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Functional interaction between leaf trichomes, leaf wettability and the optical properties of water droplets

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Abstract. Because CO_2 diffuses 10000 times more slowly through water than air, there may be strong selective pressure for increased water repellency in terrestrial plant leaves. In the present study, leaf trichomes appeared to have a strong influence on leaf water repellency (i.e. degree of water droplet formation on the leaf surface) as well as the retention of droplets on the leaf. Based upon evaluation of 38 plant species from 21 families, we found that leaves with trichomes were more water repellent, especially where trichome density was greater than $25\,\mathrm{mm}^{2}$. However, droplet repellency and retention were both high in some species where trichomes entrapped droplets. Finally, the lensing effects of water droplets on leaf surfaces increased incident sunlight by over 20-fold directly beneath individual droplets. These results may have important implications for such processes as stomatal function, whole leaf photosynthesis, and transpiration for a large variety of plant species.

Key-words: leaf wettability; water droplets; trichomes; droplet retention; droplet optics.

Introduction

There has been a long-standing interest in the interaction of the leaf surface of terrestrial plants with liquid water. Common precipitation events such as rain, dewfall, ground fog and cloud mist may generate leaf wetness for large parts of a day for many native plants (Berg, 1985; Harrington & Clark, 1989) and both adaxial and abaxial surfaces are frequently affected. The influence of leaf wetness on pathogen invasion has been a long-standing concern (e.g. Hollier, 1985; Reynolds *et al.*, 1989). In addition, the use of spray applications for irrigation and pest management in agricultural systems (Bukovac, Flore & Baker, 1979; Guzman & Gomez, 1987) has generated a broad interest in the water absorption characteristics of leaf surfaces (Fogg, 1947; Challen, 1960, 1962; Holloway, 1970).

As early as 1898, Stahl suggested that dew on leaf surfaces might inhibit early morning transpiration. Although Stone (1957, 1963) suggested a positive effect of dew on plant transpiration, only very recently have studies clearly shown important influences of natural leaf surface wetness on plant gas exchange (Smith & McClean, 1989).

The purpose of the current study was to evaluate the potential importance of leaf trichomes and pubescent layers to the formation, distribution, and retention of water droplets on a leaf surface. We present evidence that associates trichome arrangement with specific effects on water droplet formation (repellency) as well as droplet retention. We also report on some lensing effects of water droplets that produced extreme amplification and variation in incident sunlight on the leaf surface. To our knowledge, there are no other reports of this phenomenon.

Materials and methods

Thirty-eight plant species (21 families) were randomly selected for study from a total of approximately 650 species in the University of Wyoming, Laramie, U.S.A., glasshouse complex (Table 1). Gross surface characteristics of adaxial and abaxial leaf sides were examined with an Olympus Model SZ-III Zoom Stereomicroscope. The following measurements for both adaxial and abaxial leaf surfaces were made on five leaves of each species: trichome density (number per unit area), trichome length and approximate trichome canopy height, contact angle of water droplets on the leaf surface (θ), and the capability for droplet retention.

Trichome structure

Average trichome density was calculated by counting the number of trichomes within a micrometer grid (2.5 × 2.5 mm) using five replicates per leaf surface and five leaves per species. Maximum trichome length and height were measured using epidermal peels from both adaxial and abaxial leaf surfaces. Trichome canopy height measured from the leaf epidermis was estimated from leaf cross sections. Because trichome are often bent or curved, this length was often less than the maximum trichome length. This interpretation of canopy height also provided an estimate of the distance water droplets would rest from the leaf surface. Mean values for both leaf surfaces were determined from 10 measurements of trichome length and five measurements of trichome canopy height per leaf.

