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THE JEWELLED ARMOR OF *TILLANDSIA*—MULTIFACETED OR ELONGATED TRICHOMES PROVIDE PHOTOPROTECTION

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ABSTRACT

Foliar trichomes of gray-leaved Tillandsioideae (Bromeliaceae) are highly reflective, suggesting a role in protecting the leaf against direct sunlight in exposed niches. The performance of photosystem II, as denoted by the chlorophyll fluorescence characteristic F_v/F_m , was determined for seven *Tillandsia* species and *Vriesea barclayana* that were exposed to excessive light, with trichomes either present or removed. Additionally, trichome structure and interaction with light was recorded using extended depth-of-field photomicrography, and reflectance quantified using a novel photographic technique. Trichomes of mesomorphic Type IV life forms (*T. cryptantha*, *T. cyanea*) and of the intermediate life form *V. barclayana* conferred reflectance of between 1 and 11%, which did not significantly influence F_v/F_m when exposed to a high light intensity of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ (photosynthetically active radiation) for one hour. However, the ornate trichomes of atmospheric species increased the reflectivity of the leaf blade by as much as 18–40%, with a positive correlation apparent between reflectance and photoprotection. Type V *Tillandsia andrieuxii*, *T. caput-medusae*, and *T. mitlaensis* have attenuated trichome wings extending perpendicular to the leaf surface and catching the light (with leaf surfaces appearing gray and fuzzy). This open configuration was observed to facilitate leaf ventilation and the condensation of water vapor on the cooler underlying cuticle, with liquid water subsequently enveloping the trichomes, suggesting a trade-off between water acquisition and light reflectance for air plants from xeric habitats. However, Type IV–V *T. albida* and *T. concolor* impound water in leaf bases and the flattened, circular, and overlapping trichome wings did not facilitate dew formation on the cuticle. For these plants with white, smooth leaf surfaces, trichomes are multifaceted and provide more effective photoprotection by scattering light in the manner of cut gemstones.

Key words: Bromeliaceae, bromeliad, epiphyte, photoinhibition, photoprotection, *Tillandsia*, trichome.

INTRODUCTION

Tillandsioideae are a subfamily of Bromeliaceae, characterized in part by peltate trichomes (plate-like leaf hairs) with a distinctive flexible shield. The majority of Tillandsioideae grow as epiphytes, which possess trichomes that play a central role in their lifestyle by allowing the leaf to absorb water and dissolved minerals and with roots that act primarily as holdfasts (the structure and absorptive mechanism of the tillandsioid trichome is described in Fig. 1). Aside from this principal role of the tillandsioid trichome in water and mineral absorption, the dry, upright trichome wings of atmospheric species (i.e., succulent epiphytes that absorb water directly over the entire leaf surface rather than from phytotelmata; Benzing 2000) reflect light, which has been proposed as an adaptation to high light intensities (Benzing and Renfrow 1971; Benzing 1976). Mechanistically, light scattering by dry trichomes has been suggested to provide photoprotection (Benzing 2000); i.e., shielding proteins in light-harvesting units from excessive light energy. Indeed, atmospheric Tillandsioideae specialize in highly exposed canopy niches that regularly experience direct sunlight. Trichomes of *Tillandsia fasciculata* Sw. reflect approximately 25% of incident visible light (Benzing and Renfrow 1971) and ecotypes of *T. caput-medusae* from Sonora, Mexico, have inherently more reflective indumenta than ecotypes from less arid sites (Dimmit 1985). However, the non-absorptive trichomes that characterize some of the more

primitive terrestrial bromeliads reflect up to 17% of visible light as a consequence of a highly irregular water-repellent micro-relief, but this is not sufficient for photoprotection against direct sunlight (Pierce et al. 2001). Indeed, trichomes conferring reflectance of up to 56% limit photosynthesis for *Encelia farinosa* A. Gray ex. Torr. (Asteraceae) in the Sonoran Desert of California (Ehleringer et al. 1976), which is clearly of adaptive significance as pubescent leaves are produced seasonally and distinct ecotypes have been discerned (Housman et al. 2002).

