Oecologia (Berl.) 36, 151–162 (1978)

Oecologia

Pubescence and Leaf Spectral Characteristics in a Desert Shrub, *Encelia farinosa* *

J. R. Ehleringer** and O. Björkman

Department of Biological Sciences, Stanford University, and
Department of Plant Biology, Carnegie Institution of Washington, Stanford, CA 94305, USA

Summary. The effects of leaf hairs (pubescence) on leaf spectral characteristics were measured for the drought-deciduous desert shrub *Encelia farinosa.* Leaf absorptance to solar radiation is diminished by the presence of pubescence. The pubescence appears to be reflective only after the hairs have dried out. There are seasonal changes in leaf absorptance; leaves produced at the beginning of a growing season have high absorptances, whereas leaves produced during the growing season are more pubescent and have lower absorptances. The decrease in leaf absorptance is the result of an increase in pubescence density and thickness. Between 400 and 700 nm (visible wavelengths), pubescence serves as a blanket reflector. However, over the entire solar spectrum (400–3000 nm), the pubescence preferentially reflects near infrared radiation (700–3000 nm) over photosynthetically useful solar radiation (400–700 nm). Leaf absorptance to solar radiation (400–3000 nm) varies between 46 and 16%, depending on pubescence; whereas leaf absorptance to photosynthetically useful radiation (400–700 nm) may vary from 81 to 29%.

Introduction

The desert environments of southwestern North America are typically characterized by high levels of incoming solar radiation, high summer air temperatures, and limited amounts of moisture (MacDougal, 1908; Shreve and Wiggins, 1964; Sellers and Hill, 1974). These environmental factors have selected for a diversity of morphological and physiological adaptations in plants to cope with the harsh conditions (MacDougal, 1908; Shields, 1950; Oppenheimer, 1960; Shreve and Wiggins, 1964). Many desert species, however, avoid the stresses imposed by high temperature and drought by restricting their activities to the relatively brief mesic periods following rains. In this category would be the ephemeral annuals and perennial shrubs with drought-deciduous leaves.

* C.I.W.–D.P.B. Publication No. 612

** *Present address and address for offprint requests:* Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

0029-8549/78/0036/0151/$02.40

Several drought-deciduous species produce new leaf types in response to the transition from mesic to xeric conditions (Shreve, 1924; Zohary, 1961; Orshan and Zand, 1962; Cunningham and Strain, 1969). By doing so, these plants are presumably able to extend the period of their activity beyond that of annual species or other drought-deciduous species that do not produce new leaf types. One such drought-deciduous species, capable of producing new leaf types in response to changes in environmental conditions, is *Encelia farinosa* (Shreve, 1924; Walter, 1931; Cunningham and Strain, 1969), a member of the Heliantheae tribe of the family Compositae. *Encelia farinosa* occurs throughout most of the Sonoran Desert, extending into portions of the Mojave desert (Shreve and Wiggins, 1964). Through the course of a growing season, *Encelia farinosa* responds to the increases in temperature and aridity by producing new leaves which are more pubescent than earlier ones (Ehleringer et al., 1976) and leaves which are thicker and contain smaller, more densely packed palisade cells (Shreve, 1923; Cunningham and Strain, 1969).

The observation that a species produced more pubescent leaves under xeric than under mesic conditions has been noted by Schimper (1903), Warming (1909), Coulter et al. (1911), and Clausen et al. (1940) and has been inferred to be an adaptation to the xeric conditions. Leaf pubescence may be of adaptive benefit to leaves by reflecting light (Billings and Morris, 1951; Pearman, 1966; Sinclair and Thomas, 1970; Ehleringer et al., 1976) in high light environments, although this is not always the case (Shull, 1929; Gausman and Cardenas, 1969, 1973; Wuenscher, 1970). Leaf pubescence may possibly increase the thickness of the leaf boundary layer (Wooley, 1964), thus reducing the rate of water loss in water limited habitats.

In a preliminary study, Ehleringer et al. (1976) have shown that leaf pubescence in *E. farinosa* may reflect up to 70% of the incoming solar radiation between 400 and 700 nm, absorbing only 29% of the radiation in these wavelengths. It is the solar radiation between 400 and 700 nm (visible spectrum) that is photosynthetically active. In contrast, green glabrous leaves typically absorb 85% of the solar radiation between 400 and 700 nm (Gates et al., 1965; Ross, 1975). *Encelia californica,* a closely related species to *E. farinosa,* occurs in more mesic habitats along the coast of southern California, and its green glabrous leaves typically absorb 84% of the 400 to 700 nm solar radiation (Ehleringer et al., 1976). As solar radiation between 400 and 700 nm represents nearly 80% of all the solar energy absorbed by leaves, pubescent *E. farinosa* leaves should be under a significantly lower heat load than glabrous leaves in similar environmental conditions.

This study will concentrate on exploring further the reflective properties of leaf pubescence in *E. farinosa* and its effect on energy balance and leaf temperature under desert conditions.

