Leaf Hairs: Effects on Physiological Activity and Adaptive Value to a Desert Shrub*

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Summary. The effects of leaf hairs on photosynthesis, transpiration, and leaf energy balance were measured on the desert shrub *Encelia farinosa* in order to determine the adaptive significance of the hairs. The pubescence reduces leaf absorptance resulting in a reduced heat load, and as a consequence lower leaf temperatures and lower transpiration rates. In its native habitat where air temperatures often exceed 40° C, the optimum temperature for photosynthesis in *E. farinosa* occurs at 25° C, and at leaf temperatures above 35° C net photosynthesis declines precipitously. An advantage of leaf pubescence is that it allows a leaf temperature much lower than air temperature. As a result, leaf temperatures are near the temperature optimum for photosynthesis and high, potentially lethal leaf temperatures are avoided. However, there is a disadvantage associated with leaf pubescence. By reflecting quanta that might otherwise be used in photosynthesis, the presence of leaf hairs reduces the rate of photosynthesis. A tradeoff model was used to assess the overall advantage of possessing leaf hairs. In terms of the carbon gaining capacity of the leaf, the model predicted that for different environmental conditions different levels of leaf pubescence were optimal. In other words, under arid conditions and/or high air temperatures, leaves of *E. farinosa* would have a higher rate of photosynthesis by being pubescent than by not being pubescent. The predictions from this model agreed closely with observed patterns of leaf pubescence in the field.

Introduction

One of the striking features of the leaves of many desert plants is the presence of pubescence (hairs). The presence of this leaf pubescence has long been positively associated with arid climates (Schimper, 1903; Warming, 1909; Coulter
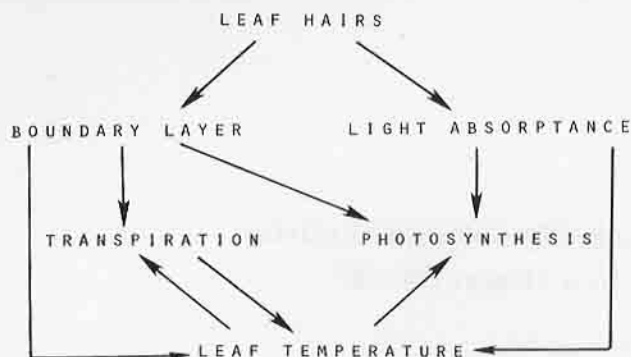
Fig. 1. Interactions between leaf hairs and leaf physiological processes

et al., 1911; Clausen et al., 1940). Largely based on these early observations of the distribution of leaf pubescence among plants, it was deduced that leaf hairs were an adaptive feature of plants occupying arid habitats (Coulter et al., 1911; Skene, 1924; Hare, 1941; Oppenheimer, 1960). There is, however, little or no experimental evidence to show that this is indeed the case.

While the adaptive significance of leaf hairs to arid land plants has not been demonstrated, several studies have concentrated on the effects of these hairs on leaf properties. These properties include the effects of pubescence on leaf spectral characteristics and the effects of pubescence on leaf boundary layer resistance. Leaf pubescence has been shown to increase light reflectance from the leaf surface (Billings and Morris, 1951; Pearman, 1966; Sinclair and Thomas, 1970; Ehleringer et al., 1976), although this is not always the case (Shull, 1929; Gausman and Cardenas, 1969; Wuenscher, 1970; Gausman and Cardenas, 1973). Leaf pubescence is thought also to possibly increase the thickness of the leaf boundary layer (Wooley, 1964; Wuenscher, 1970).

In recent studies, Ehleringer et al. (1976) and Ehleringer and Björkman (1978a) have documented the effects of leaf pubescence on leaf spectral properties in the desert shrub *Encelia farinosa*. It was found in those studies that during the course of a growing season *E. farinosa* produces leaves with different amounts of leaf pubescence. The variation in leaf pubescence is of sufficient magnitude to reduce the leaf absorptance to photosynthetically active solar radiation (400 to 700 nm) from 81 to 29 percent and the leaf absorptance to total solar radiation (400 to 3000 nm) from 46 to 16 percent. In contrast, *E. californica*, a closely related but nonpubescent species had a leaf absorptance of 84 percent (400 to 700 nm). The thickness of the hairs in densely pubescent *E. farinosa* leaves can be as thick as 0.35 mm.

The purposes of this study are to determine (1) What are the effects of the leaf pubescence in *E. farinosa* on physiological activity, and (2) the overall impact of leaf pubescence in order to assess its possible adaptive significance.

The presence of leaf hairs is thought to modify leaf properties and physiological processes through several defineable interactions (Fig. 1). The leaf hairs may modify leaf absorption and boundary layer characteristics. The decrease

in solar radiation absorption may be limited to the 400 to 700 nm (photosyntheti-cally useful wavelengths) or it may also be significant in the 700 to 3000 nm waveband (heating effects only). A decrease in absorptance in the shorter wave-band will directly affect the process of photosynthesis and transpiration. Photo-synthesis is a temperature dependent process at both low and high light levels (Björkman, 1973; Ehleringer and Björkman, 1978b). Transpiration will be de-pendent of leaf temperature, since the saturation water vapor pressure at leaf temperature is a determining factor in the driving force for transpiration (Gates, 1965).

An increase in leaf boundary layer resistance will directly influence both photosynthesis and transpiration through its effect on restricting 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 was discussed previously.