Direct measurements of photoinhibition and specifically of photoprotection by trichomes of gray-leaved *Tillandsia* L. have not been made previously. The present study investigates the hypothesis that highly reflective foliar trichomes photoprotect the leaf, as evidenced by photosystem II chlorophyll fluorescence characteristics. The nomenclature follows Luther (2002) and life forms or ecophysiological types follow Benzing (2000), as summarized by Pierce et al. (2001).

MATERIALS AND METHODS

Plant Material and Cultivation

The *Tillandsia* species and *Vriesea barclayana* listed in Fig. 2 (authorities noted in Table 1) were obtained from Bird Rock Tropicals (Carlsbad, California, USA), with the exception of *Tillandsia cyanea* (Bouquet Florist, Crookes, Shef-

Fig. 1.—Transverse views of the tillandsioid trichome in dry and wet configurations (not to scale); based on the photomicrographs and descriptions of Benzing (1976, 2000). The “shield” is comprised of dead central disc cells, ring cells, and wing, and the “stalk” is comprised of live dome and foot cells. When dry, the wing stands erect, exposing the underlying leaf surface and trichome undersides to rainwater, thus avoiding the water repellency typical of dense trichome layers (Pierce et al. 2001). Rainwater or dew enters the cells of the trichome shield, which lack cuticle and cell contents. As the central disc swells the increased pressure is directed by the differentially thickened ring cell walls to flatten the wing against the cuticle, promoting water uptake by enhancing capillary movement of water towards the central disc (Benzing 1976). Transverse walls of the dome cells are uncutinized, allowing water uptake via osmosis, transport between cells, and ultimately into the leaf. Dome cell ultra-structure suggests that mineral nutrients are taken up actively (Benzing 2000). As the leaf surface dries, collapse of the central disc seals the dome cells, preventing evaporative water loss (Benzing 1976).

field, UK). Life forms ranging from soft-leaved Type IV species with extensive phytotelmata (*T. cryptantha*, *T. cyanea*) to succulent Type V species with extremely limited phytotelmata (*T. andrieuxii*, *T. caput-medusae*, *T. mitlaensis*) and intermediate life forms (*T. albida*, *T. concolor*, *V. barclayana*) were investigated. Plants were cultivated in the UK under glass (16–29°C, 39–92% relative humidity [RH], 16 h photoperiod), with shade cloth limiting light intensity to 20% of ambient light (e.g., on a cloudless day, with full sunlight of 1600 $\mu\text{mol Quanta m}^{-2} \text{s}^{-1}$, plants experienced 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The commercial nutrient solution BabyBio (pbi Home and Garden Ltd., Middlesex, UK) was diluted ($\times 0.4$ of recommended strength) to provide 3.2 mM N, 0.3 mM P, and 0.1 mM K, with all leaf surfaces inundated daily using a hand-nebulizer, for a minimum of two weeks prior to experimentation.

Reflectance of Light by Leaf Surfaces

Reflectance of light by leaf blades of each species was quantified from photographs, using barium sulfate as a stan-

dard (BaSO_4 ; absolute reflectivity of 99.3% over the wavelength range 300–800 nm; Munsell Color, New Windsor, New York, USA). Barium sulfate powder was made into an aqueous paste (50% w/v) painted on the mid-leaf portion of the leaf blade surface, and left to dry.¹ The leaf was photographed on tungsten color-reversal film with even lighting provided by four 20W halogen lamps. Photographs were slightly underexposed to avoid over saturation of the lighter portions of images. The image was digitized using a DFS PrimeFilm 1800u transparency scanner (Jessops, Leicester, UK). Corel Photo-Paint vers. 9 imaging software (Corel Corporation, Ottawa, Ontario, Canada) was used to compare the luminosity of pixels representing the barium sulfate standard and pixels representing adjacent leaf surface proper (use of Corel software to determine luminosity values is described by Pierce et al. 2001). Portions of the leaf blade were also denuded of trichomes using sticky-back plastic, as described by Pierce et al. (2001), and thus the reflectance of the trichomes was determined by comparing intact and denuded surfaces.

