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## Ecophysiology of leaf trichomes

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1 **Ecophysiology of leaf trichomes**

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## 29 **Abstract**

30 This review examines how leaf trichomes influence leaf physiological responses to abiotic  
31 environmental drivers. Leaf trichomes are known to modulate leaf traits, particularly radiation  
32 absorptance, but studies in recent decades demonstrate that trichomes have a more expansive role  
33 in the plant-environment interaction. Although best known as light reflectors, dense trichome  
34 canopies modulate leaf heat balance and photon interception, and consequently affect gas  
35 exchange traits. Analysis of published studies shows that dense pubescence generally increases  
36 reflectance of visible light and near-infrared and infrared radiation. Reflective trichomes are also  
37 protective, reducing photoinhibition and UV-B related damage to leaf photochemistry. Little  
38 support exists for a strong trichome effect on leaf boundary layer resistance and transpiration, but  
39 recent studies indicate they may play a substantive role in leaf water relations affecting leaf  
40 wettability, droplet retention and leaf water uptake. Different lines of evidence indicate that  
41 adaxial and abaxial trichomes may function quite differently, even within the same leaf. Overall,  
42 this review synthesizes and reexamines the diverse array of relevant studies from the past 40  
43 years, illustrating our current understanding of how trichomes influence the energy, carbon and  
44 water balance of plants, and highlighting promising areas for future research.

45

46 **Keywords:** leaf hairs, pubescence, energy balance, reflectance, boundary layer, gas exchange

47

## 48 **Introduction**

49 Trichomes are a morphologically diverse array of epidermal appendages that serve many  
50 functions and occur on numerous plant organs. Structurally, trichomes may be unicellular or  
51 multicellular, and are classified as either glandular or non-glandular (reviewed in Werker 2000).  
52 Glandular trichomes often house and secrete defensive compounds (Wagner *et al.* 2004), but  
53 both trichome types play a role in plant defense against herbivores and pathogens (e.g. Allen *et*  
54 *al.* 1991; Wagner 1991; Hanley *et al.* 2007; Stavrianakou *et al.* 2010). However, trichomes are of  
55 interest across a broad array of disciplines including phylogenetic analysis (Beilstein *et al.* 2008)  
56 and as a model system for studying cell differentiation (Szymanski *et al.* 2000; Yang and Ye  
57 2013). For the study of leaf physiological traits, trichomes, and the pubescent layers they form,  
58 are perhaps best known as light reflectors (Ehleringer *et al.* 1976), and have long been thought to  
59 be important in modulating leaf boundary layer dynamics (Haberlandt 1928). However, this

60 long-standing view has been appended in recent decades, illustrating the impact of these  
61 common leaf features on leaf heat balance and gas exchange. New data reveal their importance  
62 in protecting against damaging ultraviolet (UV) radiation and modulating water relations on leaf  
63 surfaces and in the mesophyll.

64 Leaf trichome density is variable, and determined by genetic and environmental factors  
65 (Walker and Marks 2000). Climate drivers such as soil water deficit, high air temperature and  
66 vapor pressure deficit (VPD) have been shown to increase leaf trichome density (Ehleringer  
67 1982, Shibuya *et al.* 2016). While leaf trichomes are a common feature across terrestrial plant  
68 families, pubescence (a dense trichome layer) has long been associated with xeric-adapted plants  
69 (Schimper 1903; Ehleringer 1984). However, studies on this topic yield mixed results, with some  
70 work showing leaf pubescence increases with aridity (e.g., Kessler *et al.* 2007), some showing  
71 higher trichome densities in plants inhabiting more mesic environments (Martínez-Natarén *et al.*  
72 2011), and others finding no clear climate-pubescence pattern (Levin 1973). Clearly, the  
73 adaptive role of trichomes is not restricted to arid environments and more work on this topic is  
74 needed.

75 Uphof (1962) and Johnson (1975) reviewed 19th and 20th century literature on the  
76 ecological aspects of plant pubescence, but much has been learned about their role in plant  
77 ecophysiology over the last 40 years. This review focuses on leaf trichomes and their influence  
78 in plant-environment interactions that drive leaf physiological processes related to energy,  
79 carbon and water balance. Topics covered include light reflectance and energy balance; UV  
80 protection; leaf wettability and water repellence; leaf water uptake; and gas exchange.

