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ECOLOGY AND ECOPHYSIOLOGY OF LEAF PUBESCENCE IN

NORTH AMERICAN DESERT PLANTS

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Abstract

The ecophysiological effects of leaf trichomes on surface spectral characteristics and boundary layer thickness were investigated for a number of Sonoran Desert plants. Dense trichome layers substantially increase leaf reflectance for all wavelengths of solar radiation between 400-3000 nm. Leaf absorptance to total incident solar radiation may be decreased by a factor of three when compared to the leaf absorptance of glabrous leaves. These changes in leaf absorptance have an effect on leaf temperature, photosynthetic rate, and transpiration rate. Leaf boundary layers are only slightly increased by dense tomentum in the desert species studied. These ecophysiological effects of trichomes on leaf activity are discussed with respect to life form and to adaptation to arid land habitats.

1. INTRODUCTION

During the past century a correlation has been established between the presence of leaf trichomes and aridity in higher plants. Haberlandt (1884), Schimper (1903) and Warming (1909) have all pointed out that leaf pubescence is a common feature of plants from Mediterranean climates and steppe, desert, and alpine habitats. These early investigators also reported that, when an individual species extended over a broad environmental gradient, in mesic habitats the species had glabrous or glabrate leaves whereas in xeric habitats the leaves were pubescent. Moreover, in many habitats the leaves of some species were glabrate during the moist period of the year and pubescent during dry periods. Johnson (1968) has studied leaf pubescence in four communities (sandy beach, old field, oak forest, and red maple swamp) which represent an increasing moisture gradient in eastern North America. He found that although the incidence of pubescence was similar in each community (70-80% of the species), the pubescence was much more dense in the drier environments.

The adaptive value of leaf hairs is generally thought to be related to water economy of the plant either through (1) an increased reflection of solar radiation which reduces leaf temperature and thus transpiration rate, or (2) by increasing the thickness of the boundary layer (layer of still air over leaf through which water must diffuse) thereby reducing transpiration rate (Haberlandt 1884; Shull 1929; Wooley 1964; Wuenscher 1970; Ehleringer and Mooney 1978). Leaf pubescence does increase leaf reflectance in many species (Shull 1929; Billings and Morris 1951; Pearman 1966; Sinclair and Thomas 1970; Ehleringer et al. 1976; Ehleringer and Björkman 1978; Ehleringer 1981a), but exceptions occur (Shull 1929; Gausman and Cardenas 1969, 1973; Wuenscher 1970). The effects of pubescence on reflectance most likely depend on the density and thickness of the indumentum. The data relating to the leaf boundary layer effect are in conflict (Haberlandt 1884; Wiegand 1910; Sayre 1920; Wooley 1964; Wuenscher 1970; Parkhurst 1976), even when only studies of the same species are considered (Sayre 1920; Wuenscher 1970; Parkhurst 1976).

Recent studies suggest that leaf pubescence may play a role in reducing herbivory by serving as a physical barrier to animal penetration or by emitting toxic or repellent compounds (Levin 1973; Johnson 1975). Leaf hairs could serve both anti-herbivore and water economy functions, but no data are available to resolve this point.

Increases in leaf pubescence are common along aridity gradients in the southwestern United States and northwestern Mexico (Shreve and Wiggins 1964; Ehleringer 1980). The

pubescence is of various types (single cell, multicellular, branched, stellate, etc.) and occurs in almost all of the higher plant families along these aridity gradients. Such ecological gradients are ideal for studying the effects and ecological significance of leaf pubescence. Since the variations in leaf pubescence are strongly correlated with aridity, and apparently not with major distributional differences in animal taxa, the pubescence gradient is more likely a response to abiotic and not biotic components.

In this paper, I would like to briefly review the physiological and ecological significance of leaf pubescence to plants in arid environments.

2. DISCUSSION

2.1 *Pubescence and Aridity Gradients*

The increase in leaf pubescence along an increasing aridity gradient is not restricted to a few species, but is widespread among many different genera and families. No one species occurs along an entire aridity gradient in southwestern North America. More typically a species distribution will span a portion of the aridity transect. On the wetter and drier sites along such a transect, a species will often be replaced by other species within the same genus. Table 1 lists some of the more common genera whose species increase in leaf pubescence with aridity. In some cases there are only two species along the gradient and the genus extends over only a portion of the aridity transect, but in several instances different species of a genus may occur along the entire aridity gradient.