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Table 1. Families and species evaluated in this study: (+) trichomes present; (−) no trichomes

Family	Species	Trichomes	
		Adaxial	Abaxial
Acanthaceae	*Hypoestes phyllostachya* Bak.	+	−
	Justica Brandegeana Wassh. & L.B.Sm.	+	+
Apiaceae	*Levisticum officinale* W.D.J.Koch	−	−
Araliaceae	*Brassaia actinophylla* Endl.	−	−
Asclepiadacea	*Ceropegia Woodii* Schlechter	−	+
Asteraceae	*Dahlia Merckii* Lehm.	+	+
	Chrysanthemum sp.	+	+
	Senecio articulana (L.f.) Schultz-Bip.	−	−
	Senecio Cineraria DC	+	+
Begoniaceae	*Begonia* sp.	−	−
Brassicaceae	*Lunaria annua* L.	+	+
Commelinaceae	*Cyanotis Kewensis* (Hassk.) C.B.Clarke	+	+
	Tradescantia navicularia Ortg.	+	+
Crassulaceae	*Echeveria pulvinata* Rose	+	+
	Kalenchoe beharensis Drake	+	+
	Kalenchoe Millotii Hamet & Perr.B.	+	+
	Kalenchoe sp.	+	+
Euphorbiaceae	*Euphorbia pulcherrima* Willd. ex Klotzsch	+	+
Fabaceae	*Medicago sativa* L.	+	+
	Samanea saman (Benth.) Merrill	+	+
Geraniaceae	*Pelargonium* sp.	+	+
Hypericaceae	*Hypericum* sp.	+	−
	Plectranthus australis R.Br.	+	+
	Plectranthus tomentosus Benth. ex E.H.Mey.	+	+
	Salvia officinalis L.	+	+
Malvaceae	*Abutilon pictum* (Gillies ex Hook. & Arn) Walp	+	+
	Hibiscuc Rosa-sinensis L.	+	+
Onagraceae	*Fuchsia* × hybrida Hort. ex Vilm	+	+
Orchidaceae	*Haemaria discolor* (Ker-Gawl.) Lindl.	−	−
Oxalidaceae	*Oxalis rubra* St.-Hil.	−	+
Piperaceae	*Peperomia obtusifolia* (L.) A.Dietr.	−	+
	Peperomia orba Bunt.	+	+
Rutaceae	*Citrus aurantifolia* (Christm.) Swingle	−	−
Urticaceae	*Pilea involucrata* (Sims) Urb.	+	+
	Unknown 1	+	−
	Unknown 2	+	+
	Unknown 3	+	+

