

#17666
H-7

19 Leaf Morphology and Reflectance in Relation to Water and Temperature Stress

JAMES EHRLINGER

*Department of Biology, University of Utah, Salt Lake City,
Utah*

1. Introduction 295
2. Influence of Environmental Factors on Leaf Pubescence 296
3. Physiological Effects of Leaf Pubescence 302
4. Summary 307

1. INTRODUCTION

It is clear from previous ecological studies that plants growing in arid habitats tend to possess leaves that have more hairs (pubescence) than similar or related plants from more mesic habitats (1-3). This trend of increasing pubescence with aridity is seen repeatedly not only along geographical clines, but also within a single habitat as drought progresses in the growing season. Largely based on these observations, it is deduced that leaf hairs are an adaptive feature of plants occupying arid habitats (1, 4, 5). Although it may seem obvious that the leaf pubescence is a means of increasing plant fitness in arid habitats, and therefore is of adaptive value, the means by which leaf pubescence is adaptive are not so clear.

Several possibilities exist for the function of leaf pubescence in plants from arid habitats. These include (a) reduction of light absorption during conditions of high temperature and drought (6-8), (b) hindrance of the diffusion of gases across the leaf-air interface (9), and (c) reduction of predation by insects and larger herbivores (10). The function of leaf pubescence may differ among various plant species, but it would not be surprising to discover that in some cases pubescence served several functions.

With respect to high temperature and water stress, the presence of leaf

hairs is thought to modify leaf properties and physiological processes through several definable interactions (Figure 19.1). The pubescence may modify leaf absorption and boundary layer characteristics. A change in leaf absorptance will directly affect photosynthesis and leaf energy balance (leaf temperature). Indirectly, a change in leaf temperature will affect the rates of transpiration and photosynthesis. A change in the boundary layer may directly influence both photosynthesis and transpiration through its effect on the diffusion of carbon dioxide into and water vapor from the leaf surface. The boundary layer will directly affect leaf temperature by modifying the rate of heat transfer from the leaf. At the same time, the boundary layer will indirectly affect both photosynthesis and transpiration through leaf temperature as discussed previously. Thus it is clear that leaf pubescence has both direct and indirect effects on leaf physiological processes, and that the interactions among leaf hairs, environmental parameters, and physiological processes are tightly coupled. An understanding of the possible adaptive value of leaf hairs cannot be obtained without first quantifying the effects of the hairs on physiological processes.

2. INFLUENCE OF ENVIRONMENTAL FACTORS ON LEAF PUBESCENCE

Although the overall impact of leaf hairs on physiological activity is not yet understood for any system, at least one study has looked at the effects of hairs and other surface features on leaf spectral characteristics along en-

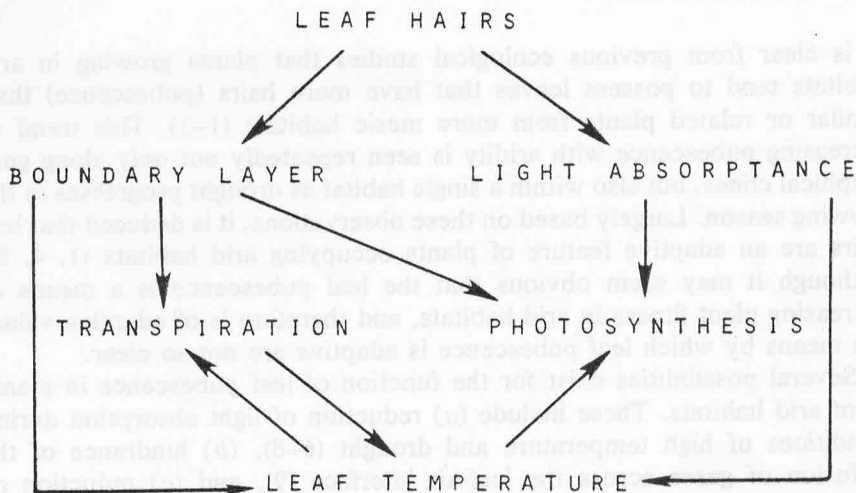


Figure 19.1. Interactions between leaf pubescence, energy exchange, and physiological processes. From Ref. 18, copyright by Springer-Verlag, Heidelberg, December 20, 1978.

vironmental clines of temperature and drought. Billings and Morris (11) compared reflectances of species from several communities and found that the reflectances of desert species were higher than those of plants from subalpine, pine forest, and shaded habitats. These investigators were comparing communities consisting of unrelated species and life forms, and several factors may have contributed to these reflectance differences.