Chlorophyll Fluorescence

Photoinhibition of photosystem II was investigated using an OS5-FL portable modulated fluorometer (Opti-Sciences, Tyngsboro, Massachusetts, USA). The degree of photoinhibition was determined from the decline in the dark-adapted ratio of variable to maximum chlorophyll fluorescence (F_v/F_m) following exposure for one hour to 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (PAR), provided by HPI-T Plus 400W high pressure iodide lamps (Koninklijke Philips Electronics N.V., Eindhoven, The Netherlands) at an air temperature of 28°C (see Pierce et al. 2001).

Trichome Structure and Density

Leaf blade trichome structure was observed via light microscopy with extended depth-of-field images of leaf surfaces and trichomes produced using the method of Rolfe and Scholes (2002). An Olympus BX50WI microscope (Olympus Optical Company, London, UK) with focus control slaved to a stepper motor (Proscan, Prior, Cambridge, UK) was used to acquire images at different focal planes at 50 μm intervals throughout the sample. Samples were illuminated from above by a 150W halogen lamp (Schott KL1500 Electronic, Schott-Fostec LLC, Auburn, New York, USA) with light delivered via a fiber optic, reflected from the sample and ultimately photographed using a cooled, back-thinned, illuminated charge-coupled device (CCD; Micro-max 880PB, Roper Scientific, Marlow, UK). Image acquisition, processing, and display functions were facilitated by Image Pro Plus vers. 4.1 software (Media Cybernetics, Silver Spring, Maryland, USA). Using DeFuzz vers. 1.0.1 extended depth of field software (Rolfe 2002), images of 1000 $\times$ 800 pixels in size were subdivided into blocks of 10² or 20²

¹ NB titanium dioxide (TiO_2) in toothpaste may be a more convenient standard than barium sulfate for use in the field or as an alternative to a powdered form when crossing international borders. Using the above technique, an absolute reflectivity of 93% ($N = 10$) was determined for Colgate Total (Colgate-Palmolive [UK] Ltd., Guildford, UK) in comparison with barium sulfate.

Fig. 2.—The seven *Tillandsia* species and *Vriesea barclayana* (Bromeliaceae) used in the present study. Pairs of coins for scale are: US quarter (left) and GB pound (right). A 30 cm rule provides scale for *T. cyanea*.

Table 1. Interactions between light (photosynthetically active radiation or PAR) and foliar indumenta of epiphytic *Tillandsia* species and *Vriesea barclayana* (Bromeliaceae: Tillandsioideae). The degree of photodamage to photosystem II, after exposure to saturating light ($1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) for one hour, is denoted by the extent of reduction in F_v/F_m (the dark-adapted ratio of variable to maximal chlorophyll fluorescence) with the leaf blade surface either intact or denuded of surface features. Values represent the mean $\pm$ 1 SE of four replicates. * Denotes significant differences in the reduction of F_v/F_m between intact and denuded treatments at the $P \leq 0.05$ level as determined by Student's t -test, ** $P \leq 0.01$, *** $P \leq 0.001$, with n.s. indicating "no significant" difference. Proportion data were arcsine transformed prior to statistical analysis and standard errors of proportion data calculated via the method of Fowler et al. (1998). Determination of photosynthetic pathway is based on tissue carbon isotope composition (Crayn, Winter, and Smith unpubl. data), in conjunction with gas exchange and titratable acidity data for *V. barclayana* (Pierce et al. 2002b). Life forms or ecophysiological types follow Benzing (2000).

Species	Life form	Photosynthetic pathway	Surface	Trichome density (stalks mm^{-2})	Reflectance from intact leaf blade (%)	Reflectance conferred by trichomes (%)	Decrease in F_v/F_m following high light exposure (%)		Significance
							Intact surface	Denuded surface	
<i>T. albida</i> Mez & Purpus	IV-V	CAM	Adaxial	41 $\pm$ 1.7	79 $\pm$ 5.1	27 $\pm$ 3.0	11 $\pm$ 1.8	31 $\pm$ 3.2	***
			Abaxial	48 $\pm$ 4.0	80 $\pm$ 5.1	40 $\pm$ 3.6	3 $\pm$ 1.1	41 $\pm$ 3.7	**
<i>T. andrieuxii</i> (Mez) L. B. Sm.	V	C ₃	Adaxial	43 $\pm$ 1.7	59 $\pm$ 4.4	25 $\pm$ 2.9	10 $\pm$ 1.8	19 $\pm$ 2.5	*
			Abaxial	48 $\pm$ 4.0	67 $\pm$ 4.7	36 $\pm$ 3.4	16 $\pm$ 2.3	39 $\pm$ 3.6	**
<i>T. caput-medusae</i> E. Morren	V	CAM	Abaxial	18 $\pm$ 1.2	58 $\pm$ 4.4	23 $\pm$ 2.8	9 $\pm$ 1.8	31 $\pm$ 3.2	*
<i>T. concolor</i> L. B. Sm.	IV-V	CAM	Adaxial	57 $\pm$ 6.2	72 $\pm$ 4.9	6 $\pm$ 1.4	12 $\pm$ 2.0	16 $\pm$ 2.3	n.s.
			Abaxial	58 $\pm$ 3.7	76 $\pm$ 5.0	18 $\pm$ 2.5	4 $\pm$ 1.2	17 $\pm$ 2.4	*
<i>T. cryptantha</i> Baker	IV	CAM	Adaxial	27 $\pm$ 1.2	62 $\pm$ 4.5	9 $\pm$ 1.8	39 $\pm$ 3.6	31 $\pm$ 3.2	n.s.
			Abaxial	25 $\pm$ 0.6	63 $\pm$ 4.6	11 $\pm$ 1.9	25 $\pm$ 2.9	33 $\pm$ 3.3	n.s.
<i>T. cyanea</i> Linden ex K. Koch	IV	C ₃ -CAM	Adaxial	48 $\pm$ 3.6	36 $\pm$ 3.4	1 $\pm$ 0.5	31 $\pm$ 3.2	31 $\pm$ 3.2	n.s.
var. <i>cyanea</i>			Abaxial	38 $\pm$ 2.0	40 $\pm$ 3.6	2 $\pm$ 0.9	10 $\pm$ 1.9	14 $\pm$ 2.2	n.s.
<i>T. mitlaensis</i> W. Weber & Ehlers	V	—	Abaxial	22 $\pm$ 0.9	83 $\pm$ 5.2	27 $\pm$ 3.0	11 $\pm$ 1.9	30 $\pm$ 3.1	*
<i>V. barclayana</i> (Baker) L. B. Sm.	IV-V	C ₃ -CAM	Adaxial	60 $\pm$ 7.1	49 $\pm$ 4.0	4 $\pm$ 1.1	37 $\pm$ 3.5	45 $\pm$ 3.9	n.s.
var. <i>barclayana</i>			Abaxial	60 $\pm$ 4.4	53 $\pm$ 4.2	8 $\pm$ 1.6	14 $\pm$ 2.1	17 $\pm$ 2.4	n.s.

pixels. Blocks that were optimally focused within each focal series were identified by standard deviation parameters and then combined to form a final montage. For investigation of trichome density, low-magnification images were taken of adaxial and abaxial surfaces of leaves from four replicate plants. For species with attenuated trichome wings, difficulty in discerning positions of individual trichomes was avoided by removing the wings with sticky-back plastic and counting the remaining trichome caps or stalks within a specified area.

Water Vapor Condensation on Leaf Surfaces

Condensation of water vapor on leaf surfaces was induced by passing a humid air stream over the leaf, viewed simultaneously by microscopy. Breath from the microscope operator (33°C, >99% relative humidity [RH]) was delivered to the leaf surface via a length of 5 mm bore butyl tubing at a rate of 0.2–0.3 L min⁻¹, as determined by rotometer (GEC-Elliott Ltd., Chelmsford, UK). Ambient laboratory conditions were 20°C and 48% RH, with leaves equilibrated to these conditions for several hours before observations were made. Images were captured at intervals of approximately 4 sec (dependent on automatically determined exposure times) by Image Pro Plus, with 30 to 50 images combined in sequence to produce time-lapse movies of condensation on leaf blade surfaces.

