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Spectral properties, gas exchange, and water potential of leaves of glandular and non-glandular trichome types in *Datura wrightii* (Solanaceae)

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Abstract. Plant trichomes commonly serve a role in mechanical and chemical defence against herbivores, but may also have the potential to alter physiology by reducing the amount of light absorbed by leaves, lowering temperatures, and reducing water loss. Populations of *Datura wrightii* Regel in southern California produce ‘sticky’ plants with glandular trichomes and ‘velvety’ plants bearing non-glandular trichomes. Because stickiness is inherited as a dominant Mendelian trait, and the proportions of sticky plants vary among populations with the moisture availability of their environment, there may be some ecophysiological differences between trichome types that contribute to their ability to survive in a particular geographic location. To examine the possible physiological significance of trichome variation, we measured the spectral properties, midday gas-exchange rates, and water potentials of *D. wrightii* leaves from sticky and velvety plants growing in a field experiment. The differences in leaf reflectance (0.9%) and absorptance (1.3%) of photosynthetically active radiation (PAR) between trichome types are too small to have any direct physiologically significant effect. Simulations of leaf temperatures based on the difference in leaf absorptances reveal that leaf temperature would be no more than 1°C lower in velvety compared to sticky plants. Gas-exchange measurements revealed no significant difference between types in their transpiration rates or stomatal conductances. In this case, trichome variation may be more important to plant defenses than to physiology.

Keywords: herbivore resistance, leaf reflectance, photosynthesis, transpiration, water relations.

Introduction

Plant characteristics that confer resistance to herbivores are sometimes accompanied by direct and indirect costs to the plant (Strauss *et al.* 2002; Koricheva 2002). *Datura wrightii* plants possessing glandular trichomes, known as ‘sticky’ plants, are protected from some herbivorous insects (van Dam and Hare 1998; Hare and Elle 2002). All plants begin producing only glandular trichomes as young seedlings, but by the age of approximately 6 weeks ‘velvety’ plants have begun producing 99% non-glandular trichomes while sticky plants continue to produce a variety of glandular trichomes (van Dam *et al.* 1999). Trichome density of velvety plants (approximately 240 trichomes mm⁻²) is more than twice that of sticky plants (approximately 100 trichomes mm⁻²). Height of the dominant trichome variety on velvety plants (approximately 0.17 mm), is just over half that of sticky plants (approximately 0.31 mm), and the height of the trichomes is much more variable on sticky plants with some reaching

nearly 1.5 mm in length. Leaf ‘stickiness’ is inherited as a simple, dominant Mendelian trait (van Dam *et al.* 1999). Although the resultant herbivore resistance would seem to be beneficial, the costs of producing sticky leaves are significant. When protected from herbivores, the viable seed production of sticky plants is 45% lower than that of velvety plants, and even in the presence of herbivores their fitness is lower (Elle *et al.* 1999; Elle and Hare 2000; Hare *et al.* 2003; Hare and Elle 2004). The frequency of the two trichome types varies among populations with sticky plants being less abundant or absent in more arid areas but more abundant in some cooler, moister coastal populations (Hare and Elle 2001).

The geographic variation in the abundance of the trichome types in *D. wrightii* populations suggests that differentially beneficial effects, other than herbivore resistance, may exist. For example, Woodman and Fernandes (1991) demonstrated that trichomes in *Verbascum thapsus* L. function both in herbivore defence and in reducing

Abbreviations used: *A*, net assimilation; *E*, transpiration; NIR, near infrared radiation; PAR, photosynthetically active radiation; PPFD, photosynthetic photon flux density; S, sticky; V, velvety; WUE, water use efficiency.

transpiration. In many species dense leaf hairs are beneficial because they reflect light and thus, shade the leaf, which reduces temperature and water loss, rather than significantly increasing the boundary layer (Ehleringer 1983). Sandquist and Ehleringer (1997, 1998) reported that *Encelia farinosa* Gray ex. Torr plants from drier habitats had greater pubescence; plants with more pubescence were able to retain their leaves longer into periods of drought and tended to have lower leaf light absorbance, stomatal conductance and photosynthetic rates.