81

## 82 **Light reflectance and energy balance**

83 Leaf trichomes are known to reflect broad-spectrum electromagnetic radiation, reducing light  
84 absorptance and modulating energy balance (Nobel 2005). But because the density of leaf  
85 trichomes varies greatly, their impact on leaf absorptance varies greatly from a moderate  
86 reduction (c. 9% in *Tussilago farfara*, Eller and Willi 1977) to a substantial reduction (c. 40%  
87 lower absorptance in densely pubescent *Encelia farinosa*, Ehleringer and Björkman 1978). A  
88 more commonly measured leaf spectral trait, reflectance, is responsible for much of the observed  
89 variability in absorptance. In general, leaf depilation results in a 7% to 10% decrease in leaf  
90 reflectance of visible wavelengths (mean  $\pm$  SE =  $8.2 \pm 0.3\%$ ; Fig. 1), though two studies found a

91 1 – 4% increase in reflectance after leaf depilation (Wuenschel 1970; Peng *et al.* 2015). Leaves  
92 with low trichome density (i.e. 1 – 5 trichomes/mm<sup>2</sup>) may exhibit spectral properties  
93 indistinguishable from glabrous leaves, particularly in photosynthetically active wavelengths  
94 (400 – 700 nm, Gausman and Cardenas 1973). Trichome density must also be considered in the  
95 context of trichome morphology. In *Pachycladon*, closely related taxa exhibited similar trichome  
96 densities, but differences in trichome morphology resulted in different leaf optical properties  
97 between two species (Mershon *et al.* 2015). A third trichome structural trait, trichome length,  
98 also affects light relations. Leaf absorptance declines with increasing trichome length, which  
99 determines the height of the trichome canopy (Ehleringer 1984) and varies with leaf ontogeny  
100 (Woodman and Fernandes 1991).

101         Several studies have described climate-driven variation in trichome patterning and leaf  
102 absorptance. Trichome patterning in several Mojave and Sonoran Desert genera varies along an  
103 aridity gradient, so that leaf reflectance increases with aridity (Ehleringer 1984). In *E. farinosa*  
104 leaf absorptance was lowest in drier regions, as lower water availability shifted the plant energy  
105 dissipation strategy away from evaporative cooling and towards reflective structural features like  
106 trichomes (Ehleringer 1984; Sandquist and Ehleringer 1998). Similarly, *E. farinosa* leaves  
107 formed during the early, moist part of the growing season exhibit much greater absorptance (c.  
108 80% of visible wavelengths) compared with leaves that develop later during drier conditions  
109 (absorptance = c. 52%; Ehleringer and Björkman 1978). The higher reflectivity of densely  
110 pubescent xeric plants cools leaves, but additionally limits photon availability to light harvesting  
111 complexes and reduces photosynthesis (see *Gas exchange*). Moreover, the high reflectivity of *E.*  
112 *farinosa*, which exhibits the lowest known leaf absorptance among North American desert plants  
113 (Ehleringer 1981), is multi-spectral, extending through visible and near-infrared (NIR) spectra  
114 when compared with closely related taxa (Ehleringer 1988). Several, but not all, studies indicate  
115 that trichomes reflect NIR (700 – 1000 nm) and infrared (IR; 1000 – 1350 nm) radiation at levels  
116 comparable to visible light (2 – 12%; Table 1). Because this spectral range includes water  
117 absorption bands (e.g., 970 nm and 1200 nm), better understanding of trichome effects on  
118 reflectance in NIR and IR spectra is needed to improve interpretation of plant water status from  
119 remote sensing products (Jones and Vaughan 2010).

120         As reflectors of broad-spectrum radiation, trichomes can play a physiologically  
121 significant role in modulating energy balance. Leaves in hot, exposed environments can regulate