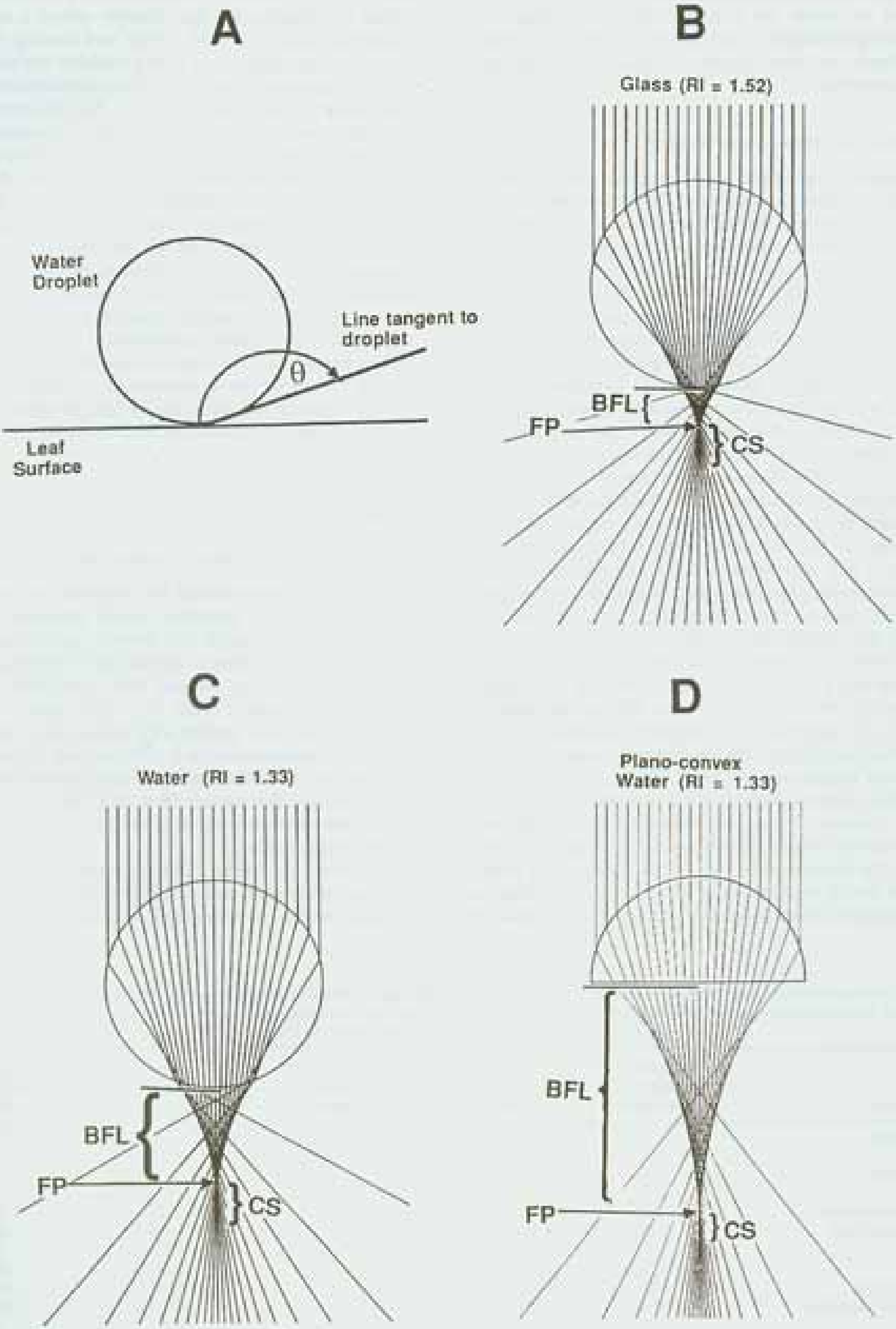
Water repellency of the leaf surface

To investigate the interaction between water droplets and trichomes, leaf surfaces were misted with a fine spray (droplets < 0.2 mm) and then observed microscopically. Natural droplet formation following dewfall was also observed in the field and compared to the spray misting technique used in the laboratory. Droplet sizes on leaves of 19 species in the field ranged from approximately 90 μm to over 6 mm in diameter.

The degree of water repellency of the leaf surface was determined by measuring the contact angle (θ) of 5 mm^3 water droplets placed on each leaf surface using a micropipette (Adam, 1963). For all leaves, θ was measured relative to the epidermis for horizontally positioned leaves even when droplets rested above the surface on trichomes (Fig. 1A). Five replicates per leaf were measured on both leaf surfaces for all species. Criteria for judging surface wettability were based on those of Crisp (1963) where $\theta < 110°$ was considered a wettable surface while $\theta > 130°$ was non-wettable. The diameter of a spherical 5 mm^3 droplet was approximately 0.4 mm. The width of more flattened droplets could be as great as 1.3 mm, depending on θ.

The amount of surface area in contact with a given water droplet was determined microscopically by measuring the contact length in cross section between the droplet and leaf surface. Contact area was estimated by assuming that the contact length of the droplet was equal to the diameter of the circle in contact with the leaf surface beneath the water droplet.

Figure 1. Droplet contact angle (θ) and ray tracings for spherical and plano-convex lenses. (A) The angle, θ, of a line tangent to the droplet through the point of contact between the droplet and leaf surface was measured. Greater θ indicates greater water repellency. Diagrams B, C and D illustrate ray tracings of collimated light passing through lenses according to Snell's Law of Refraction. BFD is the back focal length, FP is the focal point, CS is the cast shadow, and RI is the refractive index. The first lens (B) has a refractive index for glass (1.52) while the second (C) has a refractive index for water (1.33). The third lens (D) is a plano-convex lens of water representing a flattend droplet. The BFD (distance from the back of the sphere to the focal point) increases approximately 2.5 times for water droplets versus the glass spheres used in the experiments.


