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The Wetting of Leaf Surfaces and Its Ecological Significances

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Abstract

Leaf wettability, indicating the affinity for water on leaf surfaces, is a common phenomenon for plants in a wide variety of habitats. The contact angle (θ) of water on leaves measured at the gas, solid and liquid interface is an index of surface wettability. Leaves are termed as “super-hydrophilic” if $\theta < 40^\circ$, “highly wettable” if $\theta < 90^\circ$, and “wettable” if $\theta < 110^\circ$. If $\theta > 110^\circ$, the leaves are classified as being non-wettable, while $\theta > 130^\circ$ for highly non-wettable and $\theta > 150^\circ$ for super-hydrophobic. Both internal and external factors can influence leaf wettability. The chemical composition and structure of leaf surfaces are internal causes, but the external environment can also influence wettability by affecting the structure and composition of the surface. The main internal factors that affecting leaf wettability include the content and microstructure of the epidermal wax, the number, size and pattern of trichomes, stomatal density, the shape of epidermal cells, and leaf water status. The leaf contact angles increased with the increasing of leaf wax content. However, studies have shown that the contact angles were more dependent on the complexity of wax structure than on the absolute amount. For trichomes, there are three types of interaction between trichomes and water droplets, including (1) low trichomes density: no apparent influence of trichomes on the location of surface moisture, droplet formation and retention; (2) medium trichomes density: trichomes appear to circle surface moisture into patches; (3) high trichomes density: trichomes appear to hold water droplets above the trichomes. In some cases, a higher stomatal density was accompanied with a higher contact angles. While, it was also observed that there was no significant correlation between contact angle and stomatal density for some species. For the effects of epidermal cells on leaf wettability, it was generally considered that the combination of a dense layer of surface wax and the convex epidermal cells was what created a hydrophobic leaf surface. However, the influence of leaf water content on contact angle of water droplets on different leaf surfaces was complex, e.g., contact angles increased with decreasing of leaf water content, contact angle remained to be constant with different leaf water content.

The ecological significances of leaf wettability include interception of precipitation, photosynthetic rate, pathogen infection and environmental quality. On leaf level, leaf surface wettability contributes to variability in interception between different plant species resulting different geometrical shapes of water on leaves (i.e., water film, patches, drops, and spherical droplets). For wettability leaves, water droplets form a layer of film on the surface that is relatively easy retained on leaves. For water repellent leaves, water on the surface produces droplets that are easily removed by wind and gravity. The spreading water film on leaves with high wettability can decrease photosynthesis due to the fact that diffusion of CO_2 is 10,000 times slower in water than in air. For pathogen infection, excess leaf wetness promotes pathogen infection in many species. However, bacterial spores did not attach firmly and did not germinate on super hydrophilic surfaces. Different leaf wettability can also influence the amount of air pollutants that can be captured, absorbed, and filtrated by leaf surfaces. However, these air pollutants may injure the leaf surface structure and result in a dramatic change in contact angles.

Keywords: Leaf surface, wettability, hydrophobic, microstructure, wax crystal, ecological significances

1. Introduction

Leaves are covered by a layer of cuticular wax, serving to decrease surface wetting and moisture loss. The epicuticular wax layer may be classified into two main types: a thin wax film that appears to be ubiquitous and a highly crystalline epicuticular wax consisting of wax crystals that is not present on all species [1, 2]. These outer layers control the wetting of leaves, which have been studied by many researchers in recent years because of the “lotus effect” (i.e., the self-cleaning properties that are a result of very high water repellence, as exhibited by the leaves of the lotus flower) [3–7].

Wetting is the ability of a liquid to maintain contact with a solid surface, resulting from intermolecular interactions when the two are brought together [8]. The degree of wetting is determined by a force balance between adhesive and cohesive forces, which is often characterized by contact angle of water measured at the gas, solid, and liquid interface [9–13]. Contact angle gives an inverse measurement of adhesion between a liquid and a solid. A lower contact angle indicates the liquid will spread over a larger area of the surface. A greater contact angle indicates the liquid will minimize contact with the surface and form a more spherical water droplet.

In a natural environment, leaf surfaces of a large variety of plants are frequently wetted by rainfall, dewfall, ground fog, and cloud mist, and both adaxial and abaxial surfaces are frequently affected. Depending on the tissue hygroscopicity, it may consist of individual drops, or of water films of thickness between a few nanometers and a few micrometers [11]. Several studies have shown that the contact angles between leaf surfaces and water droplets range from 0° to 180° , depending on plant species [3, 4, 9, 10, 12–25]. The differences in physical and

chemical properties of leaf surfaces possibly lead to the different contact angles of leaves. These surface properties include the number and pattern of trichomes [12–14], the three-dimensional microstructures of epicuticular cells [3, 4, 15], the microstructures and compositions of wax crystals/films [3, 4, 16–18], and the number and distribution of stomata [12, 13, 19].

Wettability is a comprehensive response at the solid, gas, and liquid phase interface of leaves and it significantly affects physiological and ecological functions of plants. For example, leaf wettability influences pollutant deposition such as acid rain [20, 26, 27], ozone [20, 21], and particulate matter [4, 18, 28, 29], for foliar nutrient leaching [22], in the control of plant disease [23, 30–36], for plant photosynthesis and yield [24, 37, 38], and in the interception of precipitation [25, 39–42]. Recent advances in the area of the wetting of leaf surfaces and its ecological significances are reviewed at present. In Section 2, we discuss the contact angles on ideal and rough surfaces (the Young equation, Wenzel model, Cassie–Baxter model, and Cassie–Baxter to Wenzel transition), the classification of leaf surface wetting, and the methodologies used to measure leaf contact angles. In Section 3, we discuss how the wax content and structure; the number, shape, and pattern of trichomes; the stomatal density; the shape of epidermal cells; and the leaf water status, affect leaf wettability. In Section 4, we discuss the influence of leaf wettability on rainfall interception, photosynthesis rate, pathogen infection, and environmental quality.