Perhaps a less complicated situation for determining the value of leaf hairs to plants is to study the response(s) of a single species or of closely related species in a genus along an aridity gradient (see Chapter 18 for use of gradients in adaptation to stress). The arid land regions of the southwestern United States provide such an opportunity. From coastal California east to the deserts of the interior, there are many examples of genera with species distributed more or less allopatrically along a gradient of increasing aridity. As aridity increases along this gradient, species within a genus that have more pubescent leaves replace those that are less pubescent. These genera represent a number of families including Compositae, Labiatae, Polygonaceae, and Rhamnaceae, suggesting that the phenomenon is of broad ecological importance and is not restricted to a specific family.

One common genus along this aridity gradient, and perhaps representative of the leaf pubescence phenomena, is *Encelia* (Compositae). *Encelia* is a genus of suffrutescent shrubs with drought deciduous leaves. In terms of habitats, this genus extends from relatively mesic, warm coastal sites in southern California to extremely hot, arid desert sites in Arizona, California, and Mexico (Figure 19.2). At the coast we find the dark green, glabrous leaved *E. californica*. In the dry interior mountain slopes the light pubescent leaved *E. virginensis* occurs. At the drier lower elevations and throughout most of the desert *E. virginensis* is replaced by *E. farinosa*, a plant with white, extremely pubescent leaves. Aridity increases along a north-to-south coastal transect, and we find that *E. californica* is eventually replaced by the lightly pubescent leaved *E. asperifolia*. At the driest sites along this coastal transect *E. palmeri* with its densely pubescent leaves occurs.

Inspection of the spectral characteristics of leaves of *Encelia* species along an aridity transect makes it clear that the increased pubescence results in a decrease in leaf absorptance (Figure 19.3). Measurements of leaf absorptance between 400 and 700 nm are of interest because it is only these wavelengths that are useful for photosynthesis, and nearly 50% of the sun's irradiance and 80% of the solar radiation absorbed by leaves is in this wave band. The absorptance to solar radiation in the photosynthetically active wavelengths for leaves of *E. californica* is 85.2% (integral of solar irradiance and leaf absorptance spectra between 400 and 700 nm), a value similar to that observed for most green leaves (12). The light layer of pubescence on *E. virginensis* leaves reduces leaf absorptance to 75.9%. Leaves of *E. farinosa*, which have different amounts of leaf pubescence depending on the aridity of the site, have leaf absorptances substantially lower than the more glabrous species.

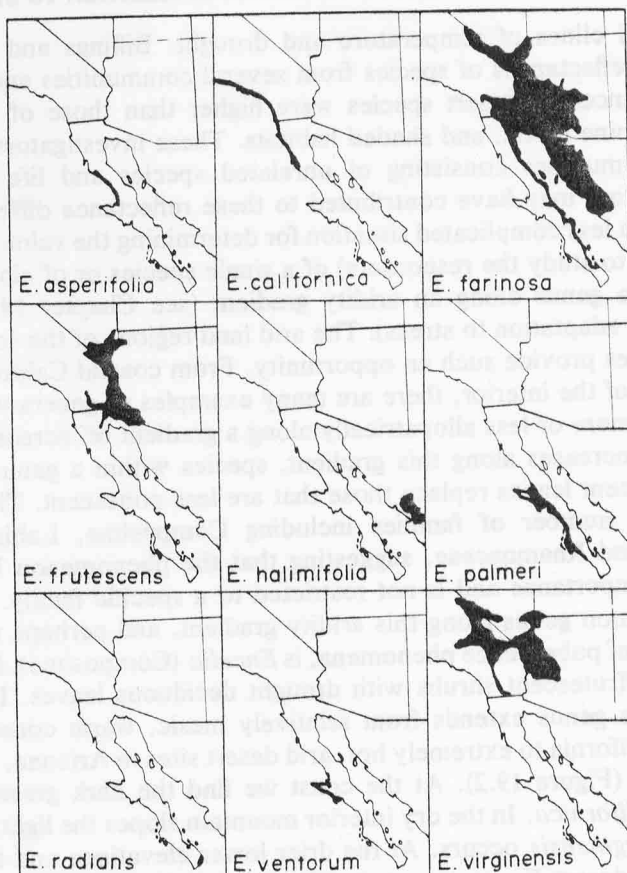


Figure 19.2. Distributions of species of *Encelia* in arid habitats of southwestern North America. *E. californica*, *E. frutescens*, *E. halimifolia*, *E. radians*, and *E. ventorum* are nonpubescent. *E. asperifolia* and *E. virginensis* are lightly pubescent, and *E. farinosa* and *E. palmeri* are heavily pubescent.