As the degree of leaf pubescence in these species increases, the percentage of light reflected by the leaf (leaf reflectance) also increases. This results in a decreased leaf absorptance. To illustrate this point, let us consider several species of *Salvia*. Along an increasing aridity gradient in southern California, *S. mellifera* occurs on the wettest sites, and is first replaced by *S. leucophylla*, and then by *S. apiana* on progressively drier sites (Munz, 1959). Figure 1 shows the leaf absorptance spectrum for these three *Salvia* species between 400 and 800 nm. *Salvia mellifera* with a glabrate, green leaf has an absorptance spectrum typical of most green leaves. On drier sites, it is replaced by the moderately pubescent, gray-leafed *S. leucophylla*. While the absorptance spectrum for *S. leucohpylla* is lower than *S. mellifera* over the visible (photosynthetically useful) wavelengths, the basic absorptance spectrum remains the same. In the heavily pubescent, white-leaved *S. apiana*, the percentage of light absorptance is much reduced below that of either *S. mellifera* or *S. leucophylla*.
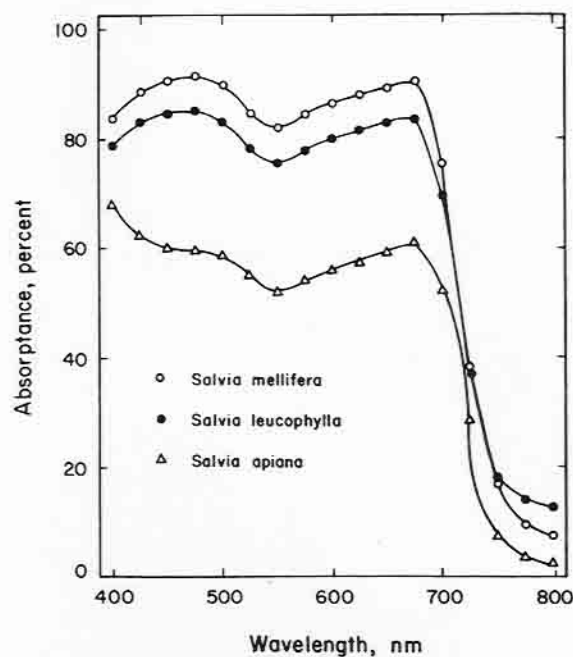
Figure 1. Monochromatic leaf absorptances between 400 and 800 nm of three *Salvia* species occurring along an aridity gradient.

Table 1. Genera which exhibit a variation in leaf pubescence along an aridity gradient in the Mohave and Sonoran Deserts.

genus	family
Arctostaphylos	Ericaceae
Artemisia	Asteraceae
Brickellia	Asteraceae
Ceanothus	Rhamnaceae
Condalia	Rhamnaceae
Encelia	Asteraceae
Enceliopsis	Asteraceae
Eriogonum	Polygonaceae
Franseria	Asteraceae
Kochia	Chenopodiaceae
Salvia	Lamiaceae
Sphaeralcea	Malvaceae
Tetradymia	Asteraceae
Viguiera	Asteraceae

Table 2. An elevational transect through Death Valley, California to demonstrate the replacement series in a group of closely related genera in the Asteraceae.

	life form	elevation (m)	absorptance (%)
Geraea canescens	annual	0–500	78
Encelia farinosa	shrub	300–800	29–81
Enceliopsis argophylla	herb	1000–1200	66
Encelia virginensis	shrub	900–1500	76

The trichomes responsible for a decreased leaf absorptance in *Salvia* are linear branched hairs. These hairs form a dense layer on the surface of the leaf, but because of the convoluted nature of the *Salvia* leaf the hairs appear as tufts.

The correlation between absorptance spectra and aridity in *Salvia* are typical of aridity gradients. Ehleringer (1980) has presented similar data for *Encelia* along a similar but more extensive aridity gradient in southern California. At the community level, Billings and Morris (1951) compared the spectral characteristics of species from several communities in the Great Basin Desert differing in aridity and they found that the average reflectance increased (absorptance decreased) as habitat aridity increased.

The pubescence which results in an increased reflectance or decreased absorptance is apparently a blanket reflector over the visible wavelengths (Ehleringer and Björkman, 1978). That is, the pubescence reflects all wavelengths between 400 and 700 nm equally well. This can be demonstrated in species of *Encelia* occurring along an aridity gradient in southern California. *Encelia farinosa* occurs in dry habitats and has pubescent leaves with a low leaf absorptance (Fig. 2). *Encelia californica* occurs at the moist end of the aridity gradient along the coast of southern California and has glabrate leaves with a spectrum typical of green leaves. When the hairs of *E. farinosa* leaves are removed and the absorptance spectrum of the now glabrous *E. farinosa* is remeasured, the spectrum is nearly identical to that of *E. californica* (Fig. 2). This suggests that in species replacements along aridity gradients (see Table 1), all species have leaves with the same basic absorptance pattern, but are covered with variable amounts of a blanket reflector.

Often, members of closely related genera occur parapatrically along aridity gradients. For example, *Encelia*, *Enceliopsis*, and *Geraea* are closely related genera occurring together in Death Valley. The lightly pubescent annual *Geraea canescens* is found at the lowest elevations (0–500 m) on the driest sites (Table 2). The leaves are green-gray with a leaf absorptance of 78% and it survives during the dry months as a seed. The heavily pubescent shrub, *Encelia farinosa*, occurs at higher elevations (300–800 m). The leaf absorptance of this species varies from 29 to 81% depending on aridity (a function of both elevation and season). *Enceliopsis argophylla*, a silver leaved perennial herb occurs on more moist sites above *E. farinosa* between 1000–1200 m. Leaf absorptance in this species is still higher at 66%. The shrub, *Encelia virginensis*, with lightly pubescent green leaves, has an absorptance of 76% and occurs at the highest, wettest elevations.
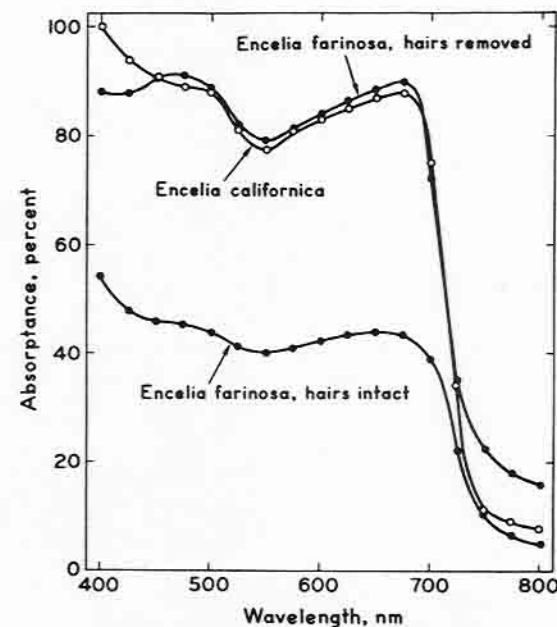