Methods and Materials

Leaf absorptances in the 400 to 700 nm band were measured with an Ulbricht integrating sphere (23 cm diameter), coated on the inside with a thin layer of magnesium oxide. Monochromatic light was provided by a xenon lamp attached to a Bausch and Laumb high intensity grating monochromator. A silicon cell attached from the outside to the inside wall was used to measure the absorptance at the different wavelengths. The theory and description of the Ulbricht integrating sphere have been discussed by Rabideau et al. (1946). Absorptances for the 400 to 700 nm band were measured by directing sunlight into the integrating sphere (via a mirror attached to a heliostat) through the same opening that was used for the monochromatic beam. Unless otherwise mentioned absorptances as used in this study are the absorptance by the leaf to solar radiation in the 400 to 700 nm waveband. A quantum sensor (model 190-SR, Lambda Instruments, Lincoln, Nebraska), attached to the integrating sphere, was used to measure leaf absorptances in the 400 to 700 nm band.

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. To evaluate the effects of leaf pubescence on solar quantum absorptance versus solar energy absorptance, absorptance curves for leaves of *E. farinosa* with different amounts of pubescence were integrated with curves of the solar quantum spectrum and solar energy spectrum at the earth's surface. Over the range of 400 to 700 nm, the absorptance differences between quantum absorption and energy absorption were less than one percent. Consequently, for practical purposes the quantum absorptance and energy absorptance by *Encelia* leaves over the visible wavelength region may be used interchangeably.

Leaf absorptances to the entire solar spectrum (400–3000 nm) were measured with a magnesium oxide coated integrating sphere (13 cm diameter) similar to the one described by Birkebak and Birkebak (1964). The differences between their sphere and the one used in this study were that in the present study 1) a filter holder was placed just outside the incoming port so that absorptances in particular wavebands could be studied and 2) the reference standards and samples were placed in the same port manually rather than with a rotational device. The integrating sphere was insulated with 2.5 cm of rubber foam on the outside to dampen any thermal gradients. A very sensitive thermopile (model BI-6, Hy-Cal Engineering, Santa Fe Springs, Calif.) was used to measure the reflectance and transmittance of leaves relative to the reference standard magnesium oxide. Absorptance was calculated as one minus the transmittance and reflectance.

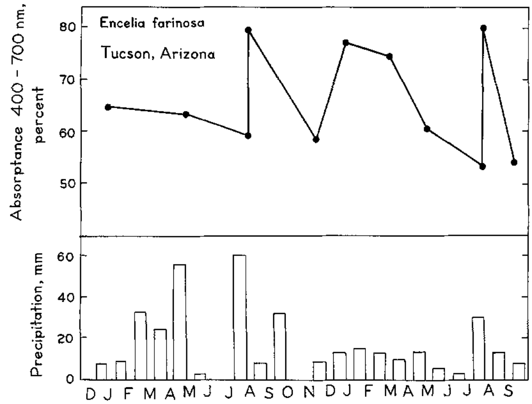
Scanning electron microscope (SEM) observations of the structure of *Encelia* leaves and leaf hairs were made with a field emission scanning electron microscope (model 100-2, Coates and Welter, Sunnyvale, Calif.). Samples were prepared by drying pieces of fresh leaf tissue kept overnight in an osmium tetroxide-filled jar. The leaf tissue was dried in acetone in seven steps, increasing from 10 to 100%. The samples were then dried using a CO_2 critical point drying apparatus (Sorvall, Newton, Conn.) and mounted on stubs. Following this step, a gold-palladium mixture was evaporated onto the leaf surfaces.

Seasonal observations of *E. farinosa* shrubs in the field were made on Tumamoc Hill, Arizona (32° 15′ N, 110° 57′ W). The Tumamoc Hill study site is located at the edge of the city of Tucson, Arizona, at an elevation of approximately 750 m. The study area is the site of the old Carnegie Institution of Washington Desert Laboratory. The vegetation of the area is characteristic for the Arizona Upland in the Sonoran Desert (Shreve and Wiggins, 1964). The dominant perennial species include *Acacia greggii, Carnegia gigantea, Cercidium microphyllum, Encelia farinosa, Ferocactus Wislizenii, Larrea divaricata,* and *Prosopis juliflora.* Rainfall patterns are Tumamoc Hill are distinctly bimodal; there are definite winter and summer rainy periods. Approximately 50% of the total annual precipitation (270 mm) falls in each of the rainy seasons. Mean daily maximum air temperatures are 38.3° C for July and 18.9° C for January (U.S. Weather Bureau records).