122 heat balance via transpirational cooling, which requires an adequate water supply, or through  
123 reduced leaf absorptance as described above (Ehleringer and Mooney 1978). In the well studied  
124 *Encelia* system, a clear ecological gradient exists whereby pubescent *E. farinosa* relies on  
125 reflective trichomes to modulate leaf temperature while nearby glabrous *E. frutescens* plants  
126 regulate leaf temperature through higher stomatal conductance and the associated latent heat  
127 exchange (Ehleringer 1988). Indeed, deprived of its normal pubescence through natural  
128 mutation, a single glabrous *E. farinosa* mutant was found to utilize high leaf conductance to  
129 maintain physiological temperatures (Ehleringer 1983). However, Ripley *et al.* (1999) found  
130 higher leaf temperatures in densely pubescent *Arctotheca populifolia* leaves, positing that this  
131 pubescence contributed to reduced stomatal conductance and latent heat loss. Similarly,  
132 Wuenscher (1970) used an energy balance approach to show that the dense pubescence of  
133 *Verbascum thapsus* reduced latent heat loss and warmed leaves by 3°K compared with depilated  
134 leaves, while Peng *et al.* (2015) found pubescent leaves were *c.* 1 – 3°K warmer than depilated  
135 alpine *Eriophyton wallichii* leaves. Modelling indicated that long trichomes would elevate leaf  
136 temperatures substantially above ambient air temperatures (*c.* 8°K) in alpine *Espeletia*  
137 *timonensis*, but field measurements showed modest leaf warming in pubescent *Espeletia* leaves  
138 (1 – 3°K; Meinzer and Goldstein 1985). Tsukaya *et al.* (2002) posited that the potential warming  
139 effect of trichomes could be ecologically important in alpine *Saussurea medusa*. They  
140 hypothesized that the dense pubescence of these high mountain plants buffered and warmed  
141 inflorescences, but a later study concluded the dense trichomes of *S. medusa* served primarily to  
142 provide protection from high light intensity rather than to warm tissues (Yang *et al.* 2008). More  
143 study is needed to determine the ecophysiological significance of the trichome-induced warming  
144 observed in the *V. thapsus*, *E. wallichii* and *E. timonensis* systems.

145 Beyond maintaining thermal balance, leaves must contend with damagingly high  
146 photosynthetic photon flux density (PPFD), which can induce photoinhibition. Leaves minimize  
147 photoinhibition by dissipating damagingly high PPFD via biochemistry (e.g. xanthophyll cycle,  
148 Demmig-Adams and Adams 1996) and/or through protective features like reflective trichomes.  
149 Several lines of evidence indicate leaves utilize both strategies. Leaf depilation resulted in  
150 greater photoconversion of violaxanthin into zeaxanthin, an indicator of enhanced xanthophyll  
151 cycle activity, following exposure to high light (Lang and Schindler 1994; Lang *et al.* 1995;  
152 Ripley *et al.* 1999). Similarly, Liakopoulos *et al.* (2006) found lower allocation to xanthophyll

153 cycle products in pubescent *Vitis vinifera* leaves. Trichomes may also play an important  
154 protective role during leaf ontogeny. In *Platanus orientalis* dense pubescence occurs in  
155 developing leaves, but is absent in mature ones. Consequently, developing pubescent *P.*  
156 *orientalis* leaves have *c.* 4% lower absorptance compared with similarly young depilated leaves  
157 (Ntefidou and Manetas 1996). The physiological significance of this reflective protection  
158 remains unclear, especially compared with the substantial investment leaves make to grow  
159 trichomes (Karabourniotis *et al.* 1995; Ntefidou and Manetas 1996), but the physical protection  
160 trichomes confer may offset the need for biochemical protection in developing tissues.

161 Finally, because of the normal orientation of leaves, studies have largely focused on  
162 spectral properties of adaxial leaf surfaces although trichomes also occur on abaxial surfaces and  
163 can exhibit conspicuously higher trichome densities than adaxial surfaces. Dense abaxial  
164 pubescence may protect stomata from damaging ultraviolet-B (UV-B) radiation  
165 (Grammatikopoulos *et al.* 1994; see *UV protection* and *Gas exchange*). Additionally, limited  
166 data indicate abaxial leaf trichomes may be important in modulating adaxial spectral properties.  
167 Eller and Willi (1977) posited that abaxial surface hairs reflect transmitted radiation, particularly  
168 NIR and IR radiation, back through the mesophyll and adaxial surface, effectively increasing  
169 adaxial surface reflectance. Data presented in a subsequent paper supported this hypothesis (Eller  
170 1977), but the small sample size ( $n = 1$  leaf) limit the conclusions that can be drawn from the  
171 study. Further studies are needed to validate this hypothesis, which could have important  
172 ramifications for the assessment of photosynthetic light-use efficiency in pubescent taxa.