The absorptance spectra for *Encelia* in Figure 19.3 were obtained at a single point in time, April, the peak of the winter growing season. Measurements of absorptances on a seasonal basis reveal that leaf pubescence in *E. farinosa* varies during the growing season (Figure 19.4). Leaves produced early in the winter growth season have little pubescence and high leaf absorptances, whereas leaves produced in the spring and summer have more pubescence and lower leaf absorptances. The change in leaf absorptance of *E. farinosa* during the course of a season and the lack of change in *E. californica* are negatively correlated with air temperatures, suggesting that leaf pubescence might serve as a mechanism for modifying leaf energy balance and regulating leaf temperatures. The reasoning behind this is that as air temperatures increase, only two possibilities exist for reducing leaf temper-

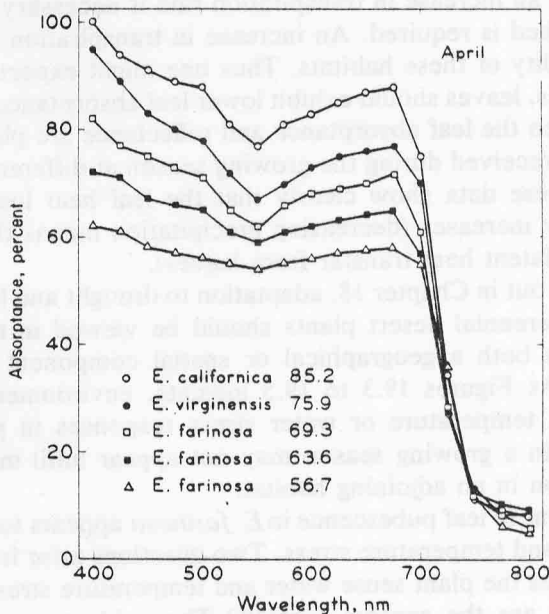


Figure 19.3. Absorbance spectra of intact leaves of *Encelia californica*, *E. virginensis*, and *E. farinosa* along an aridity gradient during April. The values adjacent to each species represents the leaf absorbance to solar radiation between 400 and 700 nm.

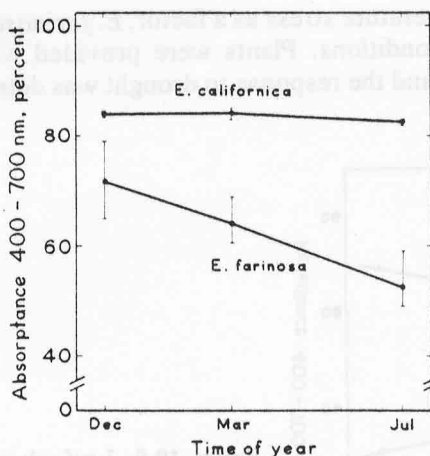


Figure 19.4. Seasonal courses of leaf absorbances (400 to 700 nm) for *Encelia farinosa* and *E. californica* from different sites. Based on data from Ref. 6.

atures: either an increase in transpiration rate is necessary or a decrease in energy absorbed is required. An increase in transpiration is very unlikely, given the aridity of these habitats. Thus one might expect that in going to more arid sites, leaves should exhibit lower leaf absorptances. This is indeed observed when the leaf absorptance and reflectance are plotted against the precipitation received during the growing season at different locations (Figure 19.5). These data show clearly that the leaf heat load is reduced as habitat aridity increases (decreasing precipitation means that less water is available for latent heat transfer from leaves).

As pointed out in Chapter 18, adaptation to drought and high temperature stresses by perennial desert plants should be viewed in two dimensions, since there is both a geographical or spatial component and a seasonal component. As Figures 19.3 to 19.5 indicate, environmental factors that result in high temperature or water stress responses in plants from one habitat early in a growing season may not appear until much later in the growing season in an adjoining habitat.

