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THE INFLUENCE OF WATER STRESS AND TEMPERATURE ON LEAF PUBESCENCE DEVELOPMENT IN *ENCELIA FARINOSA*¹

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ABSTRACT

The degree of leaf pubescence development in the arid land shrub *Encelia farinosa* Gray is affected by air temperature, leaf water potential, and previous history of the apical meristem during the current growing season. Changes in leaf pubescence levels change leaf spectral characteristics and affect both leaf temperature and photosynthesis. Decreasing leaf water potentials and increasing air temperatures both independently increase pubescence development as measured by decreased leaf absorptances. During any one growing season leaf absorptance may change reversibly coincident with air temperature changes, but with respect to water stress leaf absorptance only decreases as the season progresses. The ecological significance of regulation of the leaf spectral characteristics is discussed.

RECENTLY several studies have investigated the ecological and adaptive aspects of leaf pubescence in desert plants (Ehleringer, Björkman and Mooney, 1976; Smith and Nobel, 1977; Ehleringer and Björkman, 1978a; Ehleringer and Mooney, 1978; Ehleringer, 1981a). For the most part, these studies have focused on the drought deciduous shrub *Encelia farinosa* Gray, which seasonally changes the amount of pubescence developing on its leaves. The changes in leaf pubescence development cause dramatic changes in leaf spectral characteristics, changing the leaf absorptance (400-700 nm) from 81% under mesic periods down to 29% under driest conditions (Ehleringer and Björkman, 1978a). The decreased leaf absorptance results in lowered leaf temperatures and rates of water loss (Ehleringer and Mooney, 1978). Since the photosynthetic apparatus in this species cannot acclimate to high temperatures (Ehleringer and Björkman, 1978b), the pubescence is an adaptive feature allowing the plant to: 1) avoid lethal leaf temperatures; and 2) maintain leaf temperatures near levels optimal for photosynthesis (Ehleringer and Mooney, 1978).

The adaptive value of leaf pubescence to *Encelia farinosa* under moderate and high air temperatures results in a tradeoff, which depends on water availability, but which results in the highest daily carbon gain for that level of drought (Ehleringer and Mooney, 1978; Ehleringer, 1980). That is, under high soil moisture conditions the leaf morphology is one with

low pubescence (high absorptance) because it is possible to reduce leaf temperature via transpiration. As the soil moisture levels decrease, transpiration levels decrease and increased leaf pubescence is produced (reduced absorptance), which again results in a decreased leaf temperature. A tradeoff occurs because the reduced leaf absorptance reduces the rate of photosynthesis to an extent proportional to the decrease in leaf absorptance. However, the rate of carbon gain by a pubescent leaf is still greater than that of a glabrate leaf, because the decrease in photosynthesis by reflecting quanta and reducing leaf temperature is less than the decrease in photosynthesis caused by absorbing those quanta and decreasing photosynthesis via increased leaf temperature.

The tight association between pubescence levels, water availability, and air temperature necessary to result in maximum carbon gain suggests a fine regulation of pubescence development by the plant. The purposes of this study were: 1) to determine the influence of naturally varying air temperatures upon the production of leaf pubescence in *E. farinosa*; 2) to determine under controlled temperatures in a greenhouse, the effect of desiccation of leaf tissue upon induction of leaf pubescence; 3) to determine the reversibility of these responses when environmental conditions were changed; and 4) to provide data on the involvement of the apical meristem in the induction of pubescence.

MATERIALS AND METHODS—Field studies of *Encelia farinosa* were concentrated at two sites: the Boyd Desert Research Center in Deep Canyon, California and at Park Headquarters, Death Valley National Monument,

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California. Precipitation at both sites falls chiefly during the winter months and averages 92 mm and 42 mm annually for Deep Canyon and Death Valley, respectively (U.S. Weather Bureau Records). The performances of watered as well as unwatered shrubs were followed at each field location. Watered plants received sufficient amounts of water weekly to saturate the soils surrounding the plant (usually about 20–40 l).