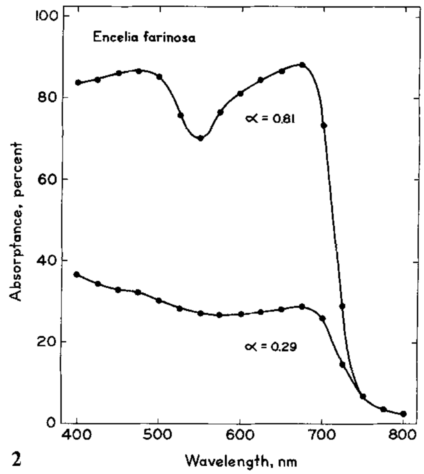
Results

Seasonal Changes in Leaf Absorptance

Seasonal observations of leaf absorptance for *Encelia farinosa* leaves on Tumamoc Hill were followed for the period December, 1974 through late September, 1976 (Fig. 1). These data show that a large variation in leaf absorptance can be found at a single site during the year. Leaf absorptances to visible solar



1



2

Fig. 1. Leaf absorptances of *Encelia farinosa* and precipitation data for Tumamoc Hill in Tucson, Arizona

Fig. 2. Extremes in pubescence differences for leaves of *Encelia farinosa*

radiation varied from a high of 80% at the beginning of a growing season to a low of 52% during the dry between growing seasons. As is characteristic of many portions of the Sonoran Desert, there is a distinct winter rain period (November through May) and a distinct summer rain period (July through September). The present results show the dramatic increase that takes place in the absorptances of *E. farinosa* leaves in response to the commencement of the rainy periods at both times of the year. The new leaves that are formed at these times of the year are very lightly pubescent and are green in color. As the season progresses, the new leaves that are formed are increasingly more pubescent and consequently have lower leaf absorptances. This variable pattern of leaf absorptance changes is seen to correlate well with the precipitation patterns. It is noteworthy that leaves formed during a single growing season appear not to have greater absorptances than the leaves formed at the beginning of the season, even though there may have been large amounts of rainfall occurring in the middle of the season.

It thus appears that the greenest leaves on a stem occur at the beginning of the season, and that all leaves formed later are progressively more pubescent. After a period of relatively little activity, such as between rainy seasons, the apical meristemic region in effect "resets" itself and once again produces green leaves in the next rainy season.

Spectral and Morphological Pubescence Characteristics

There is a significant difference in the amount of pubescence present on leaves of *E. farinosa* at different times during the growing season. To characterize the effects that the observed extremes in pubescence have on leaf absorptance, the absorptance spectrum of a lightly pubescent, greenish *E. farinosa* leaf was compared to that of a heavily pubescent, white *E. farinosa* leaf (Fig. 2). The greenish leaf showed a strong absorptance at most wavelengths between 400 and 700 nm, whereas the absorptance at all wavelengths between 400 and 700 nm of the heavily pubescent was very much reduced. Leaf absorptances in the 400 to 700 nm waveband were 81 and 29% for the lightly pubescent and heavily pubescent leaves, respectively. This large difference could conceivably arise in either of two ways or a combination of these two ways. First, the thickness of the pubescent layer could increase and the reflectance would increase proportionally; second, the thickness of the pubescent layer could remain constant and the density of hairs within the layer could increase thereby causing an increase in light reflectance. To explore this matter further, samples of leaves with absorptances similar to the two leaves of Figure 2 were observed using the scanning electron microscope (SEM). Figure 3 shows micrographs of cross-sections and dorsal views of the two leaf types at a magnification of 150 X. The lightly pubescent leaf seen in cross-section (Fig. 3A) has rather loosely arranged hairs, approximately 0.1 mm thick and of relatively low density. A dorsal view of this leaf (Fig. 3B) reveals that the pubescence is sufficiently scattered to expose most of the upper epidermal surface.

The heavily pubescent leaf (Fig. 3C) in contrast possesses an extremely thick layer of hairs on either side of the leaf. The thickness of these pubescence layers averaged 0.3 mm on each side, equivalent to the thickness of the photosynthetic leaf tissue itself. The pubescence layer is not only thicker, but the hairs appear to be more densely arranged than in the lightly pubescent leaf. Whether there is an increase in hair density or whether the hairs are just much longer and give the appearance of an increase in number is not clear from these micrographs. A dorsal view of the heavily pubescent leaf shows the tangled nature of this layer. The flat epidermal surface can not be seen. Thus, all light absorbed by the photosynthetic tissues of a heavily pubescent leaf must diffuse through the hairs by multiple reflection. The significance of this phenomenon will be discussed later.

Increased magnification of the leaf hairs of the lightly pubescent leaf reveals that the hairs are multicellular and turgid (Fig. 4A). The leaf hairs appear to consist of some five to six cells. From additional light microscope observations, it is known that the cells of the hairs in lightly pubescent *E. farinosa* leaves are alive and fluid-filled. On some of these hairs, however, the tip cell or a portion of this cell is dead and has shrunk to assume a ribbon-like shape.

Closer examination of the leaf hairs of the heavily pubescent leaf shows that the hairs are mostly dead and air-filled (Fig. 4B). These hairs are extremely long and laterally compressed, giving a curly ribbon-like appearance. Cross-sections of leaves under the light microscope support the SEM Observation that the reflective hairs are dead and air-filled.