2. Criteria and measurement of leaf wettability

2.1. Surface wetting and contact angle

2.1.1. The Young equation

A droplet on a solid surface wets the surface to a certain degree. To what extent a surface gets wet can be described by the contact angle. Contact angle is defined as the angle formed by a liquid at the three-phase boundary where the liquid, gas, and solid intersect (Figure 1). The contact angle directly provides information on three interfacial free energies involved: solid–gas/vapor (γ_{sg}), liquid–gas/vapor (γ_{lg}), and solid–liquid (γ_{sl}) [43]. The balance of forces of a water droplet on an ideal surface (i.e., the surface is flat, rigid, perfectly smooth, and chemically homogeneous, and has zero contact angle hysteresis) is explained by Young’s equation [44]:

$$\gamma_{lg} \cos \theta = \gamma_{sg} - \gamma_{sl} \quad (1)$$

where θ is the intrinsic contact angle of a solid. Water droplets form contact angles of 90° when $\gamma_{sg} = \gamma_{sl}$ ($\cos \theta = 0$). Water droplets spread (i.e., $\theta < 90^\circ$) on leaf surfaces when $0 < \gamma_{sg} - \gamma_{sl} < \gamma_{lg}$ ($0 < \cos \theta < 1$). Water droplets spread completely on leaf surfaces when $\gamma_{sg} - \gamma_{sl} = \gamma_{lg}$ ($\cos \theta = 1$). The contact angles between water droplets and leaf surfaces are greater than 90° when $\gamma_{sg} - \gamma_{sl} < 0$ ($\cos \theta < 0$).

When $\gamma_{sg} - \gamma_{sl} < \gamma_{lg}$ ($\cos\theta < 0$). Water droplets spread (i.e., $\theta < 90^\circ$) on leaf surfaces when $0 < \gamma_{sg} - \gamma_{sl} < \gamma_{lg}$ ($0 < \cos\theta < 1$). Water droplets spread completely on leaf surface when $\gamma_{sg} - \gamma_{sl} = \gamma_{lg}$ ($\cos\theta = 1$). The contact angle between the water droplet and the leaf surface is greater than 90° when $\gamma_{sg} - \gamma_{sl} < 0$ ($\cos\theta < 0$).

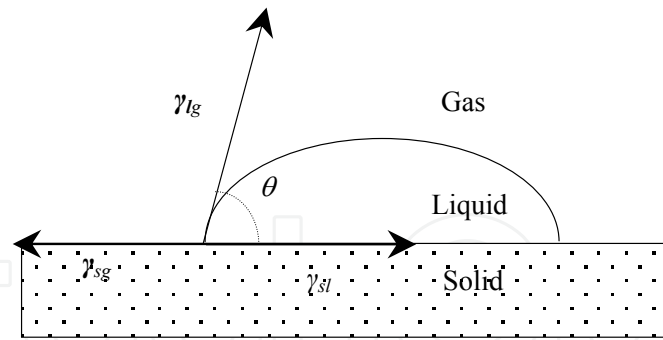


Figure 1. Wetting of a solid surface with water, with air as the surrounding medium.

Wenzel model

Young's equation applies strictly to an ideal surface. However, most leaf surfaces in nature are not perfectly smooth, rigid, or chemically homogeneous [3, 4, 12–18, 45, 46]. Wenzel [47] modified Young's equation to account for contact angles formed on rough, rigid, or chemically homogeneous surfaces because of leaf surface properties [3, 4, 12–18, 45, 46]. Wenzel [47] modified Young's equation to account for the contact angle formed on rough surfaces (θ_r) by adding a roughness factor (r) as follows:

$$\cos\theta_r = r \cos\theta \quad (2)$$

The roughness factor is defined as the actual contact area to apparent contact area, and acts as an amplification of the effect of the surface chemistry, i.e., smaller changes in θ become larger changes in θ_r . The value of $\theta = 90^\circ$ is the changeover in sign of the cosine term. When $\theta > 90^\circ$, θ_r is larger than θ , and the effect of increasing roughness is to further increase the θ_r toward to 180° . However, when $\theta < 90^\circ$, θ_r is smaller than θ , and the effect of increasing roughness is to further reduce the θ_r toward to 0° . Thus, the Wenzel roughness emphasizes the intrinsic tendency of a surface toward either complete wetting or complete non-wetting [48].

Wenzel's equation accounts for the surface roughness. It describes the homogeneous wetting regime in which water fills the roughness grooves on the surface, as seen in Figure 2a. However, it does not describe contact angle hysteresis that occurs on heterogeneous surfaces [49]. Contact angle hysteresis is defined as the difference between the advancing contact angle (i.e., the contact angle at the advancing edge of a liquid drop, θ_a) and the receding contact angle (i.e., the contact angle at the receding edge of a liquid drop, θ_r) (Figure 3). A more complex model is needed to measure how the apparent contact angle changes when various materials are involved. This heterogeneous surface, as shown in Figure 2b, is explained using the Cassie–Baxter equation [50]:

Cassie–Baxter model

Wenzel's equation accounts for the surface roughness. It describes the homogeneous wetting regime in which water fills the roughness grooves on the surface, as seen in Figure 2a. However, it does not describe contact angle hysteresis that occurs on heterogeneous surfaces [49]. Contact angle hysteresis is defined as the difference between advancing contact angles (i.e., the contact angle at the advancing edge of a liquid drop, θ_a) and receding contact angles (i.e., the contact angle at the receding edge of a liquid drop, θ_r) (Figure 3). A more complex model is needed to measure how the apparent

where θ_1 is the contact angle for component 1 with areal fraction f_1 , and θ_2 is the contact angle for component 2 with area fraction f_2 present in the composite material. This equation takes on special meaning when in a two-component system with one component being air with a contact angle of 180° . With $\cos(180^\circ) = -1$ and $f_2 = 1 - f_1$, Eq. (3) can be reduced to

Eq. (4) implies that with a small f_1 and a large θ_1 , it is possible to create surfaces with a very large contact angle. Eq. (4) implies that with a small f_1 and a large θ_1 , it is possible to create surfaces with a very large contact angle.