From Figure 1, it is thus clear that leaf hairs can be expected to have both direct and indirect effects on physiological leaf processes. The interactions between leaf hairs, leaf physical characteristics, and the rates of physiological processes are tightly coupled. An understanding of the possible adaptive signifi-cance, if any, of the leaf hairs to the plant can not be obtained without first quantifying the effects of the hairs on physiological processes.

Methods and Materials

Leaf absorptances in the 400 to 700 nm band were measured with an Ulbricht integrating sphere (23 cm diameter) in a manner similar to that described by Ehleringer and Björkman (1978a).

For laboratory measurements of photosynthesis, transpiration, and leaf biochemical parameters, plants were grown from seed in 10 cm pots containing perlite. These were watered twice daily with nutrient solution (Medina, 1970). The plants were grown in phytocells (environmental growth facilities capable of precise control of the temperature, CO_2, and water vapor levels) under either a 35° C day and 25° C night regime (phytocell A) or a 20° C day and a 15° C night regime (phytocell B). Light was provided by natural sunlight. Attenuation of the solar beam by the phytocell glass and structural support was about 20 percent. A more complete description of the phytocells has been provided by Björkman et al. (1973).

For gas exchange measurements on an incident light basis, a single attached leaf was inserted into a ventilated open system leaf chamber (total volume 150 ml) similar to that described by Björkman and Holmgren (1963). Light was provided from a 2.5 kW short arc xenon lamp (Christie Electric Corp., Los Angeles) in conjunction with appropriate lenses, heat filters, and neutral density filters. Quantum flux incident on the leaves was continuously monitored with silicon cells that had been calibrated against a quantum sensor (model LI 190-SR, Lambda Instruments, Lincoln, Nebraska). Over 95 percent of the radiant energy was in the 400 to 700 nm waveband. For field measurements of photosynthesis, light was provided by a 1000 W metal arc lamp (Sylvania) together with appropriate housing and power supply (Hubbell Lighting Division, Oakland, California).

Leaf temperature was measured with very fine copper-constantan thermocouples attached to the lower surface and was adjusted by controlling the temperature of the leaf chamber water jackets. Gas from a cylinder containing 21 percent oxygen in nitrogen (CO_2 free air) was continuously and precisely mixed with 1.00 percent CO_2 in nitrogen by a high capacity gas mixing pump (model G-27/3-F, Wösthoff OHG, Bochum, Germany). The resulting gas stream was humidified by passing through a vessel, maintained at 5° C above the desired dew point. The vessel contained a large

area of Miracloth, which was wetted by capillary uptake of water that had been slightly acidified with sulfuric acid. The gas stream was then passed through a dual coil water jacketed condenser whose temperature was kept at the desired dew point. A small portion of this humidified gas stream was passed at a constant rate (250 ml min^{-1}) through a humidity sensor (hygrometer HM-111, Weathermeasure Corp., Sacramento, California) and then through the reference cell of a differential CO_2 analyzer (Model 865, Beckman Instruments, Fullerton, Calif.). Another portion (300 to 800 ml min^{-1}) was passed via an electronic flowmeter (model DP45, Validyne Corp., Northridge, California) to the leaf chamber. A portion (250 ml min^{-1}) of the gas returning from the chamber was passed through another humidy sensor, the sample cell of the differential CO_2 analyzer, and then through an oxygen analyzer (model 209, Westinghouse Electric Corp., Pittsburgh, Pa.). All sensor inputs were connected to a real time computer based data acquisition system (model S-9, Non-Linear Systems, Del Mar, California) described earlier by Björkman et al. (1973). The system was programmed to make appropriate linearizations, corrections, and conversions; and to compute rates of CO_2 and water vapor exchange, stomatal conductance to gaseous diffusion, and intercellular CO_2 pressure. It also provided a record of the incident quantum flux, leaf temperature, and of the oxygen, CO_2 and water vapor partial pressures in the leaf chamber. Several parameters were continously displayed on analog recorders, providing a backup record and permitting a qualitative assessment of the experimental manipulations. The gas exchange system was housed in a mobile laboratory which allowed use of the same system for both field and laboratory measurements.

Light absorptance values for individual leaves used in the experiments were determined with the apparatus described above.

In the photosynthesis—light response experiments, leaves were first exposed to light at an intensity of about 200 nE cm^{-2} s^{-1} (400 to 700 nm). After a constant photosynthetic rate had been obtained, the light was lowered in steps to total darkness, at each step allowing the leaf to attain a constant photosynthetic rate before advancing to the next lower light level. Leaf temperature was held constant during each experiment at 30° C. The CO_2 partial pressure was that of normal air (310 to 330 µbar) and the water vapor pressure deficit was kept at about 10 mbar.

For measurements of the temperature dependence of photosynthesis, the rates of photosynthesis and transpiration were initially measured with leaf temperature equal to 30° C. Incident light level was 170 nE cm^{-2}s^{-1}, ambient CO_2 pressure 325 µbar, and water vapor deficit less than 10 mbar. After photosynthetic equilibrium had been reached, the leaf temperature was lowered in several steps (usually 5° C each), again with a wait for equilibrium before the next temperature change. When photosynthesis at the lowest temperature had been measured, leaf temperature was increased to 30° C. After the photosynthetic rate at 30° C this second time had achieved a rate equal to the original value, the leaf temperature was increased in steps of 5° C each.

