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RESEARCH ARTICLE

Variability in leaf wettability and surface water retention of main species in semiarid Loess Plateau of China

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Abstract

Leaf wettability, adhesion or repulsion of water drops, varies greatly among species and plays an important role in plant–soil hydrological relations. This study aimed to examine the variability in leaf wettability among species in different habitats and growth periods, and their relationships with plant surface water retention in the semiarid Loess Plateau of China. The leaf adaxial and abaxial contact angles, the surface water retention of leaves and individual plants, and general plant traits of 68 species belonging to 28 families were examined from May to August in 2017. Results showed that leaf water contact angles ranged from 27.3° to 133.4° and leaves with higher contact angles normally had lower variation coefficients. Leaf wettability was affected by internal properties (including leaf side, family, and leaf age) and external conditions (growth period), whereas the life form and slope aspect did not show significant effects. There were 47 species having higher contact angles on adaxial than abaxial surfaces, and the differences were significant in 23 species. Gramineous and leguminous species were more unwettable than compositae and rosaceous species. New leaves were more unwettable than old leaves. Surface wettability increased from May–June to July–August period. Leaf wettability was positively correlated with leaf surface water retention and was the best predictor of individual plant surface water retention compared with other plant traits. Leaf wettability showed interspecific differences associated with family and growth stage and can be a considerable variable in predicting canopy interception and evaluating vegetation hydrological function in drought environments.

KEYWORDS

family, growth period, habitat, leaf wettability, rainfall interception, species, surface water retention

1 | INTRODUCTION

Leaf wettability, adhesion or repulsion of water drops, is an important plant functional trait and varies greatly among species and communities (Brewer & Nunez, 2007; Fernández et al., 2017; Holder, 2007). The natural surfaces of leaves have been found to range from completely wettable to virtually nonwettable (Aryal & Neuner, 2016). As a result of rainfall, dew, or ground fog, leaf wetting occurs frequently in natural environment, and its extent and duration are affected by leaf surface properties (Pandey & Nagar, 2003; Wang, Shi, Li, Yu, & Zhang, 2013). Leaf surface is covered with a cuticle, serving as the interface between leaves and the surrounding atmosphere, and the physicochemical properties of cuticle determine the surface wettability (Fernández, Guzmán-Delgado, Graça, Santos, & Gil, 2016; Müller & Riederer, 2005). For instance, when the cuticular waxes were removed from the surface, the contact angles of *Nelumbo nucifera* (lotus) and *Colocasia esculenta* leaves dropped significantly and became wettable (Burton & Bhushan, 2006). A high density of trichomes and stomata on surfaces were generally related to decreased leaf wettability (Pandey & Nagar, 2003; Rosado & Holder, 2013; Wagner, Fürstner, Barthlott, & Neinhuis, 2003). These surface morphological features are variable during plant growth and greatly influenced by external habitat conditions, such as rainfall, air temperature, and humidity (Tanakamaru, Takehana, & Kimura, 1998; Koch, Hartmann, Schreiber, Barthlott, & Neinhuis, 2006; Aryal & Neuner, 2010; Zhu et al., 2014). Some researchers indicated that leaves in dry habitats tended to be less wettable as a functional response to replenish more rainfall into the soil and improve water availability (Brewer & Nunez, 2007; Holder, 2007). Leaf wettability was found to decrease significantly with increasing altitude in Nepalese Himalayas, which was considered as an important adaptation to protect leaves from surface wetting under cold and freezing environments (Aryal & Neuner, 2010).

Leaf wetting has both positive and negative effects on leaf and plant function (Goldsmith et al., 2016). Leaves may benefit from surface wetting by direct uptake of water or reducing transpiration water loss, thereby alleviating leaf water deficits (Eller, Lima, & Oliveira, 2013). High wettability can be harmful because water droplets or films on leaf surfaces may slow stomatal CO_2 diffusion by about 10,000 times, causing instantaneous suppression of gas exchange and chronic damage to photosynthetic apparatus (Brewer & Nunez, 2007; Ishibashi & Terashima, 1995; Pandey & Nagar, 2003). Furthermore, the enhanced sunlight passing through water droplets, the leaching of foliar nutrients, and the adhesion of pathogens and dust may occur synchronously on excessive wetting leaves, causing leaf tissue damage (Aryal & Neuner, 2010; Barthlott & Neinhuis, 1997). Hence, the decreased surface wettability and covariation in leaf morphological features can be seen as an adaptive trait due to the functional advantage in certain environments (Goldsmith et al., 2016; Holder, 2007).

At the ecosystem level, leaf wettability has hydrological significance for investigating canopy interception of rainfall and managing water resources (Holder & Gibbes, 2017; Rosado & Holder, 2013). Canopy interception loss refers to the amount of rainfall temporarily retained on vegetation surfaces and evaporates back into the atmosphere during and after rainfall (Zhang, Wang, Hu, Pan, & Paradeloc, 2015). The interception loss accounts for 10–50% of gross rainfall, directly influencing rainfall partitioning into throughfall or stemflow, that is, the net rainfall into the ground (Li et al., 2016). The vegetation that intercepts more rainfall may decrease the soil water availability and surface run-off in arid and semiarid environments (Llorens & Domingo, 2007; Zhang et al., 2015). During a rainfall event, canopy water storage is mainly controlled by the rainfall properties such as rainfall amount and intensity and the canopy properties such as leaf area index and canopy projected area (Li et al., 2016; Wang, Zhang, Shao, & Wang, 2013). Leaf wettability may be an additional canopy parameter for explaining the variation of water storage because high hydrophilic species may retain more rainfall and therefore increase interception loss (Holder, 2012). Studies related to leaf wettability allow us to predict rainfall interception loss more precisely and may contribute to current hydrological models (Rosado & Holder, 2013; Sikoraka et al., 2017).

Recent studies showed that the implementation of the Grain to Green Programme (GTGP) on the Loess Plateau of China has almost doubled the vegetation cover and declined the soil erosion levels to historic values (Chen et al., 2015; Zhou, Zhao, & Zhu, 2012). However, low water availability and high water consumption rates by plants may cause soil desiccation and vegetation degradation, particularly in rainfed environments, where precipitation is the only source of soil water (Duan, Huang, & Zhang, 2016; Llorens & Domingo, 2007). Balancing the hydrological effects induced by vegetation is crucial for sustainable vegetation growth and development in the region (Chen et al., 2015; Duan et al., 2016). An understanding of regional variability in leaf wettability among species and its role in contributing to rainfall interception may provide insight into predicting hydrological processes and evaluating vegetation function, whereas relevant researches were fairly limited (Holder & Gibbes, 2017). Therefore, we chose 68 common species in the semiarid loess hilly–gully region and examined the water contact angles, general plant traits, and leaf/plant surface water retention, focusing on the dual surface of leaves in different habitats and growth periods. Our objectives were to (a) examine the variation range and patterns in leaf wettability of the main species in the area; (b) evaluate possible internal properties (leaf side, life form, family, and leaf age) and external conditions (growth period and slope aspect) affecting leaf wettability; (c) determine the relationships of leaf wettability and plant traits with leaf/plant surface water retention. Specifically, this study examined whether leaf wettability can explain the variation in rainfall interception at both leaf and individual plant level, which may provide a significant foundation in species selection for vegetation restoration in this region.