Development of leaf pubescence in *E. farinosa* appears to be a function of both drought and temperature stress. Two questions arise from the previous data: How does the plant sense water and temperature stress in its environment? Where are the sensors located? The evidence available suggests that these environmental sensors and control over pubescence occurs in the active apical meristems (13, 14). To investigate the question of response to water and temperature stresses, two sets of experiments were conducted, each aimed at eliminating one environmental stress to determine plant response to the other.

To eliminate temperature stress as a factor, *E. farinosa* plants were grown under greenhouse conditions. Plants were provided with a near constant aerial environment, and the response to drought was determined. As soil and

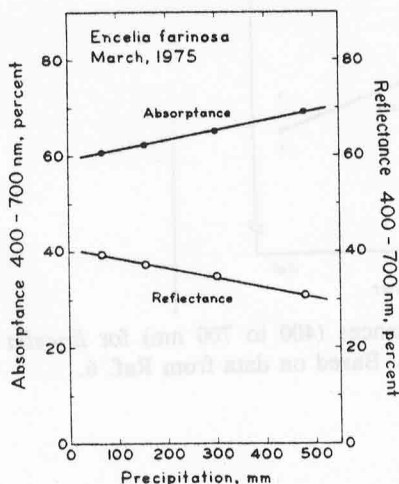


Figure 19.5. Leaf absorptance and reflectance (400 to 700 nm) of *Encelia farinosa* from various sites as functions of the precipitation received at each site during the growing season. Sites were initially chosen so that air temperatures at each site were similar. Based on data from Ref. 6.

leaf water potentials decreased, *E. farinosa* produced leaves that were progressively more pubescent, consequently having lower and lower leaf absorptances (Figure 19.6). At leaf water potentials near -10 bars leaves were lightly pubescent and leaf absorptance was about 78%. As leaf water potentials declined, leaf absorptance declined in a linear fashion. Below about -40 bars these plants did not produce new leaves; rather, they were drought deciduous and became inactive (14).

From both field and laboratory observations it appears that once a plant has been subjected to a mild water stress, removing the water stress does not result in the production of less pubescent leaves. Rather, the apical meristem continues to produce leaves with pubescence equal to the largest water stress encountered, until leaf water potentials have fallen below -40 bars (= dormancy?). Rewatering after a stress of -40 bars allows the apical meristem to "reset itself" and once again produce leaves with less pubescence and higher leaf absorptances.

The relationship between pubescence on *E. farinosa* leaves and temperature was determined with field-grown plants that received supplementary water throughout the year. The amount of leaf pubescence as measured by leaf absorptance was negatively related to mean maximum air temperature of the habitat (Figure 19.7). The variation in leaf absorptance due to temperature change, however, was much less than that due to water potential changes under the ranges of these factors normally found in nature. Although these plants were watered frequently, it is likely that to some extent leaf water potential covaried with air temperature. Nevertheless these results suggest

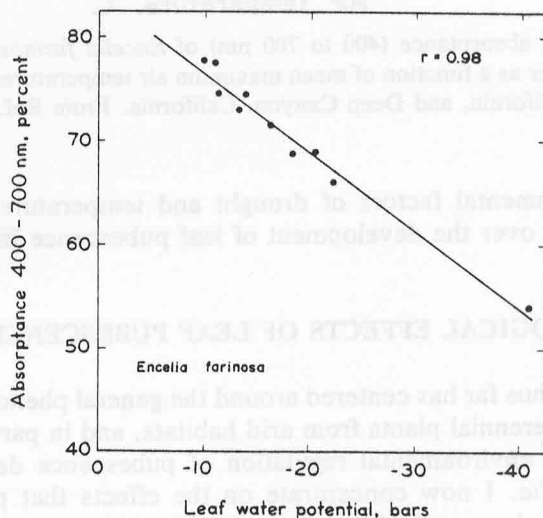


Figure 19.6. Leaf absorptance (400 to 700 nm) of *Encelia farinosa* as a function of midday leaf water potential. Plants were grown in tubs in a greenhouse and allowed to dry out slowly. From Ref. 14.