The cross-section of the lightly pubescent leaf clearly shows the mesic characteristic of that leaf type. The palisade cells are loosely arranged and relatively large in size. Overall the palisade-mesophyll cell layers are thin when compared to those of the heavily pubescent leaf. The heavily pubescent leaf is much thicker and its cells are more closely packed and smaller in size than those of the mesic leaf type. This is in spite of the fact that both leaf types developed under conditions of full sunlight.

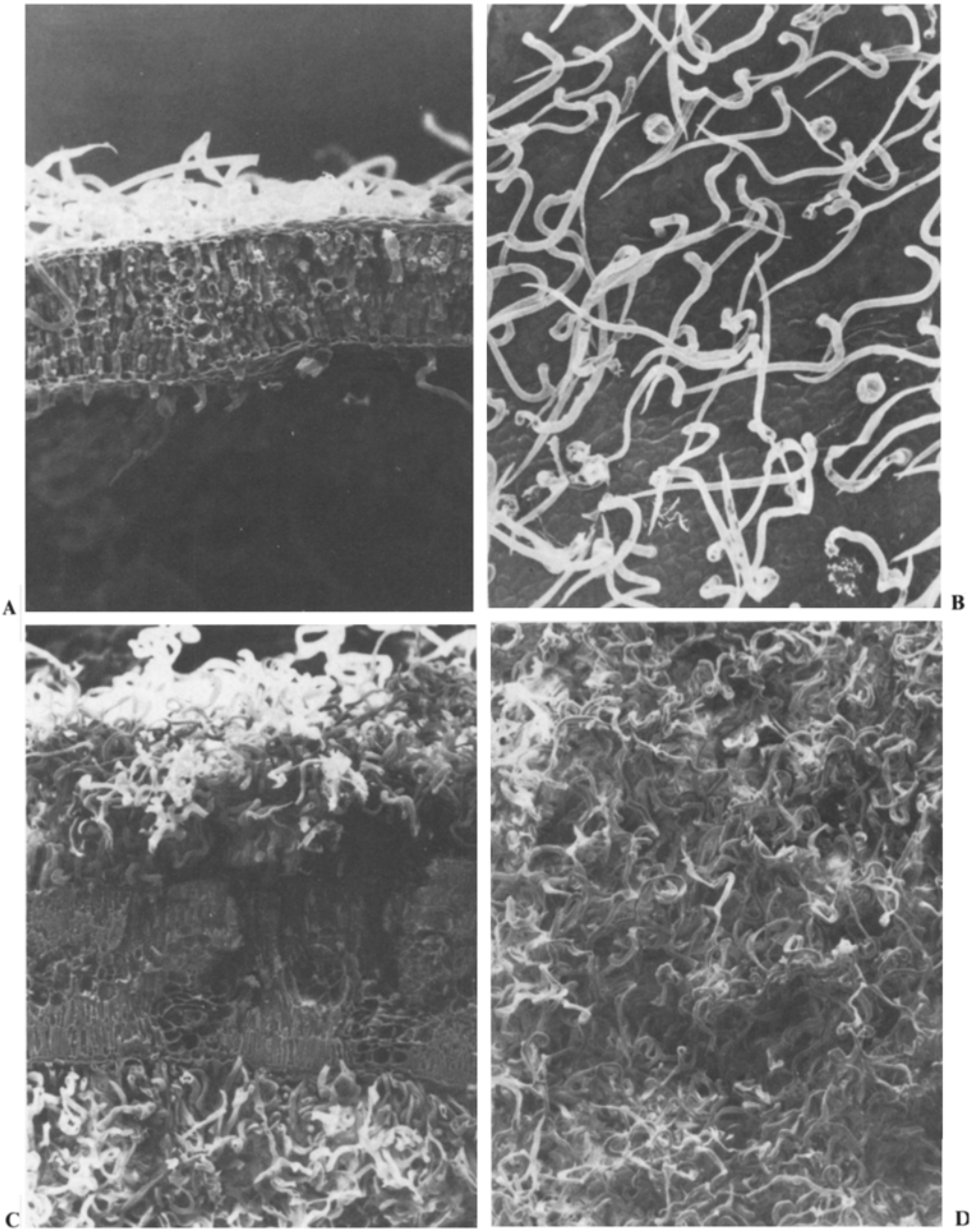
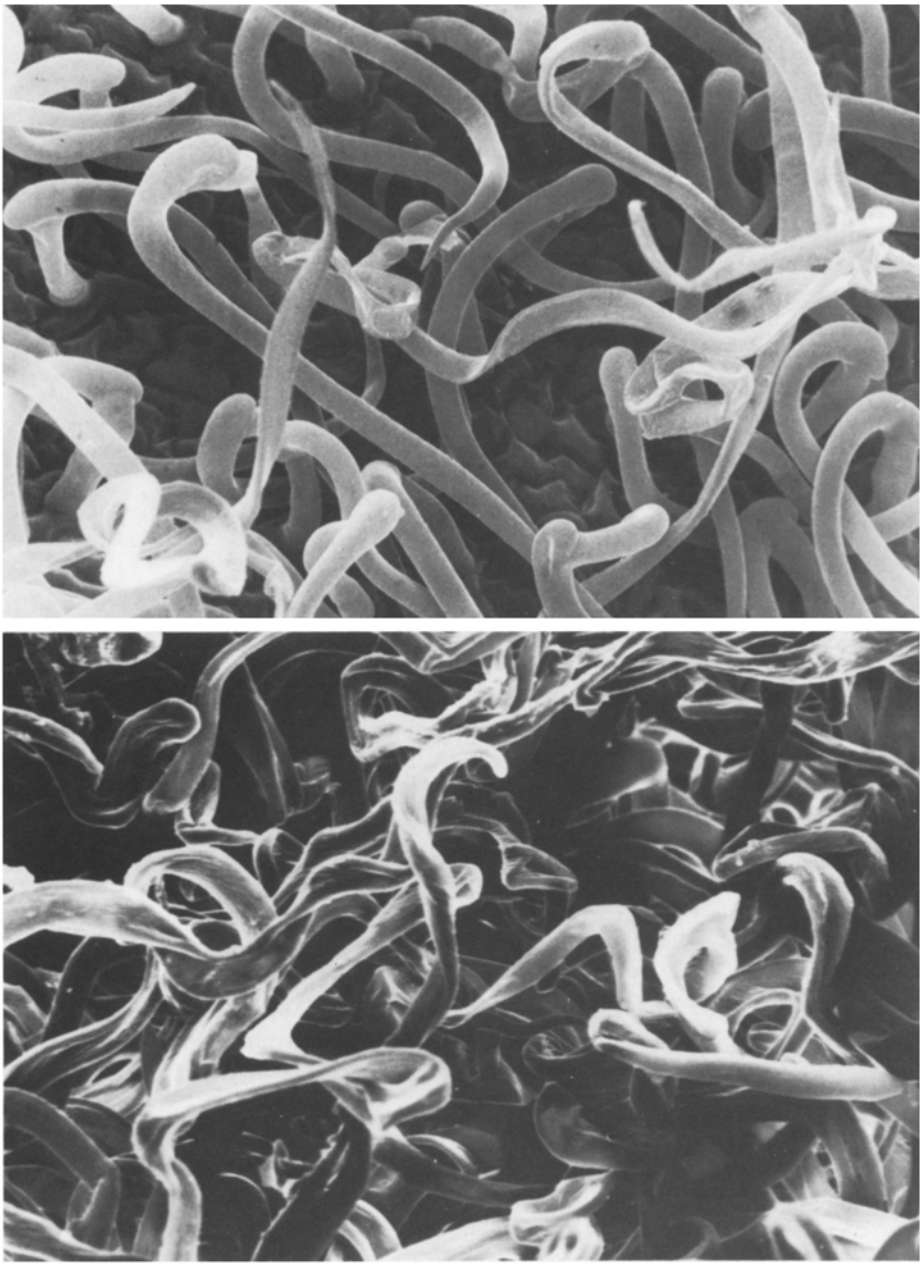