A
Water Droplet
Line tangent to droplet
θ
Leaf Surface
B
Glass (RI = 1.52)
BFL
FP
CS
C
Water (RI = 1.33)
BFL
FP
CS
D
Plano-convex Water (RI = 1.33)
BFL
FP
CS

Droplet retention was determined by placing a 0.5 cm^3 droplet of water on a horizontal leaf surface and measuring the angle of inclination at which the droplet first began to move. Smaller angular values indicate poor retention.

Optical properties of water droplets

The optics of spherical water droplets can be characterized from known properties of spherical (ball) lenses. Light rays passing through a spherical lens are only partially condensed because of lens thickness and an imperfect focal point that is generated according to Snell's Law of Refraction (Williams & Becklund, 1972) (Fig. 1B, C). Ray tracing analysis was used to make empirical estimates of the focal distances measured from the back side of the lens. The quantitative effects of sunlight focusing by spherical water droplets on a leaf surface were estimated by measuring irradiance levels of sunlight (PAR, photosynthetically active radiation, 0.3–0.7 μm) passed through precision-ground glass spheres (Edmund Scientific, New Jersey, U.S.A.). The optical properties measured for the glass spheres were converted to those of water droplets according to the difference in the refractive indices between the glass lenses (1.52) and water (1.33). By comparing the refractive indices and corresponding ray tracings of glass (Fig. 1B) versus water lenses (Fig. 1C), we also estimated the spatial effects that actual water droplets would have on sunlight focusing; for example, focal distance and projected spot size. The back focal length (measured from the back of the lens to the incident surface) of a spherical water droplet was about 2.5 times that of a glass sphere with an identical diameter according to ray tracing analysis (Fig. 1B, C).

Effects of non-spherical water droplets ($\theta < 110°$) on light focusing were approximated by comparing properties of spherical lenses to those of plano-convex lenses. As illustrated in Fig. 1C, the shape of a plano-convex lens is representative of water droplets that are not perfectly spherical but are flattened due to lower θ. Actual measurements of PAR beneath glass lenses were taken by aligning the lens directly above a modified quantum sensor (LICOR 190S) and moving the lens away from the sensor in a path parallel to the suns rays. PAR at the centre of the projected spot was measured by modifying the quantum sensor so that the area of the sensing surface was reduced to 1.0 mm^2. The sensor area was always less than one-fifth of the area of the smallest discernible spot projected by any lens used. A micromanipulator (1 μm resolution) was used to measure actual distances from the surface. Both the size of the projected focal spot and its irradiance level were measured. The size of the projected spot was measured directly on a transparent sheet of tracing paper. For all measurements, full sunlight (without lens focusing) was recorded before and periodically during the lens measurements. Glass spheres with different diameters (0.5–3.5 cm in 0.5 cm increments) were used to empirically determine the influence of lens (droplet) size on projected spot size, focal length and PAR.

Results

Trichome structure, water repulsion and retention

Leaf surface characteristics for all species are summarized in Table 2, including mean trichome length, trichome canopy height and density, and mean θ (i.e. surface water repellency) and droplet retention angles for the leaf. Of the 76 leaf sides evaluated, 56 had trichomes present (Table 1). The group without trichomes included species with leaf surfaces that were extremely hydrophobic ($\theta > 170°$) as well as some very hydrophyllic sides that had an almost continuous film of water over the leaf surface ($\theta < 15°$). Mean θ values for all leaf sides with or without trichomes were 104 and 82°, respectively (Table 2).

