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James Ehleringer, Olle Bjorkman, Harold A. Mooney

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Leaf Pubescence: Effects on Absorptance and Photosynthesis in a Desert Shrub

Abstract. *The presence of leaf pubescence (leaf hairs) in* Encelia farinosa, *a desert species of the Composite family, reduces the absorptance of photosynthetically active radiation (400 to 700 nanometers) by as much as 56 percent more than a closely related but nonpubescent species,* E. californica, *a native of the relatively moist southern California coast. Pubescence in* E. farinosa, *which increases through the growing season, modifies the leaf energy balance and dramatically reduces the photosynthetic rate. The reduction in the photosynthetic rate is caused by decreased light absorption rather than decreased carbon dioxide conductance through the boundary layer.*

There is a tendency among higher plants for leaf pubescence to increase along environmental gradients of decreasing precipitation (*1*). From observations of the distribution of leaf pubescence among plants, it has been deduced that pubescence is an adaptive feature of plants occupying arid habitats (*2*). This is because pubescence can potentially reduce the heat load of leaves by increasing the reflectance from the leaf surface, which reduces the amount of radiation absorbed. The adaptive value of a reduced radiation load to plants growing in hot or arid climates in terms of reducing leaf temperatures and decreasing transpirational losses is great (*3*), yet the consequences of reduced light absorptance on the net photosynthetic rate have not been considered.

This report is concerned with the absorptance values in the photosynthetically active spectral range (visible spectrum, 400 to 700 nm) of *Encelia farinosa*, a drought-deciduous shrub with white, densely pubescent leaves, as compared with those of a closely related species, *E. californica*, which has green, nonpubescent leaves. The two species are allopatric in their distributions; *E. californica* is restricted to the relatively moist coastal regions of southern California, and *E. farinosa* occurs in the dry desert areas of the southwestern United States.

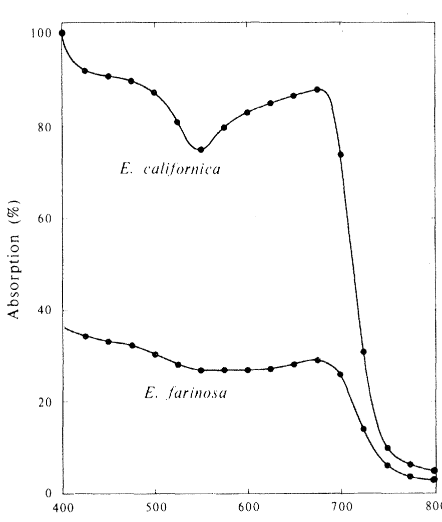

Fig. 1. Absorption spectra of intact leaves of *Encelia californica* and *E. farinosa* over the wavelengths 400 to 800 nm as determined with an Ulbricht integrating sphere.

Previous measurements have indicated that plants with pubescent leaves often (*4, 5*), but by no means always (*6*), absorb less light in the visible spectrum than green nonpubescent leaves. The upper surface of green leaves normally absorbs 80 to 90 percent of the quanta in the photosynthetically active wavelengths (*7*). In contrast, pubescence reduces absorptance to as little as 68 percent (*8*).

Leaf absorptance spectra were measured with a Bausch & Lomb high intensity grating monochromator attached to an Ulbricht integrating sphere, according to the theory and description of Rabideau *et al.* (*9*). Solar absorption coefficients for the 400- to 700-nm spectral range were calculated from the absorption spectra of the upper leaf surface in conjunction with the solar spectrum at the earth's surface. The calc'lated solar absorption coefficients thus represented the integrated percentage of quantum absorption by the leaf over the photosynthetically active wavelengths. The percentage of quanta absorbed is not necessarily equivalent to the percentage of energy absorbed, since quanta of different wavelengths contain different amounts of energy. However, over the range of 400 to 700 nm, the percentages were nearly identical for leaves of *Encelia*.

The nonpubescent *E. californica* exhibits a spectrum typical of intact green leaves (Fig. 1), but in the pubescent *E. farinosa*, the absorptance values are sharply reduced. This particular *E. farinosa* spectrum was obtained from active leaves in the extreme environment of Death Valley, California, during September 1975. Since transmittance through the leaf hairs was less than 1 percent, the pubescent layer appears to serve as a blanket reflector, decreasing the light absorbed by approximately 56 percent below the values of *E. californica* at all wavelengths. The differences between the two spectra are due only to differences in pubescence. The chlorophyll contents of leaves from both species were equivalent (about 40 $\mu g\ cm^{-2}$), and the thicknesses of the epidermis and mesophyll layers were similar. Integrated solar absorption coefficients from these spectra are 84.8 and 29.0 percent for *E. californica* and *E. farinosa*, respectively, making *E. farinosa* the most extreme case known in which pubescence reduces light absorption by the leaf. It is likely that other species exist with similarly low absorptances, yet they have not been measured because their leaves are quite small compared to those of *Encelia*.

Field observations of solar absorption coefficients for both species were made in December 1974, March 1975, and July 1975. Samples of *E. californica* were collected at Point Mugu (362 mm mean annual precipitation) and San Diego (240 mm) in southern California, and *E. farinosa* was sampled at Superior (433 mm), Tucson (270 mm), Tonopah (155 mm), and Ehrenberg (90 mm) in southwestern Arizona. Five representative samples were collected from each site. The means of all samples of a species at a given sampling time were reduced to a single value.