Results

Pubescence and Net Photosynthesis

Since pubescence increases light reflectance, less light is available for photosynthesis in pubescent leaves. The net photosynthetic rate of E. farinosa can thus be expected to be reduced at light intensities below those required for light saturation. This decrease in net photosynthetic rate under light limited conditions should be proportional to the increase in amount of light reflected. Additional effects on photosynthesis could result if the pubescence increases the boundary layer, thus increasing the resistance to CO_2 diffusion into the leaf.

To assess the effects of leaf pubescence on photosynthesis, the light dependence of net photosynthesis in individuals of E. farinosa differing in leaf absorptance (and thus amounts of pubescence) and also in non-pubescent E. californica leaves were measured in normal air. Leaves of E. farinosa used in the experiments had absorptances of 80, 65, 54 and 44 percent (400 to 700 nm). The absorptance of E. californica leaves was 88 percent.
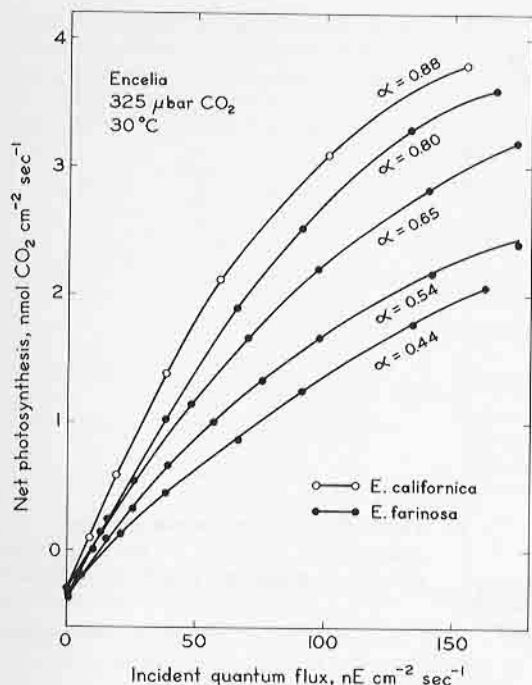
Fig. 2. Net photosynthesis versus incident quantum flux for leaves of *Encelia farinosa* differing in pubescence and for *E. californica*

Leaves of *Encelia* differing in their degree of pubescence differed sharply in their photosynthetic response to incident light intensity (Fig. 2). Maximum photosynthetic rates decrease as pubescence increases and unlike many species, photosynthesis in *Encelia* is not light saturated even at light intensities approaching full noon sunlight (200 nE cm^{-2} s^{-1}). It is also evident that as leaf absorptance is reduced the incident quantum yield (initial slope of net photosynthesis light curve) also declines. In other words, the number of quanta incident on the leaf that are required to fix CO_2 into carbohydrate increases as leaf absorptance decreases. To determine if there is any change in the intrinsic efficiency of the photosynthesis of pubescent leaves, the quantum yield on an absorbed light basis must be known. Calculations of the absorbed quantum yields for all five sets of data reveal quantum yields ranging from 0.049 to 0.052 mole CO_2 per absorbed einstein. These values are quite similar to the quantum yields found for C_3 species in general (Ehleringer and Björkman, 1977). The fact that the quantum yields of the various curves in Figure 2 are similar on an absorbed quantum basis indicates that leaf pubescence serves primarily to reflect quanta, rather than to increase the CO_2 diffusion pathway.

The differences in net photosynthetic rates between the various curves in Figure 2 seem to be explained on the basis of light reflection by the pubescence alone. If the photosynthetic data are replotted as a function of the absorbed quanta rather than incident quanta, and the small differences in dark respiration
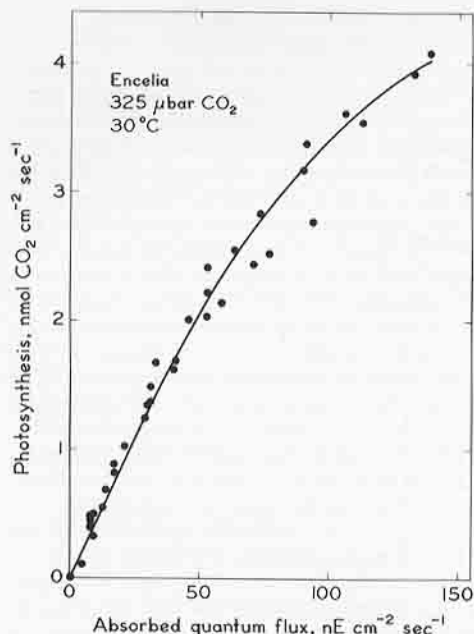
Fig. 3. Photosynthesis versus absorbed quantum flux for leaves of *Encelia farinosa* differing in pubescence and for *E. californica*

rates are removed, then all net photosynthetic measurements lie on a single curve (Fig. 3). These data also indicate that the observed differences in photosynthetic rates between *E. californica* and *E. farinosa* are due to differences in light absorptance and not other factors. That the differences between light response curves of leaves differing in pubescence can be removed by plotting the data on an absorbed quanta basis suggests that the possible effects of the leaf hairs on the boundary layer are small in *E. farinosa*.

Leaf Hairs and the Boundary Layer

It has been proposed by several investigators that the leaf hairs will act to increase the boundary layer resistance. If this effect is significant, the presence of pubescence should modify photosynthesis, transpiration, and leaf temperature. Photosynthesis data for leaves presented in the preceding section showed that while there were significant differences in the photosynthetic rates of leaves on an incident light basis, all of the differences were removed by plotting the rates on an absorbed quanta basis. This information suggests that the impact of the leaf hairs on boundary layer resistance is small.

