowground biomass at depths of 20–60 cm) explained 71% of the variance of LNRR in the deep layer (Fig. 5b). Belowground biomass negatively affected LNRR in the deep layer. Although
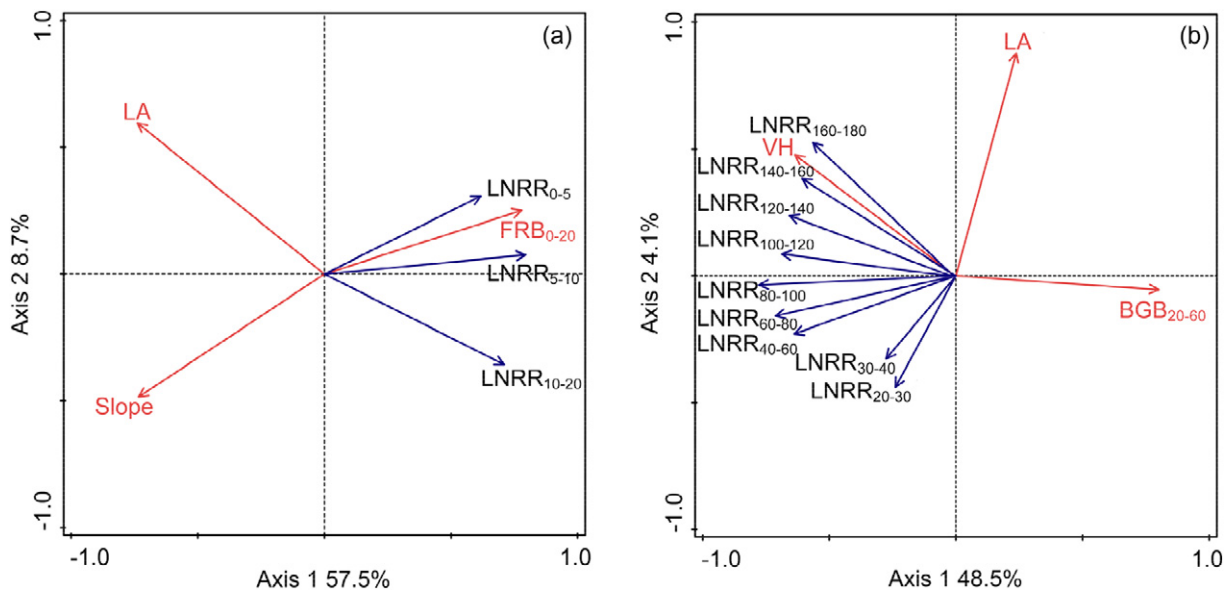