2 | MATERIALS AND METHODS

2.1 | Site description

The study was conducted at the Ansai Research Station of Soil and Water Conservation, Chinese Academy of Sciences (109°19′23″E, 36°51′31″N; 1,068–1,309 m a.s.l.), Shaanxi Province, China. The station is located in the semiarid region of northwestern China, with mean annual rainfall of 540 mm. Rainfall during the growing season between April and October accounts for 85–95% of the annual total, with July to September accounting for 60–80% (Xu, Li, & Shan, 2008). The average annual temperature is 8.8°C, with an average low of −6.9°C in January and an average high of 22.6°C in July. The annual sunshine duration is ~2,400 hr and the frost-free period is ~160 days. The soil type is classified as Calcic Cambisols. The vegetation type was previously dominated by shrub–grasslands and has changed dramatically with the implement of GTGP. In Ansai country from 1995 to 2010, the forestland increased from 12.4% to 37.8% (in terms of total area) and the shrub–grassland and cropland decreased from 52.6–39.5% to 36.7–19.7%, respectively (Zhou et al., 2012). Common herb species today include *Artemisia gmelinii*, *Bothriochloa ischaemum*, and *Lespedeza davurica*; common trees include *Ginkgo biloba*, *Juglans regia*, and *Robinia pseudoacacia*; common shrubs include *Periploca sepium*, *Hippophae rhamnoides*, and *Caragana korshinskii*; and common crops include *Zea mays*, *Helianthus annuus*, and *Glycine max*.

TABLE 1 Leaf contact angle of adaxial and abaxial surfaces and leaf and plant surface water retention of 68 species included in the study

Family/species	Life form	Leaf contact angle (°) Adaxial	Leaf contact angle (°) Abaxial	Leaf surface water retention (g m^{-2})	Plant surface water retention (g g^{-1})
Aceraceae					
Acer truncatum Bunge	Tree	73.5 ± 5.4a	85.9 ± 0.5a	80.5 ± 15.4	n.d.
Anacardiaceae					
Rhus typhina Nutt	Tree	91.9 ± 2.6b	132.0 ± 2.3a	70.7 ± 11.8	n.d.
Asclepiadaceae					
Periploca sepium Bunge	Shrub	73.4 ± 2.0b	95.1 ± 3.0a	107.7 ± 9.3	n.d.
Chenopodiaceae					
Chenopodium album Linn.	Herb	126.8 ± 2.9a	126.8 ± 2.2a	67.7 ± 8.8	0.14 ± 0.02
Kochia scoparia Linn.	Herb	127.3 ± 1.7a	123.5 ± 4.8a	98.9 ± 15.2	n.d.
Compositae					
Artemisia giraldii Pamp.	Herb	102.6 ± 7.6b	124.4 ± 6.5a	124.8 ± 15.1	n.d.
Artemisia mongolica (Fisch. ex Bess.) Nakai	Herb	107.9 ± 7.2a	118.0 ± 2.3a	90.6 ± 3.7	0.60 ± 0.07
Cirsium setosum (Willd.) MB.	Herb	71.8 ± 2.8a	73.6 ± 5.9a	114.2 ± 8.6	0.41 ± 0.03
Dendranthema indicum (Linn.) Des Moul.	Herb	82.5 ± 3.1b	131.0 ± 1.2a	148.2 ± 11.2	0.68 ± 0.07
Helianthus annuus Linn.	Herb	27.3 ± 0.8b	46.2 ± 3.5a	179.2 ± 6.2	n.d.
Heteropappus altaicus (Willd.) Novopokr.	Herb	92.0 ± 4.0a	92.0 ± 3.8a	213.0 ± 17.4	0.78 ± 0.10
Ixeridium sonchifolium (Maxim.) Shih	Herb	117.3 ± 2.4b	129.1 ± 2.2a	110.7 ± 8.9	0.42 ± 0.05
Leontopodium leontopodioides (Willd.) Beauv.	Herb	117.3 ± 7.6a	121.9 ± 5.2a	182.5 ± 7.4	0.66 ± 0.08
Mulgedium tataricum (Linn.) DC.	Herb	123.8 ± 2.5a	124.7 ± 2.7a	103.6 ± 7.7	n.d.
Saussurea japonica (Thunb.) DC.	Herb	84.3 ± 6.5b	113.8 ± 4.0a	164.0 ± 19.5	0.43 ± 0.05
Taraxacum mongolicum Hand.-Mazz.	Herb	45.6 ± 2.3a	48.1 ± 2.7a	145.7 ± 9.8	0.51 ± 0.03
Convolvulaceae					
Pharbitis nil (Linn.) Choisy	Herb	67.0 ± 6.1a	76.8 ± 8.1a	108.3 ± 10.9	0.61 ± 0.09
Elaeagnaceae					
Hippophae rhamnoides Linn.	Shrub	83.4 ± 3.0b	102.6 ± 3.7a	107.2 ± 9.4	n.d.
Geraniaceae					
Geranium wilfordii Maxim.	Herb	80.3 ± 4.5a	81.2 ± 3.8a	165.3 ± 14.9	0.50 ± 0.04
Ginkgoaceae					
Ginkgo biloba Linn.	Tree	109.2 ± 4.1a	127.6 ± 2.6a	67.6 ± 4.3	n.d.
Gramineae					
Bothriochloa ischcemum (Linn.) Keng	Herb	104.0 ± 5.8a	113.6 ± 2.6a	87.4 ± 19.4	n.d.
Bromus inermis Leyss.	Herb	121.3 ± 0.7a	105.0 ± 1.1b	52.5 ± 2.8	n.d.
Cleistogenes caespitosa Keng	Herb	108.1 ± 6.0a	66.4 ± 2.8a	163.2 ± 27.5	0.40 ± 0.06
Leymus secalinus (Georgi) Tzvel.	Herb	123.4 ± 2.8a	116.3 ± 2.9a	70.2 ± 6.4	0.12 ± 0.01
Panicum virgatum Linn.	Herb	127.0 ± 2.1a	107.7 ± 9.1a	62.6 ± 8.7	n.d.
Phragmites australis (Cav.) Trin. Ex	Herb	117.2 ± 3.7b	127.1 ± 2.2a	64.6 ± 4.4	0.15 ± 0.02
Setaria viridis (Linn.) Beauv.	Herb	132.8 ± 2.1a	90.7 ± 3.4b	81.0 ± 22.5	n.d.
Zea mays Linn.	Herb	63.2 ± 3.4a	48.8 ± 5.0a	185.2 ± 14.5	n.d.
Juglandaceae					
Juglans regia Linn.	Tree	84.5 ± 3.2a	80.8 ± 2.4a	68.3 ± 4.1	n.d.
Lamiaceae					
Dracocephalum moldavica Linn.	Herb	74.3 ± 3.5b	88.3 ± 3.5a	131.6 ± 25.5	0.54 ± 0.08
Leonurus artemisia (Lour.) S. Y. Hu	Herb	59.0 ± 1.9b	68.6 ± 3.2a	189.8 ± 21.3	0.73 ± 0.09
Leguminosae					
Astragalus adsurgens Pall.	Herb	127.3 ± 2.1a	126.8 ± 2.2a	95.9 ± 6.9	0.25 ± 0.03
Astragalus melilotoides Pall	Herb	128.9 ± 3.1a	121.6 ± 2.4a	106.5 ± 10.9	n.d.
Caragana korshinskii Kom.	Shrub	120.3 ± 1.4a	110.5 ± 5.2a	120.6 ± 8.2	n.d.
Glycine max (Linn.) Merr.	Herb	47.0 ± 1.8b	103.7 ± 5.3a	117.6 ± 4.1	n.d.
Glycyrrhiza uralensis Fisch.	Herb	50.3 ± 4.6a	55.5 ± 3.7a	196.6 ± 16.8	1.25 ± 0.03