In this study, we examined spectral properties, midday gas-exchange rates, and water potentials of leaves of sticky and velvety *D. wrightii* plants growing in an experimental population to determine whether there may be ecophysiological differences that could contribute additional costs or benefits to the production of glandular trichomes and help explain the geographic variation in their abundance. There are at least two ways that trichomes may directly affect the physiology of the two types. Firstly, if water is lost as glandular trichome exudate then sticky plants may be subjected to increased water-stress that could be measured by differences in transpiration or leaf water potential. Secondly, if non-glandular trichomes reflect enough light to shade velvety plants then they may experience lower leaf temperatures, resulting in differences in gas-exchange rates. Trichomes may further contribute to temperature differences by conducting heat from the leaf surface and by contributing to boundary layer depth and stability. An understanding of the role that variation in trichome morphology has on leaf physiology permits a comparison of trichomes as physiological *v.* defensive adaptations in *D. wrightii*.

Materials and methods

Datura wrightii Regel is a perennial plant native to California and found elsewhere in North America growing in sandy or disturbed areas (Nee 1993). The plants used in this study were growing in an experimental plot at the University of California Riverside Agricultural Experiment Station (33.9654° N, 117.3452° W, 298.7 m above sea level). Three full-sib families were derived from crosses between parent plants from three different local populations to control for genetic variation in an ongoing competition study. Only plants growing in the herbivore-protected, low-density groups with plants 5 m apart, less than one third of their density in natural populations, were included in this study.

The growing season for the *D. wrightii* in this southern California site ranges from about February to December. This study was conducted towards the second half of the growing season (August–November) in 2002, after a period of considerable heat and drought. Leaf spectral properties were measured in August, diurnal leaf water potential was measured in September, and midday (1000–1400 hours) gas-exchange rates were measured on six dates from September to November 2002. Mean (\pm standard deviation) monthly maximum and minimum temperatures during the study were $34.0 \pm 3.4^\circ\text{C}$ and $15.2 \pm 1.6^\circ\text{C}$ for August, $34.2 \pm 5.9^\circ\text{C}$ and $15.5 \pm 2.6^\circ\text{C}$ for September, and $25.3 \pm 5.3^\circ\text{C}$ and $11.2 \pm 1.9^\circ\text{C}$ in October. Plants received only 81 mm of rainfall during the 2001–2002 rainy season and virtually none after 26 April 2002. Total monthly precipitation during the study was 0 mm in August, 0.5 mm in September, and 1.0 mm in October.

In August 2002, the spectral properties of leaves from plants growing in the field plots were measured in the laboratory with an LI-1800 portable spectroradiometer and an 1800 12S external integrating sphere (LI-COR, Lincoln, NE). One leaf was taken from each of 27 sticky and 22 velvety plants from among the three different families. For each sample, reflectance, transmittance, and absorbance were calculated from measured values and integrated at 50-nm intervals over the PAR wavelengths of 400–700 nm and over the near infrared radiation (NIR) wavelengths of 750–1100 nm. Integrated values were analysed by a two-factor (type by family) ANOVA using the PROC GLM procedure of the SAS/STAT statistical software (SAS Institute 1989) after log-transforming the data to ensure normality. In this analysis, type was a fixed effect and family was a random effect. When interactions were not statistically significant, the interaction mean square was pooled with the error mean square when appropriate (Sokal and Rohlf 1995). Mean squares for the interaction and overall error in the ANOVA were pooled for reflectance, transmittance, and absorbance of PAR and for reflectance of NIR (Sokal and Rohlf 1995).