Fig. 4. Redundancy analysis (RDA) ordination biplots showing the relationships between LNRR in the surface (0–20 cm, a) and deep (20–180 cm, b) soil layer and the explanatory variables. Correlation coefficients of the first two axes with explanatory variables are shown in Table S6 and S7. Notes: LNRR, log response ratio; LA, leaf area; VH, vegetative height; BGB, belowground biomass; FRB, fine root biomass. Lower case numbers refer to soil depth (cm).
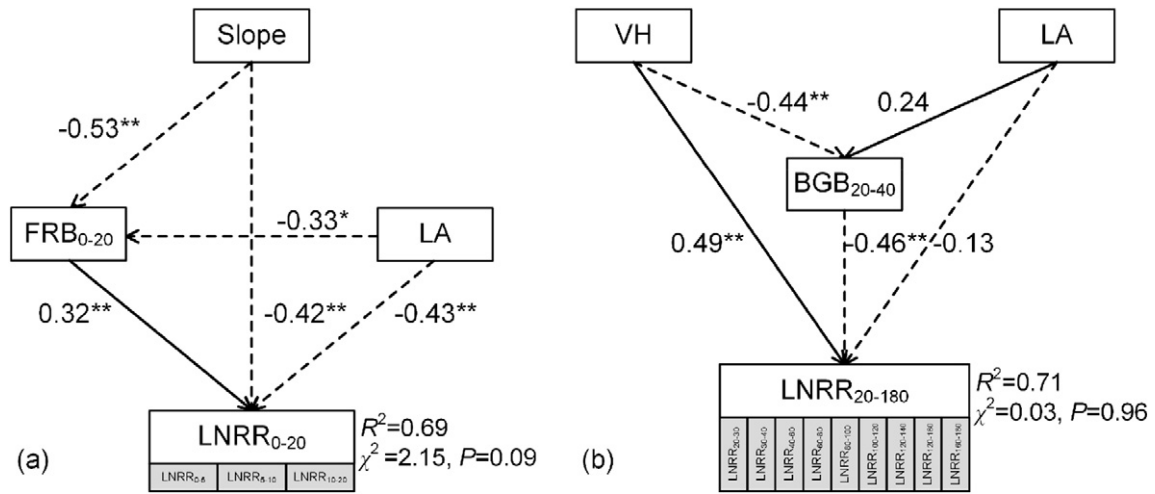
Fig. 5. Structural equation modeling (SEM) examining the direct and indirect effects on LNRR in the surface (0–20 cm, a) and deep (20–180 cm, b) soil layer. Abbreviations are the same as in Fig. 4. Double-layer rectangles represent the first component from the PCA conducted for LNRR (Fig. S1). Solid and dashed arrows indicate significant positive and negative effects, respectively. Statistics for model fitting are indicated at the bottom right of each panel. The numbers adjacent to arrows are standardized path coefficients. $^*P < 0.05$, $^{**}P < 0.01$.

leaf area performed no clear effect on LNNR ($P < 0.05$), vegetative height and leaf area had direct effects on LNRR and also jointly affected LNRR via their effects on belowground biomass.

4. Discussion

4.1. Temporal and vertical changes in vegetation effects on soil moisture

Based on our in-situ removal experiment, the vegetation effects on soil moisture (LNRR) revealed an increasing trend with soil depth (Fig. 2b), whereas their temporal variations exhibited a consistently decreasing trend (Fig. 3b, d). In contrast to the control (bare land), vegetation cover had primarily negative effects on soil moisture, which supported our first hypotheses. In general, vegetation cover influenced soil moisture by altering a series of hydrological processes such as precipitation infiltration, root water uptake, and soil evaporation (Anderegg et al., 2018; Aranda et al., 2012). As mentioned in the introduction, these processes created potentially conflicting contributions to the grass effects on soil moisture. For example, root water uptake and soil evaporation contributed to soil water consumption, whereas precipitation infiltration actually represented the opposite. Hence, the direction and magnitude of the LNRR was contingent on the resultant forces of these processes.

High variations in the LNRR existed in the surface layer over the two growing seasons. During drought periods, vegetation consumed root-zone soil water for transpiration, which resulted in negative effects on soil moisture (Hansson et al., 2019). In contrast, root channels served to redistribute precipitation inputs and enhanced water storage following rains (Wu et al., 2017). Thus, precipitation replenishment abated, and even reversed, negative effects during wet periods (Seneviratne et al., 2010). Therefore, it was reasonable that vegetation cover imparted positive effects on soil moisture in the surface layer during wet periods, relative to bare lands (Fig. 3b). Similar results were also reported in other studies (Gross et al., 2008; Wu et al., 2016). Given the likely significant seasonal changes in precipitation, the considerable variations in the surface soil moisture occurred during the transition from drought to wet periods (Fig. 3a), which was consistent with previous studies (Cao et al., 2011; Ziadat and Taimeh, 2013). Overall, vegetation cover reduced the negative effects on soil moisture in the surface layer over those in deep soil layer, and demonstrated high temporal variations with rainfall patterns.