173

#### 174 **UV protection**

175 Mounting evidence indicates that trichomes play a significant protective role against damaging  
176 UV-B radiation. Trichomes on *Quercus* and *Arctotheca* leaves strongly absorbed UV radiation  
177 and reduced UV-B related damage to photosystem II photochemistry (Skaltsa *et al.* 1994;  
178 Karabourniotis and Bornman 1999; Ripley *et al.* 1999), while trichome absorbance of *c.* 60% of  
179 incident UV-B protected *Olea* leaves from mutagenesis and prevented stomatal closure  
180 (Karabourniotis *et al.* 1992; Karabourniotis *et al.* 1993; Grammatikopoulos *et al.* 1994). This  
181 UV-B protection may be particularly important in developing leaves (Karabourniotis *et al.*  
182 1995). Recently, Yan *et al.* (2012) showed that UV-B exposure stimulated trichome formation in  
183 several *Arabidopsis* lines. Much of this UV protection stems from flavonoid compounds in

184 trichome cell walls and cuticular waxes that confer substantial UV-B protection (Liakopoulos *et*  
185 *al.* 2006). Beyond absorbing and filtering UV spectra, trichome canopies can reflect UV-B  
186 radiation (Holmes and Keiller 2002). Microprobe measurements showed that UV-A and UV-B  
187 radiation were sharply attenuated in the light environment beneath *Olea* and *Quercus* trichome  
188 layers, presumably due to enhanced reflectance (Karabourniotis and Bornman 1999). This UV  
189 protection appears to be dynamic and driven by microclimate, because levels of UV-B protective  
190 compounds and trichome density were correlated with tree canopy position and UV-B exposure  
191 (Liakoura *et al.* 1997). Minimizing exposure to damaging UV-B radiation is important in the  
192 arctic-alpine lifezone (Caldwell *et al.* 1980). Although pubescence is not necessarily indicative  
193 of a high capacity to reflect UV radiation (Robberecht *et al.* 1980), some trichomes may play a  
194 significant protective role in a changing atmosphere. Future work should examine whether  
195 trichomes offset the need for biochemical UV-B protection by conferring physical protection in  
196 environments with high levels of UV-B such as the alpine lifezone.

197

#### 198 **Leaf wettability and water repellence**

199 Water accumulation on leaf surfaces can occlude stomata, limit gas exchange, and promote  
200 pathogen growth and spread on leaves. Consequently, features of the leaf surface vary their  
201 degree of water wettability, droplet retention or repellence. Wettability is determined by the  
202 droplet contact angle with the leaf surface ( $\theta$ ), with  $\theta$  values  $>90^\circ$  being associated with  
203 unwettable surfaces and  $\theta$  values  $<90^\circ$  termed wettable surfaces (Bhushan and Nosonovsky  
204 2010; Fernández and Khayet 2015). In a broad survey, Brewer *et al.* (1991) found leaves with  
205 dense pubescence (*c.* 100 trichomes/mm<sup>2</sup>) exhibited lower wettability ( $\theta = c.$  173°), while leaf  
206 surfaces with medium trichome densities (*c.* 20 trichomes/mm<sup>2</sup>) were more wettable ( $\theta = c.$  73°).  
207 Similarly, Fernández *et al.* (2014a) found intermediate trichome densities (*c.* 59 trichomes/mm<sup>2</sup>)  
208 resulted in lower wettability compared with low trichome densities (*c.* 5 trichomes/mm<sup>2</sup>) on  
209 adaxial surfaces of wheat leaves. Trichomes also play a role in water retention and repellence.  
210 Brewer *et al.* (1991) found that leaves with dense pubescence generally exhibited low droplet  
211 retention, while leaves with medium trichome densities had higher droplet retention. In peach  
212 fruit, trichome surfaces are relatively nonpolar compared with leaf cuticle surfaces, which may  
213 limit interactions between water and densely pubescent surfaces (Fernández *et al.* 2011) and  
214 promote a more water repellent surface. However, numerous leaf surface features influence drop



215 repellence, e.g., surface cuticle chemistry (Fernández *et al.* 2014b). Such leaf water repellency  
216 may be important in modulating abiotic processes, such as stomatal occlusion and gas exchange  
217 (Smith and McClean 1989), or biotic interactions, such as fungal or bacterial growth and spread  
218 on leaf surfaces (Allen *et al.* 1991; Stavrianakou *et al.* 2010). Future studies should further  
219 examine the physicochemical properties of trichomes and elucidate their influence on water-  
220 surface relations.