As shown in Table 2, three types of interactions between trichomes and water droplets were evident. Among the leaf surfaces with trichomes, there was a

Table 2. Leaf surface characteristics. Mean values are for trichome density and length, trichome canopy height, contact angle of water droplet (θ), and retention. Plus and minus values are standard errors; sample sizes (number of leaf sides representing a total of 38 species) are in parentheses. Sample sizes are not equal for each group because some plants died during the study

Trichomes	Trichome density (no. per mm^2)	θ (degrees)	Rentention (degrees)	Trichome length (mm)	Trichome canopy height (mm)
Trichomes absent	—	82 ±14(2)	25 ±5(14)	—	—
Trichomes present:					
all sides pooled	32 ± 7(56)	104 ±16(55)	25 ±3(43)	0.42 ±0.04(56)	0.25 ±0.03(48)
no interactions	6 ± 2(29)	84 ±10(29)	30 ±4(21)	0.32 ±0.04(29)	0.14 ±0.03(25)
lift droplets	99 ±17(14)	173 ± 5(14)	16 ±4(14)	0.48 ±0.13(14)	0.41 ±0.03(14)
segregate droplets	20 ± 4(13)	73 ±10(13)	46 ±3(13)	0.60 ±0.10(13)	0.35 ±0.07(9)

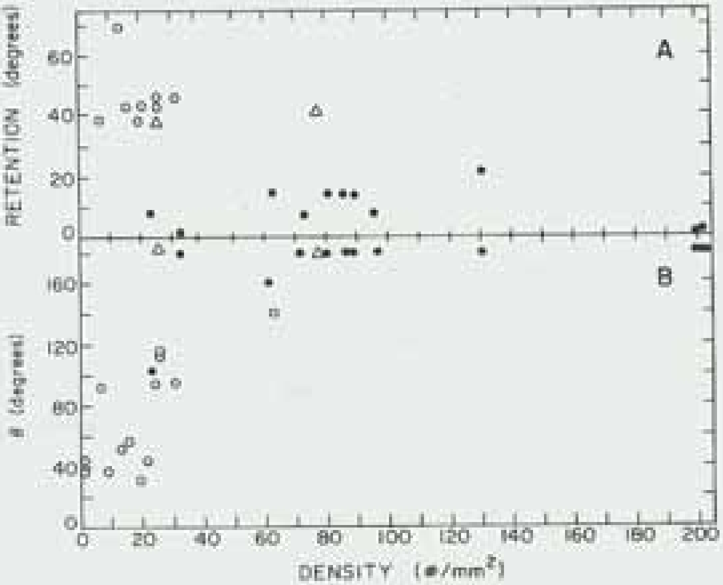


Figure 2. Retention and contact angle (θ) for water droplets on leaves. Open circles are for leaf surfaces that segregated water into patches. Closed circles represent leaf surfaces with trichome canopies that held droplets well above the leaf epidermis. Open triangles represent surfaces that had both high contact angles and retention. (A) Droplet retention as a function of trichome density for 21 leaf sides from 15 species. (B) Apparent contact angle (θ) as a function of density for 27 leaf sides from 16 species.

group that had no apparent interaction between trichomes and water droplet formation or retention. In this group, trichome density was relatively low, and usually a film of water formed on the leaf surface.

Trichomes appeared to hold water droplets above the leaf epidermis in a second group of leaf surfaces ('lift droplets' on Table 2) that had high water repulsion (θ = 173°) and trichome density. Droplets resting on the trichome canopy were small and numerous. Also, droplet retention was relatively low ($\bar{x}$ = 16°).

In a third group of leaf surfaces ('segregate droplets' on Table 2), trichomes appeared to have a strong influence on the location of surface water by encircling individual water patches. These leaf surfaces were characterized by relatively high retention ($\bar{x}$ = 46°) and wettable surfaces, but variable and relatively low θ ($\bar{x}$ = 73°) and trichome density.

The specific influence of trichome density on droplet retention and leaf wettability is illustrated inn Fig. 2. In general, low trichome density ($<30\,\mathrm{mm}^{-2}$) corresponded to higher droplet retention and lower θ, while high trichome density ($>40\,\mathrm{mm}^{-2}$) corresponded to lower droplet retention and higher repulsion. Leaves that segregated water into patches (open circles) had relatively high droplet retention and lower θ, while surfaces that had well developed trichome canopies (closed circles) tended to have lower retention and greater θ (Fig. 2). Two species had trichome canopies that lifted water droplets away from the surface, but also had relatively high retention (open triangles in Fig. 2). This high retention appeared to involved hydrophyllic trichomes even though a relatively high water repellency (high θ) still existed for the leaf surface.