Figure 2. Monochromatic leaf absorptances between 400 and 800 nm for *Encelia farinosa* with hairs intact and with the hairs removed and the absorptance spectrum for an intact *E. californica* leaf. (From Ehleringer and Björkman 1978).

2.2 *Leaf Absorptance and Life Form*

The size, shape, and density of leaf hairs varies among arid land species. Both glandular and nonglandular leaf hairs occur in these species. Most of the nonglandular hairs found are simple and linear; however, the glandular hairs often range from simple to complex.

In annual species of arid lands, the hairs are most often simple and linear (Figs. 3-6). These hairs are of both glandular and nonglandular types and are always present in low densities relative to that found in other life forms. The hairs are large, often exceeding the thickness of the photosynthetic tissues by a factor of three to five times (Figs. 7-10).

Herbaceous perennial species may have leaf hairs similar to annuals or may have much more dense pubescence layers (Figs. 11-14). The dense hair layers are typically linear and nonglandular. Light microscope observations suggest that in leaves with thick indumentum, the hairs are dead and air filled. As the pubescence layer becomes thicker in these perennials, the epidermal surface becomes obscured (Figs. 12, 14). In thick pubescent leaves, the incoming light penetrates to the photosynthetic tissues only after multiple reflection.

Leaf pubescence in shrubs follows a pattern similar to that found in herbaceous perennials. However, there are probably more variations in leaf hair types in shrubs. For instance the linear hairs may be unbranched or branched as in *Salvia* (Figs. 15, 16) which also has less conspicuous glandular trichomes (Fig. 15).

Different hair types may vary in frequency as in *Encelia* which has two glandular and one nonglandular hair type (Figs. 17-20). In *Encelia* species with high leaf reflectances (e.g., *E. actonii*, *E. farinosa*, *E. palmeri*), most of the hairs are of the linear type. These linear hairs are greatly increased in length. In contrast, leaves of *E. frutescens* and *E. virginensis* have higher frequencies of glandular hairs, lower frequencies of linear hairs which remain relatively short, and low leaf reflectances. It is not possible to measure spectral characteristics of individual hairs, but the nonglandular hairs are probably responsible for the increased leaf reflectance.

The range of leaf absorptances for many species of Mohave and Sonoran Desert plants have been measured (Ehleringer, 1981a). When these data are arranged according to life form, only shrubs and herbs exhibit a wide range of leaf absorptances, even though all life forms may have pubescent leaves (Fig. 21). Tree and annual species all have high leaf absorptances. Small variations in these absorptances are attributable to changes in leaf thickness and thus to small changes in leaf transmittance. The wide range of leaf absorptances occurring in cacti results not from hairs, but rather from surface waxes and spines.