Table 1 lists the experimental observations of the leaf and boundary layer resistances to water vapor transfer of *E. farinosa* and *E. californica* under a variety of leaf absorptances and growth regimes. It is clear from this table that the combined leaf and boundary layer resistance does vary. This resistance

Table 1. Minimum leaf and boundary layer resistance to water vapor at high light levels as measured using a gas exchange system for leaves of *Encelia farinosa* and *E. californica* grown under a variety of conditions

	r_{min} (s cm^{-1})	Leaf absorptance (percent)
Encelia farinosa		
Phytocell		
35°/25° C	1.1	65
20°/15° C	0.5	80
Death valley garden		
Winter	0.8	62
Summer	0.7	65
Encelia californica		
Phytocell		
35°/25° C	1.2	88
20°/15° C	0.6	88

varies from 0.5 s cm^{-1} to 1.1 s cm^{-1} in leaves of *E. farinosa*. This range, while suggestive of a change in boundary layer resistance as a function of the corresponding differences in leaf absorptances, is likely a result of the differences in growing conditions. If a comparison of the minimum leaf and boundary layer resistances of the essentially glabrous *E. californica* leaves is made against *E. farinosa* leaves grown under similar environmental conditions, it is seen that there is a stronger agreement between the resistance values within a treatment than within a species when grown under different growth conditions. One possible explanation for the observed differences is that there were differences in the stomatal size and/or frequency under different growth regimes. No direct measurements of these characteristics were made, however.

It should be possible to calculate an estimate of the additional boundary layer resistance arising from the presence of the hairs. We assume that the transfer of gases through the boundary layer is only by diffusion, that is to say there is no turbulent transfer. We also assume no tortuosity effects on gas diffusion caused by the hairs. The increase in the thickness of the boundary layer will then be equal to the thickness of the leaf hairs. Knowing the increased thickness of the boundary layer, we can calculate the increase in boundary layer resistance from the equation:

$$r = L/D,$$

where r is the additional boundary layer resistance for water vapor caused by the hairs, L is the thickness of the pubescence layer, and D is the diffusion coefficient for water vapor in air. From this equation the maximum expected increase in boundary layer resistance for a heavily pubescent *E. farinosa* leaf (0.35 mm thick pubescence) will be about 0.15 s cm^{-1}. A common boundary layer resistance will be approximately 0.3 s cm^{-1}. This means that under extreme conditions, pubescence may increase the boundary layer by about 50 percent.

However, even under extreme pubescence conditions, the hairs will have only a small effect on transpiration in natural conditions. This is because leaf resistances to water vapor are commonly greater than 5 s cm^{-1} at those times when leaves are heavily pubescent (Ehleringer, 1977). The effect of the hairs on the total resistance to CO_2 transfer for photosynthesis will be even less than the minimal effect they have on transpiration.

Leaf Energy Balance

An analysis using the energy budget equations as developed by Raschke (1960) and Gates (1962, 1965) was used to investigate the effects of changes in leaf absorptance to total solar radiation on leaf temperature. The heat transfer equations were amended to include the effects of hairs on boundary layer resistance. Included in this modification were the relative differences that hairs would have on the rates of transfer of heat, CO_2, and water vapor. Because of the lack of hair thickness versus leaf absorptance data, the thickness of the hair layer was assumed to be directly proportional to the leaf reflectance.

Simulations of the leaf temperature under midday solar radiation loads for spring (30° C air temperature) and summer conditions (40° C air temperature) were performed (Fig. 4). The predicted leaf temperatures are plotted against leaf absorptance (400 to 3000 nm) as a series of curves, each curve representing a different leaf conductance to water loss. The values of the environmental parameters used in both the spring and summer simulations were total solar radiation of 94 mW cm^{-2}, diffuse solar radiation of 4 mW cm^{-2}, long wave downward radiation of 42 mW cm^{-2}, wind speed of 200 cm s^{-1}, air relative humidity of 20 percent, and a soil temperature equal to air temperature. These values are typical of observed midday values. The values of the leaf parameters were similar to those found in the field: a leaf angle of 30° and a leaf width of 2 cm.

Under spring noon conditions, predicted leaf temperatures of *E. farinosa* can vary as much as 8° C, from 26° to 34° C depending on leaf absorptance (10 to 50 percent) and leaf conductance (Fig. 4). Leaf temperatures are predicted to exceed air temperatures under most conditions of leaf absorptance and leaf conductance. In order to maintain leaf temperature close to or below air temperature, a leaf absorptance below 30 percent in combination with a moderate leaf conductance or a 50 percent absorptance (typical green leaf) and a very high leaf conductance are required. The options for maintaining low leaf temperatures are clear—either a heavy investment in leaf pubescence to reduce leaf absorptance or an abundant water supply to maintain the high leaf conductance. The predicted consequence for an *E. farinosa* leaf that has little or no pubescence and a low transpiration rate is a leaf temperature of up to 5° C greater than air temperature.