RESULTS

Reflectance of visible light from intact leaves of the study species ranged from 36% for *Tillandsia cyanea* (adaxial surface, ecophysiological Type IV) at one extreme to 83% for *T. mitlaensis* (abaxial surface, Type V; Table 1). The proportion of visible light reflected by trichomes only was 1–11% for Type IV *T. cryptantha* and *T. cyanea* and the intermediate Type IV-V life form of *V. barclayana*. This did not reduce the magnitude of photodamage following exposure to intense light for one hour, as denoted by a decline in dark-adapted F_v/F_m compared between intact and denuded surfaces (Table 1). Trichomes of the adaxial surface of Type IV-V *T. concolor* similarly reflected only 6% of incident light, which did not photoprotect the leaf. However, trichomes on abaxial surfaces of this species reflected 18%, significantly reducing photodamage ($P \leq 0.05$), as did abaxial (40%) and adaxial (27%) reflectance from trichomes of Type IV-V *T. albida* ($P \leq 0.01$ and $P \leq 0.001$, respectively; Table 1). High reflectances were recorded for Type V species, which also significantly photoprotected leaves (i.e., 23–36%; *T. andrieuxii*, *T. caput-medusae*, and *T. mitlaensis*; Table 1). Trichome layers of Type IV-V and Type V species were variable in densities with respect to Type IV species (Table 1).

The reflectance of visible light from the abaxial surfaces of the bromeliads studied was directly proportional to the degree of photoprotection conferred (denoted by the decrease in F_v/F_m vs. reflectance; $y = 0.8244x - 0.8155$, $r^2 = 0.9$, $P = 0.003$; Fig. 3). High reflectivity was not dependent on trichome density per se. For example, relatively low densities of trichomes were associated with high reflectivity and photoprotection for *T. caput-medusae* and *T. mitlaensis* (18 ± 1.2 and 22 ± 0.9 trichome stalks mm⁻², re-

Fig. 3.—The relationship between percent reflectance of visible light by trichomes and photoprotection (the extent of decline in F_v/F_m circumvented by trichomes of intact surfaces, compared to denuded surfaces) for abaxial leaf blade surfaces of *Tillandsia albida* (*T. alb.*), *T. andrieuxii* (*T. and.*), *T. caput-medusae* (*T. c.-m.*), *T. concolor* (*T. con.*), *T. cryptantha* (*T. cry.*), *T. cyanea* (*T. cya.*), *T. mitlaensis* (*T. mit.*), and *Vriesea barclayana* (*V. bar.*).

spectively, cf. 60 ± 4.4 stalks mm⁻² for low-reflectivity *V. barclayana*; Table 1).

Photomicrographs of trichome structure and the indumentata of abaxial leaf blade surfaces for each species are presented in Fig. 4–16. The trichome wings of *T. albida* and *T. concolor* have multifaceted surfaces that reflect light (Fig. 4, 8, 12), with the extensive wing of *T. albida* conferring the greatest reflectivity and photoprotection of any species studied (Table 1). Such faceted wing surfaces were not apparent for the other species studied, with reflection from trichomes of *T. andrieuxii*, *T. caput-medusae*, and *T. mitlaensis* occurring along the edges of the radial cells that comprise the wing (Fig. 6, 11, 13). These trichome wings are elongated along a single axis, inclined away from the leaf surface.

For *T. caput-medusae* and *T. mitlaensis* low-trichome densities and erect trichome wings expose underlying epidermis on which condensation readily occurred and from which trichomes became wetted. (Note that no condensation was observed on trichome wings; Fig. 13, 14; time-lapse movie images are available on request). For species with immobile, flattened, plate-like trichomes, it was possible to induce condensation on the trichome wings (e.g., *T. albida*; Fig. 15, 16), but considerable time was required, even at the extreme air temperature and humidity differences imposed in the present study, compared to the almost instantaneous condensation occurring on the smooth cuticles of *T. cryptantha* and *T. cyanea* (data not shown).

DISCUSSION

The trichome wings of gray-leaved *Tillandsia* spp. reflect enough light to protect photosystem II against intensities equivalent to full sunlight. However, high reflectivity results from different trichome structures and arrangements for each life form. The Type V life form of *T. caput-medusae* has a relatively sparse covering of trichomes, but the individual trichome shields are large and the wings extend almost per-

Fig. 4–11.—Photomicrographs of trichome layers on abaxial leaf blade surfaces digitally enhanced to increase apparent depth of field.—4. *Tillandsia albida*.—5. *Vriesea barclayana*.—6. *T. andrieuxii*.—7. *T. caput-medusae*.—8. *T. concolor*.—9. *T. cryptantha*.—10. *T. cyanea*.—11. *T. mitlaensis*.

Fig. 12.—Photomicrograph of an isolated multifaceted trichome of *Tillandsia albida*, digitally enhanced to increase apparent depth of field.

pendicular to the leaf surface. This photoprotects the leaf, but also allows leaf ventilation and the condensation of water vapor on the underlying cuticle, and thus in its liquid form, the water ultimately wets the trichomes (time-lapse movies available on request). Similar trichome configurations also allow condensation on the cuticle of *T. mitlaensis* and condensation readily occurs on the smooth surfaces of mesomorphic Type IV *T. cyanea* and *T. cryptantha*. (Note that these species bear trichomes with small, immobile shields that lay flat against the leaf surface.)

Leaves of epiphytes are cooler than the surrounding air during the night and part of the day due to evaporative cooling (S. Pierce unpubl. data). In contrast, the slender, erect trichome wings of *T. caput-medusae* have a higher surface area to mass ratio than the succulent leaves and lack cell contents; trichome temperature will probably track air temperature more rapidly than will the leaf temperature. Thus, in nature, dew probably forms on the cooler cuticle rather than the trichome wing, as observed here in the laboratory (i.e., the cuticle, not the trichome wing, is the nucleus for dew formation; Fig. 14). At its simplest, attenuation of the trichome wing can thus be considered a tradeoff between photoprotection and water acquisition from dew formation, potentially of critical importance for Type V species that have no significant water-impoundment capacity or absorptive roots. Indeed, for epiphytes that may endure long, dry seasons in exposed situations without access to soil water (and thus cannot rely on evaporative cooling) alternative methods of regulating leaf energy balance are of critical importance. Trichome layers with a greater reflectance of incident visible light also reflect infrared wavelengths (e.g., *Pitcairnia integrifolia* Ker Gawl.; Pierce et al. 2001) and reflection of visible light will reduce the need for radiation-

Fig. 13–16.—Condensation on representative abaxial leaf blade surfaces of *Tillandsia* species.—13–14. *T. caput-medusae*.—13. Dry.—14. With condensation forming on the leaf cuticle.—15–16. *T. albida*.—15. Dry.—16. With condensation forming on the trichome wing. Arrows denote the position of example droplets of liquid water. These images are frames from time-lapse movies presented at The Third International Conference on the Comparative Biology of the Monocotyledons (available on request).

less energy dissipation (i.e., the conversion of excess light to heat), thus also cooling the leaf. This is evident as leaf temperatures increase in full sunlight when trichomes are removed from *T. circinnata* Schltdl. (Benzing 1976).

However, interpretation of attenuated trichomes as an adaptation to mediate leaf energy balance may be complicated by further trichome-mediated phenomena. A number of Type V species with attenuated trichomes are native to cloud forests and foggy deserts (e.g., *T. plumosa* Baker, *T. tectorum* E. Morren; D. H. Benzing pers. comm.), including *T. andrieuxii* investigated in the present study (Smith and Downs 1977). Wet trichomes hold a film of water over the stomata and impede gas exchange (Benzing et al. 1978; Pierce et al. 2001, 2002a). However, the present study demonstrated that inclined, attenuated trichome wings allow ventilation of the underlying leaf surface; this could facilitate drying in moist habitats and attenuated trichome wings potentially wick water away from the stomata. (Note that trichomes are attenuated only on the abaxial surfaces of hypostomatic *T. andrieuxii* and a moist habitat is reflected in its use of C_3 photosynthesis; Table 1.) Additional selection pressures, which shape the structure and function of trichomes for particular species, are detailed by Benzing (2000).

