Temperatures of Desert Plants: Another Perspective on the Adaptability of Leaf Size

Abstract. *Surface temperatures of perennial plants in the Sonoran Desert of California ranged from 20°C above air temperature to over 18°C below air temperature during rapid growth periods following rain. Desert cactus with large photosynthetic stem surfaces had the highest temperatures and lowest transpiration rates. Perennial plants with relatively small leaves had moderate transpiration rates and leaf temperatures close to air temperature. Desert perennials with relatively large leaves had leaf temperatures well below air temperature along with the greatest accompanying transpiration rates of over 20 micrograms per square centimeter per second, but also had correspondingly low temperatures for maximum photosynthesis. The low leaf temperatures measured for these large-leafed species are an exception to the more common pattern for desert plants whereby a smaller leaf size prevents overheating and leads to reductions in transpiration and increased water-use efficiency. The contribution of a larger leaf size to a lower leaf temperature, and thus higher rate of photosynthesis for these large-leafed species, may represent an adaptive pattern previously unrecognized for desert plants.*

Desert plants tend to have small leaves compared with congeneric or closely related species living in more mesic environments (*1*). This morphological characteristic acts to reduce transpiration per unit ground area (*2*) and, possibly more important, may result in less transpiration per unit leaf area (*3*), thereby increasing the water-use efficiency of the plant by reducing the amount of water transpired per amount of CO_2 fixed during photosynthesis (*4*). The reduction in transpiration per unit leaf area as a leaf gets smaller (without complicating changes in leaf shape) is brought about by a greater convective heat dissipation which acts to cool a leaf that may typically be warmer than the air temperature as a result of solar heating. A cooler leaf will have a smaller decrease in the water vapor concentration from the inside of the leaf to the surrounding air (because of the exponential effect of temperature on the saturation content of water in air) and thus a reduced driving force for transpiration.

This report deals with the relationships among leaf size, temperature, and the accompanying transpiration and photosynthetic rates measured for a variety of perennial desert plants that are abundant in the Coachella Valley area of the Sonoran Desert of Southern California. I found that several large-leafed species had extremely low leaf temperatures coupled with high transpiration rates, in addition to correspondingly low temperature ranges for maximum photosynthesis. These low temperatures occur because of the large leaf size and high transpiration rate which uncouple air and leaf temperature through the large boundary air layer resistance to sensible heat flux and a high latent heat loss.

Table 1 shows that leaf temperatures of the perennials with the larger leaves ranged from 8.4° to 18.1°C below air temperature. These maximum depressions of leaf temperature below air temperature are somewhat greater than previously reported for a variety of plants (*5*). The coolest leaves for these species tended to be the largest leaves that were found inside the leaf canopy and were shaded from direct sunlight for most of the day. Cactus stem temperatures ranged from 14°C above air temperature for shaded surfaces to 22°C above for sunlit surfaces. Leaf temperatures for the shrubs with smaller leaves (< 1.5 cm) remained within −0.9° to +2.4°C above air temperature depending on their exposure to direct sunlight. All surface temperatures were measured by means of 36-gauge copper-constantan thermocouples pressed firmly to the leaf or stem (Cactaceae), but avoiding penetration of the cuticle.

