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Temperature and Water Relations for Sun and Shade Leaves of a Desert Broadleaf, *Hyptis emoryi*

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ABSTRACT

The temperature and water relations of sun versus shade leaves of *Hyptis emoryi* Torr. were evaluated from field measurements made in late summer. Throughout most of the day sun leaves had higher temperatures and higher resistances to water vapour diffusion, but lower transpiration rates and lower stem water potentials, than did shade leaves. Leaf absorptivity to solar irradiation was less for 1.5-cm-long sun leaves (0.44) than for 4.0-cm shade leaves (0.56). For both leaf types the stomatal resistance increased as the water vapour concentration drop from the leaf to the air increased.

Energy balance equations were used together with the measured temperature dependence of photosynthesis to predict the effect of variations in leaf absorptivity, length, and resistance on net photosynthesis. The influence of leaf dimorphism on whole plants was determined by calculating daily photosynthesis and transpiration for plants with various percentages of sun and shade leaves. A hypothetical plant with all sun leaves in the sun had about twice the photosynthesis and half the transpiration ratio as did plants with sun leaves in the shade or shade leaves in the sun or shade. Plants with both sun and shade leaves had the highest predicted photosynthesis per unit ground area. The possible adaptive significance of the seasonal variation in sun and shade leaf percentages observed for individual *H. emoryi* bushes is discussed in terms of water economy and photosynthesis.

INTRODUCTION

In addition to intraspecific differences in leaf size, colour, or shape caused by edaphic factors, mature leaves on the same plant may vary morphologically depending on the season and the leaf location in the canopy (Hanson, 1917; Shields, 1950; Esau, 1965; Walter, 1973). Specifically, sun leaves, which occur in the more exposed positions, are typically smaller, thicker, lighter in colour, and more pubescent than shade leaves. Vogel (1968, 1969) found that the deeply lobed sun leaves of *Quercus alba* had greater convective heat exchange than did shade leaves. Leaf thickness is particularly sensitive to the illumination level during development, the thicker sun leaves having more highly developed palisade and spongy mesophyll regions (Turrell, 1936; Cormack and Gorham, 1953; Jackson, 1967; Nobel, Zaragoza, and Smith, 1975; Nobel, 1976). The much higher photosynthetic rates reported for sun versus shade leaves at light saturation have been variously attributed to increased photosynthetic enzyme activity (Björkman, 1970; El-Sharkawy and Hesketh, 1965; Grahl and Wild, 1973), variations in the number of

chlorophyll molecules per photosynthetic unit (Pearlstein, 1971; Goodchild, Björkman, and Pylotis, 1972), or decreases in the effective mesophyll resistance to CO₂ uptake due to a greater mesophyll cell surface to leaf area ratio (Nobel *et al.*, 1975; Nobel, 1976). Turrell (1965) felt that the increase in internal surface area for sun leaves would increase transpiration. However, Tanton and Crowdy (1972) provided evidence that the majority of evaporation from a leaf occurs at the inner sides of the guard cells and other epidermal cells, and so transpiration would be only slightly influenced by differences in mesophyll cell surface area. More recently, Meidner (1976) found that leaf epidermal strips, without underlying mesophyll tissue, transpired at about the same rates as intact leaves, further indicating that transpiration is relatively independent of leaf thickness.

This study quantifies the temperature and water relations of sun versus shade leaves of *Hyptis emoryi* Torr. (Labiatae) so that the possible adaptive significance of this particular form of leaf dimorphism can be evaluated. Specifically, plant transpiration and photosynthesis were determined from field and laboratory measurements on single leaves. Influences of various leaf morphological parameters were calculated using electrical analogue equations describing water vapour and CO₂ diffusion as well as energy balance relations for leaves under various conditions. Results are discussed in terms of seasonal water conservation and photosynthesis.

MATERIALS AND METHODS

Plant materials and site characteristics

Field experiments were conducted at the Philip L. Boyd Deep Canyon Desert Research Centre located near Palm Desert, California (116° 22' W, 33° 39' N, elevation 300 m). The Centre is situated on a large alluvial plain draining approximately 130 km² of the north and east slopes of the Santa Rosa mountains. Soil analysis showed a high sand and gravel content, but a low clay content. The perennial vegetation is numerically dominated by *Larrea tridentata* Sesse and Moc. ex DC., *Opuntia bigelovii* Engelm., and *Ambrosia dumosa* Gray with considerable interspecific clumping in their spatial distributions. The terrain is cut by several drainage plumes from less than a metre to several metres deep and up to 100 m across. These wash areas contain large numbers of *Cercidium floridum* Benth., *Hymenoclea salsola* Torr. and Gray, *Beloperone californica* Benth., and *Hyptis emoryi* Torr. Abundant annuals include species of *Schismus*, *Plantago*, *Cryptantha*, *Phacelia*, and *Camissonia*.

H. emoryi is an erect shrub with numerous slender straight branches, usually three to eight major branches growing slightly outward from the base, and a mean diameter approximately equal to the height for mature plants. Unless otherwise indicated, measurements reported here were made on an irrigated *H. emoryi* bush located adjacent to the north side of the Research Centre. This plant was 1.5 m tall, had a mean diameter of 1.7 m, and manifested a wide range of leaf sizes. Periodic waterings were continued throughout the duration of the experiments to maintain the soil water potential above -10^5 Pa (-1.0 bar) at a depth of 10 cm. Except where indicated otherwise, the data are means for five leaves and were obtained on 9-10 September 1975.

Leaf resistance and temperature

Total leaf resistance to water vapour diffusion (R_{wv}) was expressed as the parallel resistances of the upper (u) and lower (l) sides of a leaf and their corresponding air boundary layers (bl):

$$R_{wv} = \frac{(R_{wv}^u + R_{wv}^{bl})(R_{wv}^l + R_{wv}^{bl})}{R_{wv}^u + R_{wv}^l + 2R_{wv}^{bl}} \quad (1)$$

R_{wv}^u and R_{wv}^l were measured directly, while R_{wv}^{bl} was calculated from the expression, $R_{wv}^{bl} = \delta/D_{wv} = (0.4\sqrt{L}/v)/D_{wv}$, where δ is the displacement boundary layer of air, L is the characteristic dimension of the leaf in the direction of the air flow (cm), v is the air speed (cm s⁻¹), and D_{wv} is the diffusion coefficient of water vapour (cm² s⁻¹) at air temperature (Nobel, 1974).

R_{wv}^u and R_{wv}^l were measured with a diffusion resistance porometer (Lambda Instruments model LI-60 with LI-15 sensor and self-constructed thin metal fittings with circular apertures for smaller leaves). The extreme temperature sensitivity of this instrument necessitated frequent calibration during the day-long experiments. Resistance values were calculated using leaf temperatures (T_1) measured with an infrared field thermometer (Barnes Engineering model PRT-10) or inserted copper-constantan thermocouples (36 American-standard-wire gauge), instead of the thermistor provided with the LI-15 sensor.

The influence of leaf position in the canopy was evaluated by moving shade leaves into the sun and sun leaves into the shade and measuring initial as well as steady-state T_1 and R_{wv} . Leaf temperature was recorded immediately after each artificial positioning so that initial transpiration could be calculated before eventual changes in R_{wv} influenced T_1 . This was possible due to the relatively long time period required for R_{wv} to approach a steady-state (5 to 10 min) compared to a new steady-state T_1 (approx. 15 to 30 s).

Leaf absorptivity

Leaf reflectivity (r) and transmissivity (t) to solar irradiation were measured in the field using an integrating sphere radiometer as described in Dunkle, Edwards, Gier, and Bevans (1960). