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Surface water storage characteristics of main herbaceous species in semiarid Loess Plateau of China

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Abstract

Plant surface water storage greatly affects rainfall interception in water-limited environments. The storage characteristics of 55 common herbaceous species and their relationships with plant morphology, biomass-related traits, and leaf wettability were examined using artificial wetting method in semiarid Loess Plateau. Results indicated that plant mass storage ranged from 0.12–1.26 g g^{-1}, and *Glycyrrhiza uralensis* and *Leymus secalinus* had the highest and lowest values, respectively. Leaf storage ratio ranged from 40.2–93.2%, with the highest value in *G. uralensis* and the lowest in *Chenopodium album*. Fifty-two species had higher storage capacities in leaves than that in stems. Gramineous and leguminous species had relatively lower mass storage and leaf storage ratio than compositae and rosaceae. Plant and leaf mass storage were negatively correlated with leaf adaxial/abaxial contact angles, and stem mass storage was negatively correlated with plant height. Storage capacities were closely related to morphological and biomass-related traits, and leaf area was a better predictor of plant and leaf storage capacities, and stem fresh weight was a better predictor at the stem level. Path analysis revealed that leaf area and adaxial contact angle were two independent variables directly affecting plant and leaf storage capacities. Their ratio (i.e., wettability index) had higher correlations with storage capacities than other single trait and multiple regression models of these traits. Our results implied that high proportions of gramineous and leguminous species in grassland community would favour reducing interception loss, and wettability index can be an effective indicator for evaluating rainfall interception and vegetation hydrological benefits.

KEYWORDS

leaf area, leaf contact angle, leaf storage ratio, species family, surface water storage, wettability index

1 | INTRODUCTION

The plant canopy is the first contact interface with rainfall and leads to spatio–temporal redistribution of rainfall into interception loss, throughfall, and stemflow (Zhang, Wang, Hu, Pan, & Paradeloc, 2015). Interception loss refers to the proportion of rainfall that

temporarily retains on plant leaves and stems and later returns back to the atmosphere through evaporation during and after rainfall events (Dunkerley, 2000). Throughfall is the portion of rainfall that passes through the canopy gaps or drips from canopy to the ground (Barbier, Balandier, & Gosselin, 2009). Rainwater runs down the trunk and subsequently delivers to the root zone, defined as stemflow

(Dunkerley, 2000). Canopy interception accounts for 10–50% of gross rainfall and is an important and sometimes dominant water balance component in dryland ecosystems (Gerrits, Pfister, & Savenije, 2010; Li et al., 2016). It can smooth rainfall intensity, thereby decreasing surface runoff and soil erosion, and affect soil water infiltration, further influencing plant growth and vegetation dynamics during rainless period (Gerrit, 2010; Zhang et al., 2017). More broadly, interception is strongly linked to biogeochemical fluxes and energy conversion in the soil–plant–atmosphere continuum (Negi, Rikhari, & Garkoti, 1998; van Dijk et al., 2015). Both changes in climate (e.g., rainfall regime) and vegetation will produce a remarkable impact on rainfall interception and make it particularly variable (Ochoa-Sánchez, Crespo, & Célleri, 2018; Zeppel, Zeppel, Wilks, & Lewis, 2014).

Canopy storage capacity is defined as the amount of water that can be stored on saturated vegetation canopy after rainfall events when the water dripping has ceased (André, Jonard, & Ponette, 2008; Wang, Zhang, Hu, Pan, & Berndtsson, 2012). Storage capacity is a key factor in controlling actual interception loss and influences leaf gas exchange, plant productivity formation, and ecosystem water balance (Brooks & Vivoni, 2008; Yu et al., 2012). Storage capacity is mainly controlled by rainfall characteristics, meteorological conditions, and canopy structure (Li et al., 2016). First, rainfall amount, duration, intensity, and rainless gap determine the input of rainfall and saturation time of canopy (Zhang, Zhao, Li, Huang, & Tan, 2016). Second, meteorological conditions such as net radiation, air temperature, relative humidity, and wind speed affect the rate of intercepted rainwater removed from canopy surface (Zhang et al., 2017). Additionally, canopy structure as the internal properties of vegetation controls the amount and timing of flow within the canopy, which is critical for explaining the effects of vegetation changes on rainfall interception (Deguchi, Hattori, & Park, 2006; Gerrits et al., 2010; Xiao & McPherson, 2011).

Canopy structure varies with plant species composition and growth stages, resulting in the variation in canopy storage capacity (Deguchi et al., 2006). For instance, the needle tree species had higher storage capacities than those of broadleaf species, mainly because the former had a tighter canopy shape with more overlapping branches and leaves (Li et al., 2016). Significant differences can even be found in species with similar genetic background (Wohlfahrt, Bianchi, & Cernusca, 2006), as storage capacity ranged from 0.5 to 4.3 mm for 13 coniferous species (Link, Unsworth, & Marks, 2004). In the leaf and leafless periods, oak trees (*Quercus brantii*) showed totally different canopy structures and storage capacities of ~1 and 0.1 mm, respectively (Fathizadeh, Hosseini, Zimmermann, Keim, & Darvishi Booloorani, 2017). Overall, plant storage capacity generally increased with the size of plants, and the biomass-related parameters were considered as reliable predictors, for example, leaf area index and aboveground biomasses of plant organs (Li et al., 2016; Wang et al., 2012). Yu et al. (2012) found that converted leaf area index (by converting stem tissues into effective leaf area) had stronger linear correlation with storage capacity. Furthermore, the significance of leaf surface wettability (Rosado & Holder, 2013), leaf shape and leaf angle of orientation (Garcia-Estringana, Alonso-Blázquez, & Alegre, 2010; Holder,

2012), and stem roughness (Livesley, Baudinette, & Glover, 2014) on storage capacity has attracted great attentions in recent years. Although it is well known that canopy structure greatly affects storage capacity, less is understood about the relative importance of those structure parameters such as plant morphology and biomass-related traits (Deguchi et al., 2006; Link et al., 2004). The integrated relationships between storage capacity and multiple structure parameters were also seldom studied.