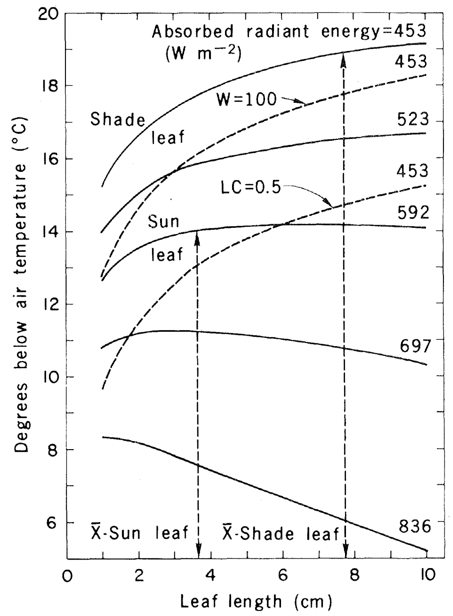

Fig. 1. Simulated leaf temperatures plotted against leaf length and absorbed radiant energy for *E. farinosa*. Microclimatic and leaf conditions were as follows: leaf conductance, 2.0 cm sec^{-1}; wind speed, 14 cm sec^{-1}; relative humidity, 20 percent; and air temperature, 42.2°C. Also plotted are curves for a simulated wind (*W*) equal to 100 cm sec^{-1} and a leaf conductance (*LC*) of 0.5 cm sec^{-1}. Leaf lengths were converted to characteristic dimensions for convective heat transfer according to Taylor (*4*). Vertical dashed lines represent mean leaf lengths measured in the field for sun and shade leaves for *E. farinosa* during growth periods with conditions nearly identical to those simulated here.

The greatest depressions of leaf temperature below air temperature occurred in the large-leafed species that also had the highest transpiration rates according to diffusion porometer measuresments of water vapor loss (Table 1). These species also photosynthesized maximally at correspondingly low temperatures as determined from CO_2 gas exchange measurements at various leaf temperatures (*6*). Apparently, for these large-leafed species, high rates of photosynthesis after rainfall occurred in part because leaf temperatures were well below air temperature. To evaluate the ecophysiological significance of the relatively large leaf size and uncharacteristically low leaf temperatures measured for these species, I conducted computer simulations of the influence of leaf size on leaf temperature using actual microclimatic measurements taken in the field during major growth periods.

Figure 1 shows the influence of leaf size on leaf temperature for a wide range of absorbed radiant energies representing entirely shaded to fully sunlit leaves of *Encelia farinosa*. Simulated leaf temperatures were computed with standard energy balance equations (*7*) which incorporated microclimatic measurements of the total incident solar irradiation, upward and downward longwave irradiation, wind speed, and water vapor concentration of the air at the leaf's position in the canopy; these equations also incorporated the measured absorptance of the leaf to solar irradiation determined with an integrating sphere radiometer (*6*). Also shown in Fig. 1 are the mean leaf lengths measured for two groups of 25 leaves chosen to represent sun and shade leaves from each of six *E. farinosa* bushes. Sun leaves were considered those that were fully sunlit throughout most of the day and shade leaves were those located within the leaf canopy, mostly shaded during the day. Calculations and measurements shown in Fig. 1 are based on field measurements taken near solar noon during a rapid vegetative growth period in late September 1976.

A typical interior shade leaf of *E. farinosa* may absorb radiant energy of 453

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W m^{-2} (less than 10 percent shortwave irradiation) compared to 592 W m^{-2} (about 40 percent shortwave irradiation) absorbed for an exposed sun leaf (Fig. 1). Higher and intermediate values for leaves in their natural canopy positions are possible depending upon variations in the orientation, exposure, and absorptance of the leaf to sunlight. The low absorbed radiant energy for shade leaves (453 W m^{-2}) leads to the greatest reduction in leaf temperature below air temperature for the measured microclimatic and leaf conditions. This low level of absorbed energy also results in the greatest changes in leaf temperature caused by variations in leaf length. Absorbed energy levels approaching fully sunlit conditions (592 W m^{-2}) substantially increase leaf temperatures and decrease the sensitivity of leaf temperature to changes in leaf size (Fig. 1). However, for *E. farinosa*, the amount of absorbed solar energy is reduced because of the presence of a reflective pubescent layer which results in considerably cooler leaf temperatures (*6, 8*).