Greenhouse studies were conducted in unshaded glasshouses during both winter and summer seasons in which daytime air temperatures ranged from 20–25 C. Greenhouse plants were grown in 20-l tubs to reduce pot-bound effects and, except for experimentally droughted plants, were watered daily.

Changes in leaf pubescence thickness and density were quantified by measuring the leaf absorbance to sunlight over 400–700 nm (visible, photosynthetically useful wavelengths). Leaf absorbance was measured using a 23-cm diameter Ulbricht integrating sphere. A heliostat was used to introduce sunlight into the integrating sphere. The leaf absorbance is a percentage measurement and thus differences in leaf absorbance are differences in the percentage of light absorbed by the leaf. Further details on the theory and measurement of leaf absorbance using this technique are described in Ehleringer and Björkman (1978a) and Ehleringer (1981b).

Leaf water potentials were measured with a Scholander-type pressure chamber.

RESULTS—Previous seasonal field observations indicated that the amount of leaf pubescence produced varied through the course of a growing season, with the greatest variations occurring in plants at the driest sites (Ehleringer et al., 1976; Ehleringer and Björkman, 1978a). Since new leaves are formed quickly, the degree of pubescence present on leaves is probably a response to recent and/or prevailing environmental conditions. Covarying with leaf pubescence through the season are air temperatures and leaf water potentials. Given this as the case, how much can the seasonal variation in pubescence production be reduced by watering the plants in the driest sites?

For this experiment, seasonal fluctuations in leaf absorbances of five watered shrubs and five unwatered shrubs were followed in Deep Canyon. The leaf absorbances of natural, unwatered shrubs followed a saw-tooth pattern, similar to previously reported studies (Ehleringer and Björkman, 1978a) (Fig. 1). The greenest leaves had absorbances as high as 85%, while leaf absorbances during the dry

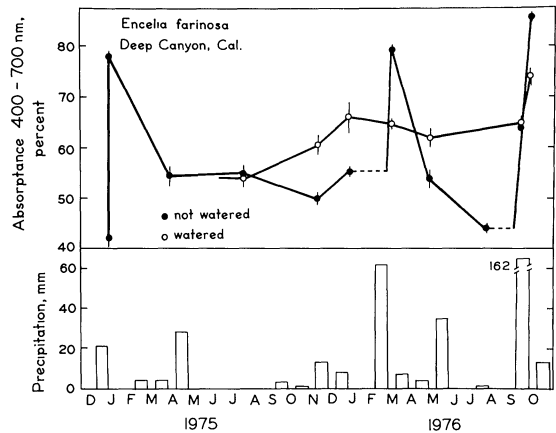


Fig. 1. Leaf absorbances (400–700 nm) for watered and unwatered *Encelia farinosa* shrubs and precipitation data for Deep Canyon, California. Data are means of five samples. Vertical bars represent ± 1 standard error.

seasons decreased to as low as 44%. In contrast, the leaf absorbances of the watered shrubs varied from 66 to 54% through the season. In response to a record rainfall of 162 mm (a tropical hurricane) at the end of this experiment, the absorbances of the watered shrubs climbed to 74%. Except for the dramatic change at the end of the experiment, the seasonal variation in leaf absorbances of the watered shrubs was only 12%, compared to a 41% variation in the leaf absorbances of unwatered plants.

The variations in leaf absorbances of unwatered shrubs followed the rainfall pattern. The highest leaf absorbances were observed at the beginning of the growing season, followed by a continual decrease through the season. Immediately following the initial rainstorm in December there was a rapid flush of larger, green leaves with high absorbances and older leaves were abscised soon after (Fig. 2). Rainfall late in the growing season after the plants had experienced only mild water stress (e.g., April, 1975 and May, 1976), did not cause the plants to develop larger, green leaves with high absorbances.