(Continues)

TABLE 1 (Continued)

Family/species	Life form	Leaf contact angle (°) Adaxial	Abaxial	Leaf surface water retention (g m^{-2})	Plant surface water retention (g g^{-1})
Lespedeza davurica (Laxm.) Schindl.	Herb	126.5 ± 2.3a	128.3 ± 1.9a	45.2 ± 7.6	0.82 ± 0.08
Medicago sativa Linn.	Herb	116.6 ± 5.6a	120.7 ± 3.2a	71.0 ± 6.8	0.19 ± 0.01
Oxytropis bicolor Bunge	Herb	111.0 ± 2.2a	113.2 ± 1.4a	99.9 ± 10.4	n.d.
Oxytropis racemosa Turcz.	Herb	130.8 ± 1.1a	96.6 ± 10.4b	182.4 ± 19.4	0.54 ± 0.06
Robinia pseudoacacia Linn.	Tree	130.0 ± 1.3b	133.4 ± 0.7a	61.2 ± 12.3	n.d.
Sophora japonica Linn.	Tree	123.0 ± 4.0a	133.4 ± 2.0a	77.3 ± 8.2	n.d.
Thermopsis lanceolata R.Br.	Herb	131.1 ± 2.3a	126.2 ± 1.6a	98.3 ± 11.2	0.35 ± 0.04
Vicia sepium Linn.	Herb	78.2 ± 4.1b	98.3 ± 3.8a	127.4 ± 14.1	0.79 ± 0.07
Linaceae					
Linum usitatissimum Linn.	Herb	125.4 ± 2.1a	114.0 ± 6.9a	92.3 ± 7.7	n.d.
Loganiaceae					
Buddleja lindleyana Fort.	Shrub	125.2 ± 1.6a	126.1 ± 2.3a	114.8 ± 8.5	n.d.
Moraceae					
Morus alba Linn.	Tree	66.4 ± 3.1a	63.5 ± 3.0a	113.2 ± 3.3	n.d.
Oleaceae					
Forsythia suspensa (Thunb.) Vahl	Shurb	74.3 ± 3.7a	72.4 ± 4.1a	73.9 ± 7.4	n.d.
Syringa oblata Lindl.	Shrub	86.6 ± 4.2a	58.3 ± 4.1b	59.2 ± 3.7	n.d.
Plantaginaceae					
Plantago depressa Willd.	Herb	39.3 ± 3.4a	45.4 ± 3.2a	166.5 ± 28.4	n.d.
Ranunculaceae					
Paeonia suffruticosa Andr.	Shrub	115.7 ± 10.0a	127.6 ± 2.1a	85.9 ± 10.3	n.d.
Thalictrum aquilegifolium Linn.	Herb	122.8 ± 2.0a	125.9 ± 1.6a	74.9 ± 16.3	0.18 ± 0.02
Rhamnaceae					
Ziziphus jujuba Mill.	Tree	78.2 ± 2.2b	87.9 ± 2.9a	131.7 ± 19.1	n.d.
Ziziphus mauritiana Lam.	Shrub	72.1 ± 4.6a	77.4 ± 5.3a	202.0 ± 29.2	n.d.
Rosaceae					
Armeniaca vulgaris Lam.	Tree	66.2 ± 3.5b	86.6 ± 2.1a	75.9 ± 10.9	n.d.
Potentilla bifurca Linn.	Herb	108.2 ± 5.1a	113.9 ± 4.2a	172.7 ± 14.5	1.18 ± 0.09
Potentilla tanacetifolia Willd. ex Schlecht.	Herb	63.3 ± 3.6b	87.6 ± 7.6a	308.0 ± 17.0	n.d.
Pyrus betulifolia Bge.	Tree	91.3 ± 2.9a	96.6 ± 2.0a	91.6 ± 7.3	n.d.
Rosa xanthina Lindl.	Shrub	124.5 ± 1.4b	129.5 ± 0.1a	110.2 ± 12.4	n.d.
Rubiaceae					
Rubia cordifolia Linn.	Herb	66.3 ± 3.1b	102.2 ± 6.0a	147.9 ± 11.3	0.52 ± 0.04
Salicaceae					
Populus tomentosa Carr.	Tree	89.9 ± 1.2b	112.9 ± 6.1a	83.2 ± 7.4	n.d.
Salix matsudana Koidz.	Tree	68.1 ± 4.9a	91.2 ± 3.4a	66.9 ± 6.1	n.d.
Sapindaceae					
Xanthoceras sorbifolia Bunge	Shrub	83.8 ± 1.9b	129.1 ± 2.3a	75.2 ± 10.9	n.d.
Simaroubaceae					
Ailanthus altissima (Mill.) Swingle	Tree	69.5 ± 5.8b	99.4 ± 4.4a	99.4 ± 11.1	n.d.
Ulmaceae					
Ulmus pumila Linn.	Tree	75.3 ± 3.2a	71.4 ± 3.4a	82.3 ± 7.0	n.d.
Valerianaceae					
Patrinia heterophylla Bunge	Herb	61.9 ± 4.5a	71.7 ± 3.6a	118.3 ± 14.2	0.42 ± 0.06
Violaceae					
Viola dactyloides Roem. et Schult.	Herb	42.6 ± 3.7b	74.5 ± 2.4a	114.1 ± 10.8	n.d.
Viola philippica Cav.	Herb	67.2 ± 5.5a	65.9 ± 3.6a	174.5 ± 18.0	n.d.

Note. Significant differences ($p < 0.05$) between adaxial and abaxial surfaces are indicated by different small letters (mean ± *SE*, n = 4–8); n.d. denotes no data.

2.2 | Meteorological conditions

Monthly records of rainfall, air temperature, and relative humidity were obtained from an automatic weather station of Ansai Research Station close to the sampling sites (0.1–3 km).