Decreasing the transpiration rate by simulating decreases in the stomatal conductance to water vapor diffusion, or increasing the convective heat exchange by simulating increases in wind speed, had quite different effects on the relation between leaf length and leaf temperature (Fig. 1). Decreasing the stomatal conductance from 1.0 cm sec^{-1} to 0.5 cm sec^{-1} for the shade leaf created a simulated increase in leaf temperature at all leaf lengths, with a greater increase for smaller leaves (≃ 2.0°C for a 1.0-cm leaf) compared to larger leaves (≃ 1.0°C for a 10-cm leaf). Increasing the wind speed tenfold (10 to 100 cm sec^{-1}) also had a more pronounced influence on the temperature of smaller compared to larger leaves. These simulated changes in leaf conductance and wind speed on leaf temperature differ from the effects of changes in the amount of absorbed radiant energy described above, in that the latter leads to greater temperature changes for larger leaves compared to smaller leaves. For example, leaf temperatures for a 10-cm leaf absorbing 453 compared to 558 W m^{-2} differ by almost 4°C, but only by 1.8°C in the case of a 1-cm leaf (Fig. 1). Larger leaves can potentially be much cooler than smaller leaves and are much more responsive to changes in absorbed radiant energy or latent heat exchange compared with smaller leaves. This enables a high degree of temperature variation for larger leaves according to their exposure to sunlight in the leaf canopy. A close coupling of leaf size to canopy exposure is reflected in the findings of Nobel (*9*), whereby leaf length in *Hyptis emoryi* was proportional to the amount of integrated illumination received by the leaf during the day. These quantitative comparisons of the potential temperature reductions of large versus small leaves (Fig. 1) suggest that a larger leaf size may be adaptive when photosynthetically optimal leaf temperatures are well below air temperature and water is available for rapid transpiration. In addition, variations in leaf size according to the location of the leaf in the canopy (that is, large shade and small sun leaves) can have an important influence on leaf temperature and thus transpiration and photosynthesis throughout a year (*6*).

Most of the potential decrease in leaf temperature below air temperature for a hypothetical sun leaf of *E. farinosa* will occur for leaves shorter than about 4 cm and for shade leaves shorter than about 8 cm (Fig. 1). Any further increases in the respective leaf sizes of these leaf types would result in only small changes in leaf temperature. Moreover, these lengths are very close to the actual mean leaf lengths for sun (3.7 ± 0.8 cm) and shade (7.7 ± 1.1 cm) leaves that were mea-

Table 1. Leaf sizes, temperatures, conductance to water vapor, and transpiration rates for a number of perennial species with relatively large leaves, plus comparative measurements for several large cactus species and smaller-leafed perennials. The leaf temperature ranges for optimal photosynthesis are also shown for several of these species during periods when the indicated leaf temperatures prevailed. All measurements were taken during rapid vegetative growth periods in 1976 and 1977 when water potentials at 20 cm were near field capacity (> − 10^5 pascals); skies were clear, relative humidity was < 20 percent, wind speeds at 4 m were < 155 cm sec^{-1}, exposed surface soil temperatures ranged from 47.6° to 66.8°C at solar noon, and total solar irradiation on a horizontal surface ranged from 704 to 1094 W m^{-2} measured at solar noon. All cactus species had nighttime stomatal openings characteristic of crassulacean acid metabolism, and thus temperature ranges for maximum photosynthesis are not shown.