The seasonal fluctuation in leaf absorbances of the watered shrubs appeared not to be related to precipitation patterns. Rather these leaf absorbances appeared to be negatively related to the seasonal fluctuations in air temperatures, although the possible interaction of water potential in addition to temperature on leaf absorbance cannot be ruled out. The leaf absorbances of the watered shrubs both in Deep Canyon and Death Valley field gardens were negatively correlated with mean maxi-

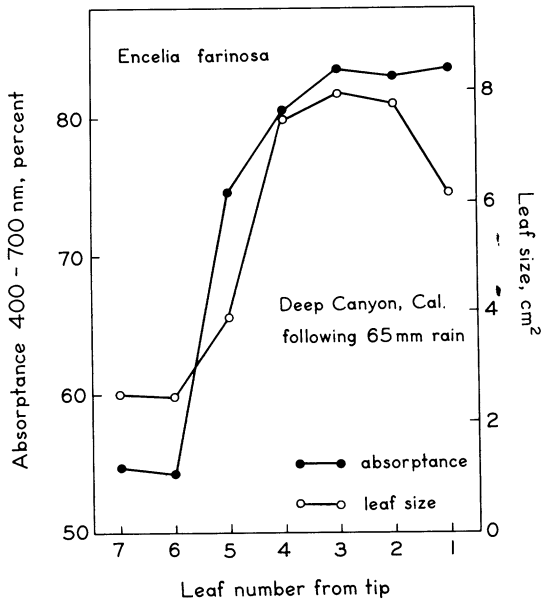


Fig. 2. Leaf absorbances (400–700 nm) of individual leaves on an *Encelia farinosa* stem following the beginning of the season rainstorm. Leaves 6–7 were developed before the rainstorm, while leaves 1–5 developed after.

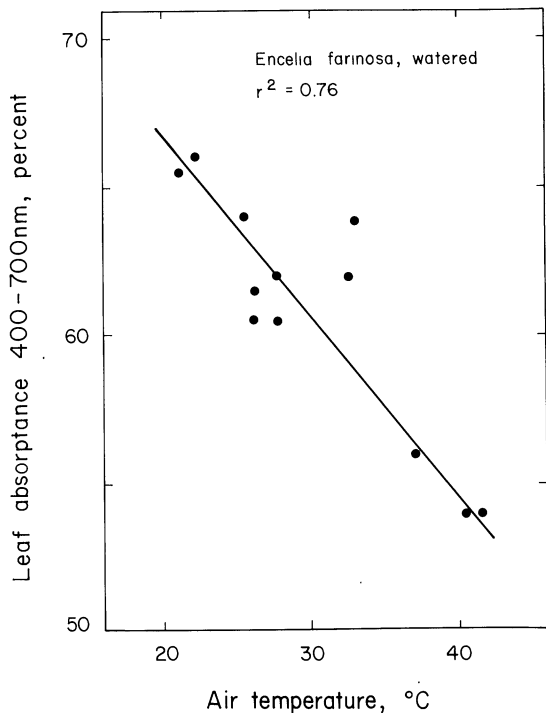


Fig. 3. Leaf absorbances (400–700 nm) of watered *Encelia farinosa* shrubs in Death Valley and Deep Canyon, California plotted against mean maximum air temperature.

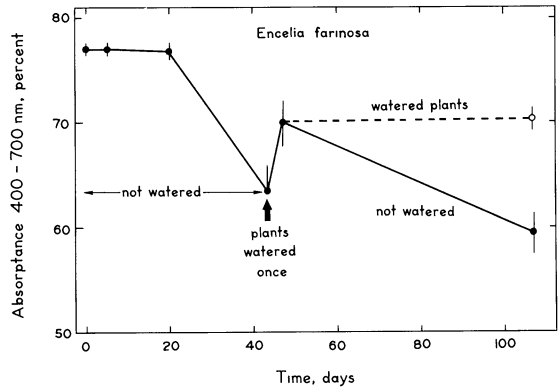


Fig. 4. Time course of leaf absorbances (400–700 nm) for *Encelia farinosa* leaves in a greenhouse drought experiment. Soils were fully saturated at the beginning of the experiment. Data are means of five samples. Vertical bars represent ± 1 standard error.

mum air temperature (Fig. 3, $r^2 = 0.76$, $P < 0.01$).