2.3 | Plant species and sampling

Sixty-eight species (including 14 tree species, 10 shrub species, and 44 herb species) belonging to 28 families were selected for measuring leaf contact angle and surface water retention (Table 1). Most herb species were selected because they are more widespread in the experimental site, and the selected trees and shrubs are also common and representative. Gramineous, leguminous, compositae, and rosaceous species were considered for comparing the differences between families, because they are the main component species in the area, accounting for 54.4% of all investigated species (Table 1). Leaf sampling was conducted from May to August because May to June is considered as a dry period and July to August as a rainy period in the region (Xu et al., 2008). Healthy and new fully developed leaves were randomly sampled at a canopy height of 2–3 m for tree species from different directions, and middle-upper leaves were sampled for shrub and herb species. Ten leaves for each species were sampled every month.

To determine the impact of leaf age on leaf wettability, withered and yellow-coloured leaves from nine species (including two tree species, one shrub species, and six herb species) were selected. To determine the effects of slope aspect, nine herb species that grow on sunny and shady slopes were specially selected. The elevation of two slopes is ~1,150 m and the distance between the slopes is ~150 m. The aspects of sunny and shady slopes are 140–150° and 320–330°, and the gradients are 20–30° and 25–35°, respectively.

Twenty-seven herb species were selected for individual plant surface water retention and general plant traits measurements (Table 1). A whole plant from each species was sampled and cut along the ground surface with shears. Leaf or plant samples were stored in a portable cool box and were immediately transported to the laboratory and kept in a freezer at 4°C, before all the measurements were completed within 2 days after sampling (Wang, Shi, et al., 2013; Wang, Shi, Li, & Wang, 2014).

2.4 | Measurements of leaf contact angle

Leaf wettability was determined by measuring the leaf contact angle (θ). Leaf surfaces with $\theta < 40°$ are normally classified as super hydrophilic, $40° < \theta < 90°$ as highly wettable, $90° < \theta < 110°$ as wettable, $110° < \theta < 130°$ as nonwettable, $130° < \theta < 150°$ as highly nonwettable, and $\theta > 150°$ as super hydrophobic (Aryal & Neuner, 2010). Here, a 10 μl droplet of distilled water was deposited on each leaf surface using a micropipette for measuring leaf contact angle. This volume was chosen to ensure the deposit of the droplet on a potentially super-hydrophobic and nonwettable surfaces, although the contact angle may be affected by the droplet weight. 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 and abaxial surfaces (each with 10 replicates) by calculating the tangential angle of a water droplet with a leaf surface. The contact angle was obtained in accordance with the photoconductive method based on 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).

2.5 | Measurements of general plant traits

The individual natural height (cm) of each species was measured with a steel ruler under natural conditions before sampling. Leaf numbers were counted and individual plant fresh weight (PW, g) was measured thereafter. Five leaves were randomly selected from each species to obtain individual leaf fresh weight (ILW, g) and individual leaf area (ILA, m^2), and the ILA was measured for the adaxial side. The ILA of each leaf was calculated by Image J software (National Institutes of Health, USA) after being photographed by a digital camera (Powershot G7X, Canon). The stem fresh weight (SW, g) was obtained after removing all leaves. The leaf fresh weight (LW, g) was calculated as

$$\mathrm{LW} = \mathrm{PW} - \mathrm{SW} \tag{1}$$

The total leaf area (TLA, m^2) was calculated as

$$\mathrm{TLA} = (\mathrm{ILA}/\mathrm{ILW}) \times \mathrm{LW} \tag{2}$$

The stem-leaf ratio (SLR) was calculated as

$$\mathrm{SLR} = \mathrm{SW}/\mathrm{LW} \tag{3}$$

An electronic balance (0.0001 g) was used to weigh all samples. To reduce the effect of wind, leaf transpiration, and water evaporation, the measurement for each sample was accomplished within 10 min in a balance room.

2.6 | Measurements of leaf and plant surface water retention

The water retained (g) on surfaces of leaf and individual plant was determined as the increased weight of their fresh samples after applying the artificial wetting method. The leaf or plant samples were weighed and then completely immersed into a bucket filled with collected rainwater for 5 min (Garcia-Estringana, Alonso-Blázquez, & Alegre, 2010). For large individual plants like *Glycyrrhiza uralensis*, they were cut into pieces to facilitate full immersion. All sample pieces were picked up carefully and held stationary in the air for 20 s. When there was no water dripping off, the samples were re-weighed. Leaf surface water retention (g m^{-2}) was calculated as the water retained per unit leaf area (m^2), and the plant surface water retention (g g^{-1}) was calculated as the water retained per unit plant fresh weight (g).

2.7 | Statistical analysis

One-way analysis of variance followed by Duncan's multiple range test was used to compare the mean values of leaf contact angles under different internal (leaf side, life form, family, and leaf age) and external factors (growth period and slope aspect) and the mean leaf/plant surface water retention values between different families.

Tamhane-T2 tests were applied for multiple comparisons when conditions of normality and homogeneity of variances were not met. Differences between contact angles of adaxial and abaxial surfaces, new and old leaves, and plants on sunny and shady slope were tested by independent sample *t* test. Pearson's product moment correlation and least squares regression analysis assessed the degree of linear association between coefficient of variation, leaf/plant surface water retention, and contact angle. The relationship between plant surface water retention and plant traits was analysed by Pearson's correlation coefficient. Analysis was processed by SPSS Statistics 20.0 (SPSS Inc. Chicago, Ill, USA). Differences were considered significant for all statistical tests at $p < 0.05$.

3 | RESULTS

3.1 | Meteorological conditions

The annual rainfall at the study site was 485.6 mm in 2017, with the highest monthly rainfall in August (130.0 mm). The rainfall during the dry period (May to June) and rainy period (July to August) accounted for 23.4% (113.8 mm) and 42.2% (204.8 mm) of annual total, respectively. The mean monthly air temperature and relative humidity ranged from −4.4°C to 23.6°C and 46.3% to 85.2%, respectively. The temperature increased gradually from January to July and declined from August to December. The relative humidity remained stable from January to April, increased gradually from May to October, and declined rapidly from November to December (Figure 1).

3.2 | Leaf wettability

In the 68 species (136 surfaces), the mean contact angle values ranged from a minimum of 27.3° in the adaxial surface of *Helianthus annuus* to a maximum of 133.4° in the abaxial surfaces of *R. pseudoacacia* and *Sophora japonica* (Table 1). The contacting states of water on leaf surfaces varied from a water film (e.g., *Plantago depressa*) to a semicircular water droplet (e.g., *Hippophae rhamnoides*) or a subround water droplet (e.g., *Chenopodium album*). According to the variability of contact angles, the species could be divided into six categories, and the super hydrophilic, highly wettable, wettable, nonwettable, and highly nonwettable species accounted for 1.5%, 41.2%, 16.2%, 35.3%, and 5.9%, respectively. No super-hydrophobic species was identified. The highly wettable species exhibited the highest variation degree compared with other categories (Figure 2a). Significant negative linear correlation was detected between variation coefficient and contact angle ($r = -0.58$; $p < 0.001$); the equation was $y = -0.14x + 24.06$ (Figure 2b).