The mean solar absorption coefficients for *E. californica* were 83.9, 83.8, and 82.4 percent, and for *E. farinosa*, 71.7,

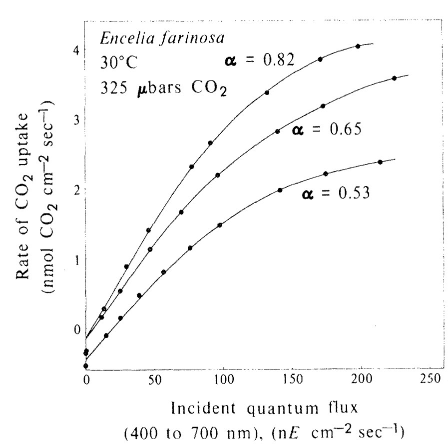

Fig. 2. Light dependence of net CO_2 uptake by single attached leaves of *Encelia farinosa* differing in their degree of pubescence. Rates were determined at a leaf temperature of 30°C, a CO_2 partial pressure of 325 μbar, an O_2 concentration of 21 percent by volume, and a water vapor pressure deficit of less than 10 mbar. Abbreviation: α, solar absorption coefficient.

63.4, and 52.5 percent, respectively, for sampling dates of December, March, and July. The range of values between sites averaged 2 and 10 percent for *E. californica* and *E. farinosa*, respectively, and the range within a site averaged 2 percent for both species. These field data show that the solar absorption coefficient for *E. californica* remains higher than that of *E. farinosa* at all times through the growing season. In addition, whereas the solar absorption coefficients for *E. californica* remained constant through the season, the coefficients for *E. farinosa* steadily declined as the season progressed. By July, *E. farinosa* averaged 30 percent less visible light absorbed than *E. californica*. This decrease in leaf absorptance by *E. farinosa* through the season occurred in conjunction with an increase in average maximum air temperatures. This correlation suggests a role for pubescence in modifying the leaf energy balance as the environment becomes more harsh so as to reduce leaf temperatures. Leaf size also decreases through the season, further providing a more favorable energy balance (*10*).

If pubescence is adaptive for *E. farinosa*, a positive correlation should exist between leaf absorptance and precipitation for sites occupied by this species. Solar absorption coefficients from each of the *E. farinosa* sites during March (the period of peak biomass) plotted against the precipitation received at the site during the current growing season before the sampling date (*11*) reveal a strong correlation ($r^2 = .995, P < .01$). This correlation suggests that (i) the reduction in energy absorbed by pubescent leaves is directly dependent on the aridity of the environment, and (ii) the degree of pubescence is a plastic response by the leaves to the amount of precipitation received. This response is responsible for most of the variation in solar absorption coefficients between *E. farinosa* sample sites. The possible correlation between pubescence and aridity on a community basis has been previously discussed (*4*), but solar absorption coefficients and correlation coefficients were not reported.

The decrease in light absorbed by pubescent *E. farinosa* leaves is sufficient to reduce the heat load of leaves. This reduction should be of selective advantage to *E. farinosa* in arid desert sites, since nearly 50 percent of the solar radiation load on the leaf is between 400 and 700 nm. Yet a reduction in the amount of light absorbed carries with it a disadvantage in that less light is available for photosynthesis. An inverse relationship between the degree of pubescence and the water availability to the plant would minimize the effects of pubescence on light-limited photosynthesis. The high correlation between solar absorption coefficients and precipitation serves as indirect evidence for such a relationship.

To determine to what degree pubescence would affect primary production, photosynthetic rates were measured on individuals of *E. farinosa* differing in their degree of pubescence. All plants were grown under conditions of sufficient water and nutrients and full sunlight in phytocells (environmentally controlled greenhouses) (*12*). Simultaneous measurements of CO_2 and water vapor exchange were made on single leaves with a leaf chamber and gas exchange system (*13*). All measurements were made in normal air (325 μbar CO_2 and 21 percent O_2).

Three significant features of the results (Fig. 2) are that (i) the incident quantum yield (slope of linear part of curve between 0 and 30 nE cm^{-2} sec^{-1}) decreases as the pubescence increases, (ii) the maximum rates decrease as pubescence increases, and (iii) unlike that in many plants, net photosynthesis under all three pubescence conditions is not light-saturated even at 200 nE cm^{-2} sec^{-1}, which is equivalent to full noon sunlight during the summer. Quantum yields on an incident light basis were 0.025, 0.033, and 0.041 for absorptances of 53, 65, and 82 percent, respectively. When calculated on the basis of absorbed quanta, the quantum yields were 0.048, 0.050, and 0.050, respectively. These yields, typical for higher plants (*14*), indicate that although pubescence in *E. farinosa* increases light reflectance and reduces net photosynthesis, it does not affect the basic photosynthetic process (CO_2 fixed per quantum absorbed). Net photosynthesis is so dramatically affected by pubescence that at a leaf absorptance of 53 percent, the net photosynthetic rate is nearly linear with light intensity up to full sunlight. Conductance values of water vapor and CO_2 into the leaf through the stomata were similar for the leaves at any given light intensity, which suggests that CO_2 diffusion limitations were not responsible for differences among the curves. When photosynthetic data from these three curves are plotted against absorbed rather than incident quanta, all data lie on a single curve; the principal differences among the curves were thus due primarily to decreases in light absorption resulting from pubescence rather than from physiological differences.

To the best of our knowledge, this study constitutes the first report that pubescence reduces the net photosynthetic rate. In our case the reduction is caused by decreased light absorption rather than by decreased CO_2 conductance through the boundary layer. Because of the dramatic effects of leaf pubescence on the energy balance and on net photosynthesis in *Encelia*, the genus appears to be a model system for studying the possible adaptive significance of pubescence and its effects on plants along aridity gradients.

JAMES EHLERINGER
OLLE BJÖRKMAN
Department of Plant Biology, Carnegie Institution of Washington, Stanford, California 94305
HAROLD A. MOONEY
Department of Biological Sciences, Stanford University, Stanford, California 94305

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