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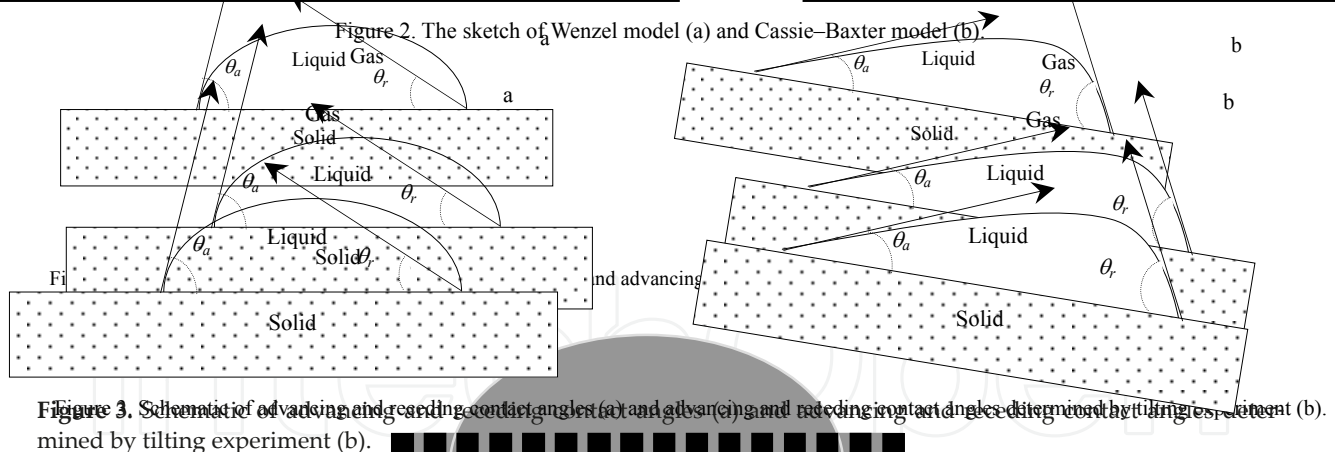
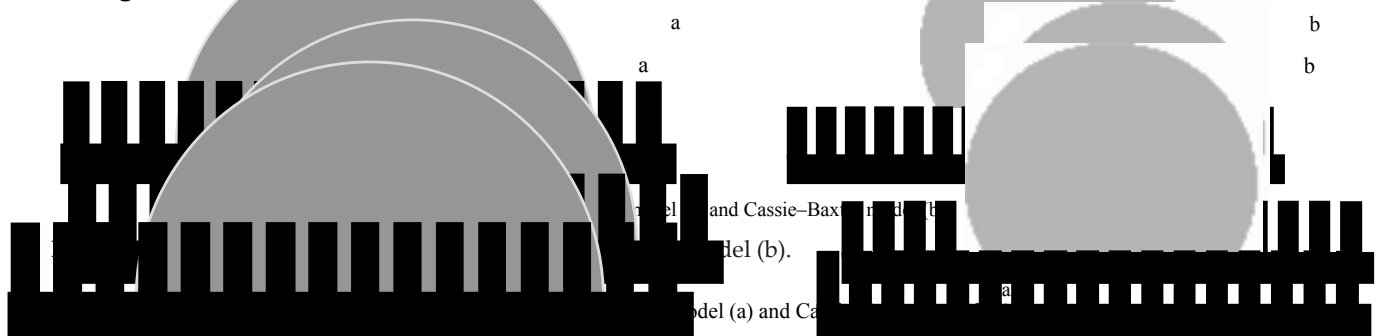


Figure 3. Schematic of advancing and receding contact angles (a) and advancing and receding contact angles determined by tilting experiment (b).

Figure 4. Sketch of a fluid drop on a hydrophilic surface where a film invades the solid texture.

In particular, Wenzel model applies in such case that the leaf surfaces with intermediate hydrophobic and intermediate hydrophilic characteristics, which remains dry beyond the water droplet. If the texture of surfaces is wettable, a film develops in the texture and the droplet sits upon a mixture of solid and liquid, consisting a composite surface (Figure 4) [51]. In this case, the contact angle between the liquid is 0° , and the equation can be written as

Eq. (5) implies that with a small f_s and a large θ_s , it is possible to create surfaces with a very large contact angle. Eq. (5) implies that with a small f_s and a large θ_s , it is possible to create surfaces with a very large contact angle.

$$\cos \theta = f_s \cos \theta_s + 1 - f_s \quad (5)$$

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$$\cos \theta = f_s \cos \theta + 1 - f_s \tag{5}$$

where f_s is solid areal fraction of the composite surface.

2.1.4. Cassie–Baxter to Wenzel transition

Some researchers studied the stability of the composite interface of superhydrophobic surfaces and the transition from composite to homogeneous interface under pressure [52, 53] and vertical vibration [54]. The intermediate state between the Wenzel and the Cassie modes is shown in Figure 5. The penetration condition is given by

$$\cos \theta = \frac{\varphi_s - 1}{r - \varphi_s} \tag{6}$$

where φ_s is the fraction of the solid/liquid interface below the drop. The penetration front propagates to minimize the surface energy until it reaches the edges of the drop, thus arriving at the Wenzel state. The fraction of the solid/liquid interface below the drop. The penetration front propagates to minimize the surface energy until it reaches the edges of the drop, thus arriving at the Wenzel state.

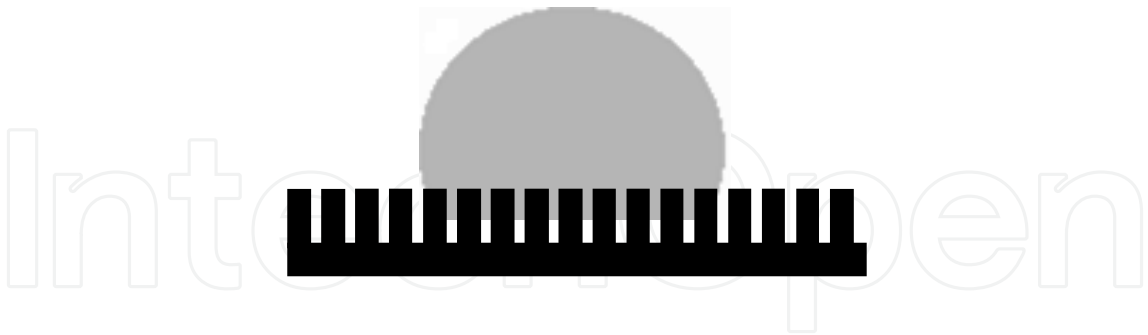
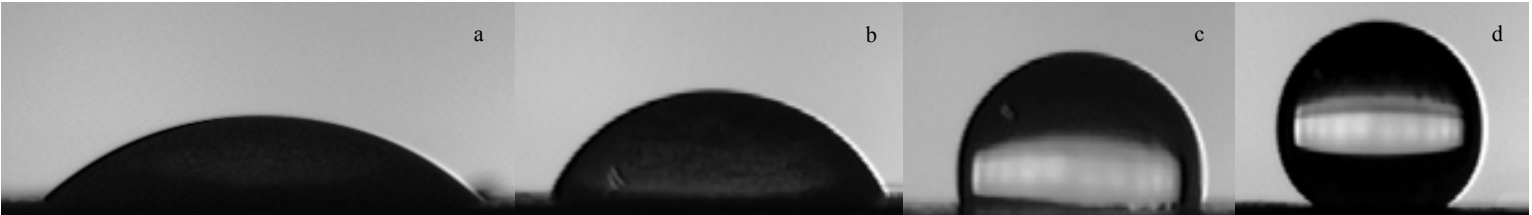


Figure 5. Intermediate state between the Wenzel and the Cassie modes.