Additional types of trichomes other than hairs can also
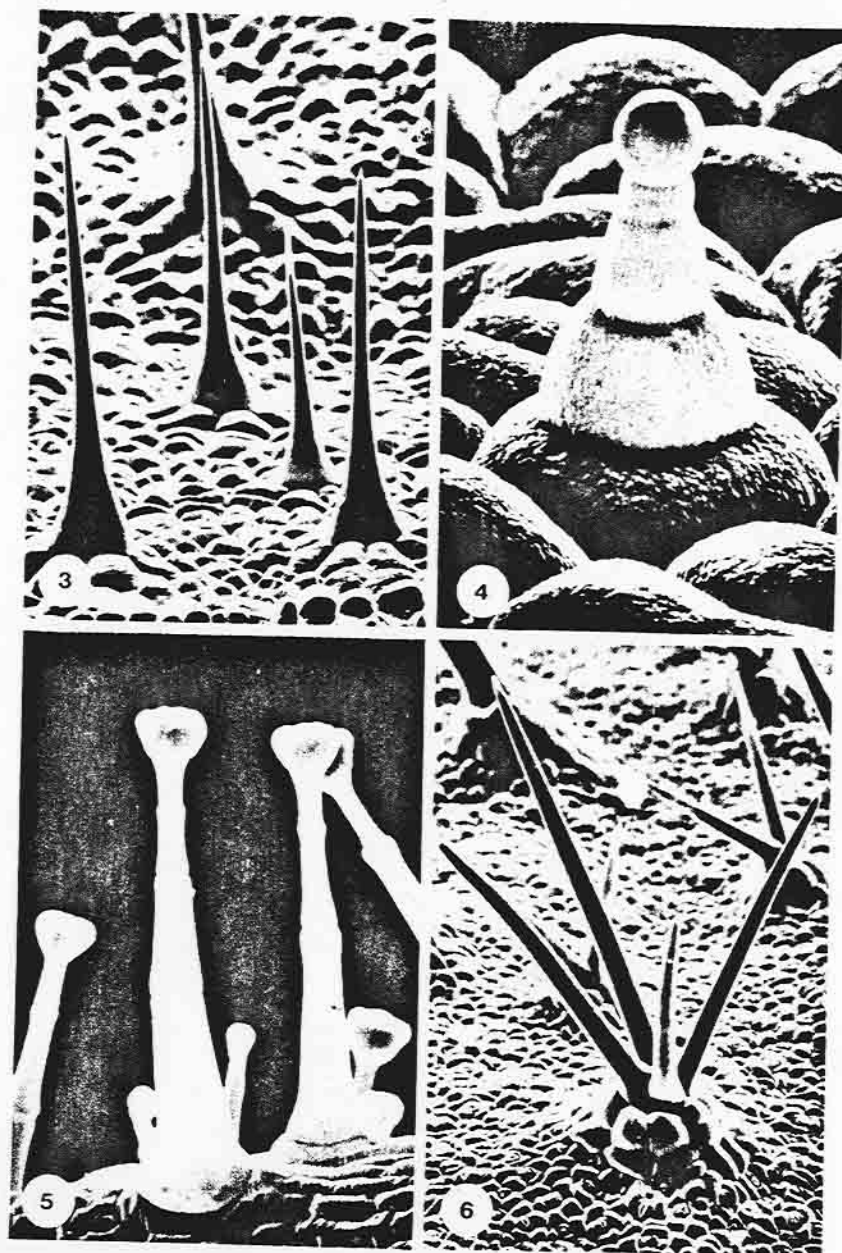
Figures 3-6. Leaf trichomes on desert annual. 3 - *Mohavea breviflora* (180X); 4 - *Abronia villosa* (740X); 5 - *Phacelia calthafolia* (240X); 6 - *Malvastrum rotundifolium* (200X).
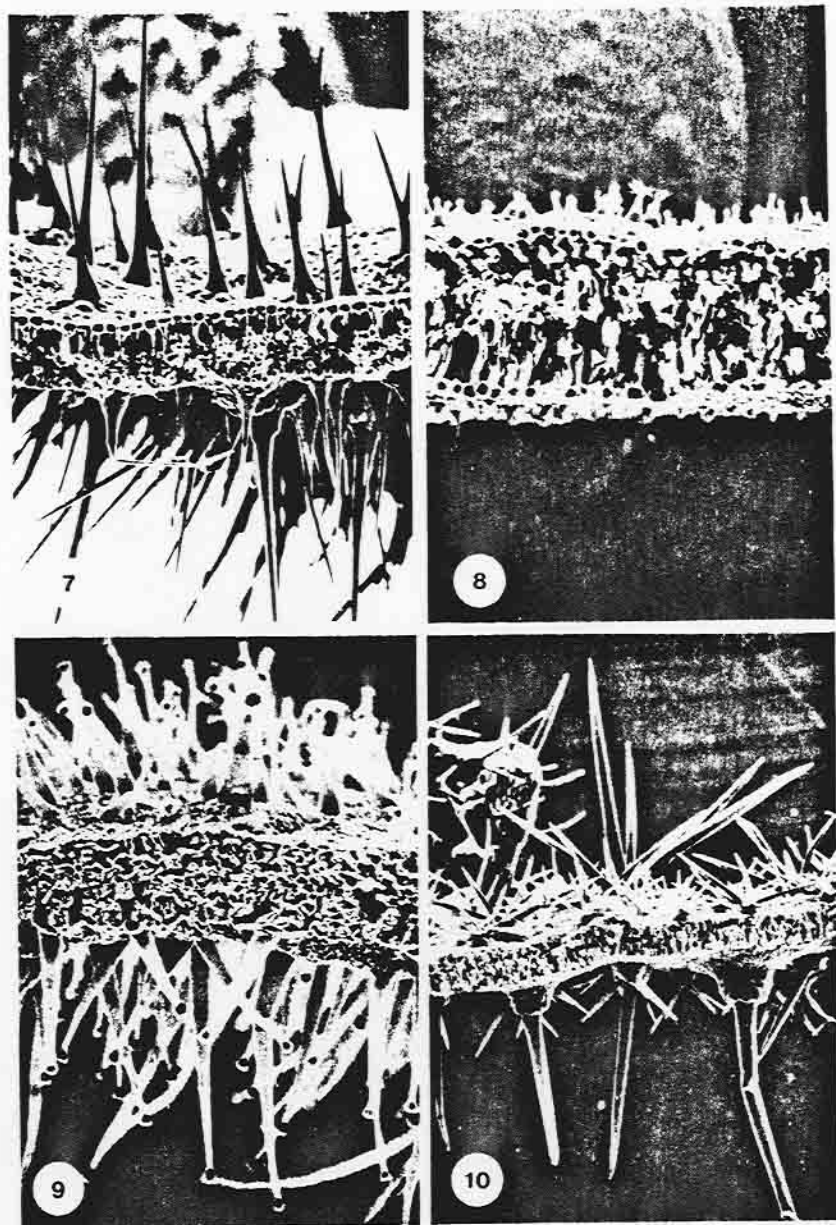
Figures 7-10. Cross section of leaves of desert annuals. 7 - *Mohavea breviflora* (68X); 8 - *Abronia villosa* (54X); 9 - *Phacelia calthafolia* (76X); 10 - *Malvastrum rotundifolium* (60X).
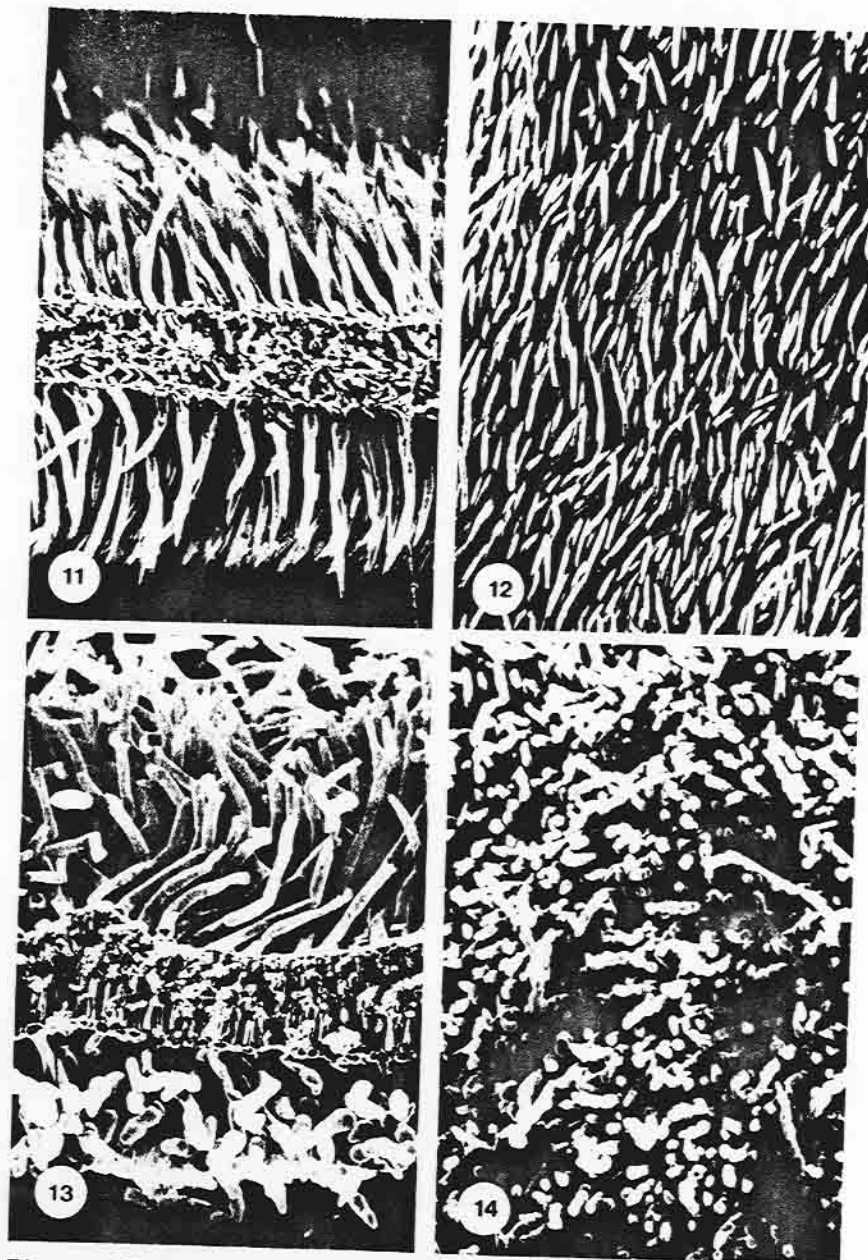
Figures 11-14. Leaf cross sections and surface views of desert perennial herbs. 11 - *Enceliopsis argophylla* (104X); 12 - *E. argophylla* (60X); 13 - *Psathyrotes ramosissima* (92X); 14 - *P. ramosissima* (64X).