In a manner similar to the field watering experiments, several greenhouse experiments were conducted to follow the changes in absorbance of successively produced leaves of watered and unwatered *E. farinosa* shrubs through time. Unwatered plants started out in the beginning of the experiment with a fully charged soil. To produce the green, high absorbance leaves necessary to begin these experiments, the apical meristems of all stems were removed. New green leaves were then produced from the axillary meristems of the uppermost leaves. For the first experiment, shrubs were grown from seed collected in Tucson, Arizona (~250 mm precipitation) where the seasonal fluctuation in leaf absorbance is approximately 55–82%. In the second drought experiment, the shrubs were from a population in Panamint Valley, California (~100 mm precipitation) where the seasonal fluctuation in leaf absorbance is approximately 40–82%.

In the first greenhouse drought experiment with ten shrubs, leaf absorbances declined when water was withheld (Fig. 4). At day 43 of the experiment, the leaf absorbances had declined from 77% to 63%. The midday leaf water potentials had fallen from -1.95 MPa to less than -6.57 MPa. At this time, leaves from all ten shrubs appeared wilted. On day 44, the soil for all of the plants was fully charged with water. For five of the shrubs, water was then applied daily to keep the soil at field capacity. The other five shrubs received no additional water for the duration of the experiment. Following the addition of the water to the soil, all plants put out new leaves which had higher

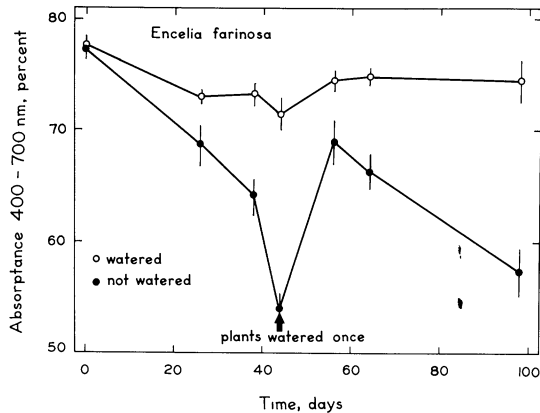


Fig. 5. Time course of leaf absorbances (400–700 nm) for watered and unwatered *Encelia farinosa* shrubs in a greenhouse drought experiment. Soils were fully saturated at the beginning of the experiment. Data are means of five samples. Vertical bars represent ± 1 standard error.

absorbances than were found on the water-stressed leaves. Leaf water potentials at this time had increased to -2.56 MPa. The new leaf absorbances averaged 70%. On day 107, 62 days after the soil had been charged with water, the leaf absorbances of the watered shrubs were still 70% and leaf water potentials were -2.13 MPa. The leaf absorbances of the unwatered shrubs had again declined, this time to 50% and leaf water potentials to less than -5.74 MPa.

Leaf absorbances of the watered shrubs did not increase above 70%, but instead remained at a constant value, even though the shrubs were well watered daily. This is very similar to the pattern of leaf absorbances seen in the field for watered shrubs. There is no simple explanation for the observation that following watering on day 45 the leaf water potential failed to return to its original value of -1.9 MPa as they were on day 0. It is clear, however, that from day 45 to day 107, both the leaf water potentials and leaf absorbances of the watered shrubs remained essentially constant, whereas in the unwatered shrubs both leaf water potentials and leaf absorbances declined together as they had previously in the period from day 0 to day 44.

In the second drought experiment, plants were divided into two groups. Five shrubs were watered to maintain the soil at field capacity. The other five shrubs were started with a fully charged soil, but additional water was withheld until midway through the experiment when the soil was again briefly charged with water. As in the first experiment, the leaf absorbances were measured at various intervals during the experiment.