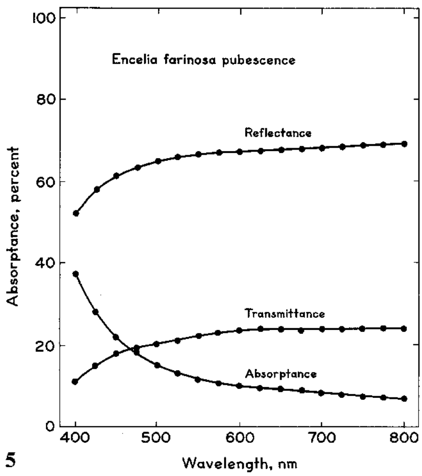
Fig. 3A–D. SEM micrographs of two *Encelia farinosa* leaves differing in pubescence. **A** shows a cross section of a lightly pubescent leaf. **B** is a dorsal view of this same leaf. **C** is a cross section of a heavily pubescent leaf. **D** is a dorsal view of the heavily pubescent leaf. Magnification on all micrographs is X 150



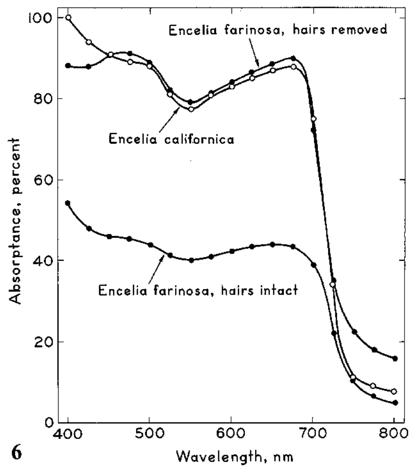
A

B

Fig. 4 A and B. Increased magnification views of leaf pubescence. **A** shows the hairs of a lightly pubescent leaf. **B** is of a heavily pubescent leaf. Magnification for both micrographs is X 700