Midday gas-exchange measurements of sticky and velvety plants were obtained using the TPS-1 portable photosynthesis system (PP Systems, Amesbury, MA) with flow rate ($300 \text{ cm}^3 \text{ min}^{-1}$), pressure (100 kPa), and leaf area (6.30 cm^2) which was set the same for all measurements. A random sample of sticky and velvety plants was taken from among the different families growing in the field experiment. The measurements of three leaves were averaged together for each plant sampled. The number of different plants sampled for gas-exchange measurements of sticky (S) and velvety (V) *D. wrightii* on the dates sampled were as follows: on 11 September S = 11, V = 13; on 17 September S = 5, V = 4; on 11 October S = 6, V = 6; on 29 October S = 6, V = 4; on 30 October S = 7, V = 7; and on 4 November S = 9, V = 7. Water use efficiency (WUE) was calculated as the ratio of net assimilation (*A*) to transpiration (*E*). The calculated gas-exchange rates were analysed by a two-way ANOVA (type \times date). The transpiration rate was square-root transformed and WUE and stomatal conductance were log-transformed to ensure normality. The photosynthetic photon flux density (PPFD) and temperature data were non-normal, and no transformation met the assumption of normality, so these variables were analysed by the Scheirer–Ray–Hare (χ^2) test (Sokal and Rohlf 1995), a non-parametric analogue of the two-way ANOVA.

In September 2002, leaf water potentials (Ψ_{lf}) of plants growing in the field plot were measured with a Model 610 pressure chamber instrument (PMS Instrument Co., Corvallis, OR). Leaf water potential was measured at 2–3-h intervals from one leaf from each of five sticky and five velvety plants throughout the day starting at 0600 hours and ending in the late afternoon. Measurements of Ψ_{lf} for sticky and velvety plants were compared using a repeated-measures ANOVA of the PROC GLM procedure (SAS Institute 1989), treating type as a fixed effect and time as the repeated variable.

To compare the measured values of gas exchange with theoretical expectations based on the measured spectral properties of the leaves, leaf temperature and transpiration were simulated by the equation of Miller (1972) as described by Ehleringer (1989) and written in the file Tleaf2.xls (Sousa 2003). Using parameters given in the program and adjusting others (Appendix 1) to match known conditions recorded by the California Irrigation Management Information System at the Agricultural Experiment Station it was possible to estimate expected leaf temperature and transpiration differences between the conditions in the leaf cuvette and ambient for the different absorbances of sticky and velvety leaves.

Results

The leaf spectral properties (Fig. 1, Table 1) differed statistically between the types in the PAR but not the NIR wavelengths. In comparison with sticky plants, velvety

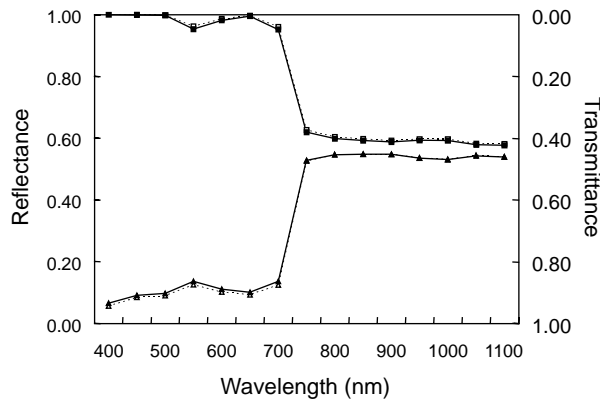


Fig. 1. Mean reflectance (triangles) and transmittance (squares) of sticky (open symbols) and velvety (closed symbols) leaves of *D. wrightii* in August 2002 in the PAR and NIR spectra (400–700 nm and 750–1100 nm, respectively). Error bars are not shown, and the standard deviation is < 0.02 for each plotted value.

leaves in the PAR wavelengths had a lower mean absorptance ($86.8 \pm 1.5\%$ v. $88.1 \pm 1.3\%$), a higher reflectance ($11.2 \pm 1.5\%$ v. $10.3 \pm 1.2\%$) and a higher transmittance ($2.0 \pm 0.6\%$ v. $1.5 \pm 0.4\%$). For NIR wavelengths, the absorptance, reflectance, and transmittance averaged over types were $5.9 \pm 2.0\%$, $54.1 \pm 1.2\%$, and $40.0 \pm 2.8\%$, respectively. There was a significant difference between the families only in their PAR transmittance, which ranged from $1.48 \pm 0.36\%$ to $1.95 \pm 0.55\%$.