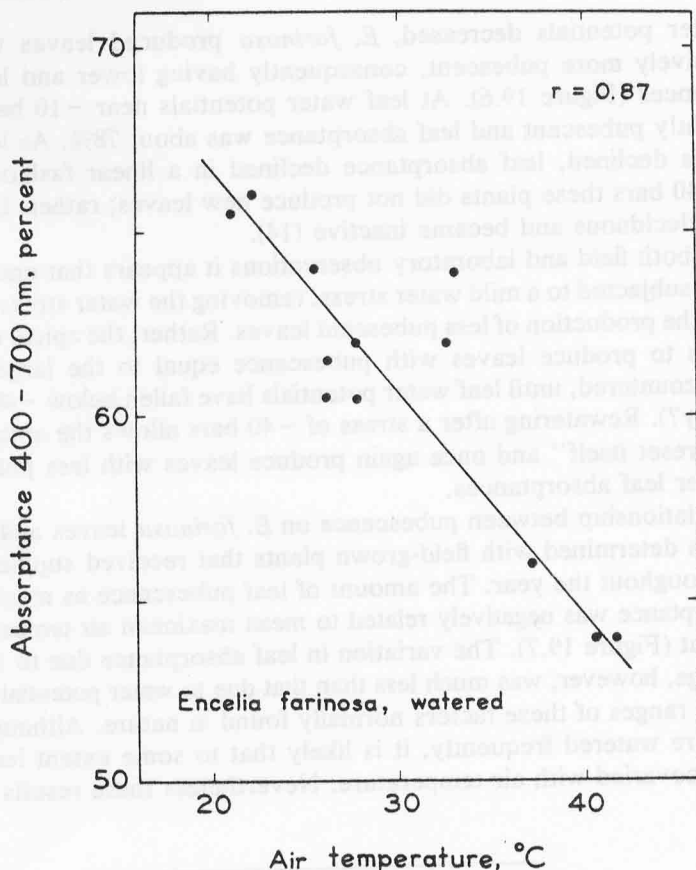


Figure 19.7. Leaf absorbance (400 to 700 nm) of *Encelia farinosa* that received supplemental water as a function of mean maximum air temperatures at field sites in Death Valley, California, and Deep Canyon, California. From Ref. 14.

that the environmental factors of drought and temperature both exert a strong influence over the development of leaf pubescence in *E. farinosa*.

3. PHYSIOLOGICAL EFFECTS OF LEAF PUBESCENCE

Our discussion thus far has centered around the general phenomenon of leaf pubescence in perennial plants from arid habitats, and in particular on leaf pubescence and environmental regulation of pubescence development in species of *Encelia*. I now concentrate on the effects that pubescence in *Encelia farinosa* has on leaf spectral characteristics, physiological processes, and carbon balance.

The presence of leaf hairs in *E. farinosa* greatly reduces absorbance by

increasing leaf reflectance, not by increasing transmittance (Figure 19.5). Studies have shown that pubescence in *E. farinosa* is a blanket reflector between 400 and 700 nm. Consequently removing leaf pubescence from *E. farinosa* yields a leaf whose absorptance spectrum is virtually identical to that of *E. californica* (15). However over the entire solar spectrum the pubescence preferentially reflects near infrared radiation (700 to 3000 nm) (15). The heat balance of the leaf and the leaf temperature are influenced by leaf absorptance over the entire solar spectrum (400 to 3000 nm) rather than just the 400–700 nm band. The correlation between these two bands, however, is very tight (Figure 19.8). Whereas the 400 to 700 nm leaf absorptance for *E. farinosa* varies from 29 to 81%, the 400 to 3000 nm leaf absorptance varies from 15 to 46%. In comparison, *E. californica*, as is typical of green leaves, has a 400 to 700 nm leaf absorptance of 50%. These changes in 400 to 3000 nm leaf absorptance have a profound effect on leaf temperature. From energy balance calculations, a change in leaf absorptance from 50 to 15% will reduce midday leaf temperature by 5.1°C at a leaf conductance to water loss of 0.5 cm/s and typical summer conditions (air temperature 40°C). Solely as a result of this difference in leaf temperatures, the transpiration rate will decrease from 840 to 550 nmol/cm²/s, a decrease of 34%.