5



6

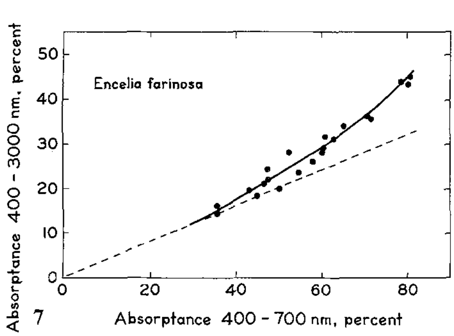
Fig. 5. Spectral characteristics of *Encelia farinosa* pubescence

Fig. 6. Leaf absorptance spectra for *Encelia farinosa* with hairs intact and after the hairs had been removed and the leaf absorptance spectrum for an intact *E. californica* leaf

In summary it would appear that increased reflectance of *E. farinosa* leaves is caused by an increase in both the thickness and the density of the leaf pubescence layer as well as in the proportion of dead air-filled cells.

To assess the absorptance properties of the thick pubescence layer, the hairs were carefully removed from the upper surface of an *E. farinosa* leaf using a razor. The absorptance of this leaf before the removal of the hairs was approximately 30% (400–700 nm). The pubescence was then mounted on a piece of clear transparent tape to create a thickness approximately equivalent to the thickness of the pubescence on the intact leaf. The absorptance of the clear tape had been measured previously and was approximately 2% at all wavelengths between 400 and 800 nm. Figure 5 shows the reflectance, transmittance, and absorptance characteristics of this thick pubescence layer. The pubescence layer appears to be serving as a blanket reflector between 400 and 800 nm, reflecting nearly 70% of the incoming light. There is a small increase in absorptance below 450 nm. This increase in absorptance by epidermal cells in the UV and near-UV regions has been reported by Gausman et al. (1975) for several sun leaf species.

If the pubescence layer is indeed a blanket reflector in the 400 to 700 nm region, the removal of the pubescence from *E. farinosa* should produce an absorptance spectrum similar to that of the closely related, but non-pubescent coastal species *E. californica*. In Figure 6 are plotted the absorptance spectra of an *E. farinosa* leaf before and after the hairs had been removed, and for comparison also that of an intact *E. californica* leaf. It is clear from these spectra that an *E. farinosa* leaf from which the pubescence has been removed is essentially identical to the non-pubescent *E. californica* leaf over the wavelengths 400 to 700 nm. A reasonable conclusion from these data is that the absorption spectra of intact *E. farinosa* leaves are the products of the spectra



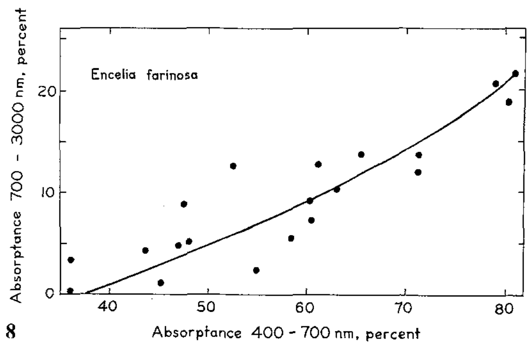


Fig. 7. Total solar leaf absorptance for *Encelia farinosa* as a function of the 400 to 700 nm leaf absorptance

Fig. 8. Leaf absorptances of *Encelia farinosa* to near infrared radiation as a function of leaf absorptance to visible radiation

of normal green leaves and that of a reflectant, pubescence, reflecting equally well at all wavelengths between 400 and 800 nm.

Leaf Absorptances—Total and near Infrared

To determine the effects that pubescence in *E. farinosa* may have on energy balance and leaf temperature via solar radiation absorptance, the 400 to 3000 nm solar absorptances of *E. farinosa* leaves with different amounts of pubescence were measured. Solar absorptance values (400–3000 nm) were found to vary from 46% in lightly pubescent leaves to 16% in heavily pubescent leaves. The 400 to 3000 nm absorptances are presented plotted against the 400 to 700 nm absorptances of the same leaf (Fig. 7). In this manner, the strong correlation between visible radiation absorptance and total solar radiation absorptance is evident. The significant variation in total solar absorptances will assuredly affect the leaf energy balance as there is nearly a three fold difference between the least and most pubescent *E. farinosa* leaves.

The dashed line of Figure 7 represents the relationship between total solar absorptance and visible radiation absorptance to be expected for a leaf that was absorbing only visible radiation, and no near infrared solar radiation. Any point lying above this dashed line then represents a leaf which is absorbing near infrared radiation (700–3000 nm). Moreover, the percentage of near infrared radiation absorbed will be directly proportional to the vertical distance between the data point and the dashed line. From the deviation of the data from the dashed line of Figure 7, it is clear that leaves of *E. farinosa* vary in the percentage of near infrared radiation absorbed. The percentage of near infrared radiation absorbed versus visible radiation absorptance has been calculated and is shown in Figure 8. The percentage of near infrared radiation absorbed by the leaf is inversely related to the degree of pubescence. In other words, heavily pubescent leaves will absorb very little if any of the sun's near infrared radiation, while lightly pubescent leaves may absorb as much as 22% of this near infrared radiation.