At an air temperature of 40° C, typical of summer conditions, predicted leaf temperatures will generally be within 5° C of air temperature (Fig. 4). The range of predicted leaf temperatures for the range of leaf absorptances and leaf conductances found in *E. farinosa* is 10° C, from 34° to 44° C. At very high leaf conductances (1 cm s^{-1}), predicted leaf temperatures are 3° to 6° C
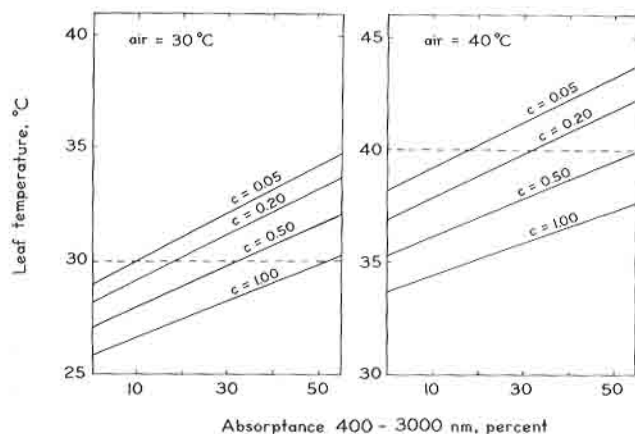
Fig. 4. Predicted leaf temperatures as a function of leaf absorptance. The plate on the left represents spring conditions at midday, whereas the right plate represents summer conditions at midday. Leaf temperatures are calculated for various values of leaf conductance to water loss

below air temperature, depending on the leaf absorptance. At these moderately high leaf temperatures, a leaf conductance of 1 cm s^{-1} will result in extremely high transpiration rates. On the other hand, a reduction in leaf conductance to a moderate (0.2 cm s^{-1}) or a low level (0.05 cm s^{-1}) in a green leaf will result in leaf over-temperatures of up to 4° C, i.e. leaf temperature exceeds air temperature by this amount. A moderate or low leaf conductance can result in a leaf under-temperature of several degrees if the absorptance is low — less than 30 percent. The point to be made here again is that either a thick pubescence layer or a large water loss rate is required to maintain leaf temperature below air temperatures. A lack of leaf pubescence and a low leaf conductance are predicted to result in large leaf over-temperatures. These leaf temperatures, approaching 45° C, may be thermally damaging or lethal to *E. farinosa*. If this is the case, the selective advantages of leaf hairs to *E. farinosa* in hot, high light environments would be great indeed.

Verification of the leaf temperature trends predicted by the energy budget calculations were made with field observations of the leaf temperatures of *E. farinosa* in Tucson, Arizona at different seasons through the year. These measurements were collected from sunlit leaves ($n = 16$) at solar noon on clear days. The mean leaf-air temperature differentials and the absolute readings of air and leaf temperatures are presented for winter, spring, summer and fall seasons.

There was not a close coupling between leaf and air temperatures (Fig. 5). Leaf temperatures were greater than air temperatures in the winter and fall seasons by as much as 2.5° C. The leaf over-temperatures resulted from different factors. In the winter, leaf conductances were high and so were leaf absorptances (near 45 percent), resulting in an over-temperature. In the fall, the leaf conductance was quite low (about 0.05 cm s^{-1}) and leaf absorptance was low. However, with very little water loss from the leaf, an over-temperature was measured, even though the leaves were quite hairy.

The leaf under-temperatures of the spring and summer seasons resulted
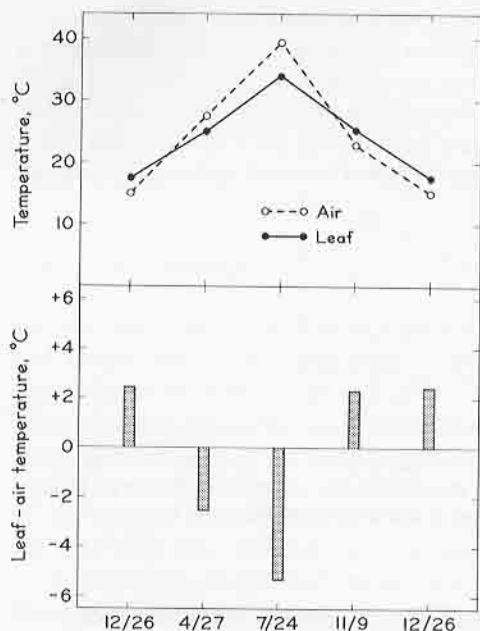
Fig. 5. Measured midday leaf temperatures for sunlit leaves of *Encelia farinosa* at Tumamoc Hill in Tucson, Arizona

from a combination of moderate leaf conductances (0.2 to 0.7 cm s^{-1}) and low leaf absorptances. Neither factor alone was of sufficient magnitude to account for the observed leaf under-temperatures. During the noon summer measurements, leaf temperatures averaged 5.3° C below the air temperature of 39.3° C. Total solar leaf absorptances of these leaves were approximately 40 percent and leaf conductances approximately 0.7 cm s^{-1}. In the spring measurements, leaf temperatures were 2.5° C below air temperature (28° C). Leaf conductances on this date were about 0.2 cm s^{-1} and leaf absorptances 30 percent.

Though the course of the year, the magnitude and direction of differences between leaf and air temperatures are associated with changes in both total solar absorptances and leaf conductances. In general, these changes in leaf temperature are quite similar to those predicted by the leaf energy budget analysis.