For a $5\,\mathrm{mm}^3$ droplet, the actual contact area measured between it and the leaf surface at a given θ is shown in Fig. 3. A rather sharp decrease in contact area occurred for θ near 0° to about 40°, followed by a much more gradual decline for θ > 40°. Contact area for θ = 10° was more than five-fold greater than that measured at θ = 140°. Theoretically, contact areas would be negligible for a perfectly spherical droplet (θ = 180°).

Focusing of incident sunlight by water droplets

The irradiance level (PAR) and size of the projected bright spot from the back of a spherical lens to the focal point (see Fig. 1B, C) are shown in Fig. 4. Measured PAR increased as the spot size decreased from the back of the lens to the focal point. The maximum measured PAR for a glass lens was approximately 20 times full sun and occurred at a focal distance of about 0.2 of the lens diameter (measured from the back of the lens). Beyond the focal point, rapid dispersion of the beam took place with no condensation of light rays (Figs 1B & 4). When the projected bright spot was largest (just beyond the back of the lens) the relative irradiance was about five times full sun. It is likely that our estimates of maximum irradiance at the focal point beneath the water droplets are conservative. The sensing surface was $1\,\mathrm{mm}^2$, but at the smallest spot size (i.e. the focal point), the projected spot was smaller than $1\,\mathrm{mm}^2$. Thus, maximum irradiance may be higher than our estimate of about 20 times full-sun. At greater distances from the back of the glass lens (>0.4 of the lens diameter) irradiance decreased from about four times full sun to much less than full sun (indicated by negative irradiance values in Fig. 4). This

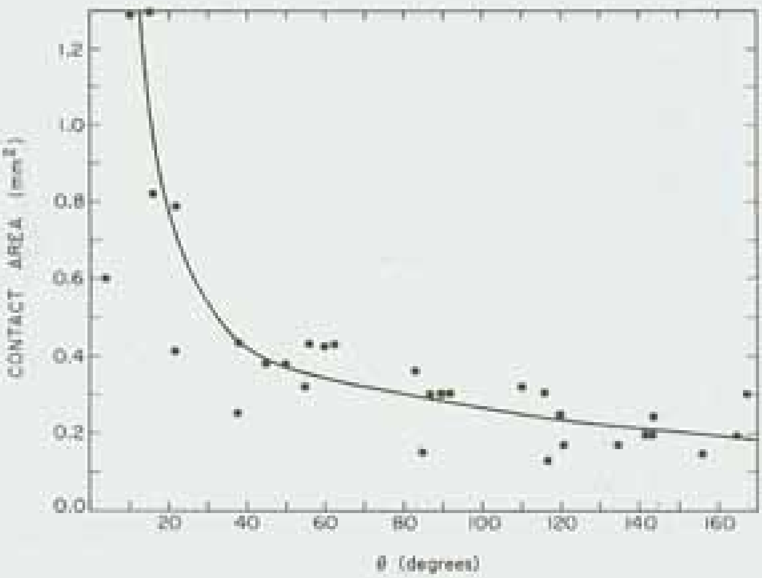


Figure 3. Contact area between a droplet and leaf surface as a function of the contact angle (θ). Droplet volume was 0.5 cm^3. Contact area is a function of both surface repellency and droplet size (e.g. as droplet size increases, θ decreases for a given surface repellency).

depletion in PAR corresponded to the region of rapid beam dispersal shown in Fig. 1B–D and can be visually detected as a cast shadow on the projection surface (see cover photo).

A plano-convex lens is a rough approximation of the shape of a water droplet with lower θ due to a less hydrophobic surface and/or greater droplet weight (Fig. 1D). Spherical and plano-convex lenses will not differ in the degree of amplification of irradiance because the condensation of light rays is directly proportional to interception area. However, the focal distance and change in spot size with distance from the lens will differ substantially. In general, spot size beneath a plano-convex lens will be much larger nearer the lens and the focal distance will be about doubled compared to a spherical lens of equal diameter.