The mean contact angle of abaxial surfaces was significantly higher than the adaxial when considering pooled data from all species ($p = 0.001$; Figure 3a; Table 2). Specifically, there was 23 species having significantly higher contact angles on abaxial surfaces than on adaxial surfaces ($p < 0.05$). Only four species (*Bromus inermis*, *Setaria viridis*, *Oxytropis psamocharis*, and *Syringa Linn*) exhibited the opposite phenomenon. In the other 41 species, there were no significant differences between contact angles on adaxial and abaxial surfaces ($p > 0.05$; Table 1). Life form had no effect on contact angle ($p > 0.05$), but greater variation in contact angles was found in herbs than in trees and shrubs (Figure 3b; Table 2). Significant differences were observed among four families; the gramineous and leguminous species had significantly higher contact angles than compositae and rosaceous species ($p < 0.05$; Figure 3c; Table 2). Species belonging to the same family may have significantly different contact angles (Table 1). For instance, the adaxial surface contact angles of three

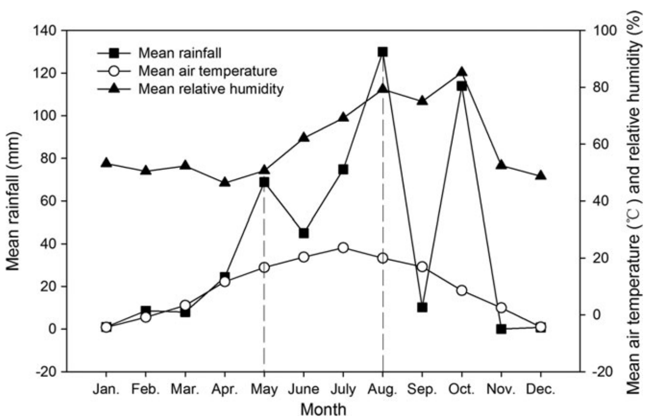

FIGURE 1 Monthly variations of rainfall, air temperature, and relative humidity in 2017. The dotted lines represent the experimental period from May to August

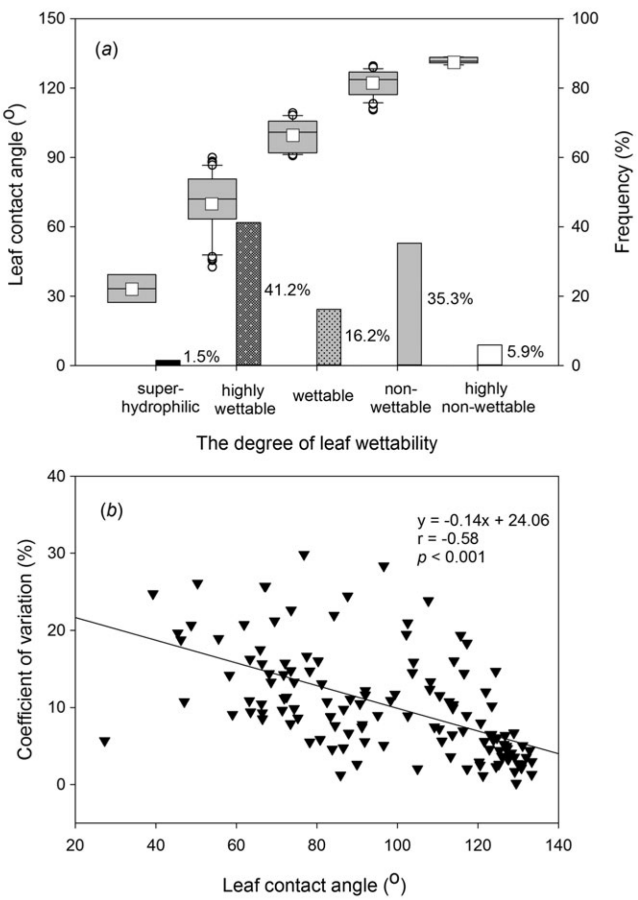

FIGURE 2 (a) Variability in leaf adaxial and abaxial contact angles of 68 species within different leaf wettability categories and the relative frequency. (b) Correlation between coefficient of variation and leaf contact angle of investigated species ($n = 136$)

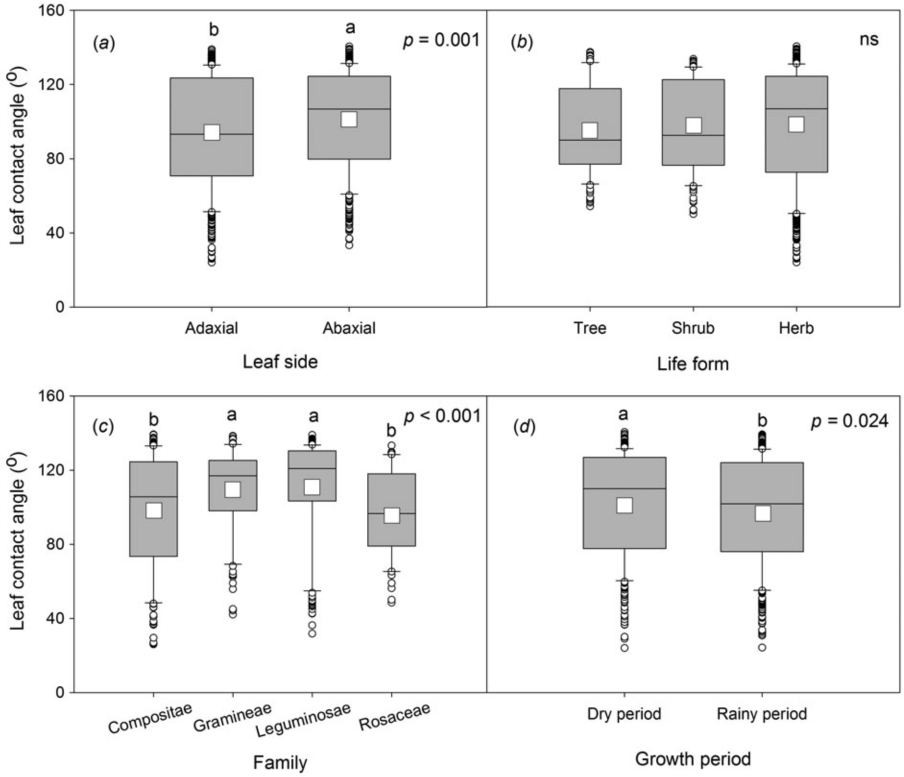

FIGURE 3 Variations in leaf contact angle under each influencing factor: leaf side (a), life form (b), family (c), and growth period (d) for 68 investigated species (n = 8–16 for each species). Squares in boxes indicate the average of contact angles under each factor. Different small letters indicate significant differences between contact angles. The significances of each influence factor on contact angle are marked on upper right (ns, $p > 0.05$)

TABLE 2 Differences in leaf contact angles between different leaf sides, life forms, families, growth periods, leaf ages, and slope aspects were analysed by one-way ANOVA or independent sample t test