Discussion

In this study, the presence of pubescence on *Encelia farinosa* leaves has been shown to result in an increased light reflectance by the leaf surface. Reflectance in the visible portion of the solar spectrum (400 to 700 nm) by *E. farinosa* leaves reaches 71% in the most extreme case (Ehleringer et al., 1976). In contrast, a normal green leaf reflects only about 10 percent of the visible solar radiation (Moss and Loomis, 1952; Gates et al., 1965; Ross, 1975). Previous studies of the reflectance properties of species with pubescent leaves have also found that light reflectance was greater than in nonpubescent leaves (Billings and Morris, 1951; Pearman, 1966; Sinclair and Thomas, 1970). The most extreme reflectance reported for upper leaf surfaces in previous studies was 32% in *Arctotheca nivea* (Pearman, 1966), a sand dune species. This value is much less than those reported for *E. farinosa.* However, the presence of leaf hairs does not always result in an increased light reflectance. The reflectance values of leaves from several pubescent species were equal to those of glabrous leaves (Gausman and Cardenas, 1969, 1973; Wuenscher, 1970). Perhaps the reflectance properties of pubescent leaves depend on whether the leaf hairs are alive and fluid filled or whether they are dead and air filled.

An understanding of the absorptance characteristics of leaves between 400 and 700 nm is valuable for two reasons. First, it is only the energy in this waveband that is useful for photosynthesis. Second, although only 50% of the sun's energy reaching the earth's surface is between 400 and 700 nm, nearly 80% of the total solar energy absorbed by green leaves is in this waveband. The explanation for this lies in the observation that, while 50% of the sun's energy at the earth's surface is between 700 and 3000 nm (near infrared), water is the only leaf component absorbing significantly in this waveband. Thus, whereas most green leaves will absorb an average of 85% of the solar energy between 400 and 700 nm (Gates et al., 1965; Björkman, 1973; Ross, 1975), the absorptance between 400 and 3000 nm averages only 50% (Birkebak and Birkebak, 1964).

Since near infrared solar radiation can not be used in photosynthesis, the main effect of absorbing this radiation is an increase in the heat load of the leaf. In general, it would therefore be to the plant's advantage to reduce the absorption of near infrared radiation in hot, arid environments. The high water content of the epidermal cells of most green leaves precludes a large reduction in the absorptance in the near infrared region. However in *E. farinosa* leaves the outer pubescent layer contains not live, water filled cells, but dead, air filled cells. As a consequence, the pubescence reduces not only the absorption of visible radiation, but also of near infrared solar radiation. As leaf pubescence increases, the near infrared radiation absorption declines faster than does the visible radiation absorption. This is highly advantageous to the leaf. These absorptance data also indicate that the pubescence does not serve as a blanket reflector over the entire solar spectrum, reducing absorptance equally at all wavelengths. Instead, the pubescence preferentially reduces the absorption in the near infrared waveband.

The reduction in absorptances of near infrared radiation is made possible by the presence of dead air filled hairs. Apparently, these hairs have a greater near infrared reflectance than water filled cells, although no measurements were made to verify this. Wong and Blevins (1967) have measured the near infrared reflectances of pubescent leaves from the composite *Gazania*. They found that the near infrared reflectance was greater for this species than it was for other glabrous species.

The advantages to having a layer of hairs in the upper leaf surface are evident from the preceding discussion. In *E. farinosa,* however, leaf hairs are present on both upper and lower surfaces in equal thicknesses. The value of having reflective hairs on the lower leaf surfaces does not become evident until one also considers components of solar radiation reflected from the ground surface and from other leaves. As the soil surface dries out, the reflectivity of near infrared radiation increases much faster than that of visible radiation (Bowers and Hanks, 1965; Bowers and Hayden, 1967). This is due to a decrease in the concentration of water in the soil. Since the dead hairs on the lower leaf surface act as a near infrared reflector, absorption of much of the photosynthetically inactive radiation reflected from the soil and other leaves is avoided.

The range of leaf absorptances to total solar radiation varies over 300%. Leaf absorptance values of the greenest and least pubescent *E. farinosa* leaves are quite similar to values reported for most leaves (Birkebak and Birkebak, 1964; Ross, 1975). However, leaf absorptances for the heavily pubescent leaves are far below those values reported for other species. The effects of this substantial decrease in leaf absorptance on leaf energy balance, leaf temperature, and transpiration rate are considered in a separate paper now in preparation.

Acknowledgments. We thank H.A. Mooney, W.R. Briggs, and J.A. Berry for their helpful comments and advice and E. Ehleringer for her constant encouragement. Permission from the University of Arizona to use the Tumamoc Hill site was greatly appreciated. This study was supported by NSF Grant BMS 75-03933 to J.E. and by a Carnegie Institution of Washington Predoctoral Fellowship.