Due to lower storage capacity and higher technical difficulty of measurement, fewer studies were conducted on herbaceous species with low and procumbent canopies when compared with trees and shrubs (Llorens & Domingo, 2007; Ochoa-Sánchez et al., 2018). However, some dense and complex grassland communities may even intercept more rainfall than trees and shrubs (Couturier & Ripley, 1973; Llorens & Domingo, 2007). Study showed that about 32% of annual rainfall was intercepted for Mitchell grass communities in Australia (Dunkerley & Booth, 1999). Several indirect or direct methods have been developed to estimate storage capacity of herbaceous species (André et al., 2008; Ochoa-Sánchez et al., 2018). Water balance method using simulated rainfall can indirectly estimate storage capacity by calculating the difference between rainfall amount and soil water content (Ochoa-Sánchez et al., 2018; Yu et al., 2012) or the increased weight of plant samples after saturated rainfall (Garcia-Estringana et al., 2010; Wang et al., 2012). While in field experiments, the complicated simulated rainfall equipment and nonconvenient transportation affect the accurate measurements for large groups of samples. Direct methods such as cantilever deflection, ray attenuation, and artificial wetting were also developed. The former two are expensive to implement and require specific and sophisticated instrumentation. In comparison, the artificial wetting method is widely used because of its simplicity, especially in scaling up the specific storage capacity to the whole canopy level (Llorens & Gallart, 2000; Wang et al., 2012; Wohlfahrt et al., 2006).

Rainfall is the main source of soil moisture in the semiarid region on the Loess Plateau of China, which is well known for its fragile ecological environment and serious soil erosion (Lu & van Ittersum, 2004; Zhang, Zhao, Liu, Fang, & Feng, 2016). The Grain to Green Programme for vegetation restoration since 1999 has almost doubled the vegetation cover and declined the soil erosion levels to historic values; however, it potentially creates conflicting demands for the limited water resources between ecosystem and humans (Feng et al., 2016; Yuan et al., 2016). Grassland is the main vegetation type and accounts for 42.9% of the land area in the region (Gang et al., 2018). Changes in coverage and species types of grassland caused by vegetation restoration are expected to greatly influence ecosystem water balance and alter land surface ecohydrological processes (Duan, Huang, & Zhang, 2016). Exploring the surface water storage characteristics of main herbaceous species and their relationships with plant structure traits contributes in revealing the internal mechanism of rainfall interception and evaluating the ecohydrological effects of vegetation restoration. Therefore, the specific objectives of this study were to: (a) quantity the storage characteristics (e.g., storage capacities of leaves, stems, and individual plants) of common herbaceous species in the region,

(b) compare the relationships between storage characteristics with plant morphological and biomass-related traits, and (c) establish a suitable variable or regression model to predict storage capacity at the plant level. These results could enhance our understanding of rainfall interception processes of herbaceous species and provide an experimental basis in species selection and the ecohydrological effect evaluation of vegetation restoration.

2 | MATERIALS AND METHODS

2.1 | Site description

The study site was in the Ansai Research Station of Soil and Water Conservation, Chinese Academy of Sciences (109°19′23″E, 36°51′31″N; 1068–1309 m above sea level), Shaanxi Province, China. It has a typical loess hilly terrain of the Loess Plateau and semiarid climate with mean annual rainfall of 540 mm and mean temperature of 8.8°C. The annual sunshine duration is ~2,400 hr and the frost-free period is ~160 days. The soil type is mainly Calcic Cambisols (Food and Agriculture Organization), originated from wind deposits and classified as silt loam. The vegetation belongs to the warm-temperate forest steppe area, which is in the transitional zone of the deciduous broadleaf forest area and grassland area. Shrub–grassland is the dominant vegetation type in Ansai country, and the total area decreased from 52.6% to 39.5% during 1995–2010 with the implementation of the Grain to Green Programme (Zhou, Zhao, & Zhu, 2012). Nowadays, in the natural vegetation, there are mainly xeric herbaceous species, including *Artemisia giraldii*, *Artemisia gmelinii*, *Bothriochloa ischcemum*, *Lespedeza davurica*, and *Stipa bungeana*, associated with a small quantity of tree and shrub communities, including *Quercus wutaishanica* and *Rosa xanthine*. The artificial vegetation is dominated by *Astragalus adsurgens*, *Hippophae rhamnoides*, *Medicago sativa*, and *Robinia pseudoacacia*, where *A. adsurgens* and *M. sativa* are fine species for the construction of local artificial grassland.

2.2 | Experimental design and plant sampling

The experiment was implemented during the growing season from May to August in 2017. After a comprehensive investigation and record of common herbaceous species at the mountain experimental field of the Ansai Research Station in May, six grassland communities with areas from 10 to 100 m^2 were selected as sample plots. When selecting plots, well-grown grasslands that cover common herbaceous species were required, and the plot area was determined by actual site situation. In total, 55 common herbaceous species were selected for measuring plant mass storage (gram per gram), that is, plant storage capacity per unit fresh weight. Gramineous, leguminous, compositae, and rosaceous species are the main component species in the area, accounting for 70.9% of the investigated species (Table 1). They were considered for comparing the differences in storage characteristics between species families. There were 27 widely distributed species selected for measuring plant, leaf, and stem storage capacities (gram

per plant). The aboveground part of individual plant was sampled for each species, which was cut along the ground surface with hand-hold shears. Five to ten individual plants for each species were sampled every month to obtain enough plant samples with different sizes and morphological traits. Only a small number of plant samples (less than 10%) had flowers and fruits, and this part of water storage is small enough to be neglected for the total plant storage. Thus, they were removed after sample collection and not included in the calculation of water storage. The samples were stored in a portable cool box and were immediately transported to the laboratory and kept in a freezer at 4°C. All the measurements would be completed within 2 days after sampling (Wang, Shi, Li, & Wang, 2014; Wang, Shi, Li, Yu, & Zhang, 2013).

2.3 | Measurements of plant morphological and biomass-related traits

The plant natural height (*H*, centimetre) of each species was measured in situ with a steel ruler. Leaf number (*N*) was counted, and plant fresh weight (PW, gram) was measured before the separation of leaves and stems for measuring the stem fresh weight (SW, gram). Leaf fresh weight (LW, gram) was calculated as the difference between PW and SW. Stem–leaf ratio (SLR) was calculated as SW divided by LW. Five to ten leaves were randomly selected from the individual plant of each species to obtain individual leaf area (ILA, square metre) and individual leaf fresh weight (ILW, gram). The ILA was calculated for the adaxial side of each leaf by ImageJ software (National Institutes of Health, USA) after being photographed by a digital camera (Powershot G7X, Canon). The total leaf area (LA, square centimetre) of the individual plant was calculated as: LA = (ILA/ILW) × LW (Garcia-Estringana et al., 2010). An electronic balance with an accuracy of 0.0001 g was used to weigh all the samples.