In contrast to Type V bromeliads, the intermediate Type IV-V life forms of *T. albida* and *T. concolor* possess rudimentary phytotelmata formed by leaf sheaths. Indeed, difficulty in inducing condensation, even with the extreme air/leaf temperature differential generated in the laboratory, suggests that in nature dew formation would not occur readily

on the indumenta of these species. Trichomes of *T. albida* form a dense layer with trichomes flattened even when dry (but still exhibiting limited hygroscopic movement) and with the extensive trichome wing decorated with concave dimples. These dimples produce a multifaceted surface that scatters incident light, thus providing the greatest reflectivity and photoprotection of any species investigated in the present study. Multiple concave facets provide additional surface area from which light is scattered, thus amplifying reflection from each trichome. Trichome wings are thick enough that the probability of reflection is equal for photons of all wavelengths (i.e., there is no iridescence; Feynman 1985) with reflected light exhibiting the same spectral composition as incident light. Similar trichome ornamentation was also evident for *T. concolor*, explaining the high reflectivity of this species despite its relatively small trichome wings. Indeed, the eight species investigated here exhibited diverse trichome wing architecture. With over 530 species of *Tillandsia* currently described (Luther 2002) and many varied life forms evident, it is likely that other light-reflecting structures and photoprotective strategies are also present within the genus. For instance, trichome wings of *T. karwinskyana* Schult. f. appear to be papillose and also catch the light (Benzing 2000).

Trichome layers are typically more prominent on the underside of leaf blades of the more primitive bromeliads, possibly to reduce transpiration (Benzing 2000) or, being water repellent, to keep stomata clear of excess water and dirt (Pierce et al. 2001). A propensity for larger trichome wings on the underside of the leaf, providing greater photoprotection for erect, more delicate, expanding leaves, may have favored the relatively upright and in-rolled leaf blades of many Type V Bromeliaceae, such as *T. caput-medusae* and *T. mitlaensis*. Thus, an erect and in-rolled morphology could be considered part of the photoprotective strategy. *Tillandsia bulbosa* Hook. has retained the in-rolled leaves typical of this life form, but not the same trichome structure, with reflectance lost as an adaptation to darker cloud forest habitats (Benzing 1980, 2000; Pierce et al. 2002a).

While trichomes of species such as *T. albida* and *T. caput-medusae* have adaptations to extremely high light, a continuum of reflectance and photoprotection is apparent for the tillandsioid trichome. Indeed, light-response analysis of *V. barclayana* indicates that even trichomes of this species modify instantaneous photosynthesis at moderate light intensities (i.e., shade the leaf and decrease both electron transport and nonphotochemical chlorophyll fluorescence quenching; S. Pierce unpubl. data), but do not prevent photodamage at high light intensities (Table 1). Trichomes, in general, are thus detrimental in terms of light capture for photosynthesis. However, trichomes throughout the subfamily share common structural and functional features essential to water and nutrient uptake and hence the epiphytic habit. The smaller number of species that have additional structural adaptations to high light therefore represent the extreme of adaptive radiation; trichomes have an inherent reflectivity that has become more pronounced during radiation into exposed niches.

To conclude, the trichomes of gray- or white-leaved *Tillandsia* exhibit adaptations in structure (wing attenuation or facets, respectively) that reflect enough light to help protect

the photosynthetic apparatus against full sunlight, whereas the lesser reflectance by trichomes of mesomorphic Type IV life forms does not and indeed is characteristic of species endemic to shaded habitats. Trichome attenuation for Type V species represents a trade-off between photoprotection and leaf ventilation that allows water acquisition via dew formation on the cooler underlying cuticle for species occupying exposed xeric niches. For Type IV-V species that are hydrated from phytotelmata and have smooth, white leaf blade surfaces, high light intensity appears to have been the overriding selection pressure acting on trichome wing architecture; these trichome wings are multifaceted and thereby extremely reflective.

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