221         Wettability and droplet retention may differ between pubescent adaxial and abaxial leaf  
222 surfaces. Brewer and Smith (1994) found no differences in wettability of adaxial and abaxial  
223 soybean leaf surfaces, but did observe lower droplet retention on abaxial surfaces in five soybean  
224 (*Glycine max*) isolines that varied greatly in trichome density. In *Quercus ilex*, Fernández *et al.*  
225 (2014b) examined the physicochemical properties of pubescent adaxial and abaxial surfaces and  
226 observed much lower wettability and greater water repellency on abaxial than on adaxial leaf  
227 surfaces. Importantly, this greater hydrophobicity was associated with chemical and structural  
228 differences in abaxial trichomes. While their analysis determined that surface chemistry was the  
229 strongest driver of these water-leaf interactions, trichomes increased surface roughness and  
230 affected wettability. While much remains unclear about physicochemical differences in adaxial  
231 and abaxial trichomes and their respective leaf surfaces, these data indicate that trichomes on  
232 different sides of the same leaf may be functionally different. Specifically, the low droplet  
233 retention observed on abaxial soybean and *Q. ilex* surfaces may limit stomatal occlusion and  
234 promote gas exchange during rainfall or when fog or dew condense on leaf surfaces.

235

### 236 **Leaf water uptake**

237 Beyond their influence on water-leaf surface interactions, trichomes also contribute to plant  
238 water uptake and water balance. Until recently, trichome-mediated uptake of water and other  
239 solutes was only observed in epiphytic bromeliads (e.g. Benzing 1976; Benzing *et al.* 1976).  
240 Trichomes positioned near bromeliad water catchment tanks absorb liquid water, while water  
241 vapor is taken up from the atmosphere by trichomes on distal portions of leaves (Martin 1994). A  
242 survey of ten bromeliad species found trichome water uptake rates between 0.2 - 0.5 mmol kg<sup>-1</sup> s<sup>-1</sup>  
243 <sup>1</sup> as their nocturnal crassulacean acid metabolism (CAM) gas exchange period began, but also  
244 attributed much of their diurnal water leakage to trichome stalks (Benz and Martin 2006).  
245 Similarly, Schmitt *et al.* (1989) observed water uptake during early phases of nocturnal CAM gas

246 exchange in *Tillandsia*, but this foliar (liquid) water uptake did not completely offset water vapor  
247 losses across the diel period (Martin and Schmitt 1989). In contrast, recent work showed that  
248 water vapor uptake by *Tillandsia* trichomes did not contribute to leaf water balance or increase  
249 photosynthetic activity (Martin *et al.* 2013). Trichome water uptake may also have been detected  
250 outside Bromeliaceae. Fernández *et al.* (2014b) found that depositing water drops on adaxial  
251 surfaces resulted in a *c.* 5% increase in leaf water content and 1 MPa increase in xylem water  
252 potential in Mediterranean *Q. ilex* leaves, while water deposition on abaxial surfaces did not  
253 change leaf water status compared with unwatered controls. (Fernández *et al.* 2014b). While  
254 their study could not determine if trichomes were associated with these changes in leaf water  
255 status, they speculated that trichomes or trichome scars may have provided a water entry  
256 pathway into tested leaves. Work by Fahn (1986) showed that trichomes of xeromorphic leaves  
257 had fully cutinized cell walls that were impermeable to a fluorescent tracer, while mesomorphic  
258 leaf trichomes were cutin deficient and exhibited tracer-permeable cell walls. Subsequent studies  
259 have failed to identify more species with tracer-permeable trichomes (e.g. Grammatikopoulos  
260 and Manetas 1994; Burrows *et al.* 2013). However, variability in cutin deposition on trichome  
261 bases could affect water permeability and should be studied further to elucidate the role  
262 trichomes play in foliar water uptake during conditions of fog, dew or rain.

263

## 264 **Gas exchange**

### 265 ***Boundary layer effects***

266 Boundary layer effects on leaf conductance are minor compared with the regulation imposed by  
267 stomata (Nobel 2005). Nevertheless, the influence of trichomes on leaf conductance has been a  
268 long interest (Johnson 1975). Early experimental work by Woolley (1964) showed up to a 40%  
269 windspeed reduction in pubescent soybean leaves when compared to depilated leaves,  
270 presumably due to an enhanced boundary layer in the pubescent leaves. In a similar manner,  
271 Wuenscher (1970) used smoke in wind tunnels to visually inspect airflow over pubescent  
272 *Verbascum* leaves, observing that laminar boundary layers in pubescent and depilated leaves  
273 were similar, but that boundary layer formation in pubescent leaves occurred above the trichome  
274 canopy and their presence effectively thickened the leaf boundary layer. Quantitatively, this  
275 trichome enhancement of the boundary layer was estimated to be  $0.013 \text{ s m}^{-1}$  in pubescent  
276 leaves, or approximately 2x that of depilated leaves ( $0.006 \text{ s m}^{-1}$ ), but only *c.* 1% of stomatal