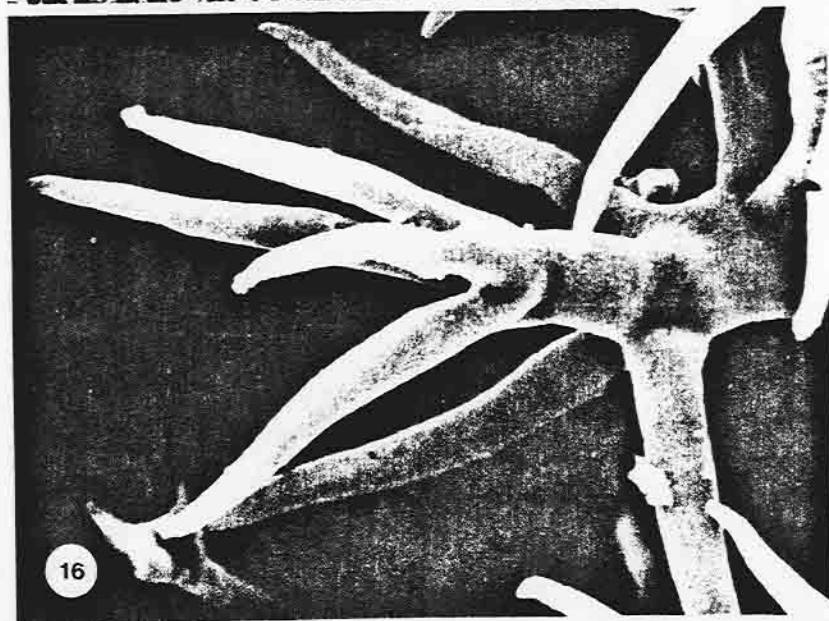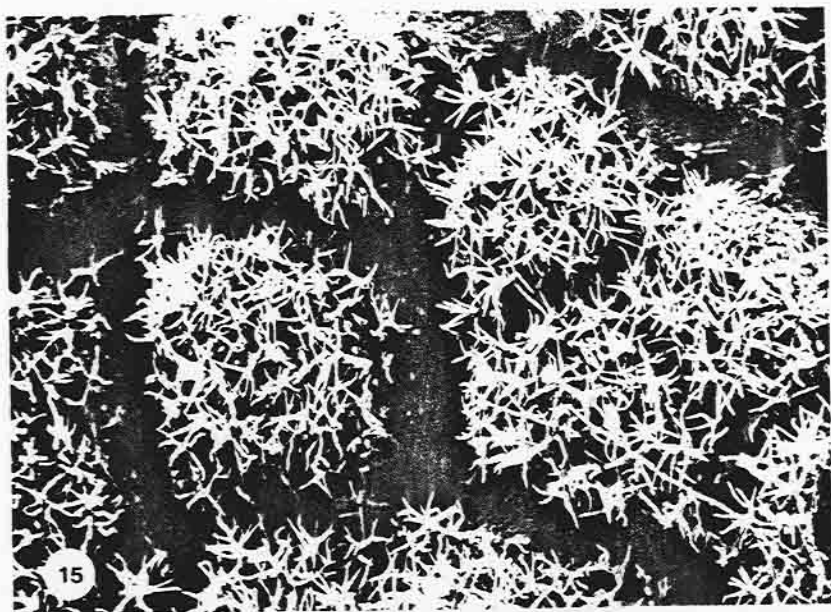
Figures 15-16. Leaf surface view and enlarged view of leaf trichomes in *Salvia leucophylla*. Figure 15 is 200X and Figure 16 is 2600X.
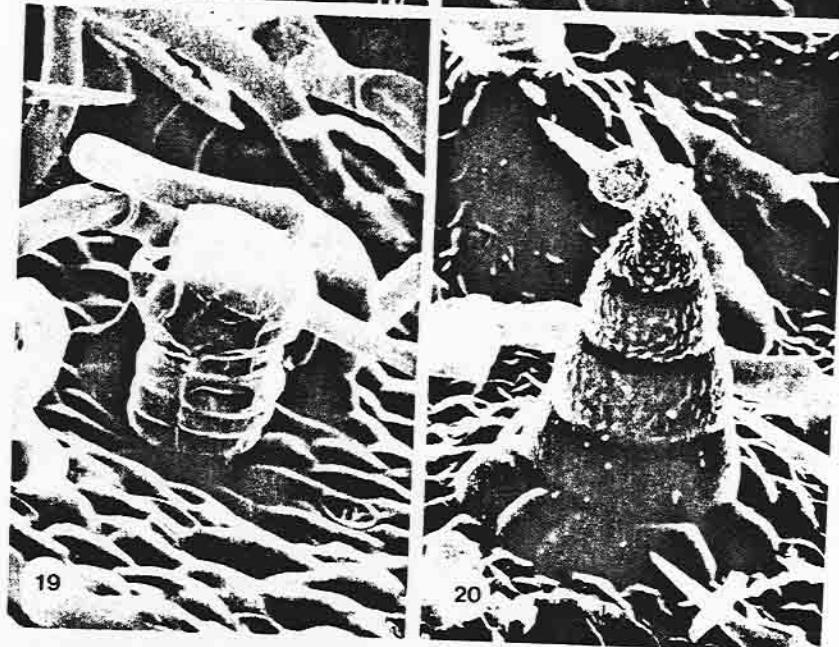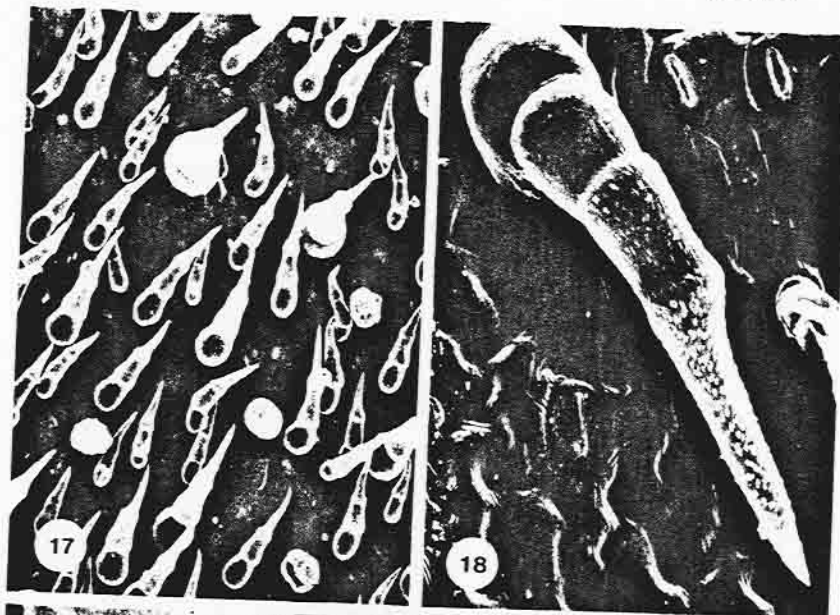
Figures 17-20. Leaf surface view of *Encelia virginensis* illustrating the density and diversity of trichomes and enlarged views of the predominant trichome types found in the species *Encelia*. Magnifications are 240X, 1080X, 880X and 650X, respectively.
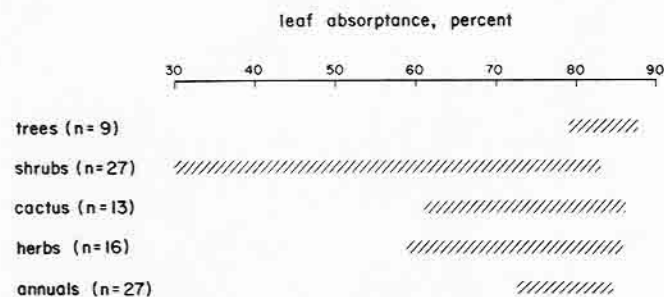
leaf absorptance, percent