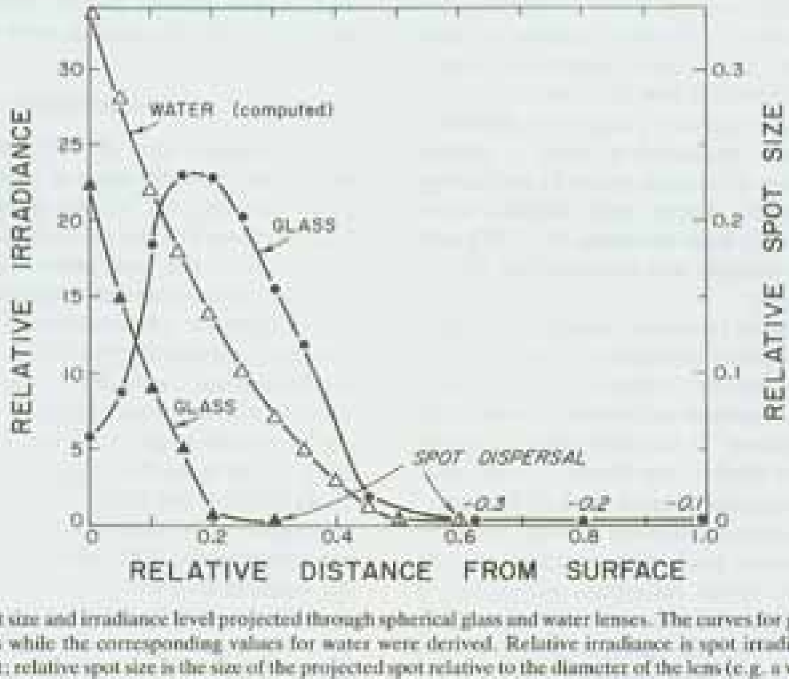


Figure 4. Relative spot size and irradiance level projected through spherical glass and water lenses. The curves for glass were generated from measured values while the corresponding values for water were derived. Relative irradiance is spot irradiance expressed as a fraction of full sunlight; relative spot size is the size of the projected spot relative to the diameter of the lens (e.g. a value of 0.2 indicates that the spot is 0.2 times the size of the lens diameter); relative distance from the surface is the distance the spot is projected away from the back of the lens relative to the original lens diameter (e.g. a value of 0.4 indicates that a spot is projected 0.4 times the lens diameter away from the back of the lens). Data for glass lenses are closed circles (irradiance) and triangles (spot size), while data for water lenses are open triangles (spot size).

Discussion

In a review of the ecological importance of plant pubescence, Johnson (1975) noted that the occurrence of trichomes was ubiquitous among plants and he suggested that, if selection pressures were important in directing the development of pubescence, there should be a correspondence between the occurrence of pubescence and certain environmental conditions. For example, a great deal of work has illustrated the importance of pubescence for reflecting sunlight and reducing temperature and water stress in desert plants (Ehleringer, 1984).

Selective pressure to shed water or isolate it to locations where it does not interfere with the photosynthetic uptake of CO_2 should be high for terrestrial plants in habitats with frequent leaf wetting events. The importance of keeping surfaces with stomata dry to promote gas exchange has been recognized in agricultural species (Raskin & Kende, 1983) and in aquatic plants with floating leaves (Sculthorpe, 1967; Hutchinson, 1975). Crisp (1963) suggested that a seemingly obvious function of hydrophobic leaves was to prevent leaf surfaces from being saturated with water. Smith & McClean (1989) reported dramatic increases on water use efficiency for naturally wetted leaves with high θ and retention. Photosyntheis was increased due to greater stomatal opening and yet, transpiration was substantially lower compared to leaves with dry surfaces.