Water use efficiency was 11.2% higher for sticky plants; however, there was also an interaction between type and date (Fig. 2, Table 2). On 30 October the mean WUE of sticky plants was $4.92 \pm 0.25 \mu\text{mol mmol}^{-1}$ or 11.82% higher than that of velvety ($t=2.88$, $df=12$, $P<0.05$). WUE was similar between the types on hot, sunny days, but on the days with lower PPFD and temperatures, sticky plants tended to have higher WUE. Stomatal conductance and E did not differ significantly between the two types on the days sampled. Overall, the mean A was significantly higher for sticky plants

(Fig. 2, Table 2). Although A was virtually identical for sticky and velvety plants on the first and last dates, the mean A for sticky plants ($12.07 \pm 2.09 \mu\text{mol m}^{-2} \text{s}^{-1}$) was 16.3% higher than that of velvety plants over the other four dates.

The pattern of diurnal Ψ_{lf} (Fig. 3) was similar for sticky and velvety plants with a midday Ψ_{lf} of -1.63 ± 0.14 MPa. Leaf water potential differed significantly across hours of the day ($F_{3,24}=286.66$, $P<0.0001$), but it did not differ significantly between the two types ($F_{1,8}=0.02$, $P=0.9022$).

The predicted leaf temperature and transpiration based on the conditions measured in the leaf cuvette on 30 October 2002 were 26.99°C , $2.51 \text{ mmol m}^{-2} \text{s}^{-1}$, and 27.08°C , $2.51 \text{ mmol m}^{-2} \text{s}^{-1}$ for velvety and sticky, respectively. The predicted difference in temperature resulting from the observed difference in absorptance amounts to only 0.09°C in this instance. This matches fairly well with what was observed, except that in the cuvette with air-flow set to 4 m s^{-1} the stomatal conductance was probably reduced resulting in a lower transpiration and slightly elevated leaf temperatures. The predicted leaf temperature and transpiration in ambient conditions were 21.94°C , $1.43 \text{ mmol m}^{-2} \text{s}^{-1}$ for velvety and 22.09°C , $1.43 \text{ mmol m}^{-2} \text{s}^{-1}$ for sticky. Although actual temperatures and transpiration rates were probably lower than those measured in the cuvette in this case, the temperature difference between types due to their difference in absorptance would be only 0.15°C and in both cases there would be no effect on transpiration.

Discussion

Despite obvious differences in trichome morphology and density, leaves from *D. wrightii* plants with glandular and non-glandular trichomes have similar physiological functionality. Although the different trichome types had slightly different spectral properties, this difference is relatively small and it did not result in significant changes in leaf temperature or transpiration rate. The higher average assimilation rate and WUE for sticky leaves may reflect some other

Table 1. ANOVA results of leaf spectral properties

ANOVA results of leaf spectral properties in the PAR and NIR spectra \times type, family, and type \times family interaction. Bold type indicates values significantly different at $\alpha=0.05$

Source	DF	Absorptance			Reflectance			Transmittance		
		MS	F	P	MS	F	P	MS	F	P
PAR										
Type	1	2.04×10^{-3}	10.36	0.002	1.56×10^{-2}	5.80	0.02	1.08×10^{-1}	7.24	0.047
Family	2	1.76×10^{-4}	0.89	0.42	1.69×10^{-3}	0.62	0.54	4.88×10^{-2}	3.28	0.01
Type \times Family	2	1.410^{-4}	0.70	0.50	2.16×10^{-3}	0.80	0.46	8.10×10^{-3}	0.53	0.59
Error	43	1.99×10^{-4}	–	–	2.710^{-3}	–	–	1.52×10^{-2}	–	–
NIR										
Type	1	2.34×10^{-2}	0.85	0.45	5.76×10^{-9}	0.009	0.925	2.36×10^{-4}	0.17	0.72
Family	2	5.29×10^{-2}	2.84	0.07	6.510^{-5}	0.40	0.67	1.64×10^{-3}	2.17	0.13
Type \times family	2	2.74×10^{-2}	1.47	0.24	1.83×10^{-4}	1.14	0.33	1.35×10^{-3}	1.79	0.18
Error	43	1.86×10^{-2}	–	–	1.60×10^{-4}	–	–	7.55×10^{-4}	–	–