Leaf contact angle (°)			Plant surface water retention (g g^{-1})		
Factors	F value	p value	Factors	Correlation coefficient	p value
Leaf side	11.92	0.001**	Plant fresh weight (g)	0.10	0.62
Life form	0.50	0.61	Leaf fresh weight (g)	0.12	0.55
Family	9.63	<0.001***	Stem fresh weight (g)	0.039	0.85
Growth period	5.08	0.024*	Plant height (cm)	−0.16	0.43
Leaf age	12.71	<0.001***	Leaf count (n)	0.27	0.17
Slope aspect	0.001	0.98	Total leaf area (m^2)	0.18	0.37
			Stem-leaf ratio (g g^{-1})	−0.064	0.75
			Adaxial contact angle (°)	−0.42	0.029*
			Abaxial contact angle (°)	−0.35	0.073

Note. The correlations between general plant traits and plant surface water retention were analysed by Pearson's correlation coefficient. Significant differences are indicated by the following:

*$p < 0.05$. **$p < 0.01$. ***$p < 0.001$.

compositae species *Cirsium setosum*, *Heteropappus altaicus*, and *Sonchus oleraceus* were 71.8°, 92.0°, and 123.8°, respectively, considered to be highly wettable, wettable, and nonwettable. The leaf age significantly affected contact angle ($p < 0.001$; Table 2). All new leaves across the nine species had higher contact angles than old leaves, and the differences were significant for six species (*Cirsium setosum*, *Dendranthema indicum*, *Potentilla tanacetifolia*, *R. pseudoacacia*, *Thermopsis lanceolata*, and *Vicia sepium*; $p < 0.05$; Figure 4a).

The contact angles during the dry period was significantly higher than that during the rainy period ($p < 0.05$; Figure 3d; Table 2). Slope aspect had no effect on contact angle ($p > 0.05$; Table 2). Six species that grew on sunny slope had higher contact angles than those from shady slope, but the differences were only significant for one species (*Artemisia mongoica*; Figure 4b).

3.3 | Leaf and plant surface water retention

Leaf surface water retention of compositae and rosaceous species was significantly higher than that of gramineous and leguminous species ($p < 0.05$; Figure 5a). Rosaceous species had significantly higher plant

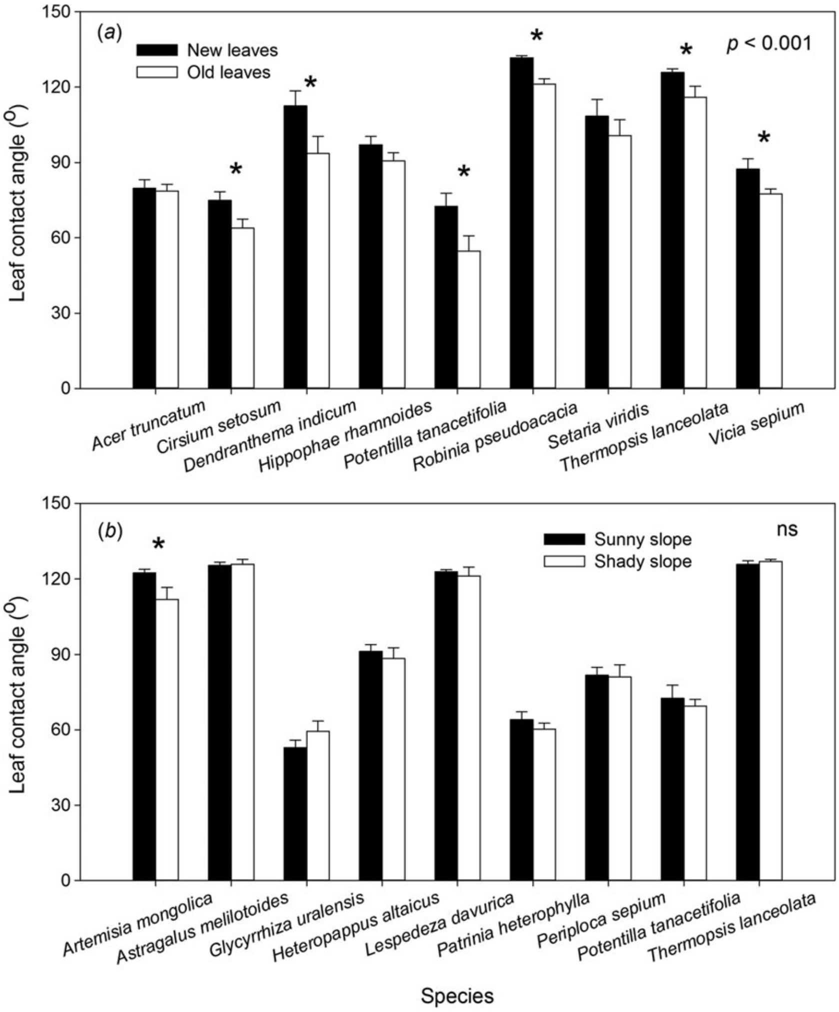

FIGURE 4 Contact angle of nine typical species for new and old leaves (a) and at sunny and shady slopes (b). Significant differences ($p < 0.05$) between leaf ages or slope aspects for each species are indicated by asterisk. The significances of leaf age and slope aspect on contact angle are marked on the upper right corner (ns, $p > 0.05$). Vertical bars represent the mean ± *SE* (n = 8–16 for each species)

surface water retention than compositae and leguminous species ($p < 0.05$), and the gramineous species showed the significantly lowest values ($p < 0.05$; Figure 5b).

Leaf surface water retention was negatively correlated with both adaxial contact angle ($r = -0.42$; $R^2 = 0.18$; $p < 0.001$) and abaxial contact angle ($r = -0.43$; $R^2 = 0.19$; $p < 0.001$); the equations were $y = -0.73x + 182.92$ and $y = -0.80x + 195.13$, respectively (Figure 6a). Plant surface water retention was negatively correlated with adaxial contact angle ($r = -0.42$; $R^2 = 0.18$; $p = 0.029$), whereas it had approximate correlation with abaxial contact angle ($r = -0.35$; $R^2 = 0.12$; $p = 0.073$); the equations were $y = -0.004x + 0.92$ and $y = -0.004x + 0.91$, respectively (Figure 6b). Other general plant traits, such as fresh weight (plant, leaf, or stem), plant height, leaf number, total leaf area, and stem–leaf ratio had no significant correlations with plant surface water retention across 27 species ($p > 0.05$; Table 2).