Retention of droplets on a leaf surface may differ depending on whether droplets are deposited as rain or as dew. Retention of rain is often low because either drops bounce from the leaf surface on impact or they do not adhere to inclined surfaces (Holly, 1976). Barr & Gillespie (1987) found that only 6% of leaf area may be covered by droplets as a result of rainfall. Our observations are similar to Holly's (1976) in that drops on surfaces with high θ ($>130°$) are unstable and tend to roll off, while drops on surfaces with low θ ($<100°$) have a lower centre of gravity and are more likely to adhere to the leaf surface. Also, the condensation of water vapour into small droplets (e.g. dewfall) may cover a much larger portion of the leaf surface and may be enhanced by surface roughness (Osment, 1963).

In the field, we have observed that droplet formation following dewfall generally results in the greatest concentration of droplets on a leaf surface. Many species were covered with a virtual monolayer of small droplets (<0.5mm in diameter) and many of these species also tended to have a dense trichome layer. Both leaf sides, even for horizontally oriented leaves, had dew deposition. Much smaller droplets appear at the beginning of dew formation while much larger sizes (>1mm in diameter) develop with time, or if droplets are shed to specific locations on the leaf where they merge. We know of no other data describing these characteristics of leaf wetting in native or agricultural species. However, from our observations of native plants in the field, a wide range of droplet sizes and concentrations occurs on leaves depending on species, location, type of precipitation and leaf orientation.

Our results suggest a strong influence of trichome density and arrangement on the wettability of leaf surfaces and the tendency for leaves to retain or repel moisture. Although trichomes were not always uniformly distributed across the leaf surface and there was some overlap in our classification of lifting versus segregating trichome canopies (Fig. 2), it appears that trichome canopies had a strong influence on the formation, repulsion, and/or retention of water droplets. Droplets lifted above the leaf surface would create a source of moist air next to the leaf surface as they evaporate (Uphof, Hummel & Staesche, 1962). Water sequestered into patches may also increase the vapour density near the leaf surface or within the leaf canopy. Thus, if droplets or patches of water are retained on leaves via the influence of trichomes, an improved photosynthetic environment (possibly enhanced stomatal opening) and lowered transpiration could result (as reported by Smith & McClean, 1989). We are currently evaluating the specific distribution of retained water across the leaf surface versus stomatal distribution in a variety of species and habitats, along with the possible involvement of trichomes.

Water droplets on leaf surfaces also have the potential to generate an extremely variable light environment across the leaf surface. The significance of elevated and variable irradiance levels depends on the total amount of leaf area involved (Fig. 3). Droplets act as condensing lenses which can focus light into bright spots many times full solar irradiance (Fig. 4). For species with monolayers of droplets created by dewfall, a large portion of the leaf surface may be affected by sunlight levels greater than full sun. However, incident sunlight may not always be amplified by water droplets because the epidermis may not be at the focal point and/or because of the light scattering that could occur within a trichome layer. Regardless, one cannot help wonder how underlying tissue could cope with such large irradiance levels (e.g. chlorophyll-containing guard cells). Droplets may also cast shadows that are far less than full-sun irradiance.

Summary

Functionally, the formation of more spherical water droplets due to greater water repellency will insure gas exchange due to the elimination of water film formation. Moreover, retention of water droplets on individual leaves and throughout the leaf canopy may lead to enhanced water use efficiency by reducing transpiration as well as increasing photosynthesis (Smith & McClean, 1989). In the present study, trichomes and pubescent layers on leaf surfaces appear to enhance water repellency by the formation of spherical droplets (high θ), and may also increase retention of droplets at steeper leaf angles. However, the focusing properties of water droplets could result in damage of epidermal (e.g. chlorophyll containing guard cells) or possibly palisade cells. In response, trichomes and pubescent layers could sequester droplets at distances away from the focal length of the droplets. For water droplets, this distance is about equal to their radius. Also, the formation of smaller droplets will reduce the amount of lens amplification by the square of the radius. Smaller droplet sizes will result in less intense and smaller projected bright spots that will be closer to the back of the droplet. More work is needed to comprehensively evaluate the functional interaction between leaf water repellency, droplet formation, the co-occurrence of trichomes and stomata, and ultimately, the ecological significance of these relationships.

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