2.2 Classification of leaf surface wetting

The larger the contact angle is, the more repellent a leaf surface shows (Figure 6). According to Aryal et al. [55] and Wang et al. [25], the judgment criteria for leaf wettability were as follows: if $\theta < 40^\circ$, $40^\circ - 90^\circ$, $90^\circ - 110^\circ$, $110^\circ - 130^\circ$, $130^\circ - 150^\circ$, and $> 150^\circ$, leaves were termed as “superhydrophilic,” “highly wettable,” “wettable,” “highly non-wettable,” and “superhydrophobic,” respectively.



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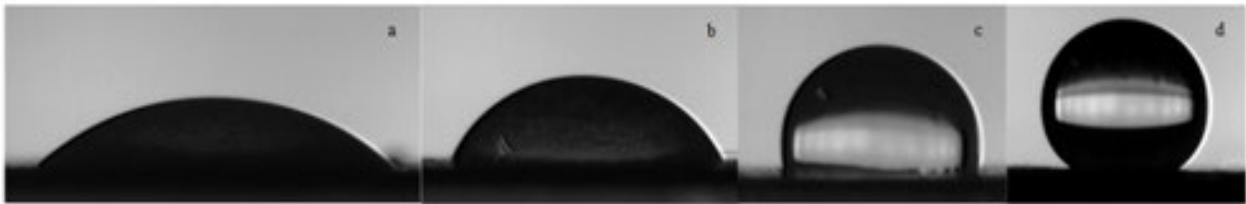


Figure 6. Images from a goniometer of a water droplet on (a) a superhydrophilic, (b) a highly wettable, (c) a non-wettable, and (d) a hydrophobic leaf surface.

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2.3. Measurement of leaf contact angle

The measuring methods of leaf contact angle include the static sessile drop method, the dynamic sessile drop method, the dynamic Wilhelmy method, and the Washburn equation capillary rise method [13–17, 28–32, 37–38, 56–78]. The contact angle is measured by a contact angle goniometer using an optical subsystem to capture the profile of a pure liquid on a solid substrate. Older systems used a microscope optical system with a back light. Current-generation systems employ high-resolution cameras and software to capture and analyze the contact angle [77]. Water droplet sizes vary between studies from 0.2 to 15 μl (Table 1). Letellier et al. [79] considered that the contact angle is dependent on not only the nature and structure of the substrate but also the size of the drops. In their study, they found that if interface is a surface and with a thermodynamic dimension (m^{SL}) of $2/3$, the contact angle does not depend on the drop mass. However, if interface is a fuzzy interface (i.e., a nonextensive phase), the contact angle depends on the surface wettable characteristics (hydrophilic vs hydrophobic), thermodynamic dimension, and water droplet volume. When $m^{\text{SL}} > 2/3$, the contact angle decreases as the volume increases if $\theta < 90^\circ$, while the contact angle value increases with increasing volume if $\theta > 90^\circ$. If $m^{\text{SL}} < 2/3$, the contact angle value increases with increasing volume when $\theta < 90^\circ$, while the contact angle value decreases as the volume increases if $\theta > 90^\circ$. However, both Knoll and Schreiber [31] and Schreiber [80] found that contact angles were independent of the droplet volumes between 1 and 10 μl . Therefore, the effects of water droplet volumes on leaf contact angles need further studies to provide relatively accurate information for comparing the results among researchers.

Methods	Water droplet size (μl)	Number of species	The measured contact angle ($^\circ$)	Location	Reference
Digital camera and image-processing software	7.5	5	52–122	Belgium	17
Microscope and image-processing software	Not reported	1	64.7–138.0	Polish	56
Digital camera and geometric analysis	0.2	1	50–85	Japan	57

Methods	Water droplet size (μl)	Number of species	The measured contact angle (°)	Location	Reference
Binocular microscope with protractor graticule	1	1	72–115	UK	58
Stereomicroscopic photo and image-processing software	5	18	109–136	United States	30
Stereomicroscopic photo and image analysis	5	38	<15–>170	United States	59
Digital camera and image-processing software	10	36	40.33–144.25	Guatemala and United States	9
Digital camera and image-processing software	10	36	40.3–144.3	Guatemala and United States	60
Digital camera and image-processing software	10	5	44.68–77.92	Brazil	61
Digital camera and image-processing software	10	33	<20–>150	Guatemala and United States	62
Automated tension meter	2	1	85–120	Greece	16
Goniometer	2	1	45–75	Germany	31
Goniometer	2	1	40.7–134.3	Spain	14
Goniometer	2	6		New Zealand	63
Goniometer	7	3	60–140	Germany	4
Goniometer	0.2	1	65–99	New England	20
Digital camera and image-processing software	7.5	1	51.2–97.7	Belgium	37
Microprojector and image analysis	2 mm diameter	1	120–150	Australia	64
Drop shape analyzer or digital camera and image-processing software	5	227	50–145	Nepal	55
Not reported	1.5 mm diameter	52	39.9–136.1	New Zealand	65
Geometric analysis with inspection microscope	5	3	85–105	United States	21
Geometric analysis with inspection microscope	5	37	0–180	Argentina	12
Bench microscope with a protractor graticule	Not reported	1	101–108	Italy	66

Methods	Water droplet size (μl)	Number of species	The measured contact angle (°)	Location	Reference
Geometric analysis with inspection microscope	2	1	75–97.2	India	67
Not reported	5	1		United States	38
Geometric analysis with inspection microscope	5	50	23.8–180	United States	68
Goniometer	5	2	66.3–129.4	Japan	23
Digital camera and image analysis	0.2	1	60–120	Japan	69
Digital camera and image analysis	1–42 mm diameter	1	15–100	Sweden	70
Goniometer	2–3 mm diameter	200	117–164	Germany	3
Goniometer and image-processing software	500 μm diameter	50	<50–141	Germany	71
Goniometer	10	11	34.57–120.38	United States	10
Geometric analysis with inspection microscope	5	5	71–130	United States	72
Goniometer and image-processing software	2 or 6	3	67.1–135.9	China	18
Goniometer and image-processing software	5	5	43–146	China	73
Goniometer	5	9	53–153.5	China	74
Goniometer and image-processing software	6	21	42.3–134.7	China	13
Goniometer and image-processing software	6	21	41.5–136.0	China	28
Goniometer and image-processing software	6	18	47.6–142.7	China	29
Not reported	10	33	Not reported	Germany	15
Goniometer	5	2	62–153	United States	75
Goniometer	2	1	50.7–86.1	Germany	32
Goniometer	15	3	100–160	Germany	45
Microprojector and image analysis	3 mm diameter	7	29–152	UK	76

Table 1. Measurement methods and water droplet sizes used to calculate leaf contact angles.