2.4 | Measurement of leaf contact angle

Leaf contact angle was measured to determine the leaf surface wettability, and larger contact angle indicates a more spherical water droplet on the surface and higher leaf water repellency (Rosado & Holder, 2013). A 10-μl droplet of distilled water was deposited on leaf surface using a micropipette for measuring leaf contact angle (Holder, 2012, 2013). Leaves were spread out to obtain a 5 × 5-mm area and fixed horizontally onto a glass plate using double-sided tape. Measurements were taken on both adaxial (θ_{ad}, degree) and abaxial (θ_{ab}, degree) surfaces (each species with 10 replicates) by calculating the tangential angle of water droplet with leaf surface. The contact angle was obtained in accordance with the photoconductive method on the basis of a charge-coupled device image and calculated by measuring the average value of the tangential angles on two sides of the water droplet. Each measurement was completed within 2 min using a JC2000C1 instrument (Powereach, Shanghai Zhongchen Digital Technology Apparatus Co., Ltd, China).

TABLE 1 The species families, Latin names, and abbreviations of 55 common herbaceous species included in the study

Family	Latin name	Abbreviations
Brassicaceae	*Torularia humilis* (C. A. Meyer) O. E. Schulz	Th
Chenopodiaceae	*Chenopodium album* Linn.	**Ca**
	Kochia scoparia (Linn.) Schrad.	Ks
Compositae	*Artemisia capillaris* Thunb.	Ac
	Artemisia giraldii Pamp.	Ag
	Artemisia gmelinii Web. ex Stechm.	Ag1
	Artemisia mongolica (Fisch. ex Bess.) Nakai	Am1
	Artemisia scoparia Waldst. et Kit.	As
	Bidens bipinnata Linn.	Bb
	Cirsium setosum (Willd.) MB.	**Cs**
	Dendranthema indicum (Linn.) Des Moul.	**Di**
	Heteropappus altaicus (Willd.) Novopokr.	**Ha**
	Ixeridium sonchifolium (Maxim.) Shih	**Is**
	Lappula myosotis Moench	Lm
	Leontopodium leontopodioides (Willd.) Beauv.	**Ll**
	Mulgedium tataricum (Linn.) DC.	Mt
	Saussurea japonica (Thunb.) DC.	**Sj**
	Sonchus arvensis Linn.	Sa
	Taraxacum mongolicum Hand.-Mazz.	**Tm**
	Youngia japonica (Linn.) DC.	Yj
Convolvulaceae	*Pharbitis nil* (Linn.) Choisy	**Pn**
Geraniaceae	*Geranium wilfordii* Maxim.	**Gw**
Gramineae	*Bothriochloa ischcemum* (Linn.) Keng	Bi
	Cleistogenes caespitosa Keng	**Cc**
	Leymus secalinus (Georgi) Tzvel.	**Ls**
	Phragmites australis (Cav.) Trin. Ex	**Pa**
	Poa annua Linn.	Pa1
	Roegneria kamoji Ohwi	Rk
	Setaria viridis (Linn.) Beauv.	**Sv**
	Stipa bungeana Trin.	Sb
Lamiaceae	*Dracocephalum moldavica* Linn.	**Dm**
	Leonurus artemisia (Lour.) S. Y. Hu	**La**
Leguminosae	*Astragalus adsurgens* Pall.	**Aa**
	Astragalus melilotoides Pall	Am
	Glycyrrhiza uralensis Fisch.	**Gu**
	Gueldenstaedtia stenophylla Bunge	Gs
	Lespedeza davurica (Laxm.) Schindl.	**Ld**
	Lespedeza floribunda Bunge	Lf
	Medicago sativa Linn.	**Ms**
	Oxytropis bicolor Bunge	Ob
	Oxytropis racemosa Turcz.	**Or**
	Thermopsis lanceolata R.Br.	**Tl**
	Vicia sepium Linn.	**Vs**
Linaceae	*Linum usitatissimum* Linn.	Lu
Polygalaceae	*Polygala tenuifolia* Willd.	Pt1
Ranunculaceae	*Thalictrum aquilegifolium* Linn.	**Ta**
Rosaceae	*Potentilla bifurca* Linn.	**Pb**
	Potentilla discolor Bge.	Pd
	Potentilla tanacetifolia Willd. ex Schlecht.	Pt
Rubiaceae	*Rubia cordifolia* Linn.	**Rc**
Scrophulariaceae	*Rehmannia glutinosa* (Gaert.) Libosch. ex Fisch. et Mey.	Rg
Umbelliferae	*Bupleurum chinensis* DC.	Bc
Valerianaceae	*Patrinia heterophylla* Bunge	**Ph**

TABLE 1 (Continued)

Family	Latin name	Abbreviations
Violaceae	Viola dactyloides Roem. et Schult.	**Vd**
	Viola philippica Cav.	Vp

Note. The abbreviations in bold represent the 27 widely distributed species selected for the separation of leaves and stems.

2.5 | Measurements of plant storage characteristics

The storage capacity of individual plant (PC, gram per plant) was determined as the increased weight of their fresh samples after applying the artificial wetting method (Garcia-Estringana et al., 2010; Llorens & Gallart, 2000; Wohlfahrt et al., 2006). The fresh plant samples were weighed (PW, gram) and then completely immersed into a bucket filled with collected rainwater for 5 min. Large-sized plants such as Glycyrrhiza uralensis were cut into pieces to facilitate full immersion. All sample pieces were picked up carefully with tweezers and held stationary in the air for 20 s. When there was no water dripping off, the samples were reweighed. Plant mass storage (PS, gram per gram) was calculated as PC divided by PW. After removing all leaves and wiping the stems dry, stem storage capacity (SC, gram per plant) was also obtained by the increased weight of stems through artificial wetting method. Similarly, stem mass storage (SS, gram per gram) was calculated as SC divided by SW. Leaf storage capacity (LC, gram per plant) and leaf mass storage (LS, gram per gram) were calculated as: LC = PC – SC and LS = LC/LW. Leaf storage ratio (LSR, percentage) was calculated as LC divided by PC. All the measurements were accomplished under the laboratory conditions within 10 min to reduce the effect of wind and water evaporation.