4 | DISCUSSION

4.1 | Leaf wettability in relation to internal properties

Leaf contact angles differed significantly between species, ranging from 27.3° to 133.4°, and the variability was closely associated with leaf side, family, and leaf age. The leaf surfaces exhibit a wide range of physicochemical properties, such as the wax structure and composition, trichome density, stomatal distribution, and epiphyll cover, which were reported to primarily determine leaf wettability (Müller & Riederer, 2005; Wagner et al., 2003; Wang, Shi, et al., 2013). Leaf adaxial surfaces were more wettable than abaxial surfaces after comparing pooled data from all species. The result was in agreement with previous studies and may be concerned with stomata distribution patterns of terrestrial plants (Smith & McClean, 1989). Typically, the abaxial surface was less wettable and had higher stomatal density than adaxial surface (Brewer & Nunez, 2007; Pandey & Nagar, 2003; Smith & McClean, 1989). Leaf wetting is beneficial to plant growth due to potential absorption of water (Fernández et al., 2017; Goldsmith et al., 2016); however, it can be harmful by greatly reducing the photosynthetic rate or promoting pathogen infection, pollutant deposition, and foliar nutrient leaching (Aryal & Neuner, 2010; Barthlott & Neinhuis, 1997; Ishibashi & Terashima, 1995). Lower wettability on abaxial surfaces may serve as a protection against water films that may be formed above the stomata to impede photosynthetic gas exchange (Brewer & Nunez, 2007). Holder (2007) also considered relative higher water repellency on leaf abaxial surfaces in cloud forests may be an adaptation to allow water to drip off and increase gas exchange for photosynthesis.

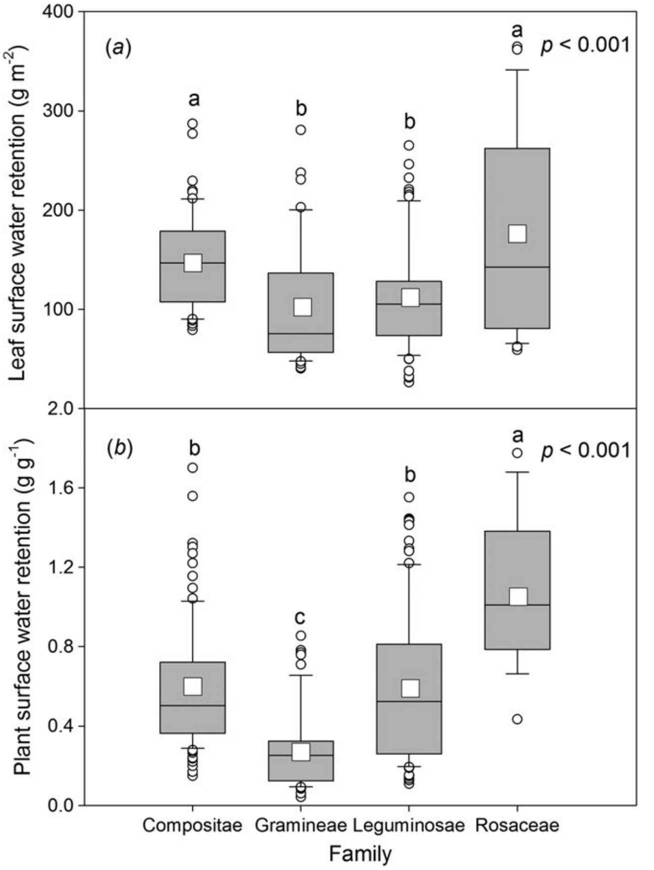

FIGURE 5 Leaf (a) and plant (b) surface water retention of investigated species belonging to four common families. Different small letters indicate significant differences between surface water retention. The significances of family on surface water retention are marked on upper right (*n* = 4–8 for each species)

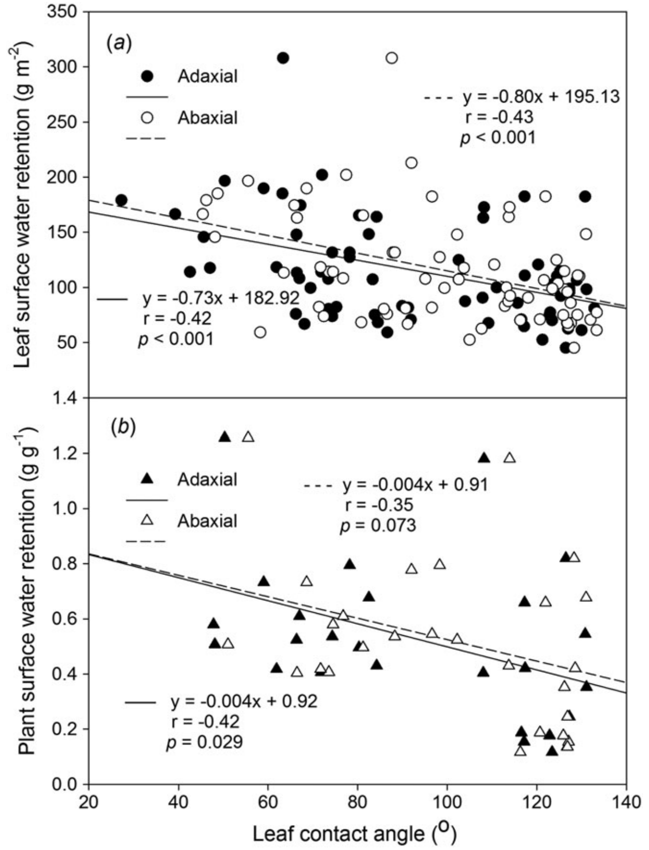

FIGURE 6 Correlations between leaf surface water retention (*n* = 68) (a) and plant suface water retention (*n* = 27) (b) with leaf adaxial and abaxial contact angle

Gramineous and leguminous species were found to be more unwettable than compositae and rosaceous species. Most aerial plant organs are covered with a cuticle consisting of a cutin matrix with cuticular waxes embedded in and deposited on the surface of the matrix (Fernández et al., 2016; Fernández et al., 2017). The epicuticular wax layer constitutes the leaf-atmosphere interface, and its main components have hydrophobic properties (Burton & Bhushan, 2006; Müller & Riederer, 2005; Wang, Shi, et al., 2013). Neinhuis and Barthlott (1997, 1998) suggested that the family or genus of a given species, to a certain extent, is relevant to the presence or absence of a prominent epicuticular wax layer on leaf surfaces, which can be observed clearly under SEM (Scanning electron microscopy). For instance, the leaves of most grasses and legumes possess prominent wax layers, which may increase their hydrophobicity (Neinhuis & Barthlott, 1997). Similarly, Wohlfahrt, Bianchi, and Cernusca (2006) indicated that graminoid leaves tended to have less water retention capacities compared with forbs. Our results also showed that not all the species belong to the same family had the similar wetting property, suggesting that plant leaf wettability is species-specific. Neinhuis and Barthlott (1997) found that water repellent leaves were more concentrated in herbs than in trees, whereas this finding was not confirmed by our results. This is probably because we selected the healthy and newly developed leaves, whereas they sampled the leaves which remained on the plants for years in evergreen tropical forests, where epicuticular waxes could be destroyed by nature environment conditions. To clarify the family or life form effect on surface wettability, further comparisons in surface wettability and morphology among a variety of plants should be conducted.