In the deep soil layer, the vegetation effects on soil moisture (LNRR) were temporally stable with rainfall patterns (Fig. 3d), which confirmed that the impacts of precipitation replenishment on deep layer soil

moisture were secondary in contrast to the root water uptake (Markewitz et al., 2010; Wang et al., 2016a). Indeed, precipitation replenishment decreased with soil depth; hence, deep soil moisture was less influenced by rainfall patterns. Rather, soil moisture in the deep layer was more susceptible to be affected by root water uptake (Choi and Jacobs, 2007). Although herb roots in this region were primarily concentrated at depths of 0–50 cm (Yang et al., 2014b) plants also consumed soil moisture that was stored below the root zone via a hydraulic lifting effect (Prieto et al., 2012). Notably, a few herb species possess deep root systems, such as alfalfa with developed taproots, which can attain 300 cm (Li et al., 2017). In such cases, the deep soil moisture was lower and less replenished by precipitation relative to the surface layer, which resulted in a clear trend of soil desiccation (Fig. 2a).

4.2. Effects of community traits on soil moisture

In this study, four traits jointly determined vegetation effects on soil moisture (LNRR) and were therefore identified as effect traits on soil moisture (Fig. 4b, d). This result supported our second hypotheses, which suggested that vegetation effect on soil moisture was associated with several plant traits. As noted above, vegetation cover had primarily positive effects on soil moisture in the surface layer during wet periods (Fig. 3b). Strong positive effects occurred in those grasslands with a set of beneficial traits (e.g., small leaves and great fine root biomass at depths of 0–20 cm) (Figs. 4b, 5a). Indeed, grasses with small leaves (e.g. Russian wormwood, *Artemisia frigida*) were conducive to limiting water losses by reducing transpiration. Moreover, small leaves might be linked to decreased canopy interception, thereby increasing throughfall (Holder and Gibbes, 2017). Alternatively, grasses with thick dense root systems in the surface layer (e.g., bunge needlegrass, Russian wormwood) more effectively improved infiltration capacities. For instance, Wu et al. (2017) found that the average root channel diameter and root channel area were significantly and positively correlated with the average infiltration rate. Thus, the overall performance of these beneficial traits led to obvious positive effects on soil moisture in the surface layer during wet periods. Furthermore, slope plays a significantly negative role in affecting LNRR in the surface layer ($P < 0.01$). Compared with other topographic and soil properties, slope becomes more important in the control of soil moisture dynamics and distribution at the watershed scale (Yang et al., 2015). Apparently, gentler slopes are much more conducive to precipitation infiltration (direct effects; Fig. 5a). Meanwhile, gentle slopes with shallow root grasses were more efficient in terms of improving infiltration and preventing runoff and soil erosion (Chen et al., 2017). Consequently, gentle slope

conditions associated with small leaves and shallow root systems contributed to the positive effects on soil moisture during wet periods. Similar results were also reported by other researchers. For example, Zirbel et al. (2017) found that plant functional traits coupled with environmental conditions shaped community assembly and ecosystem functioning during vegetation restoration.

Our results further illustrated that vegetation cover primarily induced deep soil moisture declines across two growing seasons (Figs. 2b, 3d), which was modulated by vegetative height, leaf area, and belowground biomass at depths of 20–60 cm (Figs. 4b, 5b). Slightly negative effects occurred in the grasslands with a set of beneficial traits: tall plants, small leaves, and undeveloped root systems at depths of 20–60 cm (Fig. 5b). Small leaves and undeveloped root systems were considered to be more conservative in their water use efficiencies (Díaz et al., 2015; Prieto et al., 2012), which was consistent with a low community transpiration rate. Although tall plants were directly related to high transpiration rates and light interception (Fry et al., 2018), those in our study likely contributed to a subtle wetting effect by intercepting incident irradiation, and lowering the soil temperature (Rosset et al., 2001). Furthermore, different trait syndromes may result in contrasting effects on soil moisture. For example, tall plants associated with developed deep root systems, such as alfalfa, intensified deep-soil drying in the Northern Loess Plateau (Zhang et al., 2018). However, tall plants combined with small leaves and shallow root systems (e.g. Russian wormwood, Fringed Sage (*Artemisia frigida*), bunge needlegrass) were seemingly conducive to reducing drying effects on deep soil moisture.