2.6 | Statistical analysis

Plant mass storage of 55 species and leaf storage ratio of 27 species were ranked from the maximum to the minimum value, respectively. The two storage characteristics were divided into four categories to better characterize their variation ranges according to the rank orders. One-way analysis of variance followed by Duncan's multiple range test were performed to compare the mean values of plant mass storage and leaf storage ratio among different families. The relationships between storage characteristics (mass storage, storage capacity, and leaf storage proportion) with plant morphological and biomass-related parameters were analyzed by Pearson's product-moment correlation. Path analysis was used to select the main plant traits directly affecting plant, leaf, and stem capacities, estimate the relative importance of plant traits to storage capacities through path coefficients, and calculate the correlations between variables. The relationships between wettability index (defined in Section 3) and storage characteristics were analyzed by Pearson's product-moment correlation. The optimal multiple regression models between storage capacities and direct influencing traits were determined by path analysis. SPSS Statistics 20.0 (SPSS Inc. Chicago, IL, USA) was used for all statistical tests at .05 probability level.

3 | RESULTS

3.1 | Plant mass storage and leaf storage ratio

Plant mass storage was divided into four categories, and >0.8 g g^{-1}, 0.6–0.8 g g^{-1}, 0.4–0.6 g g^{-1}, and <0.4 g g^{-1} accounted for 9.1% (5 species), 23.6% (13 species), 36.4% (20 species), and 30.1% (17 species), respectively. G. uralensis had the highest plant mass storage (1.26 g g^{-1}) across all species, and Leymus secalinus was the lowest one (0.12 g g^{-1}; Figure 1). For leaf storage ratio, the category of >90%,
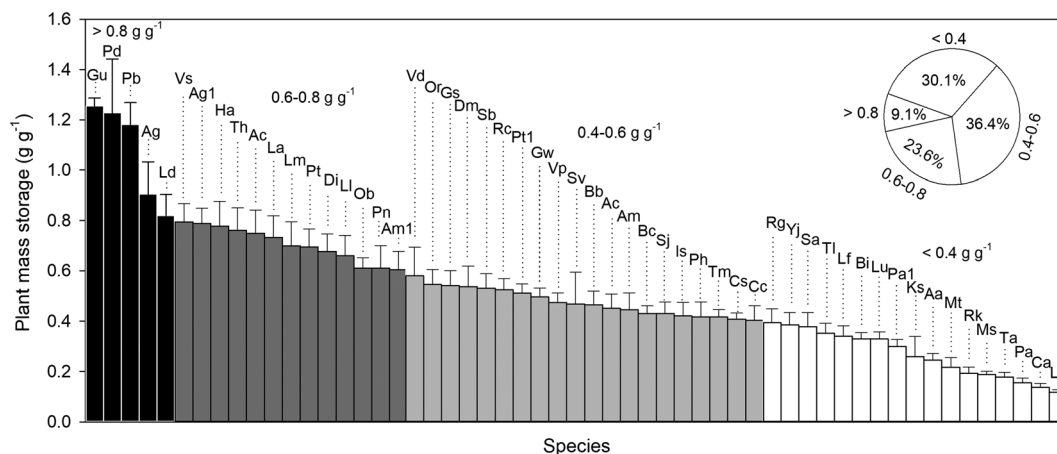

FIGURE 1 The rank order of plant mass storage of 55 common herbaceous species. The pie chart represents the proportion of four categories: >0.8 g g^{-1}, 0.6–0.8 g g^{-1}, 0.4–0.6 g g^{-1}, and <0.4 g g^{-1}

70–90%, 50–70%, and <50% accounted for 11.1% (3 species), 51.9% (14 species), 25.9% (7 species), and 11.1% (3 species), respectively. The highest and lowest leaf storage ratio were 93.2% and 40.2%, which were found in *G. uralensis* and *Chenopodium album*, respectively (Figure 2).

The average value of plant mass storage in rosaceous species was significantly higher than that in all species; leguminous and compositae species (*P* < .05; Figure 3a) and the gramineous species showed the lowest value (*P* < .05). The average value of leaf storage ratio in compositae species was significantly higher than that in all species and leguminous species (*P* < .05, Figure 3b), with the gramineous species being the lowest (*P* < .05). Rosaceous species was not compared because only one species belonging to rosaceae was measured for leaf storage ratio. There was a positive correlation between plant mass storage and leaf storage ratio (*r* = .55, R^2 = .30, *P* = .003), and the linear regression equation was *y* = 1.05*x* – 0.22 (Figure 4).

3.2 | Relations between plant storage characteristics with morphological and biomass-related traits

Plant mass storage was negatively correlated (*P* < .05) with leaf adaxial (*r* = −.41, R^2 = .17) and abaxial contact angles (*r* = −.36, R^2 = .13). Leaf mass storage was also negatively correlated (*P* < .05) with leaf adaxial (*r* = −.42, R^2 = .18) and abaxial contact angles (*r* = −.34, R^2 = .12). Plant height, leaf number, leaf area, fresh weights of individual plant and its components (i.e., leaves and stems), and stem–leaf ratio had no correlations with both plant and leaf mass storage (*P* > .05). Stem mass storage was only correlated with plant height (*r* = −.50, R^2 = .25, *P* = .007) within all plant traits (Figure 5).

Plant, leaf, and stem storage capacities were positively correlated with plant height, leaf number, leaf area, plant fresh weight, and fresh weights of leaves and stems (*P* < .01, Figure 5). Leaf adaxial and abaxial contact angles were negatively correlated (*P* < .05) with plant and leaf storage capacities and had no correlations with stem storage capacity (*P* > .05). Stem–leaf ratio had no correlations with plant and leaf storage capacities (*P* > .05), whereas it was positively correlated with stem storage capacity (*P* = .002). Leaf area (*r* = .69, .66; R^2 = .48, .44) and plant fresh weight (*r* = .68, .65; R^2 = .46, .42) were better predictors of plant and leaf storage capacities. Stem fresh weight (*r* = .82, R^2 = .67) and plant fresh weight (*r* = .71, R^2 = .50) were better predictors of stem storage capacity. Leaf storage ratio was positively correlated with leaf fresh weight (*r* = .41, R^2 = .17, *P* = .007) and was negatively (*P* < .05) correlated with leaf adaxial (*r* = −.67, R^2 = .45) and abaxial contact angles (*r* = −.47, R^2 = .22). The other morphological and biomass-related traits had no correlations with leaf storage ratio (*P* > .05).