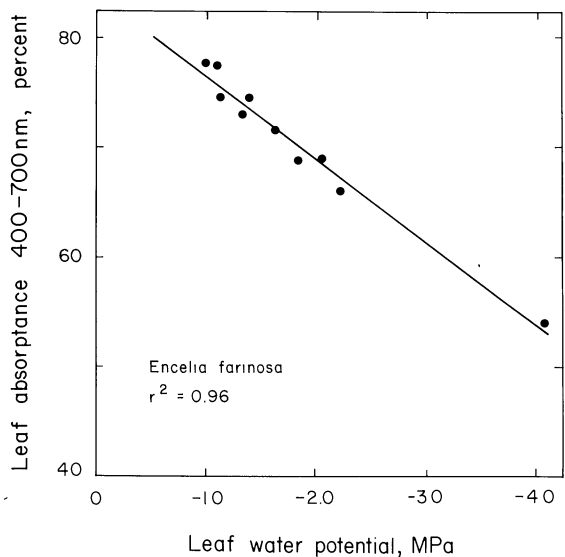


Fig. 6. Leaf absorbances (400–700 nm) of *Encelia farinosa* shrubs in the second drought experiment (Fig. 5) plotted as a function of leaf water potential.

The leaf absorbances of the watered shrubs remained constant for the 98 day duration of the experiment at approximately 75% (Fig. 5). Leaves from shrubs which did not receive water had absorbances which continually declined from the time of soil moisture saturation. Leaf absorbances of unwatered shrubs declined from 77% on day 0 to 54% on day 44. These shrubs were watered once on day 45. Following this watering, the leaf absorbance increased but then followed a continual decline again. Midday leaf water potentials of the watered shrubs ranged from -1.0 to -1.63 MPa, whereas the water potentials of the unwatered shrubs ranged from -1.07 to -4.07 MPa. When the leaf absorbances of droughted and nondroughted shrubs are plotted against leaf water potentials (Fig. 6), a strong negative relationship is observed ($r^2 = 0.96$, $P < 0.01$). It should be kept in mind though that both leaf water potentials and leaf absorbances were measured on mature leaves. The leaf water potential inducing a specific pubescence production level during development may be somewhat higher.

The results of the greenhouse drought experiments suggest that high leaf absorbances can only be obtained if the water potential is kept high at the time when the meristematic region is first activated. This period of high leaf absorbances can be maintained by providing the shrubs continuously with adequate soil moisture, thus avoiding any plant water stress. However, once the stem has experienced low water potentials only leaves with progressively

greater amounts of pubescence are formed until the meristematic region has undergone severe drought stress (less than -4.0 MPa) and is then given adequate moisture. Providing the plant with adequate moisture at a time when the plant has only experienced a moderate level of water stress fails to produce leaves of greater leaf absorptance under both greenhouse and field conditions. It is interesting to note that field plants become drought deciduous at about -4.0 MPa.

The irreversibility of the relationship between pubescence development (leaf absorptance) and water stress (leaf water potential) suggests that some part of the plant is able to detect levels of water stress and to regulate pubescence development depending on the greatest extent of water stress imposed on the plant. It was hypothesized that the apical meristem exerted a large control over the pubescence development.

To test this hypothesis, five plants were grown in a greenhouse with daily watering (no water stress, midday $\psi_{\text{leaf}} \sim -1.6$ MPa), allowed to dry out until visibly water stressed (midday $\psi_{\text{leaf}} \sim -4.2$ MPa), and then rewatered to field capacity and soil moisture maintained at this level (midday $\psi_{\text{leaf}} \sim -1.7$ MPa). At this point, 49 stems from these shrubs were chosen and their leaf absorptances were measured; they averaged 69%. The apical meristems were removed on approximately half of these stems ($n = 23$), and allowed to remain as control on the others ($n = 26$). Plants were watered daily for 30 days and then the absorptances of the developed leaves on the two sets of stems were determined. The absorptances of the axillary activated meristem leaves now averaged 81% and the control meristem leaves still averaged 68%. The difference between the treatment and control was significant ($F = 224.7$, $P < 0.01$).