3. Main factors influencing leaf wettability

3.1. Leaf wax

Leaves of higher plants are covered by a cuticle consisting of a cutin matrix with waxes embedded in and deposited on the surface of the matrix [80, 81]. The cutin fraction is a polyester-type biopolymer composed of hydroxyl- and hydroxyepoxy fatty acids, whereas the cuticular waxes are a complex mixture of long-chain aliphatic and cyclic compounds [45]. The major compound classes of plant cuticular waxes are *n*-alkanes (chain-length C_{21-35}) and smaller proportions of iso- and anteiso-homologues, primary alcohols (C_{22-40}), fatty acids (C_{16-34}), aldehydes (C_{21-35}), secondary alcohols (C_{21-35}), with a tendency for mid-chain hydroxylation, ketones (C_{21-35}), β -diketones (C_{22-36}), and *n*-alkyl esters (C_{32-64}) resulting from the combination of long-chain primary alcohols and fatty acids [1, 81, 82]. The cuticular waxes vary enormously between and among different species, different leaf developmental stages, and even between leaf sides [1, 13, 18, 25, 81, 83]. The main components of epicuticular wax always have hydrophobic properties, having contact angles of 94° – 109° [84]. However, the contact angles of the investigated leaves cover a wide range (0° – 180°), suggesting that the physicochemistry of the cuticular wax (e.g., wax content, composition, and microstructure of cuticular wax) influence leaf surface wettability [4, 17, 24, 62, 63, 75]. Meanwhile, the external environments (e.g., precipitation, temperature, water stress, ozone, and acid rain) can influence the wettability through altering the leaf structures [20, 21, 45, 85–87].

Studies have shown that wax content had distinct effects on leaf wettability [13, 19, 45, 88]. A study conducted by Koch et al. [45] showed that the contact angle increased with the increasing of leaf wax content for the three investigated species (*Brassica oleracea*, *Eucalyptus gunnii*, and *Tropaeolum majus*). Wang et al. [13] investigated the contact angles of water droplets on leaves of 21 plant species and their relation with leaf wax contents. They found that leaf contact angles increased with increasing of wax contents. However, the correlation was not significant. Burton and Bhushan [88] measured the contact angles of *Nelumbo nucifera* and *Colocasia esculenta* for both with wax and without wax (removed using acetone). And they found that the contact angle dramatically reduced to less than 90° when the wax was removed from the surface. Their results suggested that the leaf material itself was a hydrophilic material, and the combination of the wax and the roughness of the leaf is what creates the hydrophobic surface. Wang et al. [13] also found that contact angles decreased after wax removal for most species, especially for hydrophobic leaves (e.g., *Ginkgo biloba*, *Rosa chinensis*, and *Berberis thunbergii*). But, an increase in contact angles for a few hydrophilic species (e.g., *Populus canadensis*, *Prunus persica*, and *Koeleruteria paniculata*) after wax removal was observed, and the observed contact angles were always less than 110° . Scanning electronic microscopy (SEM) showed that removal of epicuticular wax by organic solvents could affect the physical appearance and perhaps structure of the foliar surface [89]. The studies of Wang et al. [13], Koch et al. [45], Kumar et al. [19], and Burton and Bhushan [88] suggested that leaf contact angle was more dependent on the complexity of wax structure than on the absolute amount.

Since leaf contact angle was more dependent on the wax structure, recent papers have highlighted the importance of wax structure on leaf wettability [4, 18, 24, 25, 39, 45, 46, 65, 73–

superhydrophobic surface (contact angle over 150°). The SEM images (Figure 7a, b) showed that the surface of the lotus leaf comprises randomly distributed, almost hemispherically topped papillae with sizes 5–10 μm (height to basal radius aspect ratio ~ 1) decorated with branchlike protrusions with sizes of about 150 nm [46, 90, 91]. Many elliptic protrusions with an average diameter of about 10 μm were uniformly distributed in the nestlike caves, forming a microstructure on taro leaf (*Colocasia*). Many nanoscale pins were also harmoniously disseminated on the whole surface, resulting in a hierarchical structure on its surface together with the formed microstructure (Figure 7c, d). This binary structure resulted in a superhydrophobic leaf surface, with a higher contact angle of about $159^\circ \pm 2^\circ$ [91]. A binary structure (Figure 7e, f) on surface of rice (*Oryza sativa*) was observed, and leaf surface had a contact angle of $157^\circ \pm 2^\circ$. On top of the surface, the papillae with average diameter of about 5–8 μm are arranged similarly. Innumerable pins about 20–50 nm were proportionally distributed on the sublayer of surface [91].

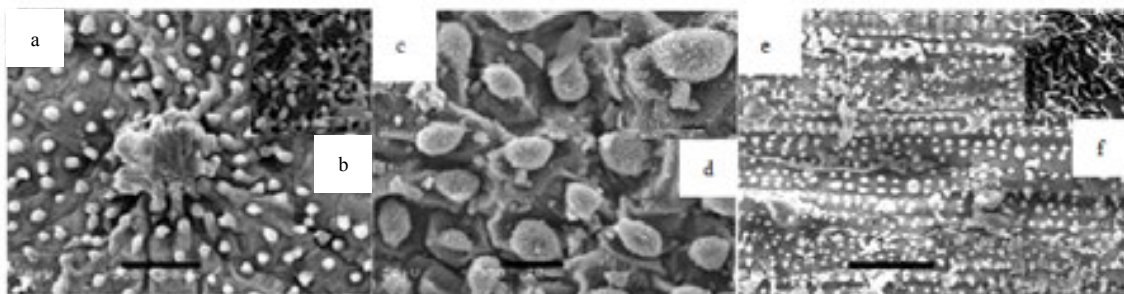


Figure 7. SEM images with different magnifications of lotus (a, b, from references [46, 90]; a: scale bar 20 μm ; b: scale bar 1 μm), taro (c, d, from reference [91]; c: scale bar 20 μm ; d: scale bar 5 μm) and rice (e, f, from reference [91]; e: scale bar 50 μm ; f: scale bar 1 μm).