Path analysis revealed that leaf area, leaf adaxial contact angle, and leaf number were the main variables directly affecting plant and leaf storage capacities, and the direct path coefficients to plant storage capacity were .59, −.28, and .29 and to leaf storage capacity were .57, −.30, and .26, respectively (Figure 6). The optimal multiple regression equations were PC = 1.01 + 0.014LA – 0.012θ_{ad} + 0.0070N (*r* = .77, R^2 = .59, *P* < .001) and LC = 0.94 + 0.013LA – 0.012θ_{ad} + 0.0060N (*r* = .74, R^2 = .55, *P* < .001; Table 2). Stem storage capacity was mainly affected by stem fresh weight, leaf number, and adaxial contact angle, and the direct path coefficients were .69, .35 and −.075, respectively (Figure 6). The optimal multiple regression equation was SC = 0.060 + 0.15SW + 0.0010N – 0.00040θ_{ad} (*r* = .88, R^2 = .77, *P* < .001; Table 2).

There was a significant correlation between leaf area and leaf number (*r* = .40, R^2 = .16, *P* < .001; Figure 6). In comparison, leaf area and adaxial contact angle were two independent variables. Leaf area was the most important plant trait to predict plant/leaf storage capacity, and the reciprocal of θ_{ad} is closely related to the degree of leaf hydrophilicity (Holder, 2013). Thus, the variable of wettability index (WI, square centimetre per degree) was established and calculated as leaf area divided by adaxial contact angle (WI = LA/θ_{ad}). The ecological significance of wettability can be understood as the degree of hydrophilicity of individual plant. General regression models showed that wettability index as a synthetic variable had higher correlation coefficients (*r* = .86, .85; *P* < .001) with plant and leaf storage capacities than
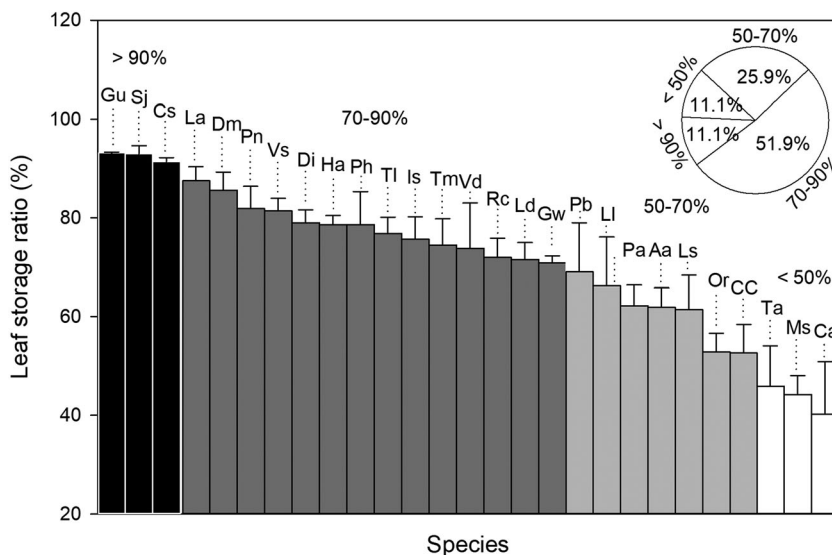

FIGURE 2 The rank order of leaf storage ratio of 27 widely distributed herbaceous species. The pie chart represents the proportion of four categories: >90%, 70–90%, 50–70%, and <50%
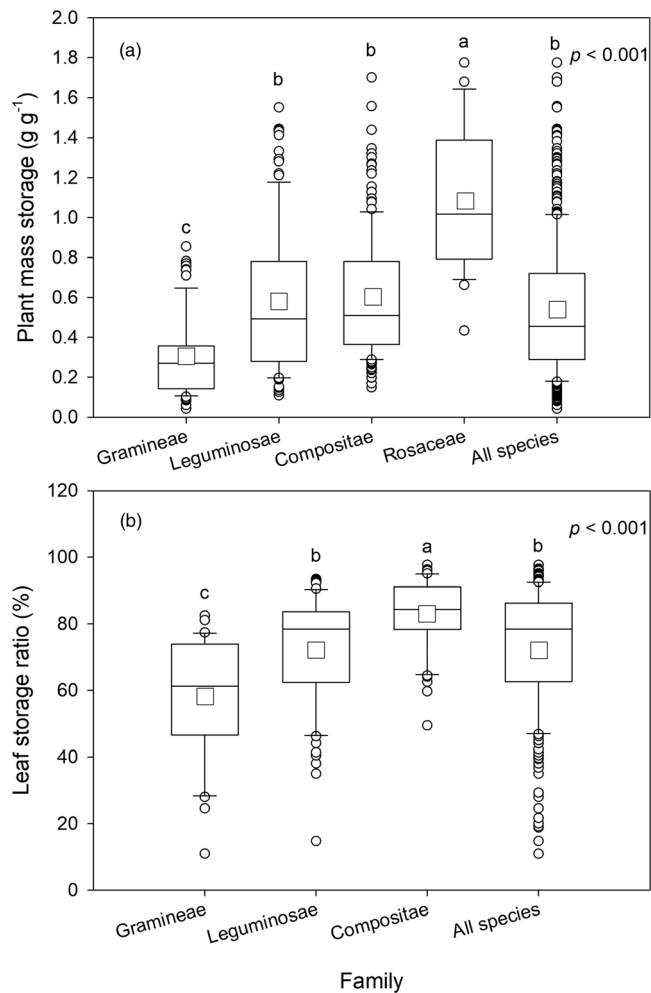
FIGURE 3 (a) Plant mass storage and (b) leaf storage ratio of herbaceous species among different families. The significances of family are marked on the upper right
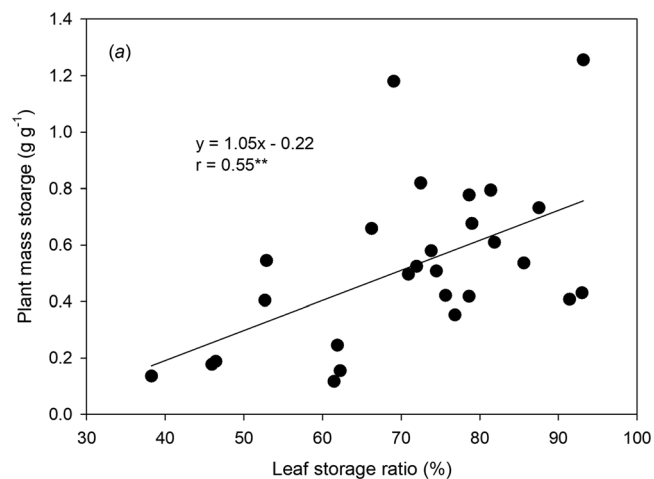