Figure 21. Ranges of leaf absorptances (400-700 nm) observed in a variety of plant species in the Mohave and Sonoran Deserts.
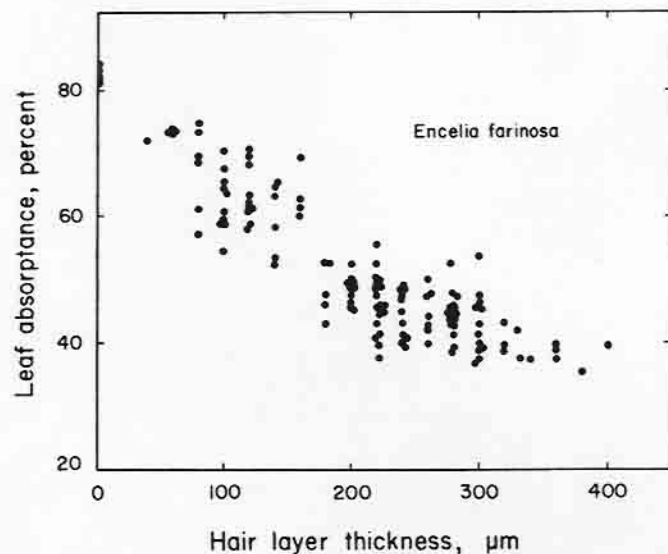