3.2 Trichomes

Barthlott et al. [2] observed surface micromorphology of at least 13,000 species, representing all major groups of seed plants. In total, 23 wax types are classified, for example, granule, platelet, plate, rodlet, thread, and tubule. For water repellency, a classical example is the lotus leaf, which has a very superhydrophobic surface (contact angle over 150°). The SEM images (Figure 7a, b) showed that the surface of the lotus leaf comprises randomly distributed, almost hemispherically topped papillae with sizes 5–10 μm (height to basal radius aspect ratio ~ 1) decorated with branchlike protrusions with sizes of about 150 nm [46, 90, 91]. Many elliptic protrusions with an average diameter of about 10 μm were uniformly distributed in the nestlike caves, forming a microstructure on taro leaf (*Colocasia*). Many nanoscale pins were also harmoniously disseminated on the whole surface, resulting in a hierarchical structure on its surface together with the formed microstructure (Figure 7c, d). This binary structure

Some papers have demonstrated that different trichome density and structure may result in different leaf wettability [3, 59, 67, 68, 92]. In a study conducted in the center Rocky Mountain (USA), a positive correlation was observed between contact angle and trichome density for 50 subalpine/montane species [68]. Brewer et al. [59] and Pandey and Nagar [67] considered that the

resulted in a superhydrophobic leaf surface, with a contact angle of about $159^\circ \pm 2^\circ$ [91]. A binary structure (Figure 7e, f) on surface of rice (*Oryza sativa*) was observed, and leaf surface had a contact angle of $157^\circ \pm 2^\circ$. On top of the surface, the papillae with average diameter of about 5–8 μm were arranged similarly. Innumerable pins about 20–50 nm were proportionally distributed on the sublayer of surface [91].

3.2. Trichomes

Trichomes, also known as hairs, are fine outgrowths or appendages on plants, which are of diverse structure (e.g., puberulent, hispid, strigose, villous, pilose, strigillose, tomentose, pubescent, downy, and articulate) and function. Plant hairs may be unicellular or multicellular, branched or unbranched. Hairs on plants are extremely variable in their presence across species and even within a species, such as their location on plant organs, size, density. Trichomes can reflect the sunlight, absorb water and nutrients, and reduce transpiration. Besides, trichomes affect the leaf wettability, which has been analyzed in some investigations [12–14, 19, 38, 68].

Some papers have demonstrated that different trichome density and structure may result in different leaf wettability [3, 59, 67, 68, 92]. In a study conducted in the center Rocky Mountain (USA), a positive correlation was observed between contact angle and trichome density for 50 subalpine/montane species [68]. Brewer et al. [59] and Pandey and Nagar [67] considered that the leaves with trichomes were more water repellent, especially where trichome density was greater than 25/mm², at which they may develop trichome canopy. The adaxial surface of leaves of *Callistephus chinensis*, having a contact angle of 139° , was densely covered with conoid trichomes, whereas the adaxial surface of leaves of *Cucurbita pepo*, having a contact angle of 70° , was sparsely covered by villous [92]. The study of Wang et al. [92] also found that the variation in structure of trichomes had great influence on leaf wettability. The adaxial surface of *N. nucifera* with waxy trichomes was extremely water repellent (high contact angle of 150°). However, the abaxial surface of *C. chinensis* with nonwaxy trichomes only had a contact angle of 97° . The wettability of hairy leaves strongly depended on the presence or absence of wax crystals on the trichomes. Leaves with nonwaxy trichomes were only water repellent for a short time after a water droplet had been applied. In contrast, leaves with waxy trichomes are extremely water repellent, although the trichomes were up to 2 mm high and only loosely distributed over the leaf surface [3].

Three types of interaction between trichomes and water droplets were evident [38, 68]. On one group of leaf surfaces (Figure 8a), trichomes appeared to have no influence on the location of surface moisture, droplet formation, or retention. In this group, the trichome density was relatively low, and usually a film of water formed on the leaf surface. The leaves of *Abutilon theophrasti*, *Helianthus tuberosus*, and *Prunus triloba* had pilose, and the trichomes may penetrate water droplet deposited on leaves, resulting in contact angles of $43^\circ \pm 2^\circ$, $46^\circ \pm 2^\circ$, and $84.8^\circ \pm 12.3^\circ$, respectively [13, 73]. The enhanced wetting observed in some plant species with “open” trichome pattern caused by capillary action, which segregated water into patches based on water drawn along the trichomes [25, 84]. In a second group, leaf surfaces showed a “segregating strategy” (Figure 8b). In this group, the trichome density was relatively low, but not as

low as that on leaf surfaces with no trichome–water interaction, and the hydrophilic trichomes encircled patches of water. Trichomes on the third group of leaf surfaces exhibited the “lifting

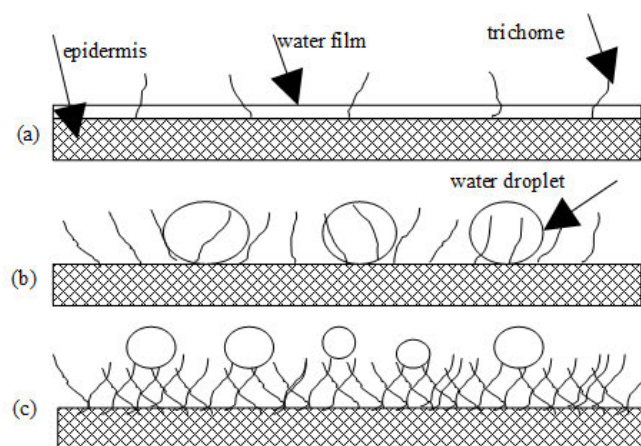


Figure 8. Types of trichome interactions with water. (a) No apparent influence of trichomes on the location of surface moisture, droplet formation or retention. (b) Segregating strategy—trichomes appear to circle surface moisture into patches. (c) Trichomes appear to hold water droplets above the trichomes. (From references [38, 68].)

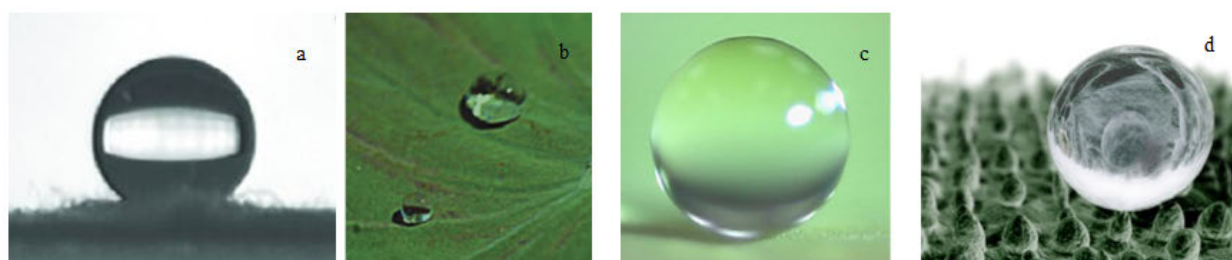


Figure 9. Water droplet on *P. acerifolia* (a, From reference [13]) and lotus leaf (b–d, From references [93, 94].)