277 resistance in those same leaves ( $0.989 \text{ s m}^{-1}$ ; Wuenscher 1970; Parkhurst 1976). Other studies  
278 suggest that trichome-induced shifts in boundary layer thickness accounted for 5 - 10% of the  
279 resistance pathway from leaf to atmosphere. Using a gas exchange approach, Ripley *et al.* (1999)  
280 found overall leaf resistance was higher in pubescent *Arctotheca populifolia* leaves ( $2.7 \text{ m}^2 \text{ s}$   
281  $\text{mol}^{-1}$ ) than in similar depilated leaves ( $2.5 \text{ m}^2 \text{ s mol}^{-1}$ ). They used the  $0.2 \text{ m}^2 \text{ s mol}^{-1}$  difference  
282 between pubescent and depilated leaves as an estimate of boundary layer resistance in *A.*  
283 *populifolia*, a value indicative of a relatively thin boundary layer (Nobel 2005). Surveying  
284 numerous bromeliad species, Benz and Martin (2006) estimated that trichomes increased the leaf  
285 boundary layer thickness up to 9.7% but concluded that, in general, the contribution of these  
286 trichome layers to resistance in the mass transport pathway from atmosphere to mesophyll was  
287 minimal.

288         Efforts to model trichome impacts indicate trichome length (height) may be an important  
289 factor in leaf boundary layer dynamics. Using empirical and model data, Ehleringer and Mooney  
290 (1978) estimated that boundary layer resistance in *Encelia* leaves with a 0.35 mm high trichome  
291 layer, while much higher than in glabrous leaves, was negligible compared with resistance  
292 imposed by stomata. However, using a similar modeling approach, Meinzer and Goldstein  
293 (1985) showed that dense, long pubescence (2.5 mm) of *E. timotensis* increased boundary layer  
294 resistance to sensible heat loss substantially (458%) under alpine conditions, potentially warming  
295 leaf tissues (see *Light reflectance and energy balance*). Modeling also revealed that trichomes  
296 were instrumental in regulating flow in the leaf boundary layer (Schreuder *et al.* 2001). Their  
297 models indicated that trichome canopy height strongly affects surface roughness and stimulates  
298 the transition from laminar to turbulent flow, thereby decreasing boundary layer resistance to  
299 water and  $\text{CO}_2$  transport and promoting gas exchange rates. Despite these insights, however,  
300 these modeling studies illustrate a deficiency in our understanding of trichome impacts on  
301 boundary layer dynamics, namely the simplifying engineering assumptions that underlie these  
302 efforts. Models assume leaves are perfectly flat objects, but the complex topography of leaves -  
303 which trichomes contribute to - likely impact surface roughness and airflow patterns in ways that  
304 are difficult to generalize (Schuepp 1993). Topographical modeling or empirical studies using a  
305 biomimetic approach are needed to clarify the impact of these surface features on leaf boundary  
306 layers.

307

308 ***Transpiration, Photosynthesis and Water-Use Efficiency (WUE)***

309 With the exception of water-exchanging trichomes, trichomes impact transpiration,  
310 photosynthesis and WUE indirectly by regulating energy absorptance and boundary layer  
311 thickness (Smith and Nobel 1977; Ehleringer and Mooney 1978). Trichome-induced leaf  
312 reflectance decreases photon availability to light harvesting complexes, resulting in lower  
313 photosynthetic rates. And, as described earlier, reflectance and absorptance vary greatly among  
314 pubescent taxa. In addition to lowering leaf temperatures, thick leaf pubescence reduced  
315 photosynthesis in *Encelia* proportional to the light attenuation imposed by different trichome  
316 canopy densities (Ehleringer *et al.* 1976; Ehleringer and Mooney 1978; Ehleringer and Björkman  
317 1978). In *Olea*, dense abaxial pubescence did not affect photosynthetic rate or stomatal  
318 conductance when exposed to white light, but supplementing white light with UV-B radiation  
319 reduced photosynthesis and stomatal conductance in depilated leaves (Grammatikopoulos *et al.*  
320 1994). Trichome-induced changes in leaf temperature also affect photosynthesis and  
321 transpiration. Trichome mediated cooling allowed *E. farinosa* leaves to maintain near-optimal  
322 temperatures for photosynthesis in hot, arid environments (Ehleringer and Mooney 1978). In  
323 field-grown *Arctotheca populifolia* the warm, depilated leaves showed slightly lower  
324 photosynthetic rate but consistently higher transpiration - conditions consistent with lower WUE  
325 - when exposed to higher PPFD (Ripley *et al.* 1999). Similarly, sun-exposed, depilated *Mallotus*  
326 *macrostachyus* leaves exhibited moderately elevated afternoon transpiration rate and lower WUE  
327 than similar pubescent leaves (Kenzo *et al.* 2008). Dense pubescence could also collect and hold  
328 fog or dew droplets above stomatal pores, reducing the leaf-to-air water potential gradient and  
329 increasing WUE (Brewer *et al.* 1991; Brewer and Smith 1994). At the crop canopy scale,  
330 trichomes reduced evapotranspiration, but not CO<sub>2</sub> exchange, resulting in greater WUE in a  
331 densely pubescent soybean isoline (Baldochi *et al.* 1983). In contrast, trichomes can sometimes  
332 themselves be conducting agents and negatively impact WUE. Water losses from *Tillandsia*  
333 (Bromeliaceae) trichomes accounted for 16% of total water conductance, an extra-stomatal water  
334 loss that contributes to reduced photosynthesis and WUE in these epiphytes (Schmitt *et al.*  
335 1989), though the broader appearance of this phenomenon among pubescent plants remains  
336 unclear.