Hair layer thickness, μm

Figure 22. The relationship between increased leaf pubescence thickness and leaf absorptance (400-700 nm) in *Encelia farinosa* (From Ehleringer 1981b).

reduce leaf absorptance. Mooney et al. (1977) have shown that epidermal salt bladders in *Atriplex* may reduce leaf absorptance to about 40%.

The high leaf absorptances of tree and annual species may be the consequence of the water relations characteristic of those life forms. In the Mohave and Sonoran Desert, tree species are restricted to water courses with greater water availability. Annual species are typically ephemeral and complete their life cycle in mesic periods before the onset of extended drought.

2.3 *Influence of Pubescence on Leaf Boundary Layer*

Increases in the height of the pubescence layer should alter the boundary layer thickness, because the pubescence layer constitutes an additional component to the boundary layer. As the boundary layer becomes thicker, the rates of transfer of heat, water vapor, and CO_2 should decrease because they must diffuse across this layer.

Boundary layers are commonly quantified as resistances and not in terms of thickness. Resistance is a functional measure which indicates the impedance to the movement of substances across the layer. A typical leaf boundary layer resistance for water vapor is approximately 0.02 s mm^{-1} (Gates 1965). The total boundary layer resistance of a pubescent leaf will be

$$r_t = r_B + r_H \qquad (1)$$

where r_T, r_B, and r_H are the total boundary layer resistance of a glabrous leaf, and additional boundary layer resistance due to the presence of hairs. Since heat and gases must diffuse across both components of the total boundary layer resistance, the impedances are in series and the total resistance is the sum of the components.

The additional boundary layer resistance from hairs can be calculated as

$$r_H = L/DA \qquad (2)$$

where L is the height of the pubescence layer, A is the fractional area of the surface not occupied by hairs and available for diffusion, and D is the diffusion coefficient.