In terms of photosynthesis, which is presumably the primary function of a leaf, pubescence may be necessary for the survival of *E. farinosa* under the hot, desert conditions of its native habitat. Figure 19.9 shows the temperature dependence of photosynthesis in *E. farinosa*. *Encelia farinosa* shows a temperature optimum for photosynthesis near 25°C and lacks the ability to acclimate the photosynthetic machinery to changes in growth conditions (16, 17). Consequently the temperature optimum remains near 25°C, and the upper limit of leaf temperatures is near 45°C. Pubescence (white leaf) allows *E. farinosa* to avoid potentially lethal temperatures and to photosynthesize close to the optimum temperature during summer conditions. Conversely, in

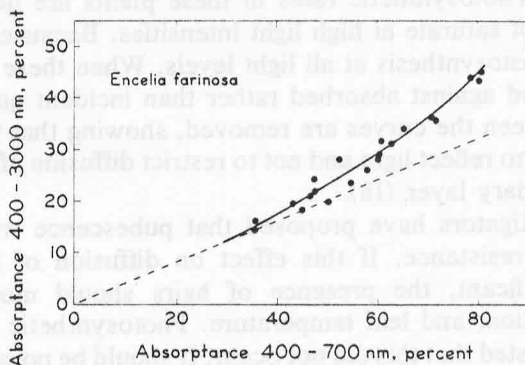


Figure 19.8. Total solar leaf absorptance (400 to 3000 nm) for *Encelia farinosa* plotted against the 400 to 700 nm leaf absorptance. From Ref. 15, copyright by Springer-Verlag, Heidelberg.

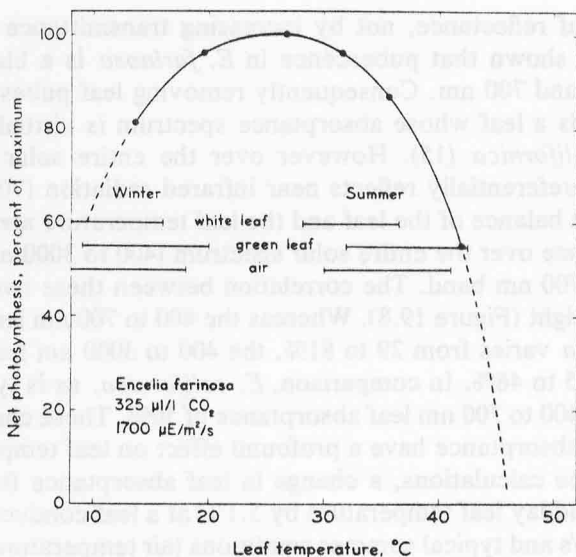


Figure 19.9. Daily ranges of air temperatures and leaf temperatures for green and white leaves of *Encelia farinosa* in the winter and summer and the temperature dependence of photosynthesis. Adopted from Ref. 18, copyright by Springer-Verlag, Heidelberg, December 20, 1978.

the winter the lightly pubescent form (green leaf) has a leaf temperature above air temperature and again closer to the temperature optimum of photosynthesis.

Our studies show, however, that pubescence in *E. farinosa* is not wholly advantageous. The presence of leaf pubescence decreases the photosynthetic rate by reflecting quanta that might otherwise be used in photosynthesis (Figure 19.10). Photosynthetic rates in these plants are quite high for C_3 plants and do not saturate at high light intensities. Because of this, pubescence affects photosynthesis at all light levels. When these photosynthetic data are replotted against absorbed rather than incident quantum flux, all differences between the curves are removed, showing that the pubescence serves primarily to reflect light and not to restrict diffusion of carbon dioxide across the boundary layer (18).

Several investigators have proposed that pubescence will increase the boundary layer resistance. If this effect on diffusion of heat and mass transfer is significant, the presence of hairs should modify photosynthesis, transpiration, and leaf temperature. Photosynthetic data presented previously suggested that this did not occur. It should be possible to estimate the additional boundary layer resistance arising from the presence of the hairs. I assume that the transfer of gases through the boundary layer is by