New leaves were found to be more unwettable than old leaves. During leaf senescence, changes in leaf wettability may occur due to changes in surface microstructure and chemical components (Zhu et al., 2014). Former studies have demonstrated that soybean leaves became easier to wet with increasing age, and low wettability at early growth stages was mainly attributed to the presence of a dense epicuticular wax layer (Puente & Baur, 2011). In senescent leaves of urban tree species, the degradation of epicuticular wax crystals was observed, making the surfaces more wettable than newly formed leaves (Wang, Shi, et al., 2013). The cover of epiphytic microorganisms on the upper surface of *Abies grandis* increased with age, which was correlated with decreased leaf water repellency of older leaves (Schreiber, 1996). The distribution of stomata and trichomes on leaf surface changes with growth stages, which also affects surface wetting properties (Fernández et al., 2014; Kolodziejek, Waleza, & Mostowska, 2006).

4.2 | Leaf wettability in relation to external conditions

There was a significant negative correlation between variation coefficient and leaf contact angle, suggesting that leaf surfaces with higher contact angles had lower variability. Low wettability surfaces mean smaller contact areas and less adhesion of water and dust particles and accumulation of pathogenic microorganisms (Koch, Bhushan, & Barthlott, 2009). Due to self-cleaning properties, these surfaces may therefore be less susceptible to adverse environmental conditions, such as acid rain (Percy & Baker, 1988), air pollution (Wang, Shi, et al., 2013), and bacterial infection (Kumar, Pandey, Bhattacharya, & Ahuja, 2004). These implied that environmental condition change would increase spatiotemporal variability in leaf wettability for highly wettable surfaces (Wang, Shi, et al., 2013).

Leaf contact angles declined from the dry period to rainy period. The stronger rainfall exposure during the rainy period and different growth stages between the two periods were primarily responsible for this decrease. The epicuticular waxes may be eroded from leaf surfaces during frequent rainfall events, resulting in that leaves become more wettable (Aryal & Neuner, 2010; Brewer & Nunez, 2007; Tanakamaru et al., 1998). After simulated rainfall, the amounts of epicuticular wax in the leaves at different positions of two barley lines decreased 10–50% (Tanakamaru et al., 1998). High leaf wettability in tropical forest species may be caused by the loss of epicuticular wax due to high precipitation totals (Holder, 2007; Neinhuis & Barthlott, 1997).

Plants on the sunny slope experience stronger solar radiation and more xeric environment than those on the shady slope, which may lead to variability of leaf properties (Auslander, Nevo, & Inbar, 2003). Leaves in dry, open or alpine habitats exhibited more water repellency than those in rainy, shade, or tropical habitats, respectively, which can be seen as a selective trait of plants in certain environments (Aryal & Neuner, 2010; Holder, 2007; Pandey & Nagar, 2003). For instance, in dry regions, high water repellent leaves can increase the limited available water to plant root systems and protect leaves from the negative effects of surface wetting (Holder, 2007). Contrary to our expectations, no significant differences in leaf wettability between the two slope aspects were found across eight species, with the exception of *Artemisia mongolica*. The phenomena can be explained in two aspects: (a) The environmental deviations between sunny and shady slopes were too limited to induce changes in leaf surface properties; (b) the response magnitude of surface properties to external environment was species dependent.

4.3 | Relationships between leaf wettability and surface water retention

Consistent with leaf wettability, compositae and rosaceous species had significantly higher leaf surface water retention than gramineous and leguminous species. This suggested a potential positive correlation between leaf wettability and leaf surface water retention. At the individual plant level, the surface water retention of leguminous species became close to compositae species and higher than gramineous species. The leguminous species investigated here generally had more leaves and smaller distances between leaves (e.g., *Lespedeza davurica*), likely increasing the water retention ability of plants (Li et al., 2016).

Leaf wettability was an important variable affecting surface water retention at the leaf level and may be the best predictor of surface water retention at the plant level compared with other general plant traits. Similarly, the leaf surface retention of *Ulmus pumila* was found to be 60% greater than that of *Catalpa speciosa*, and the adaxial contact angles of *Catalpa speciosa* was more than double the *Ulmus pumila* at the same time (Holder, 2012). Holder (2013) found that the rank order of total leaf surface retention of a branch corresponded to the rank order of leaf hydrophobicity across seven species. However, the correlation was not statistically significant ($p > 0.05$), and the relationship between leaf hydrophobicity with individual plant surface retention were not compared. In the present study, leaf wettability is most suitable for predicting plant surface water retention involving 27 herb species is compelling. The plant traits considered did not include some leaf surface properties such as water droplet retention, leaf roughness, or surface free energy (Wang et al., 2014). These characteristics are also important for water adhesion on leaf surfaces, which should be quantified and compared in the related research (Aryal & Neuner, 2010; Holder, 2013; Wang et al., 2014). Approximate correlation between the abaxial contact angle and plant surface water retention was probably because water on abaxial surfaces tended to aggregate into large droplets and dripped down easily under the influences of surface tension and gravity (Wang et al., 2014).

The results of the study presented a leaf and plant level analysis of how leaf wettability influence surface water retention, and their relationships need to be further assessed at the canopy level. Rainfall redistribution by vegetation canopy and its spatial variation directly affect hydrological processes such as throughfall, stemflow, run-off, and infiltration (Holder & Gibbes, 2017; Llorens & Domingo, 2007). Highly nonwettable leaves may contribute to add hydrological inputs beneath the canopy, thus improving the water supply for vegetation in water-limited regions (Holder, 2007). When changes in vegetation occur due to the climate change or human influences, the water balance in the ecosystem may also be largely influenced (Brooks & Vivoni, 2008). For instance, the GTGP in the Loess Plateau since 1999 has effectively reduced soil erosion; however, the conflict emerged between the limited soil moisture and the large water demand of extensive vegetation (Duan et al., 2016; Zhou et al., 2012). It is imperative to select suitable vegetation types that not only can effectively control soil erosion but also balance the soil water availability and water consumption of plants (Chen et al., 2015; Duan et al., 2016). The species-specific and seasonal changes of leaf wettability are additional topics worth studying in evaluating the vegetation hydrological function for sustainable development in this region.

5 | CONCLUSIONS

Leaf contact angles ranged from 27.3° to 133.4° in the 68 species, and leaves with higher contact angles had lower variation coefficients. There was a significant variability in leaf wettability between different leaf sides, families, leaf ages, and growth periods, and the effects of life form and slope aspect were not significant. New leaves were more unwettable than old leaves, and rainfall exposure during the rainy period significantly increased the leaf surface wettability. Leaf wettability and surface water retention were both associated with family, where gramineous and leguminous species were more water repellent than compositae and rosaceous species. Leaf wettability is an applicable hydrological variable for judging surface water retention of different species at both leaf and plant level compared with other plant traits. Species with hydrophobic leaf surfaces (e.g., grasses and legumes) are more appropriate for vegetation restoration and construction in the semiarid Loess Plateau due to their lower surface water retention capacity. The seasonal changes of leaf wettability should also be considered to accurately predict rainfall interception by plants during a whole growth period. Further researches should be taken at multiple scales to evaluate the hydrological effect of leaf wettability for establishing suitable vegetation and promoting sustainable management.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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