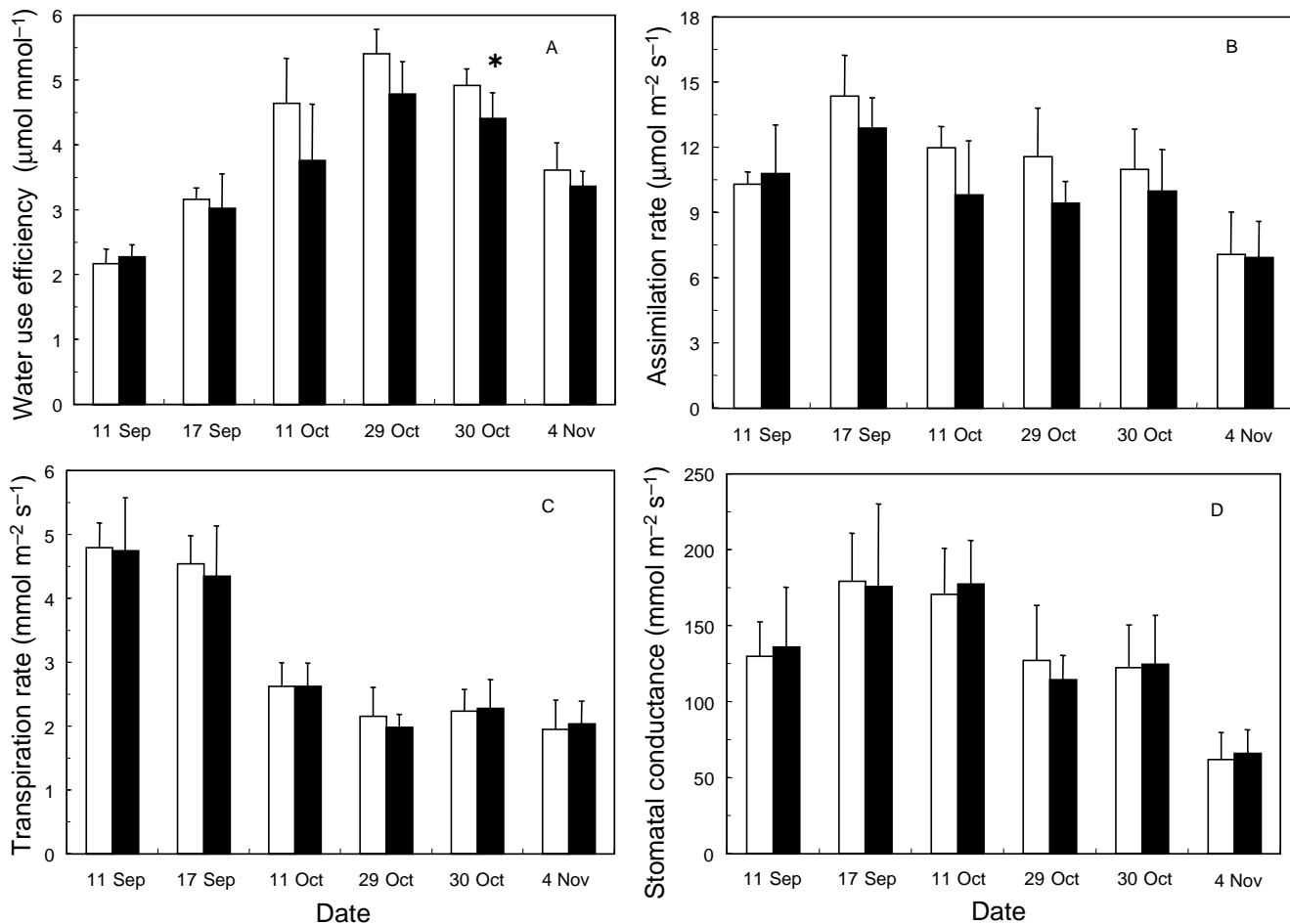


Fig. 2. Midday water use efficiency (A), assimilation rate (B), transpiration rate (C), and stomatal conductance (D) for sticky (open bars) and velvety (coloured bars) *D. wrightii* plants growing in an experimental field. All values shown in the graphs are means + standard deviations. * indicates the day on which there was a significant date \times type interaction.

type-associated physiological differences, but they are not the direct result of increased reflectance or decreased absorbance of PAR or NIR by the trichomes themselves.

The effect of reduced absorbance would only be physiologically important if the trichomes reflected or absorbed enough radiation to shade the leaf and result in a reduced temperature, thereby reducing transpiration and water loss. The review by Johnson (1975) showed that most studies find that pubescence has very little effect on transpiration rate.

Ehleringer and Mooney (1978) demonstrated in *Encelia* species that the contribution of trichomes to boundary layer resistance is relatively insignificant compared with, in that study, their ability to act as a reflector of radiation. Unlike species such as *Encelia* that have air-filled, reflective trichomes, the leaf hairs of *D. wrightii* do not act as a reflective shield against incoming PAR and NIR. Using the leaf energy-balance equation of Miller (1972), we were able to model possible effects of trichome type differences in

Table 2. ANOVA results for gas-exchange measurements

ANOVA results for gas-exchange measurements \times trichome type, sampling day, and for type \times day interactions. Boldface font indicates values significantly different at $\alpha=0.05$

Source	DF	Water use efficiency			Assimilation rate			Transpiration rate			Stomatal conductance		
		MS	F	<i>P</i>	MS	F	<i>P</i>	MS	F	<i>P</i>	MS	F	<i>P</i>
Type	1	0.0279	11.50	0.0011	21.57	6.67	0.0118	0.00257	0.13	0.7246	0.000042	0.00	0.9496
Day	5	0.2960	121.92	0.0001	55.38	17.13	0.0001	1.89	92.14	0.0001	0.366	35.08	0.0001
Type \times day	5	0.0064	2.63	0.0302	4.28	1.40	0.2346	0.00367	0.18	0.9699	0.0017	0.16	0.9752
Error	73	0.0024	–	–	3.23	–	–	0.0205	–	–	0.0104	–	–

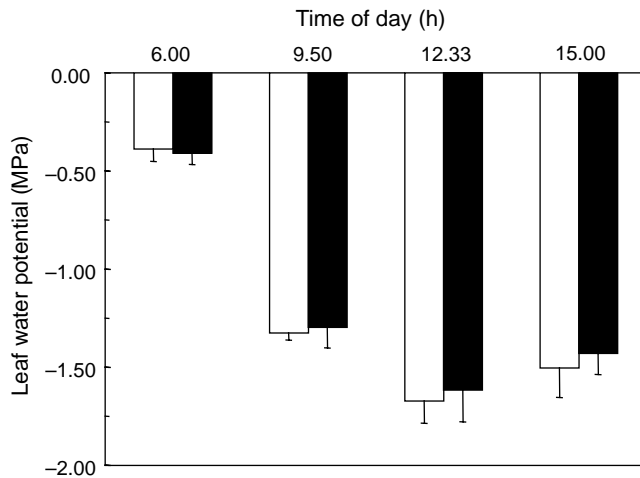


Fig. 3. Diurnal leaf water potentials (mean – standard deviation) of sticky (open bars) and velvety (closed bars) plants.

absorptance, demonstrating that the measured absorptance differences between trichome types result in a temperature difference of only a few hundredths to several tenths of a degree Celsius.