As indicated in this study, aboveground traits accounted for a large fraction of the variation in LNRR across 36 sites via CWM indices (Table 1), which suggested that mass ratio process (reflected by CWM), rather than niche complementary (reflected by FD), primarily determined the effects of vegetation cover on soil moisture. This result was consistent with many other studies, which revealed that most ecosystem properties such as carbon and nutrient cycling would be determined by the aggregated traits of dominant species (Faucon et al., 2017; Zuo et al., 2018). As soil available water and nutrients are low in this area (Yang et al., 2015), relatively few species are very abundant. Consequently, niche complementarity had a weak effect on soil moisture in this study, where species diversity was lower and trait values were in a narrow range. This idea is supported by other studies in drylands (van der Sande et al., 2018). Meanwhile, our results suggested that aboveground traits could regulate the vegetation effect on soil moisture through belowground traits (Fig. 5). One potential mechanism that explained this result was that soil water status was variably driven by top-down forces (regulation by consumers) (Wardle et al., 2004). For example, plants with small leaves were considered as a conservative strategy in water use efficiency. In this case, shallow root systems could adequately meet the water requirements for plant growth, which further improved rainfall infiltration. Finally, the beneficial traits did not clash between the strong positive effects in the surface layer and the slight drying effects in the deep layer. For example, vegetation with a greater allocation of roots in the surface layer not only assisted with the replenishment of surface soil moisture during wet periods, but also reduced the consumption of deep soil moisture due to reduced root allocation to the deep layer. Accordingly, beneficial community structures for soil moisture in grasslands might be summarized as tall plants with small leaves and shallow root systems (Fig. 6).

4.3. Implications for management

To improve degraded ecosystems, land preparation and vegetation plantation efforts were implemented in water-limited regions such as the Loess Plateau of China (Wei et al., 2019; Yu et al., 2015). Vegetation plantations have severely modified community functional structures and further altered ecosystem functioning (Quétier et al., 2007; Zhang et al., 2019b). Consequently, ecosystem functioning may be estimated from the overall performance of effect traits (Gross et al., 2008). For example, alfalfa was an introduced pasture characterized by small leaves but deep root systems, which was not consistent with the beneficial trait syndromes for soil moisture identified in this study. This result was confirmed by other studies, where alfalfa induced temporally stable soil desiccation compared with native grassland (Yang et al., 2014b; Zhang et al., 2018). As we conducted an in-situ vegetation removal experiment to identify effect traits, the influences of slopes on soil moisture were also isolated (Figs. 4a, 5a). Our study iterated that slope gradients and effect traits cooperatively determined the vegetation effects on soil moisture at the small watershed scale. Natural slopes can be easily transformed into flat surfaces by diverse terracing measures such as counter-slope terraces and fish-scale pits, which markedly improved soil water retention (Wei et al., 2019).