Leaf Temperature and Photosynthesis

The temperature dependence of photosynthesis was measured under high light intensities and normal atmospheric conditions (Fig. 6). The response curve is relatively flat between 20° and 30° C, with a temperature optimum occurring at 25° C. Below 20° C and above 30° C, the temperature dependence of photosynthesis is quite steep. The shape of this response curve does not appear to change when the plants are grown under a variety of controlled growth condi-
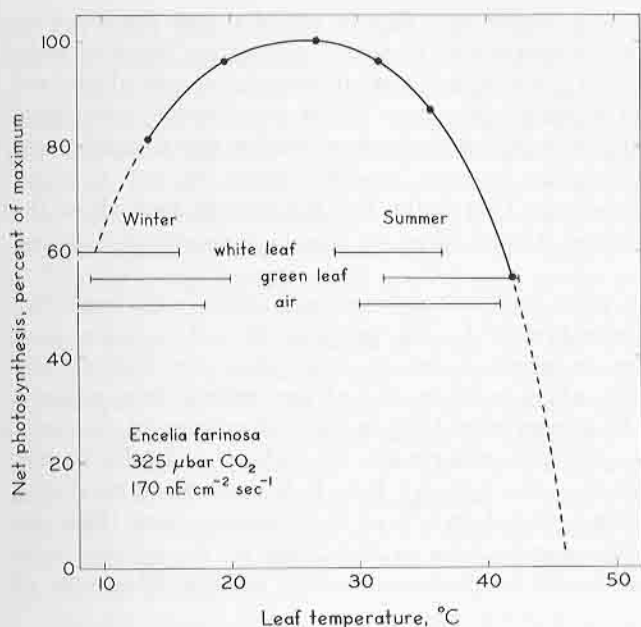
Fig. 6. Daily ranges of leaf temperatures for "green" and "white" leaves of *Encelia farinosa* in the winter and summer and the temperature dependence of light saturated photosynthesis

tions or with season in the field (Strain and Chase, 1966; Ehleringer and Björkman, 1978 b).

Leaves of *E. farinosa* are able to cope with the high summer air temperatures and for much of that time even to photosynthesize at near optimal temperatures because of the presence of leaf pubescence. The reflective properties of the hairs reduce the heat load of the leaf resulting in a leaf temperature much lower than that of the air. How this difference between leaf and air temperature works to be an advantage is shown in Fig. 6. In this figure, the daily range of air temperatures measured between 0900 and 1600 on a clear winter day (December 26) and a clear summer day (July 24) are plotted together with the curve for photosynthesis as a function of leaf temperature. The measured range of *E. farinosa* leaf temperatures is plotted for these same two days. For the summer day, the actually measured leaf temperatures are those of the "white" leaves. The temperatures of the "green" leaves are those predicted by the energy budget for leaves similar to the "white" leaves, but differing in the total solar absorptance. Conversely, the actually measured winter leaf temperatures are those of the "green" leaves and the "white" leaf temperatures are those predicted by the energy budget for leaves similar to the "green" leaves, but differing in total solar absorptance.

These data clearly show the effects of winter over-temperatures and summer leaf under-temperatures. A leaf over-temperature in winter allows the photosyn-

thetic process to operate at a higher rate than it would if leaf temperatures were equal to or below air temperatures. Similarly, during the summer when air temperatures exceed 35° C, a summer leaf under-temperature allows the leaf to photosynthesize at a greater rate than if leaf temperature were equal to or above air temperature. Perhaps even more important is that a pronounced leaf under-temperature in the hot summer months allows the leaf to avoid extremely high leaf temperatures. That is the leaf pubescence may allow the leaf to be physiologically active at times when the temperatures would be otherwise lethal.

If the summer leaves were "green" rather than "white", the predicted midday leaf temperature would be 41° C. This temperature is 4° C higher than the measured temperature. In terms of net photosynthesis, the "white" leaf is able to operate at a rate which is 82 percent of the optimal rate, whereas the "green" leaf would be photosynthesizing at only 60 percent of this rate. In terms of water loss, for equal leaf conductances the "white" leaf will transpire at a rate 23 percent lower than the "green" leaf. If leaf conductance during the summer months declined to $0.2 \, cm \, s^{-1}$ as it frequently does, then the "white" leaf would be photosynthesizing at 75 percent of the optimal rate, whereas the "green" leaf would be photosynthesizing at only 35 percent of the optimal rate.

During the cooler winter months, the situation is reversed. A "green" leaf will then have a greater photosynthetic rate than a "white" leaf. This difference in the photosynthetic rate can be attributed to the "green" leaf having a higher leaf temperature (and closer to the optimum) than the "white" leaf.

Tradeoff Analysis-Model and Predictions

The presence of leaf hairs on *E. farinosa* has both advantages and disadvantages. To analyze the overall effect of the hairs on leaf performance, a combined leaf energy budget-photosynthesis model was used.

Before the model could be employed, it was necessary to decide what overall factor(s) was being selected for/against by the presence of the hairs. Since the pubescence appears to be most directly affecting the processes of photosynthesis and transpiration, it is likely that selection for pubescence in *E. farinosa* involved the maximization/minimization of either of these two processes or the ratio of the two. The three possibilities are that in response to the aridity and high temperatures of the desert environment, leaf pubescence is a mechanism to 1) minimize transpirational losses, 2) maximize the photosynthesis/transpiration ratio, or 3) maximize the carbon gaining capacity of the leaf. It is unlikely that leaf pubescence is a mechanism to minimize water loss from the leaf perse. This is because to minimize water loss from the leaf the stomates would be kept closed – thus reducing photosynthesis to essentially zero. Maximizing the photosynthesis/transpiration ratio will have the same effect as minimizing transpiration. That is, to maximize the photosynthesis/transpiration ratio in a C_3 plant, the stomates must be almost closed. Thus, it is unlikely that selection would favor a maximizing of this ratio. It is, however, quite possible that leaf pubescence is a mechanism to maximize the carbon gaining capacity of

the leaf. Two points speak in favor of pubescence as a mechanism serving this function in *E. farinosa*. First, CO_2 assimilation is the primary function of the leaf. Second, leaves of *Encelia* are drought-deciduous and not active for long periods during the year. Hence one would expect that any mechanism that will allow the leaf to photosynthesize at a higher rate during the brief period of activity and to extend this period would be selected for. Consequently, in the tradeoff analysis it is hypothesized that pubescence is an adaptive mechanism serving to maximize the carbon gaining capacity of the leaf.