Because sticky and velvety leaves had similar water potentials and transpiration rates, the two types were not likely experiencing different levels of water stress. Although gas-exchange measurement conditions are necessarily unnatural, the lack of difference in E suggests that the contribution of evaporation of water from glandular trichome exudate to leaf water loss is relatively small. The leaf water potential measurements also reveal, at least in this environment, that there were not significant differences in plant moisture stress at the individual leaf level. In the drought resistant tomato species, *Lycopersicon pennelli*, a lower trichome density and a higher WUE are found than in *Lycopersicon esculentum*. However, the relatively higher WUE is due to lower stomatal conductance, which also reduces the rate of photosynthesis (Kebede *et al.* 1994; Martin *et al.* 1994). In *D. wrightii*, the higher WUE reflects the higher assimilation rate during the observation period, comprised of mostly relatively cooler days, in sticky plants than in velvety plants. It has been suggested that low WUE may be a successful strategy in drought-tolerant plants when competing for water in an arid environment (DeLucia and Heckathorn 1989), although the existence of drought tolerance differences between sticky and velvety *D. wrightii* has not been examined. While these midday punctual measurements of gas exchange give us only a snapshot of the variation that necessarily occurs diurnally and seasonally, the similarities and differences observed suggest that the physiological variation between the types is not directly due to the spectral properties of the trichomes themselves.

We have shown with our measurements and leaf temperature simulation that in *D. wrightii* slight differences in

absorptance of PAR and NIR do not contribute significantly to differences in transpiration, water potential or leaf temperature. Of course, leaf trichomes may have other functions and we should be cautious in our interpretation of their significance (Press 1999). Although we were not able to distinguish possibly linked genotypic variation for photosynthetic rate from genetically-determined morphological variation between the trichomes types, the higher photosynthetic rate found for sticky plants may deserve further examination. Leaf hairs have been shown in several different species to contain compounds that can absorb UV-B (280–320 nm) radiation and protect tissues, especially young tissues, from damage (Karabourniotis *et al.* 1992; 1994). Leaf orientation, size, and arrangement could also have a much greater effect on leaf temperature and water relations (Geller and Smith 1982; Shaver 1978; Smith 1978; Mooney *et al.* 1977). Future studies may examine how such factors contribute to possible differences in photosynthetic response and photoinhibition between the trichome types while controlling for other sources of genotypic variation.

Overall, the absence of substantial differences in physiological function in this study suggests that there are only relatively small physiological advantages of either trichome type for primary productivity and water use. In contrast, the differences in trichome morphology strongly influence which herbivorous insects attack sticky and velvety plants and the amount and type of damage that those herbivores inflict (van Dam and Hare 1998; Hare and Elle 2002). We predict that natural selection is more likely to act on sticky and velvety plants based upon those plants' relative susceptibility to herbivorous insects than on their slight differences in physiological capacity.

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Appendix 1. Parameter settings for leaf temperature simulation

Leaf orientation to the incident solar radiation was determined based on the mean leaf angle of 19.9° previously reported by Ehleringer and Werk (1986) and the solar elevation of 41.94° calculated with the Solar Position Calculator (Cornwall *et al.* 2003). The coefficient of absorptance of total solar radiation (300–4000 nm) was calculated based on its relationship to absorptance to visible radiation (400–700 nm) published by Ehleringer (1981). For sticky and velvety leaves the absorptances (300–4000 nm) were set at 0.556 and 0.547, respectively. Ehleringer (1981) also reported a similar leaf absorptance for this species (84% absorptance to visible radiation, which would be 0.527 to total solar radiation). Leaf width was set to 0.09 m based on previously reported leaf dimensions, which do not differ significantly by type (Forkner and Hare 2000)

	Leaf cuvette	Ambient
Solar radiation	630 W m ⁻²	
Vapour density of air	8.8 g m ⁻³ , 51% relative humidity	
Wind velocity	4 m s ⁻¹	1 m s ⁻¹
Air temperature	26°C	20°C
Leaf orientation	0°	28°