3.3 Stomatal density

3.3. Stomatal density

Stomatal density and aperture (length of stomata) vary under a number of environmental factors such as atmospheric CO_2 concentration, light intensity, air temperature, photoperiod (daytime duration), and pollutants [85, 95–98]. Previous studies have shown that the contact surface was higher than that on adaxial surface [9, 12, 13, 65, 68], which was consistent with the stomatal distribution on leaf surfaces. The results of Brewer and Nuñez [12] showed that the surface with the greatest concentration of stomata was the least wettable. In a study conducted in Xi'an by Wang et al. [13], they found that a higher stomatal density was accompanied with a higher contact angle. However, the relationship between leaf contact angle and stomatal density was not shown a

angle on abaxial surface was higher than that on adaxial surface [9, 12, 13, 65, 68], which was consistent with the stomatal distribution on leaf surfaces. The results of Brewer and Nuñez [12] showed that the surface with the greatest concentration of stomata was the least wettable. In a study conducted in Xi'an by Wang et al. [13], they found that a higher stomatal density was accompanied with a higher contact angle. However, the relationship between leaf contact angle and stomatal density was not shown a simple linear relationship. The studies of Juniper and Jeffree [99], Brewer and Smith [38], and Kumar et al. [19] indicated that no significant correlation was observed between contact angle and stomatal density.

3.4. Epidermal cells

A gradient in the cell shape directly related to the contact angle of leaf surfaces was observed in some studies conducted by Wagner et al. [15] (Figure 10), Haines et al. [39], Neinhuis and Barthlott [4], Wang et al. [18], and Wang et al. [25]. Wang et al. [25] found that the leaves with convex epidermal cells with wax crystals, for example, *Cynanchum chinense*, *Agropyron mongolicum*, and *Anemone vitifolia*, had higher contact angles and lower water droplet adhesion. However, the leaves with smooth epidermal cells, such as *Populus simonii* and *Cynanchum komarovii*, had lower contact angles and higher water droplet adhesion. Haines et al. [39] found that the combination of a dense layer of granular wax and the convex epidermal cells was what created a hydrophobic surface of *L. tulipifera*. Wang et al. [18] and Neinhuis and Barthlott [4] both found that the leaf surfaces with convex epidermal cells had higher contact angles than those with flat epidermal cells, and the differences in leaf microstructure could also lead to the differences in leaf wettability during the whole growing season. These studies suggested that the combination of the wax and the convex epidermal cells can create a higher leaf contact angle. However, Neinhuis and Barthlott [3] observed the micromorphological characteristics of 200 water-repellent plant species by using SEM. They found that the scale of the epidermal relief ranged from 5 μm in multipapillate epidermal cells up to 100 μm in large epidermal cells. These variations in scale had almost no effect on leaf wettability of the investigated plant species.

3.5. Leaf water status

Leaf water status of plants is also a key factor in the wetting of leaf surfaces. Quantitative studies on the wetting by water of the exterior surfaces of leaves of *Sinapis arvensis* and *Triticum vulgare* showed that contact angles varied markedly on the detached leaves during the wilting process. This change was reversible on the recovery of turgor, and the magnitude of the contact angle of water droplets on a leaf surface showed a diurnal fluctuation characteristic with a range of as high as 30°. The change of contact angle could be explained by a function of leaf water status in rapidly wilting leaves. In addition, this change of contact angle was related to the corrugation of the leaf surfaces [76]. Weiss [100] studied the relationship between the contact angle of distilled water droplets and the leaf water potential as a function of time of a day on three different types of leaf surface: alfalfa (*Medicago sativa*), a smooth, waxy surface; dry edible beans (*Phaseolus vulgaris*), a corrugated, relatively waxless surface; and soybeans (*Glycine max*), a dense pubescent, corrugated, relatively waxless surface. The results showed

Ecological significance of leaf wettability

Interception of precipitation

Rainfall interception of forest areas is an important hydrological process that alters the quantity, timing, and distribution of water input and output on a catchment. On leaf level, leaf surface characteristics contribute to variability in interception between different plant species, resulting in different geometrical shapes of water on leaves (i.e., water film, patches, drops, and spherical droplets) [65]. Wang et al. [25] investigated leaf water drop adhesion of 60 plant species from Shaanxi, northwest China. The adhesion of water droplets to leaves covered a wide range of area, from 4.09 to 88.87 g/m² on adaxial surfaces and 0.72 to 93.35 g/m² on abaxial surfaces. The combined values for adaxial and abaxial surfaces in a single species ranged from 5.67 to 159.59 g/m². Wilson et al. [40] found that the leaf maximum water storage capacity of

potato was 150 g/m². They also reported that leaf water accumulation in the upper position of the canopy always exceeded that in the lower canopy, and clumping caused less water accumulation in the upper canopy and greater accumulation in the lower half compared to the random case. Tanakamaru et al. [41] compared leaf water retention by young and old leaves of *Cryptomeria japonica* and used values of 56 and 128 g/m², respectively. They attributed this difference in leaf water retention to the epicuticular wax of this species, which was very susceptible to erosion by rainfall. Haines et al. [39] explored the relation between water storage capacities and leaf wettability. They reported that *L. tulipifera*, having a low wettability, captured less water compared to those captured by *E. hieracifolia* and *Platanus occidentalis*, having a high wettability. Hanba et al. [24] reported values of 202, 210 g/m² and 120, 116 g/m² for the adaxial and abaxial surface of bean and pea, respectively. A survey of 50 subalpine/montane species indicated that moisture accumulation differed among species and habitats [68]. Wohlfahrt et al. [42] investigated the water storage capacities of nine plant species in Stubai Valley and found that the maximum water storage capacities covered a wide range from 13.2 to 314.0 g/m². They found the correlations between leaf maximum water storage capacity and leaf perimeter, hemisurface area, shape factor, and specific leaf area were all not significant and suggested that other parameters than those investigated were responsible for determining the maximum water storage capacity for plant species. Therefore, Wang et al. [25] explored leaf physical (roughness) and physicochemical (surface free energy, its dispersive and polar components, and work of adhesion for water) properties in relation to the adhesion of water droplets on leaves. The adhesion of water droplet on leaves decreased as leaf roughness increased but positively correlated with surface free energy, its dispersive component, and work of adhesion for water. However, a significant power correlation was observed between adhesion of water droplet and the polar component of surface free energy. These results indicated that leaf roughness, surface free energy, its components, and work of adhesion for water played important roles in leaf water droplet adhesion.