This trait-based framework not only mediated the effects of restoration projects on ecosystem multifunctionality (Gross et al., 2017), but also proved applicable in supporting effective restoration schemes that could easily be managed by restoration practitioners (Zhu et al., 2015; Zirbel et al., 2017). We recognized that vegetation effects on soil moisture were intimately correlated with several functional traits, and the prevalence of particular trait syndromes were jointly conducive to soil water retention,
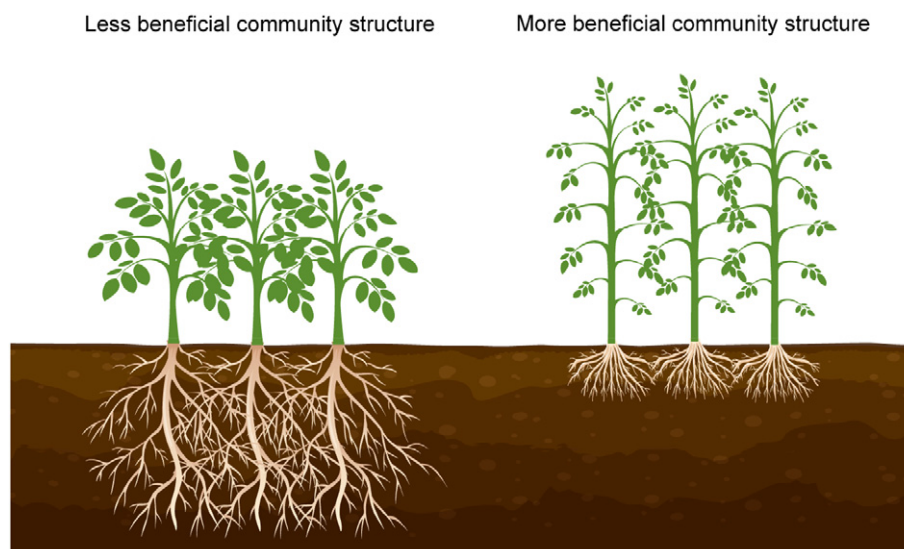
Less beneficial community structure   More beneficial community structure

Fig. 6. Conceptual diagram of beneficial community functional structure (right) and the contrast (left) for soil moisture.

which benefitted vegetation restoration and ecosystem rehabilitation (Fu et al., 2016). In turn, soil water retention assisted with the control of soil erosion by modifying soil properties and reducing surface runoff (Ola et al., 2015). These findings implied that the goal of restoratively enhancing water conservation and its accompanying outcomes might be achieved by manipulating the functional structures of plant communities. Here, we proposed such a two-step restoration scheme. First, we selected the appropriate species from a local species pool, in terms of their overall performance of beneficial trait syndromes. Second, we assembled plant communities by imitating zonal vegetation, inclusive of species compositions and plant density. To summarize, our results represented an attempt to link the effects of vegetation cover on soil moisture to plant traits and provided trait-based restoration guidelines to conserve soil moisture. Further studies should integrate additional model simulations and empirical tests to provide effective solutions for the development and management of ecological restoration projects in the Chinese Loess Plateau and other water-limited regions.

5. Conclusions

We found that, over time, vegetation cover primarily induced soil moisture decreases in the deep soil layer (20–180 cm) by 19.44% compared with an in-situ unvegetated control. However, vegetation cover increased soil moisture content in the surface layer by 6.81% during wet periods (semimonthly rainfall >30 mm). By integrating various functional traits, we linked the vegetation effects on soil moisture to particular trait syndromes. Vegetative height, leaf area, and shallow root allocation were identified as the effect traits on soil moisture. These results supported our initial hypothesis that vegetation cover induced significant changes in soil moisture and vegetation effect on soil moisture was related to plant traits. Additionally, our work proposed that beneficial community structures for water resource conservation were characterized by tall plants with small leaves and shallow roots. As a powerful measure for reducing slope gradient and runoff connectivity, terracing further enhanced these beneficial effects on soil moisture. Such findings are expected to provide important references for future restoration strategies toward augmenting the efficiency of water conservation and ecological restoration in dry and degraded regions.

CRediT authorship contribution statement

Qindi Zhang: Conceptualization, Methodology, Software, Investigation, Writing - original draft.**Wei Wei:**Resources, Writing - review & editing, Supervision.**Liding Chen:**Writing - review & editing.**Lei Yang:** Investigation, Writing - review & editing.**Yiqi Luo:**Writing - review & editing.**Andong Cai:**Methodology, Software.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.137355.

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