The leaf energy budget equation used in the model was developed by Raschke (1960) and by Gates (1962, 1965) and modified as described earlier. A linear solution was used to calculate leaf temperature. The calculation of net photosynthesis was based on a Gaastra type diffusion equation as presented by Ehleringer and Miller (1975). The only difference between the equations used in the current simulations and those presented earlier by Ehleringer and Miller (1975) is that instead of using a mesophyll resistance versus photosynthesis relationship, a mesophyll conductance versus photosynthesis relationship was calculated. The mesophyll resistance was then calculated as the inverse of the mesophyll conductance. This change was made to provide more sensitivity to the factors affecting the photosynthetic rate.

The model was designed to answer the following question: For a given combination of air temperature and degree of aridity, what value of all the possible leaf absorptance values for *E. farinosa* yields the highest photosynthetic rate? Leaf conductance to water vapor diffusion was used as a parameter reflecting the degree of habitat aridity. That is, an arid site is characterized by having a low leaf conductance (such as 0.05 cm s^{-1} for water vapor), whereas a mesic habitat would be characterized by having a high leaf conductance (1.00 cm s^{-1}).

A combination of several factors make such an analysis possible for *E. farinosa*. First, the evidence available shows that *E. farinosa* leaves are the same as *E. californica* except for variable amounts of a near-blanket reflector. Second, on an absorbed quantum basis, there are no differences in the photosynthetic response to light by either *E. farinosa* leaves differing in pubescence or between *E. farinosa* and *E. californica* leaves. Third, the temperature dependence of light saturated photosynthesis does not change seasonally or with growth conditions.

The predictions of the tradeoff analysis show that the amount of pubescence yielding the highest carbon gaining capacity depends on the environmental conditions (Fig. 7). If water is freely available (i.e., leaf conductance is 1.0 cm s^{-1}), the optimal leaf absorptance is the greenest possible leaf (leaf absorptance equal to 80 percent) for air temperatures up to $42°$ C. However, the model predicts that above $42°$ C, even when water is freely available, the greatest rate of carbon gain will be by a leaf whose absorptance is less than 80 percent. As air temperature increases above $42°$ C, the optimum leaf absorptance will decline continuously. If the aridity of the environment is increased (that is if in the model leaf conductance is decreased), the point at which a reduced leaf absorptance is beneficial shifts to even lower air temperatures. As aridity increases, the optimal leaf absorptance is predicted to decline at an earlier temperature and to decline more rapidly as a function of air temperature.
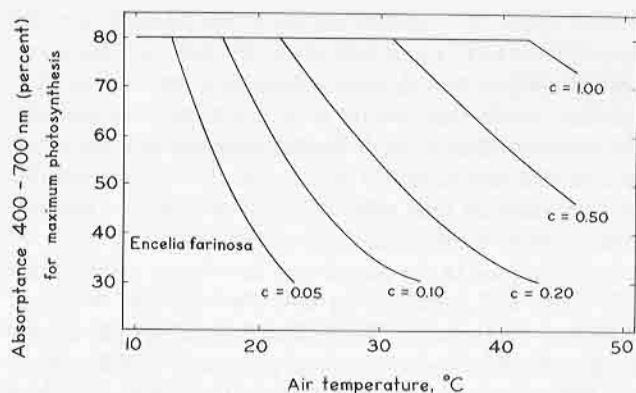
Fig. 7. Predicted optimum leaf absorptances for various combinations of air temperature and drought stress. Drought stress is represented by different values of leaf conductance to water loss

The reason for the model prediction that the optimum leaf pubescence varies with environmental conditions is that there is a tradeoff between the decline in photosynthesis caused by an increased reflectance and the increase in photosynthesis caused by a decrease in leaf temperature. A leaf with a certain degree of pubescence is predicted to have a greater rate of photosynthesis than a somewhat less pubescent leaf if the gain in photosynthesis resulting from a reduction in leaf temperature exceeds the gain in photosynthesis that would result from an increased light absorption.

Discussion

The pubescence of *E. farinosa* modifies the heat balance of the leaf. Increased pubescence results in a reduced heat load on the leaf by reducing the amount of energy absorbed. Over the ranges of leaf pubescence found in *E. farinosa*, the leaf absorptance to total solar radiation varied by a factor of 3 (Ehleringer and Björkman, 1978a). The three fold difference in absorptance means that for moderately and heavily pubescent leaves significantly less energy must be dissipated by transpiration in order for the leaf to remain at a given temperature. Since the relationship between water vapor pressure and temperature is exponential, the savings in terms of water loss can be substantial at moderate and high temperatures. This reduction in water loss should not be confused with a decrease in water loss resulting from a reduction in leaf conductance.

It has been noted that *E. farinosa* leaves produced during the hot summer months are much thicker than leaves produced during the cooler winter months (Shreve, 1924; Cunningham and Strain, 1969). While part of the increased thickness is undoubtedly due to pubescence, it appears that the palisade layer is also thicker. In our studies we did not observe a relationship between photosynthetic rate and leaf thickness, but instead a strong relationship between photosynthetic rate and leaf absorptance. This is in contrast to a recent report

by Smith and Nobel (1977) that photosynthetic rate in *E. farinosa* is dependent on leaf thickness, but not dependent on leaf absorptance.