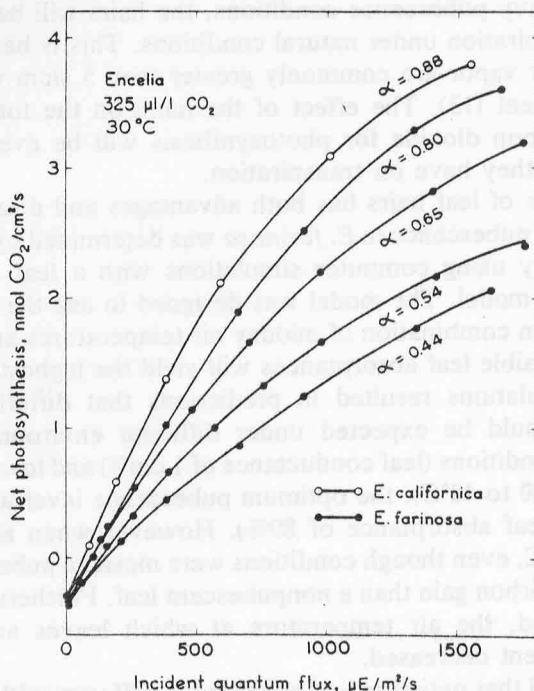


Figure 19.10. Relationship between net photosynthesis and incident quantum flux density for leaves of *Encelia farinosa* differing in pubescence and for *E. californica*. Alpha values represent leaf absorptance (400 to 700 nm) estimates. Thus the lower the alpha value, the greater will be the thickness of the pubescence layer. Adopted from Ref. 18, copyright by Springer-Verlag, Heidelberg, December 20, 1978.

diffusion, that is, there is no turbulent transfer, and I also assume no tortuosity effects on gas diffusion caused by the hairs. The increase in thickness of the boundary layer will then be equal to the thickness of the layer of leaf hairs. Knowing the increased thickness of the boundary layer, we can calculate the increase in boundary layer resistance as

$$r = \frac{L}{D} \quad (19.1)$$

where r is the additional boundary layer resistance for water vapor caused by the hairs, L is the thickness of the pubescent layer, and D is the diffusion coefficient for water vapor in air. The maximum expected increase in boundary layer resistance for a heavily pubescent *E. farinosa* leaf (0.36 mm thick pubescence) will be about 0.15 s/cm. A common boundary layer resistance will be approximately 0.3 s/cm. This means that under extreme conditions, pubescence may increase the boundary layer resistance by 50%. However

even under heavy pubescence conditions, the hairs will have only a small effect on transpiration under natural conditions. This is because leaf resistances to water vapor are commonly greater than 5 s/cm when leaves are heavily pubescent (13). The effect of the hairs on the total resistance to transfer of carbon dioxide for photosynthesis will be even less than the minimal effect they have on transpiration.

The presence of leaf hairs has both advantages and disadvantages. The overall value of pubescence to *E. farinosa* was determined by Ehleringer and Mooney (18) by using computer simulations with a leaf energy budget-photosynthesis model. The model was designed to ask the following question: For a given combination of midday air temperatures and aridity, what value of all possible leaf absorptances will yield the highest photosynthetic rate? The simulations resulted in predictions that differing amounts of pubescence should be expected under different environmental regimes. Under mesic conditions (leaf conductance of 1 cm/s) and low to moderate air temperatures (20 to 40°C), the optimum pubescence level was the greenest possible leaf (leaf absorptance of 80%). However when air temperatures were above 40°C, even though conditions were mesic, a pubescent leaf had a higher rate of carbon gain than a nonpubescent leaf. Furthermore, as habitat aridity increased, the air temperature at which leaves are predicted to become pubescent decreased.

It is predicted that optimum leaf pubescence will vary with environmental conditions because there is a tradeoff between the decline in photosynthesis caused by an increased reflectance (see Figure 19.10) and the increase in photosynthesis caused by a decrease in leaf temperature (see Figure 19.9) (18). Because the photosynthetic machinery of *E. farinosa* does not acclimate to temperature changes, pubescence may become advantageous whenever leaf temperatures exceed the photosynthetic temperature optimum. Predictions from the model agree with field observations of pubescence levels by Ehleringer et al. (6), Ehleringer and Björkman (15), and Smith and Nobel (8).

Simulation results of the total daily carbon gain and transpiration loss by *E. farinosa* leaves under wet and dry conditions during the winter and summer seasons are in agreement with predictions from midday conditions by Ehleringer and Mooney (18). These simulations reveal that nonpubescent leaves are expected to have higher daily rates of carbon gain than are pubescent leaves, except when environmental conditions are hot and dry (Figure 19.11). Under the four environmental regimes considered in Figure 19.11, however, the pubescent leaves will have a lower daily water loss. As a consequence, the photosynthesis/transpiration ratio of pubescent leaves in the summer is predicted to be greater than that of glabrous leaves. With respect to natural selection, these simulation results and respective field observations would suggest that plant fitness in this perennial shrub may be maximized not by minimizing water loss, nor by maximizing the pho-