337

338

339 **Concluding remarks**

340 Much has been learned about the ecophysiology of leaf trichomes in the last 40 years, and recent  
341 developments suggest we may be underestimating the physiological significance of these  
342 conspicuous leaf appendages. The reflectivity of pubescent layers that plant scientists have noted  
343 for nearly a century (e.g. Haberlandt 1928) is now recognized to have demonstrable impacts on  
344 leaf energy balance, with substantial downstream effects on photosynthesis and transpiration  
345 (Ehleringer and Mooney 1978). Little evidence has emerged to indicate trichomes strongly  
346 modulate boundary layer resistance, rather it appears that their influence on leaf energy balance  
347 occurs primarily through their regulation of leaf energy absorptance and leaf conductance. Heat  
348 energy that is deflected does not have to be dissipated via evaporative cooling, minimizing water  
349 loss. Low density trichome canopies have negligible impact on leaf spectral properties and water  
350 relations indicating that their evolutionary role is related to defense, not physiology (Woodman  
351 and Fernandes 1991; Hanley *et al.* 2007). Newly recognized effects, such as the protection leaf  
352 trichomes confer against UV-B radiation and photoinhibition, may prove useful in future crop  
353 development (e.g. Kataria and Guruprasad 2015). Similarly, the recent finding that trichomes  
354 play an important role in leaf-surface water interactions and foliar water status in *Quercus*  
355 (Fernández *et al.* 2014b) should be explored in other plant systems. The ecological significance  
356 of leaf water uptake has gained much attention recently (e.g. Limm *et al.* 2009), and the role  
357 trichomes play in this process should be examined more closely.

358         The functional variation of trichomes on the same leaf also points to new avenues of  
359 research. We now know from two lines of evidence that trichomes on different sides of the same  
360 leaf function differ in their water relations (Brewer and Smith 1994; Fernández *et al.* 2014b).  
361 Through their potential to influence leaf energy gain and water uptake on adaxial surfaces, and  
362 gas exchange on abaxial surfaces, trichomes can exert substantial influence over factors that  
363 drive leaf physiology. And, as we seek incremental advances in functional plant morphology and  
364 crop improvement, better understanding of these trichome traits may be valuable in reaching  
365 those goals.

366

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370

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579 **Table 1.** Change in NIR and IR leaf spectral reflectance post-depilation. For each species, the  
 580 change in reflectance (% difference; depilated - intact trichomes) was calculated at 50 or 100 nm  
 581 increments between 750 - 1350 nm. Standard deviation of the mean (SD) is shown to illustrate  
 582 the relatively low variability in NIR and IR reflectance spectra compared with visible reflectance  
 583 spectra (Fig. 1).

584

Species	Spectral range (nm)	% difference (mean $\pm$ SD)	Source
<i>Verbascum thapsus</i>	750 - 1300	-0.2 $\pm$ 0.3	Wuenschel 1970
<i>Tussilago farfara</i>	750 - 1350	-2.6 $\pm$ 1.6	Eller & Willi 1977
<i>Tussilago farfara</i>	800 - 1300	-8.4 $\pm$ 0.6	Eller 1977
<i>Encelia farinosa</i>	750 - 800	-12.5 $\pm$ 2.1	Ehleringer & Bjorkman 1978
<i>Aechmea dactylina</i>	750 - 850	1.0 $\pm$ 0.0	Pierce et al. 2001
<i>Ananas comosus</i>	750 - 850	1.7 $\pm$ 0.6	Pierce et al. 2001
<i>Pitcairnia integrifolia</i>	750 - 850	-7.7 $\pm$ 0.6	Pierce et al. 2001
<i>Catopsis micrantha</i>	750 - 850	-3 $\pm$ 0.0	Pierce et al. 2001
<i>Saussurea medusa</i>	750 - 800	-5.4 $\pm$ 0.5	Yang et al. 2008