Species	Family	Solar time (hours)	Leaf lengths* (cm)	Air temperature (°C)	Leaf temperature (°C)	Leaf conductances (cm sec^{-1})	Transpiration rates (μg cm^{-2} sec^{-1})	Temperature ranges for 90 percent maximum photosynthesis (°C)
Large-leafed perennials								
Encelia farinosa	Compositae	1206	3.6 − 8.2	43.6	25.5 − 31.4	0.54 − 2.0	11.1 − 25.8	26.3 − 32.4
Datura metaloides	Solanaceae	1220	4.3 − 9.7	43.7	26.1 − 36.3	0.60 − 1.8	16.9 − 22.2	27.5 − 35.5
Eriogonum inflatum	Polygonaceae	1315	4.0 − 7.0	38.6	28.4 − 35.0	0.47 − 1.4	14.1 − 23.0	29.0 − 35.1
Hyptis emoryi	Labiatae	1202	3.4 − 8.3	41.4	26.0 − 32.2	0.54 − 1.7	12.6 − 19.1	26.5 − 32.6
Sphaeralcea ambigua	Malvaceae	1210	2.9 − 7.6	40.5	24.6 − 31.8	0.59 − 1.9	13.1 − 21.3	25.4 − 33.2
Mean ± standard deviation			6.1 ± 1.3	41.6	27.9 ± 2.4	1.3 ± 0.2	18.6 ± 2.5	26.9 − 33.5
Cactus								
Opuntia basilaris	Cactaceae	1245	7.4 − 16.2	41.3	48.2 − 61.5	<0.01	<1.26	
Opuntia bigelovii	Cactaceae	1155	3.1 − 5.4	41.6	46.5 − 49.3	<0.02	<0.70	
Echinocactus acanthoides	Cactaceae	1310	15.0 − 23.2	41.5	50.2 − 56.7	<0.02	<1.03	
Mamillaria dioica	Cactaceae	1330	3.6 − 4.7	41.3	49.8 − 58.1	<0.01	<1.09	
Mean ± standard deviation			12.4 ± 3.6	41.4	52.7 ± 2.1	<0.02	<0.96	
Small-leafed perennials								
Larrea tridentata	Zygophyllaceae	1218	<1.5	40.7	40.9 − 43.1	0.09 − 0.23	3.9 − 11.3	34.4 − 39.1
Ambrosia dumosa	Compositae	1149	<1.0	39.2	39.1 − 41.6	0.11 − 0.31	4.1 − 14.4	33.6 − 39.3
Hymenoclea salsola	Compositae	1213	<1.0	36.6	36.3 − 36.8	0.08 − 0.27	2.7 − 9.5	
Dalea schottii	Leguminosae	1300	<1.5	36.8	35.9 − 37.2	0.09 − 0.39	3.0 − 13.9	32.1 − 38.6
Mean ± standard deviation			<1.3	38.3	38.8 ± 2.2	0.22 ± 0.03	8.3 ± 1.9	33.4 − 39.0

*Stem diameters for cactus.

sured in the field in September 1976 during the microclimatic conditions chosen to simulate the leaf temperatures in Fig. 1. Similar mean leaf sizes were also measured in the field for the other four large-leafed species based on selection of sun versus shade leaf types during rapid growth periods (Table 1). This correlation provides evidence that leaf size may have an important functional role in the regulation of leaf temperature and, in combination with high transpiration rates, may act to reduce leaf temperatures to more optimal photosynthetic levels, particularly for rapid growth periods when water is abundant. Without abundant water and high transpiration rates a larger leaf size contributes to warmer leaf temperatures, often well above air temperature, and the accompanying changes in transpiration and photosynthesis.

A major portion of the photosynthetic production of these perennials may occur during relatively short periods following rainfall at almost anytime of the year (*6*). The probability of rain is nearly the same for any month except May and June, with substantial precipitation occurring in the late summer and fall months. Average maximum air temperatures for these months are generally above 30°C, while absolute maximum temperatures average above 40°C. In addition, these high temperatures usually persist for up to 6 or 7 hours during the day, over 50 percent of the total daily photosynthetic period. During these warm periods following rainfall, temperature reductions favoring photosynthesis appear to take priority over water conservation. This relationship is in contrast to the high water conservation of smaller leaves with moderately low leaf conductances that are characteristic of most desert species (*10*), although maximizing photosynthesis at some cost to water-use efficiency has been previously considered as a potential strategy for desert plants (*4, 11*). This adaptive pattern may represent an evolutionary alternative to the biochemical alterations needed for raising the temperature range for optimal photosynthesis, a prerequisite for water-conserving desert plants with relatively large leaves or photosynthetic stems.