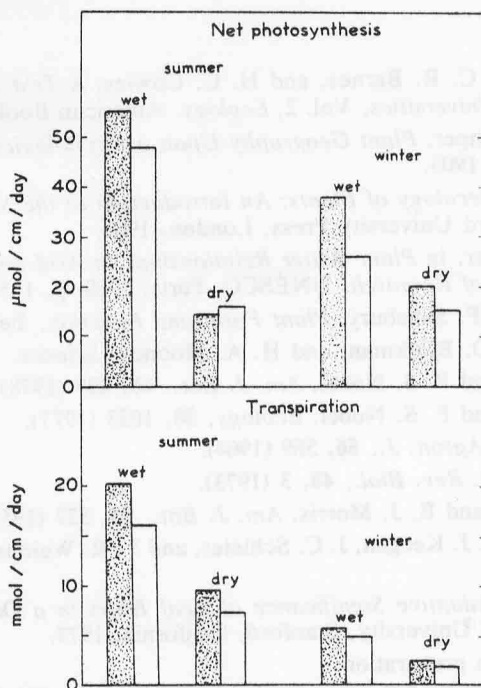


Figure 19.11. Daily rates of carbon gain and water loss for pubescent leaves (leaf absorbance 400 to 700 nm = 50%: open histograms) and for nearly glabrous leaves (leaf absorbance 400 to 700 nm = 80%: shaded histograms) of *Encelia farinosa* under wet (leaf conductance = 0.5 cm/s) and dry (leaf conductance = 0.2 cm/s) conditions in the winter (max/min air temperatures = 20/5°C) and summer (max/min air temperatures = 40/25°C) seasons.

tosynthesis/transpiration ratio, but rather through maximizing the carbon-gaining capacity of the leaf.

4. SUMMARY

I suggest that leaf pubescence has adaptive value to *E. farinosa* in its native desert habitats, because the hairs allow the leaf to gain a higher rate of carbon under arid conditions than the leaf could acquire without hairs, to avoid potentially lethal high leaf temperatures, and to lose less water daily, which allows the plant to extend its growth for a longer period into the drought. To a species that appears to be unable to acclimate its photosynthetic characteristics when faced with increasing air temperatures, the use of leaf hairs to produce a reflective surface is a viable alternative mechanism in adapting the plant to its environment.

REFERENCES

1. J. M. Coulter, C. R. Barnes, and H. C. Cowles, *A Text Book of Botany for Colleges and Universities*, Vol. 2, *Ecology*, American Book, New York, 1911.
2. A. F. W. Schimper, *Plant Geography Upon a Physiological Basis*, Clarendon Press, Oxford, 1903.
3. E. Warming, *Oecology of Plants: An Introduction to the Study of Plant Communities*, Oxford University Press, London, 1909.
4. H. Oppenheimer, in *Plant Water Relationships in Arid and Semi-arid Conditions: Reviews of Research*, UNESCO, Paris, 1960, p. 105.
5. F. Fritsch and F. Salisbury, *Plant Form and Function*, Bell, London, 1965.
6. J. Ehleringer, O. Björkman, and H. A. Mooney, *Science*, **192**, 376 (1976).
7. W. K. Smith and P. S. Nobel, *Am. J. Bot.*, **65**, 429 (1978).
8. W. K. Smith and P. S. Nobel, *Ecology*, **58**, 1033 (1977).
9. J. T. Woolley, *Agron. J.*, **56**, 569 (1964).
10. D. A. Levin, *Q. Rev. Biol.*, **48**, 3 (1973).
11. W. D. Billings and R. J. Morris, *Am. J. Bot.*, **38**, 327 (1951).
12. D. M. Gates, H. J. Keegan, J. C. Schleieter, and V. R. Weidner, *Appl. Opt.*, **4**, 11 (1965).
13. J. Ehleringer, *Adaptive Significance of Leaf Hairs in a Desert Shrub*, Ph.D. thesis, Stanford University, Stanford, California, 1977.
14. J. Ehleringer, in preparation.
15. J. Ehleringer and O. Björkman, *Oecologia*, **36**, 151 (1978).
16. B. R. Strain and V. C. Chase, *Ecology*, **47**, 1043 (1966).
17. J. Ehleringer and O. Björkman, *Plant Physiol.*, **62**, 185 (1978).
18. J. Ehleringer and H. A. Mooney, *Oecologia*, **37**, 183 (1978).