FIGURE 4 The relationship between plant mass storage and leaf storage ratio. Significance differences are indicated: $^*P \leq .05$; $^{**}P \leq .01$; $^{***}P \leq .001$

other single traits, even higher than the optimal multiple regression equation ($r = .77, .74$; Table 2; Figure 7). Wettability index was also positively correlated ($P < .05$) with plant mass storage ($r = .40$), leaf mass storage ($r = .42$), and leaf storage ratio ($r = .48$; Figure 7).

4 | DISCUSSION

Plant surface water storage controls the amount of water that can be held on vegetation canopy during rainfall events. Interception loss and water utilization of grassland would increase during vegetation restoration in the semiarid Loess Plateau, greatly affecting rainfall availability and land surface ecohydrological processes (Duan et al., 2016). Our study was motivated by the limited understanding about the rainfall storage of herbaceous species and their relations with plant functional traits in the region. We quantified the storage characteristics of 55 common herbaceous species, evaluated the relationships between storage characteristics with morphological and biomass-related traits, and established the wettability index to more accurately predict storage capacity. The results of this study may provide the theoretical basis for the construction of reasonably structured grassland in terms of its ecohydrological benefits.

4.1 | Plant storage characteristics

Plant mass storage, expressed in storage capacity per unit fresh weight, differed significantly among species, ranging from 0.12 to 1.26 g g^{-1}. The values were basically in agreement with other researchers. Storage values were found to range from 0.23 to 2.26 g g^{-1} in the nine Mediterranean shrubs (Garcia-Estringana et al., 2010). Wang et al. (2012) estimated that the storage values of three dominant xerophytic shrubs in Northwestern China were 0.41, 0.51, and 0.73 g g^{-1}, respectively. Besides, some researchers calculated the plant storage capacity per unit leaf area, and the values covered a wide range from 13.2 to 314.0 g m^{-2} for nine herbaceous plants (Wohlfahrt et al., 2006). Actual interception loss was also found to vary from one plant species to another by monitoring 22 local rainfall events (Ufoegbune, Ogunyemi, Eruola, & Awomeso, 2010). The above findings implied that the differences in surface storage between species should be considered in accurate estimation of rainfall storage capacity at both individual plant and community level (Couturier & Ripley, 1973; Llorens & Gallart, 2000; Yu et al., 2012). Leaf storage ratio was also species dependent between 40.2% and 93.2%, and storage capacities of leaves were higher than those of stems for 52 species (55 species in total). Greater storage capacities in leaves have also been confirmed (Wohlfahrt et al., 2006; Yu et al., 2012), and the higher leaf storage ratio, the greater mass storage was recorded in this study. These indicated that leaves play a more important role than stems in canopy interception processes for herbaceous species.

Plant mass storage and leaf storage ratio showed variability associated with species family, as the values of gramineous and leguminous species were lower than those of compositae and rosaceous species. Researchers have confirmed that graminoid leaves tend to have less
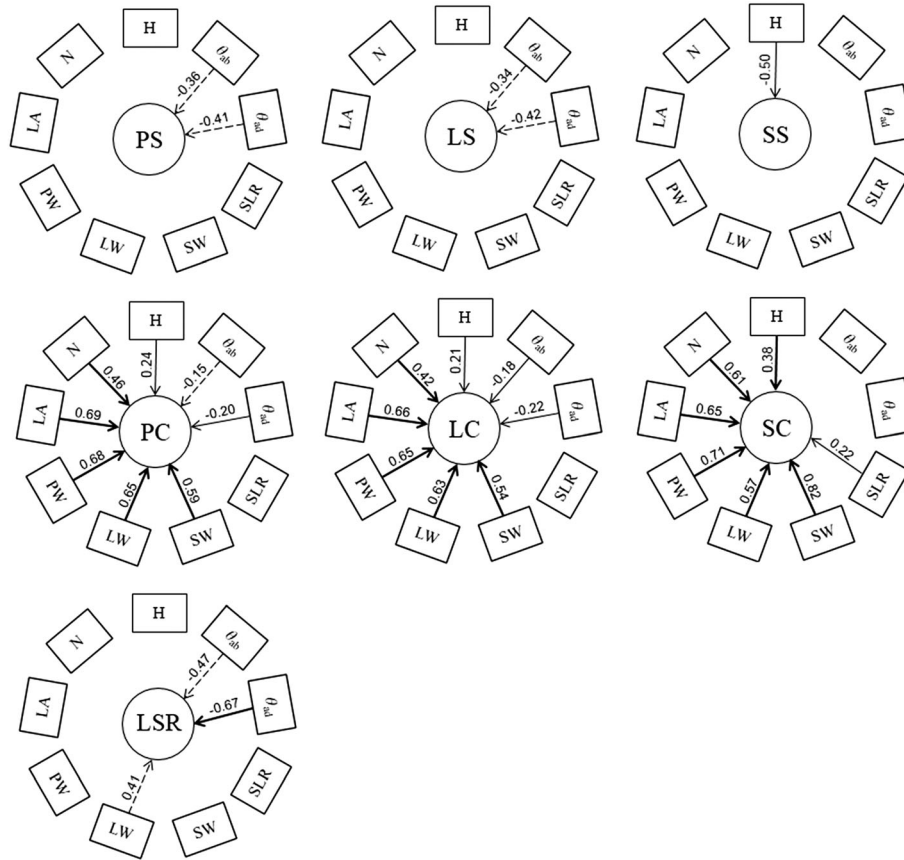
FIGURE 5 The correlations between plant storage characteristics with plant morphological and biomass-related traits (PS, LS, SS: plant, leaf, and stem mass storage; PC, LC, SC: plant, leaf, and stem storage capacities; LSR: leaf storage ratio; H: plant height; N: leaf number; LA: leaf area; PW, LW, SW: plant, leaf, and stem fresh weight; SLR: stem–leaf ratio; θ_{ad}/θ_{ab}: leaf adaxial/abaxial contact angle). The numbers above the lines are Pearson correlation coefficients. The bold solid line represents $P \leq .001$; solid line represents $P \leq .01$; and dashed line represents $P \leq .05$ (the same as Figures 6 and 7)
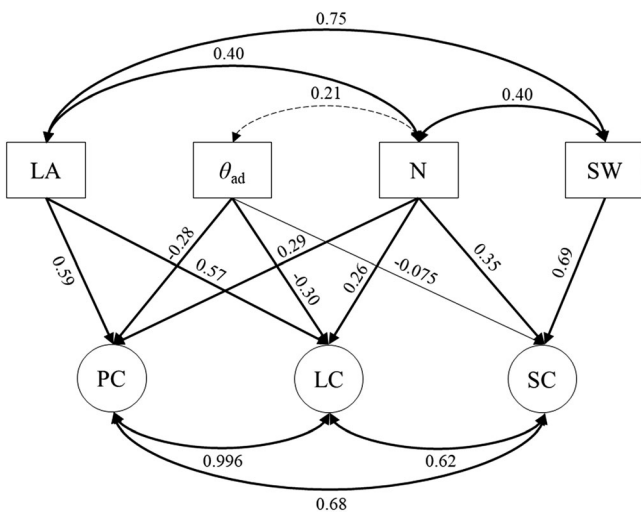