The thickness of the indumentum on leaves of varying pubescence has been measured in *Encelia farinosa* (Fig. 22). Leaf absorptance decreased asymptotically as the hair layer increased in thickness. Moderately pubescent leaves have hair layer thicknesses in the range of 100-200 μm. In extremely pubescent leaves with very low leaf absorptances, the pubescence may approach 400 μm. Assuming that A from equation 2 has a value in the neighborhood of one, the maximum increase in leaf boundary layer resistance for water vapor due to hairs will be approximately 0.017 s mm^{-1}. This represents almost a doubling of the
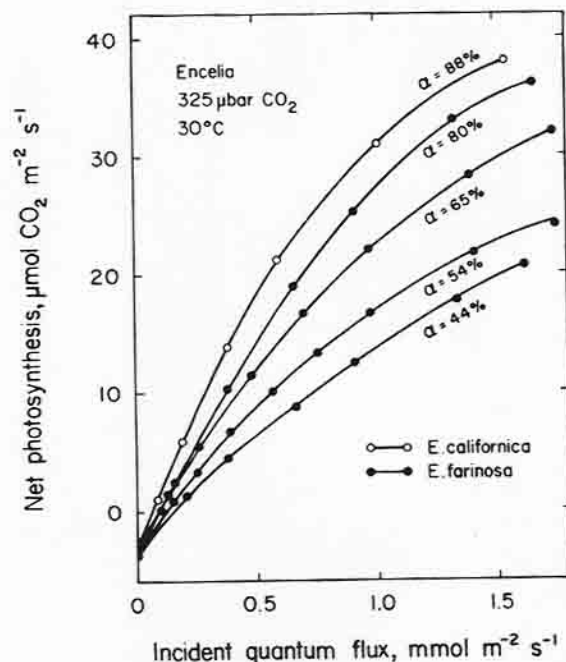
Figure 23. The relationships between quantum flux and photo-
synthesis in *Encelia* differing in leaf absorptance (α). (Based on
data from Ehleringer and Mooney, 1978).

Table 3. Effects of changes in pubescence on leaf temperature and
water loss in *Encelia farinosa* under mid-day summer conditions.

	green leaf	white leaf
absorptance (%)		
400–700 nm	85	40
400–3000 nm	50	17
leaf temperature (°C)	41.8	38.5
transpiration rate ($\mu g\ cm^{-2}\ s^{-1}$)	9.2	7.4

boundary layer resistance. However, functionally the effect on
transpiration will be small.

The rate of water loss from a leaf will depend on the
movement of water across both the boundary layer and stomatal
pore resistances. A typical stomatal resistance for a pubescent
E. farinosa leaf will be 0.5 s mm^{-1} (Ehleringer, 1977). This
makes a total resistance to water loss of 0.52 s mm^{-1} if we
neglect any additional resistances due to presence of the hairs.
If the effects of hairs on boundary layer resistance are included,
the total resistance becomes 0.537 s mm^{-1}; a change of only 3%.
Consequently, the effects of hairs on boundary layer resistance
are negligible in *Encelia* and probably also in all other arid
land plant species.

2.4 *Effects of Pubescence on Ecophysiology*

A thick pubescence layer therefore has a significant effect
on leaf spectral characteristics, but not on the total leaf layer
resistances to water loss. Ehleringer and Mooney (1978) have
addressed the question on how changes in leaf absorptance will
affect leaf physiology.

With respect to transpiration and photosynthesis, both direct
and indirect effects may occur. A decrease in solar radiation
absorption will directly affect photosynthesis by reflecting
quanta that might otherwise be used in carbon fixation. Leaf
temperature is affected by decreasing the heat load on the leaf.
Indirectly, a change in leaf temperature will affect both trans-
piration and photosynthesis. Transpiration will be modified
since the saturation water vapor pressure at leaf temperature is
a determining factor in the driving force for transpiration
(Gates 1965). Photosynthesis will be modified as it is tempera-
ture dependent at both low and high light levels (Björkman 1973;
Ehleringer and Björkman 1977, 1978).

In *Encelia farinosa* the effects of increased light
reflectance by pubescence on photosynthesis are dramatic. In an
analysis of photosynthesis light response curves with individual
leaves of differing pubescence, Ehleringer and Mooney (1978)
found that (1) *E. farinosa* leaves were not light saturated by
noon irradiances and that (2) increased pubescence levels reduced
photosynthetic rate at all light intensities (Fig. 23). The
differences in rates of photosynthesis among the differentially
pubescent leaves appeared to result solely from differences in
leaf absorptance properties. When the rates of photosynthesis
were expressed on an absorbed quantum flux basis rather than as
incident quantum flux, the differences among the curves
disappeared (Ehleringer and Mooney, 1978).

The effects of changes in leaf absorptance on leaf
temperature and transpiration rate can be calculated using energy

budget calculations (Gates, 1965; Ehleringer and Mooney, 1978). To illustrate this, let us consider the hypothetical situation of a "green" and "white" leaved *E. farinosa* (Table 3). The 400-700 nm leaf absorptances for "green" and "white" leaves are 85% and 40%, respectively. The total solar energy leaf absorptance (400-3000 nm) for these leaves would then be 50% and 17% (Ehleringer, 1981a). Under midday summer conditions (clear sky, 40°C air temperature, 20% relative humidity), the "green" leaf temperature is calculated to be 41.8°C and the "white" leaf 38.5°C. As a consequence, the transpiration rate of the "green" leaf is 9.2 μg cm^{-2} s^{-1} versus 7.4 g cm^{-2} s^{-1} for the "white" leaf. This 24% difference in water loss is likely to be of adaptive value to plants growing in arid habitats and may be one means of extending physiological activity into drought periods.

3.   CONCLUSION

Leaf pubescence is abundant in desert plant species, and often increases in thickness in conjunction with increased aridity. A thick leaf hair layer results in reduced leaf absorptance (increased leaf reflectance). In the Mohave and Sonoran Deserts, these decreased leaf absorptances are found primarily among herbs and shrubs, but not among annuals or trees. Pubescence has little effect on the total leaf resistance to water loss, but does have a significant effect on leaf temperature, photosynthesis, and water loss through increased light reflectance.

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