4.2. Photosynthetic rate

The effect of leaf surface wettability on plant photosynthesis stems from the fact that diffusion of CO₂ is 10,000 times slower in water than in air [9, 12, 24, 38, 72, 101]. Surface wetness induces different changes in leaf photosynthesis among species because leaf surface wettability varied greatly (i.e., from being covered almost completely by water to being water repellent) [24, 68]. For alpine and subalpine plants, natural dew depressed assimilation by 77% in species having wettable leaves, whereas assimilation was stimulated by 14% in species having nonwettable leaves [101]. For bean and pea, a 22% stimulated assimilation rate was obtained for nonwettable pea leaves in the 72-h mist-treated artificial surface, but the wettable bean leaves were on the contrary, which decreased 28%. They postulated that the photosynthetic responses to wetness are due to the change in stomatal regulation [24]. The results of Brewer and Smith [72] indicated that surface wetting, either from natural events or spraying irrigation might lead to significant reduction in CO₂ exchange and growth potential in agricultural species. Leaf surface wetness caused the greatest decline in photosynthesis for the surfaces with the lowest contact angle, which was due to the fact that water physically blocked stomatal pores.

4.3. Pathogen infection

Different plant species vary widely in pathogen infection, perhaps due to leaf micromorphology, surface chemistry, and degree of leaf wetness [19, 81, 102–104]. Water droplets on the leaf surface can be an important source of water for pathogen infection. Excess leaf wetness promotes pathogen infection in many native and agricultural species [19]. Kuo and Hoch [33] found that pycnidiospores of *Phyllosticta ampellicida* could only germinate on substrata on which they were firmly attached. Such surfaces had contact angles of $>80^\circ$. When pycnidiospores were deposited on more wettable surfaces, they did not attach firmly and did not germinate. Such surfaces had contact angles of $<40^\circ$. A significant increase in leaf wettability of wheat (*Triticum aestivum* L. cv. 'Minaret') was observed when the leaves were infected by *Pseudomonas putida*. The densities of *P. putida* decreased when leaf wettability increased [82]. The degradation of epicuticular wax crystals was observed with leaf age [7, 10, 18] and under environmental conditions [56, 87], which offered, in general, a more suitable microhabitat for most phyllosphere organisms [31–32]. In this way, these features increased the coverage by epiphytic microorganisms [31–32]. Huber and Gillespie [34] studied the relation between leaf surface wettability and pathogen infection. They found that the factors (e.g., micrometeorology, leaf wettability, and plant structure) that influenced the duration of dew all influence the pathogen infection. Pinon et al. [35] found that infection by *Melampsora larici-populina* on poplar leaves was dependent on the duration of leaf moisture. They also suggested that leaf wettability should be considered as an additional trait when breeding poplar for durable resistance to *M. larici-populina*, as this characteristic is likely to be a useful defense against all pathotypes of the pathogen. In addition, Cook [36] considered that the difference in leaf wettability provided a quick and discriminating technique for the preliminary screening of cultivars and lines within cultivars of peanut for resistance to *Puccinia arachidis*.

4.4. Environmental quality

It is universally accepted that trees and other vegetation are effective at trapping and absorbing many pollutants, such as particulate matters, CO, NO₂, and SO₂ [17–18, 56, 105–108], and they can act as biological absorbers or filters of pollutants [18, 105–107]. Leaf as the multifunctional interface between plants and environment is also continuously exposed to high levels of varieties of air pollutants. Air pollutants may cause plants both acute and chronic damages on anatomical and morphological characteristics [17–18, 56, 109, 110], leading variations in leaf wettability. Therefore, leaf wettability is potentially a good indicator to point out differences in urban habitat quality [18, 56]. Adams and Hutchinson [26] investigated the ability of four species (cabbage: *Brassica oleracea*; sugar beet: *Beta vulgaris*; radish: *Raphanus sativus*; sunflower: *Helianthus annuus*) to neutralize acid rain with contrasting leaf surfaces (e.g., wettability, droplet retention, hairiness, and thickness of epidermal waxes). Droplets were neutralized on the leaves of radish, and sunflower which had lower contact angles, causing a pH increase of between 0.3 and 1.5 pH units. On leaves of cabbage and sugar beet, which had larger contact angle, however, droplets were generally acidified. The wettability of leaves of *P. vulgaris*, *Vicia faba*, *Pisum sativum*, and *Brassica napus* from emergence to full expansion exposed to simulated acid rain at pH values between 5.6 and 2.6 were investigated by Percy and Baker [27, 111]. Leaf contact angles in all species decreased on leaves exposed to simulated acid rain at pH ≤ 4.6 relative to those exposed at pH 5.6. The variations in epidermal wax and epidermal membrane

could have important consequences for leaf wettability [111]. Ozone exposure decreased contact angles of *Populus nigra*, *Populus euramericana*, and *Populus menziesii* foliage, and the effects of ozone on cuticular interactions with liquid water varied with the ozone exposure regime and species [21]. Neinhuis and Barthlott [4] and Wang et al. [18] observed the seasonal changes in leaf wettability, the relation between the particulate matter accumulation and leaf wettability. They reported that *G. biloba* and *S. japonica*, having nonwetable leaf surfaces, did not show significant seasonal changes in contact angle and particulate matter ability during the growing season. However, *Q. robur*, *Fagus sylvatica*, *C. deodara*, and *P. acerifolia*, having wettable leaf surfaces, showed significant seasonal variations in contact angle and particulate matter capturing ability during the growing season. Besides, they found that the particulate matter capturing ability of leaves of *Q. robur*, *F. sylvatica*, *C. deodara*, and *P. acerifolia* increased with the decrease in contact angle.

5. Conclusions

Leaf surfaces represent the key interfaces between plants and their environment, which influence the biodiversity and biomass, nutrient and water balance, biogeochemical cycle, and productivity of ecosystems. Leaf surface wettability, indicating the affinity for water on the leaf surface, is a common phenomenon for plants in a wide variety of habitats, which directly affect leaf photosynthesis, canopy interception, pathogen infection, and environmental quality. Many studies concentrated on the differences in leaf surface wettability and its relation with leaf microstructure. Leaf surface wettability has been considered to be of great theoretical and academic importance, and studies focused on the ecological significances of leaf wettability should be encouraged in the future.

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