References

Billings, W.D., Morris, R.J.: Reflection of visible and infrared radiation from leaves of different ecological groups. Am. J. Bot. **38**, 327–331 (1951)

Birkebak, R., Birkebak R.: Solar radiation characteristics of tree leaves. Ecology **45**, 646–649 (1964)

Björkman, O.: Comparative studies on photosynthesis in higher plants. In: Photophysiology, Vol. 8, pp. 1–63. New York: Academic Press 1973

Bowers, S.A., Hanks, R.J.: Reflection of radiant energy from soils. Soil Sci. **100,** 130–138 (1965)

Bowers, S.A., Hayden, C.W.: A simple portable reflectometer for field use. Agron. J. **59**, 490–492 (1967)

Clausen, J.D., Keck, D., Hiesey, W.M.: Experimental studies on the nature of species. I. The effect of varied environments of western North American plants. Carnegie Inst. Washington Publ. 520 (1940)

Coulter, J.M., Barnes, C.R. Cowles, H.C.: A text book of botany for Colleges and Universities, Vol. II. Ecology. New York: Amer. Book 1911

Cunningham, G.L., Strain, B.R.: An ecological singificance of seasonal leaf variability in a desert shrub. Ecology **50**, 400–408 (1969)

Ehleringer, J., Björkman, O., Mooney, H.A.: Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub. Science **192**, 376–377 (1976)

Gates, D.M., Keegan, H.J., Schleter, J.C., Weidner, V.R.: Spectral properties of plants. Appl. Optics **4**, 11–20 (1965)

Gausman, H.W., Cardenas, R.: Effect of leaf pubescence of *Gynura aurantiaca* on light reflectance. Bot. Gaz. **130**, 158–162 (1969)

Gausman, H.W., Cardenas, R.: Light reflectance by leaflets of pubescent, normal, and glabrous soybean lines. Agron. J. **65**, 837–838 (1973)

Gausman, H.W., Rodriguez, R.R., Escobar, D.E.: Ultraviolet radiation reflectance, transmittance, and absorption by plant leaf epidermises. Agron. J. **67**, 720–724 (1975)

MacDougal, D.T.: Botanical features of North American deserts. Carnegie Inst. Washington Publ. 99 (1908)

Moss, R.A., Loomis, W.E.: Absorption spectra of leaves. I. The visible spectrum. Plant Physiol. **27**, 370–391 (1952)

Oppenheimer, H.R.: Adaptation to drought: xerophytism. In: Plant-water relationships in arid and semi-arid conditions, pp. 105–138. Paris: UNESCO 1960

Orshan, G., Zand, G.: Seasonal body reduction of certain desert half shrubs. Bull. Res. Counc. Israel Sec. D. Bot. **110**, 35–42 (1962)

Pearman, G.I.: The reflection of visible radiation from leaves of some western Australian species. Aust. J. Biol. Sci. **19**, 97–103 (1966)

Rabideau, G.S., French, C.S., Holt, A.S.: The absorption and reflection spectra of leaves, chloroplast suspensions, and chloroplast fragments as measured in an Ulbricht sphere. Am. J. Bot. **33**, 769–777 (1946)

Ross, J.: Radiative transfer in plant communities. In: Vegetation and atmosphere, Vol. 1, pp. 13–55. London: Academic Press, 1975

Schimper, A.F.W.: Plant geography upon a physiological basis. Oxford: Clarendon 1903

Sellers, W.D., Hill, R.H.: Arizona Climate 1931–1972. Tucson: Univ. of Arizona 1974

Sheilds, L.M.: Leaf xeromorphy as related to physiological and structural influences. Bot. Rev. **16**, 399–447 (1950)

Shreve, E.B.: Factors governing seasonal changes in transpiration of *Encelia farinosa*. Bot. Gaz. **77**, 432–439 (1924)

Shreve, F., Wiggins, I.L.: Vegetation and flora of the Sonoran Desert. Stanford: Stanford University Press 1964

Shull, C.A.: A spectrophotometric study of reflection of light from leaf surfaces. Bot. Gaz. **87**, 583–607 (1929)

Sinclair, R., Thomas, D.A.: Optical properties of leaves of some species in arid South Australia. Aust. J. Bot. **18**, 261–273 (1970)

Walter, H.: Die Hydratur der Pflanze. Jena: Fischer 1931

Warming, E.: Oecology of plants: an introduction to the study of plant communities. London: Oxford University Press 1909

Wong, C.L., Blevin, W.F.: Infrared reflectances of plant leaves. Aust. J. Biol. Sci. **20**, 501–508 (1967)

Wooley, J.T.: Water relations of soybean leaf hairs. Agron. J. **56**, 569–571 (1964)

Wuenscher, J.E.: The effect of leaf hairs of *Verbascum thapsus* on leaf energy exchange. New Phytol. **69**, 65–73 (1970)

Zohary, M.: On hydro-ecological relations of the Near East desert vegetation. In: Plant-water relationships in arid and semi-arid conditions, pp. 199–212. Paris: UNESCO 1961

Received December 15, 1977