FIGURE 6 Path analysis between plant, leaf, and stem storage capacities with plant morphological and biomass-related traits. The numbers above the single-headed and double-headed arrow lines are path coefficients and Pearson correlation coefficients, respectively

storage capacities compared with forbs (Wohlfahrt et al., 2006; Yu et al., 2012). Such differences may be associated with the variability in leaf wettability, adhesion, or repulsion of water drops, determined by leaf surface physico-chemical properties (Brewer & Nunez, 2007; Fernández et al., 2017). The leaf surfaces of most grasses and legumes were covered with prominent epicuticular wax layers, which can be observed clearly by scanning electron microscopy (Neinhuis & Barthlott, 1997). The epicuticular wax layer constitutes the interface between leaf and atmosphere, and its main components have hydrophobic properties (Müller & Riederer, 2005). Thus, dense epicuticular wax layers were generally associated with decreased leaf surface wettability (Koch, Bhushan, & Barthlott, 2009). Our previous data also proved that leaves of gramineous and leguminous species were more water repellent (higher leaf contact angles) than those of compositae and rosaceous species (Xiong et al., 2018). However, not all species belonging to the same family had similar leaf wettability. For example, the leaves of leguminous *G. uralensis* were highly wettable, although most leguminous leaves were considered as hydrophobic. Therefore, leaf wettability was species-specific, which cannot be judged merely

TABLE 2 The optimal regression models between plant, leaf and stem capacities with plant morphology, biomass-related traits, and wettability index

	Regression models	
Dependent variables	LA, θ_{ad}, N, SW	WI
Plant storage capacity (PC, gram per plant)	PC = 1.01 + 0.014LA – 0.012θ_{ad} + 0.0070N, r = .77, R^2 = .59***	PC = –0.060 + 1.55WI, r = .86, R^2 = .74***
Leaf storage capacity (LC, gram per plant)	LC = 0.94 + 0.013LA – 0.012θ_{ad} + 0.0060N, r = .74, R^2 = .55***	LC = –0.14 + 1.43WI, r = .85, R^2 = .72***
Stem storage capacity (SC, gram per plant)	SC = 0.060 + 0.15SW + 0.0010N – 0.00040θ_{ad}, r = .88, R^2 = .77***	SC = 0.076 + 0.13WI, r = .63, R^2 = .40***

Note. The multiple regression models were analyzed by path analysis, and the general linear regression models were analyzed by Pearson's product-moment correlation.

Abbreviations: LA, leaf area; θ_{ad}, leaf adaxial contact angle; N, leaf number; SW, stem fresh weight; WI, wettability index.

Significance differences are indicated:

*$P \leq .05$. **$P \leq .01$. ***$P \leq .001$.
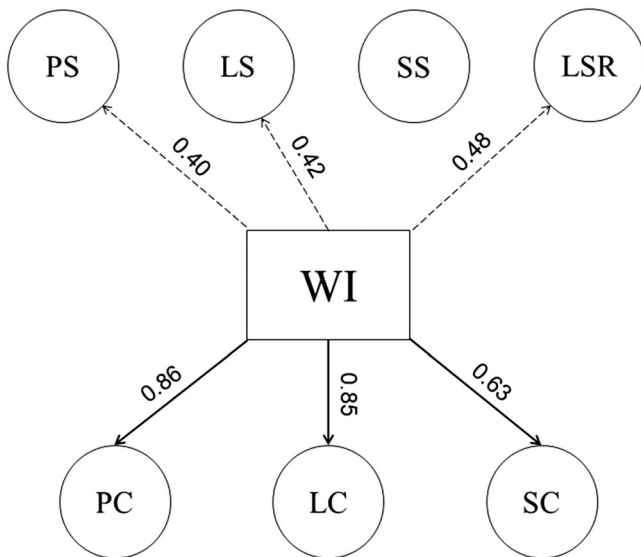
FIGURE 7 The correlations between plant storage characteristics and wettability index. The numbers above the lines are Pearson correlation coefficients

by species family. To clarify the effects of family on leaf wettability, detailed leaf surface physico-chemical properties (e.g., distributions of wax, trichomes, and stomata) that affect leaf wettability should be investigated among more quantities and varieties of plants.