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7. The specific energy balance equations used to calculate the leaf temperatures in Fig. 1 are given in (*6*). These calculated leaf temperatures were found to be accurate to within ± 0.5°C under a wide range of environmental conditions.
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Photoejection of Electrons from Flavins in Polar Media

Abstract. *Riboflavin and 12 of its derivatives have been shown to form solvated electrons under ultraviolet irradiation (253.7 nanometers) in various water-methanol solvent mixtures. The highest quantum yield of solvated electrons (about 0.03) was obtained for flavins containing tyrosine on a side chain in the isoalloxazine N-3 or N-10 position. The splitting of hydrogen atoms from excited flavin molecules was also observed. From the results presented here, it can be determined that the semiquinone transients are formed not only by way of the flavin triplet, as usually suggested, but also by the attack of the electrons and hydrogen atoms on flavin molecules in the ground state. This is important, because the flavin radicals remaining after the electron-ejection or hydrogen-splitting processes must also be considered in the subsequent reaction mechanisms. The electron-ejection process from electronically excited flavins has important implications in the photobiology of these compounds.*

It has been shown that riboflavin and other isoalloxazines with substituents on the N-10 position in air-free polar solutions can be photobleached, and alteration to the aliphatic side chain is mainly responsible for this process (*1–4*). The solvent influences the kind of products formed in the photochemical reactions, which can be divided into two groups: reversible and irreversible. In the first group of products, the carbon skeleton of the side chain remains intact; however, it is oxidized. As a result of investigations of kinetic isotope effects with specifically deuterated isoalloxazines that have substituents on the N-10 position, it has been found that these processes can be initiated by intramolecular hydrogen abstraction (*2, 4, 5*). In the second group, at least a part of the carbon skeleton of the side chain is removed or the isoalloxazine nucleus is fragmented (*6*). Hydrogen abstraction occurs preferentially from the OH-bearing side-chain carbon most proximal to the ring system.

In addition, a completely reversible photoreduction of riboflavin has also been observed (*1, 2, 7*). Flash photolysis investigations showed that the reduction process is easier to achieve in alcohols with sufficiently labile hydrogens than in other solvents. The following solvents have been used, with the effectiveness decreasing in the order: 2-propanol, *tert*-butanol, 2-propyl acetate, and *tert*-butyl acetate (*8*). The same investigators found

Table 1. Substituents in formula **1**.

Compound	Substituents
1	$R_1 = CH_2(CHOH)_3CH_2OH$; $R_2 = H$ (riboflavin)
2	$R_1 = (CH_2)_5CONHCH(COOCH_3)CH_3$; $R_2 = H$
3	$R_1 = (CH_2)_5CONHCH(COOH)CH_2CH_2SCH_3$; $R_2 = H$
4	$R_1 = CH_2CONHCH(COOCH_3)CH_2C_6H_5$; $R_2 = H$
5	$R_1 = CH_2CONHCH(COOCH_3)CH_2C_6H_4CH_3$; $R_2 = H$
6	$R_1 = CH_2CONHCH(COOCH_3)CH_2C_6H_4OH$; $R_2 = H$
7	$R_1 = (CH_2)_5CONHCH(COOCH_3)CH_2C_6H_4OH$; $R_2 = H$
8	$R_1 = CH_2CONHCH(COOCH_3)CH_2$-indole; $R_2 = H$
9	$R_1 = (CH_2)_5CONHCH(COOCH_3)CH_2$-indole; $R_2 = H$
10	$R_1 = CH_3$; $R_2 = CH_2CONHCH(COOCH_3)CH_2C_6H_5$
11	$R_1 = CH_3$; $R_2 = CH_2CONHCH(COOCH_3)CH_2C_6H_4OH$
12	$R_1 = CH_3$; $R_2 = CH_2CONHCH(COOCH_3)CH_2$-indole
13	8α-*S*-(*N*-Acetyl)-L-cysteinylriboflavin

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