In the desert environments occupied by *E. farinosa*, the gains as measured by reductions in leaf temperature and water loss are large. As an example, let us compare the differences in leaf temperature and water loss between a moderately pubescent leaf with an absorptance of 25 percent and a green nonpubescent leaf with a leaf absorptance equal to 50 percent. If both leaves are allowed to have a leaf conductance of 0.5 cm s^{-1}, then this 25 percent difference in leaf absorptance is predicted to result in a leaf temperature decrease of 2.2° C and a decrease in water loss of 1.9 µg cm^{-2} s^{-1}.

It was previously shown that leaf pubescence in *E. farinosa* will result in lower leaf temperatures and less water loss. Over long periods of little or no precipitation, conditions characteristic of desert habitats, this gain should be reflected in the capacity of the plant to extend the duration of active growth into these drought periods.

The reduction in leaf temperature during periods of high air temperature and low water availability are beneficial to photosynthesis in *E. farinosa*. The optimum leaf temperature for photosynthesis is 25° C and when leaf temperatures exceed 30° C net photosynthesis declines precipitously. Be reflecting radiation, the leaf pubescence maintains the temperature of the leaf below that of the air, so that the leaf temperature remains closer to the thermal optimum for photosynthesis. As the season progresses, ambient air temperatures steadily increase and this is accompanied by an increase in leaf reflectance (Ehleringer et al., 1976). The net result is that during most of the season the leaf is able to operate at a temperature near the thermal optimum. In the winter months when air temperatures are low, the pubescence is greatly reduced (Ehleringer et al., 1976; Ehleringer and Björkman, 1978a) and therefore the energy absorbed is increased. Leaf temperatures exceed air temperatures and again become closer to the thermal optimum for photosynthesis.

The significance of pubescence in maintaining lower leaf temperatures is not only that it permits the photosynthetic system to operate closer to the thermal optimum, but also that extremely high leaf temperatures are avoided. Leaf temperatures above about 45° C result in no net carbon gain and prolonged exposure to such high temperatures are probably lethal to *E. farinosa* leaves (Strain and Chase, 1966; Ehleringer and Björkman, 1978b). Yet air temperatures during the months often approach and even exceed 45° C in *E. farinosa* habitats (Shreve and Wiggins, 1964; Sellers and Hill, 1974). Since the photosynthetic temperature compensation point for *E. farinosa* appears not to vary with growing conditions or time of year, the presence of leaf pubescence allows *E. farinosa* leaves to fix carbon at times of the year when, if the pubescence were absent, the leaf temperatures would result in a net carbon loss.

The overall adaptive significance of leaf pubescence in *E. farinosa* must be analyzed in terms of its net benefit to the leaf. As is generally considered to be the case with most adaptations, leaf pubescence has a cost or loss partially offsetting any potential gain. In *E. farinosa* the leaf pubescence reduces leaf temperature, reduces the rate of water loss, and increases the rate of photosynthesis at high air temperatures. On the other hand, leaf pubescence reduces

the rate of photosynthesis at all light intensities encountered in the field. The leaf energy budget-photosynthesis model used to evaluate the tradeoffs involved predicted that different amounts of pubescence will be selected for under different environmental conditions. Experimental evidence to support the model predictions can be seen in the field observations of leaf absorptances.

The model predicts that at the beginning of the growing season, when water is abundant, the leaves should be as green as possible. It has been previously shown that during both the cool winter and hot summer seasons, the leaves initially developing on the stem after the first rain storms of the season have high leaf absorptances (Ehleringer and Björkman, 1978a).

Another prediction of the model is that as air temperatures increase, the leaf absorptances should decline. Seasonal field observations support this prediction (Ehleringer et al., 1976). During the course of a growing season, the air temperatures increase even at the wettest sites. Correspondingly, the absorptance of the leaves produced declines.

The model predicts that if a transect were taken along an aridity gradient and if each site along this gradient had a similar air temperature, one should expect to see a gradation in leaf pubescence on the shrubs along this transect. Specifically, the model predicts that on the driest sites the leaves would be the most pubescent and on the wettest sites the least pubescent. Field observations of the leaf absorptances of *E. farinosa* leaves growing at several sites receiving different amounts of precipitation yet but having similar air temperatures, support the model prediction. Ehleringer at al. (1976) found a strong positive correlation between precipitation and leaf absorptance.

Air temperatures in native *E. californica* habitats rarely exceed 20° C during the growing season. The model predicts that if air temperatures remain low, the leaves should not be pubescent. Observations show that leaves of *E. californica* are never heavily pubescent and the leaf absorptance remains near 80 percent throughout the growing season (Ehleringer et al., 1976).

In summary, the model shows that the leaf hairs are adaptive to *E. farinosa* in its native desert habitats. While it is clear that leaf hairs are of benefit for heat balance purposes, it seems possible that these hairs may also serve an antiherbivore function. The agreement between the leaf absorptances predicted by the tradeoff model and the field observations are quite close. The leaf hairs serve as a morphological mechanism to maximize the carbon gaining capacity of the leaf in the diverse and fluctuating desert environments. To a species which appears unable to adjust its physiological characteristics when faced with increasing air temperatures, the use of leaf hairs in *E. farinosa* to produce a reflective surface is a viable alternative mechanism in adapting the plant to its environment.

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