DISCUSSION—This study has demonstrated that pubescence development in *Encelia farinosa* changes dramatically through the growing season and is influenced by current temperature and water stress as well as by previous history of the apical meristem. Shreve (1923), Ehleringer et al. (1976), Smith and Nobel (1977), and Ehleringer and Björkman (1978a) have shown that pubescence development increased with dry conditions late in the growing season. Our measurements indicate that both temperature and leaf water potential influence the degree of pubescence development. Under more or less constant water availability in the field, leaf absorptances of *E. farinosa* varied 12% as temperature changed seasonally;

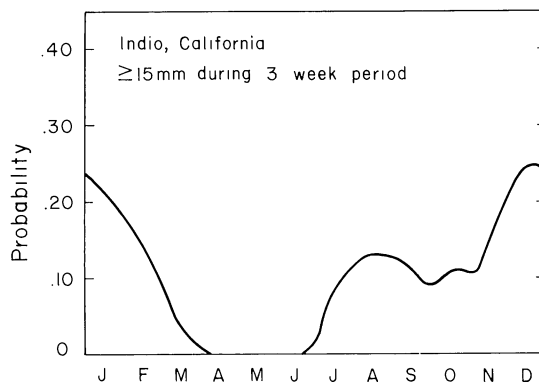


Fig. 7. The probability of receiving 15 mm or more precipitation in a 3-wk period as a function of the time of year in Indio, California. This location is near the Deep Canyon study site. Based on data from Gifford, Ashcroft and Magnuson (1967).

whereas with constant temperatures (greenhouse conditions), leaf absorptance varied 31% as water availability (leaf water potentials) declined.

At first glance these results are not consistent with those of Smith and Nobel (1978) in which, under a factorial experimental design, leaf pubescence levels (as measured by absorptance) in *E. farinosa* changed very little with water availability (under high light) except at low temperatures. The Smith and Nobel study lasted only 25 days. However, if in their study the plants had been partly water stressed (when brought in from the field) and now were actively growing, then only decreases in temperatures (Fig. 3) and not increases in water availability (Fig. 6) would result in leaf absorptance changes. This arises because partially water stressed apical meristems are unable to once again produce green high absorptance leaves until they have undergone dormancy ($\psi_{\text{leaf}} < -4.0$ MPa).

The irreversibility of pubescence development is clear from field observations (Fig. 1; also in Ehleringer and Björkman, 1978a). Once an active apical meristem has been partially stressed, it appears that only leaves with pubescence levels equal to the "driest" conditions that the plant has been exposed to are produced. That the "sensor" for water stress and "memory" for previous history during the growing season are perhaps located in the active apical meristem is suggested by the experiments with apical meristem removal. The advantage to the plant of this lack of reversibility may be that because high precipitation events late in the growing season are rare. The data available indicate that indeed the probability of these late season storms is quite low

(Fig. 7). From March to the end of the winter season (main growing period), the probability of receiving a storm that would significantly increase soil moisture conditions is less than 4%. Given this, maintaining the current pubescent leaf could result in greater net photosynthetic gains to the plant than would be expected from excision of the current leaf followed by production of a less pubescent leaf that may be active for only a brief period of time.

The mechanisms by which these leaves become more pubescent under water stress are presently unknown. The development and growth of these linear hairs requires extensive cell elongation at a time when a plant is undergoing stress, a phenomenon which usually results in the cessation of growth activities (Hsiao, 1973). One component of this process is that elongating hair cells may contain higher osmotic concentrations than the rest of the leaf, resulting in the higher turgor pressures necessary for the extensive cell wall growth.

This study has investigated the means by which pubescence levels in *Encelia farinosa* are regulated. The apical meristem appears to regulate the extent of pubescence on newly formed leaves in a manner which is consistent with the notion that carbon gain and survival are maximized.

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