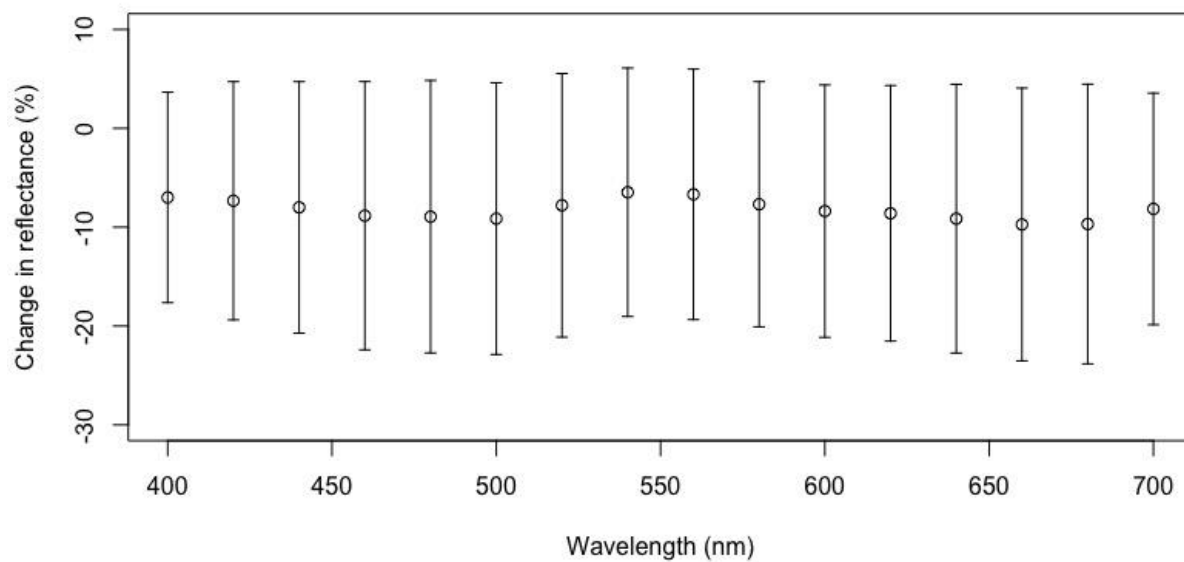
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587 **Figure caption**

588 Figure 1. Change in adaxial leaf reflectance of visible spectrum radiation after leaf depilation.  
589 Reflectance spectra pre- and post-depilation were extracted from the literature (*Verbascum*  
590 *thapus*, Wuenschel 1970; *Tussilago farfara*, Eller and Willi 1977; *Encelia farinosa*, Ehleringer  
591 and Björkman 1978; *Platanus orientalis*, Ntefidou and Manetas 1996; *Aechmea dactylina*,  
592 *Ananas comosus*, *Pitcairnia integrifolia*, *Catopsis micrantha*, Pierce *et al.* 2001; *Saussurea*  
593 *medusa*, Yang *et al.* 2008; *Eriophyton wallichii*, Peng *et al.* 2015). Reflectance data for *E.*  
594 *farinosa* were calculated from absorptance data presented in Ehleringer and Björkman (1978),  
595 and assume that leaf transmittance was negligible. For each species, the change in reflectance  
596 (depilated - intact trichomes) was calculated at 20 nm increments between 400 - 700 nm, the  
597 most commonly reported spectrum. Mean change in reflectance was calculated at each  
598 wavelength interval by incorporating the reflectance data from all species listed above. Means  
599 summarize the range of species-specific changes in reflectance patterns observed after leaf  
600 depilation including *E. wallichii* ( $+2.1 \pm 0.5\%$ ; mean  $\pm$  1 SE) and *E. farinosa* ( $-42.3 \pm 0.3\%$ ).  
601 Bars represent  $\pm$ 1 SD of the mean, and illustrate the range of spectral reflectance observed in  
602 pubescent leaves.  
603

604 **Figure**  
605



606  
607 **Figure 1**