Plant and leaf mass storage were negatively correlated with leaf contact angle and positively correlated with wettability index. The difference in contact angle between blade surface and water droplet would lead to different contact states, varied from a water film to a semicircular or subround water droplet (Rosado & Holder, 2013). When leaf contact angle is high, rainwater falling on leaf surface tend to drop more easily under the influences of gravity or any meteorological and biotic disturbances (Holder, 2013; Xiong et al., 2018). The adaxial leaf contact angle of Catalpa speciosa was double than

that of Ulmus pumila, and the surface storage of U. pumila leaves was 60% greater than that of C. speciosa at the same time (Holder, 2012). The rank order of leaf surface storage of a branch across seven species is the opposite of their rank order of leaf contact angle (Holder, 2013). Wettability index was defined in Section 3 as the degree of hydrophilicity of individual plant. Significant negative relationships between plant mass storage with leaf adaxial/abaxial contact angles and wettability index were expected, although the correlation coefficients were relatively low (r = –.41, –.36, .40). This is probably because the water retention on plant surface is a complicated process, also affected by water droplet features (e.g., water quality and droplet diameter; Šikalo & Ganić, 2007), leaf surface properties (e.g., leaf roughness, and leaf surface free energy; Brewer & Nunez, 2007; Wang et al., 2014), leaf morphology (e.g., leaf shape, and leaf angle; Holder, 2012), and stem or bark "wettability" (Crockford & Richardson, 2000). In this study, the rosaceous Potentilla bifurca had a high plant mass storage of 1.18 g g^{-1}, although the leaves were nonwettable. We speculated that numerous and dense leaves of this species may increase its storage capacity under the equivalent plant weight. There was a negative correlation between stem mass storage and plant height. Taller herbaceous plants were normally accompanied by greater stem length and diameter, resulting in the water retained on stems more likely to gather into larger droplets at the bottom and easily dropping down under the influences of surface tension and gravity (Wang et al., 2014; Wohlfahrt et al., 2006).

4.2 | Linkages between plant storage capacity with morphological and biomass-related traits

Plant storage capacity increased linearly with leaf, stem, and plant fresh weight, plant height, leaf number, leaf area, and leaf contact angle, which emphasized the importance of plant structure traits in influencing rainfall interception. Leaf area had the highest explanation (48, 44%) for the variation of plant and leaf storage capacities than

other traits followed by plant fresh weight. The results were consistent with the findings of Wang et al. (2012) who considered that leaf area and plant dry biomass could better predict storage capacities of shrubs than canopy projection area and sample volumes. Similarly, the water stored by shrubs was related to plant biometric characteristics, in which the fresh total biomass had the highest correlation coefficient (Garcia-Estringana et al., 2010). Biomass-related parameters (e.g., woody and total biomass) were the best predictors for interception of four dominant tree species in the northern China (Li et al., 2016). For herbaceous species, Wohlfahrt et al. (2006) found that the predictive power of morphological traits for storage capacity was low, such as leaf length, shape factor, and specific leaf area and suggested that the dependence of storage capacity on morphological traits was highly species-specific. Taking one with another, considering the pooled data from 27 herbaceous species, our results have good applicability and reliability.

Because of low predictability of single plant trait to storage capacity, and the interspecific differences between their relationships, it is necessary to establish more suitable parameters or models (Barbier et al., 2009; Fathizadeh et al., 2017; Wohlfahrt et al., 2006). Path analysis was used in this study to divide the correlations between storage capacities and plant traits into direct and indirect effects. Leaf area, adaxial contact angle, and leaf number showed larger direct effects on storage capacity. Considering the independence and ecological significances of leaf area and adaxial contact angle, wettability index was established and could be understood as the degree of hydrophilicity of individual plant. The explanation of this new indicator for plant storage capacity increased to 74%, even higher than optimal multiple regression model of plant traits (59%). In natural environments, the vegetation storage capacity is affected synchronously by canopy, rainfall, and meteorological characteristics, which increases the difficulties of accurate prediction using a single variable (Crockford & Richardson, 2000; Li et al., 2016; Zhang et al., 2017). We suggested that wettability index could better reflect plant structural characteristics and compensated for the limitation of single variable on the storage capacity estimation of herbaceous species.

At the community or large-scale level, researchers recognized that leaf area index (LAI), canopy cover fraction, and aboveground biomass had strong relationships with canopy storage capacity, especially for LAI (Pitman, 1989; Wang et al., 2012; Yu et al., 2012). It is reasonable to assume that LAI, combined with contact angle data of regional species, can more accurately estimate grassland storage capacity in a large area. With the development of remote sensing observation, it provides good opportunity for quickly obtaining efficient data on vegetation structure properties at the regional scale (Cui & Jia, 2014). Certainly, this hypothesis still needs to be verified and enriched by field experiments. Further, Fathizadeh et al. (2017) showed that canopy structure variables performance to predict storage capacity of oak forest varied seasonally from leafed to leafless period. Hence, a comprehensive consideration of seasonal changes in LAI and leaf wettability of species may be useful for accurately predicting interception loss and evaluating hydrological function of grassland communities during the whole growing season.

5 | CONCLUSION

Plant mass storage and leaf storage ratio were species-specific, ranging from 0.12–1.26 g g^{-1} (55 species) and 40.2–93.2% (27 species), respectively. Storage capacities of leaves were higher than stems for most species, indicating that leaves play the leading role in retaining rainfall for herbaceous species. Surface storage and leaf storage ratio of gramineous and leguminous species were lower than those of compositae and rosaceous species, suggesting that species differences should be considered in accurate quantification of canopy interception. In the grassland restoration and construction on water-limited Loess Plateau, when gramineous and leguminous species account for a large proportion under similar coverage, rainfall interception loss would be reduced, thus improving soil water replenishment.

Within all plant traits, leaf adaxial contact angle and leaf area were the most appropriate indicators for estimating plant mass storage and storage capacity, respectively. Wettability index, integrating the two former variables, had the highest correlations with plant and leaf storage capacities, even higher than multiple regression of plant traits. These findings could contribute to the ecohydrological effect evaluation of degraded vegetation rehabilitation so as to establish suitable vegetation for sustainable development in large scale in rainfed regions. In addition, more detailed investigations of plant structure traits (e.g., leaf surface physico-chemical properties, leaf angle, and stem roughness) should be involved, which can better reveal the mechanisms of plant rainfall storage and how changes in structural variables may affect ecohydrological processes.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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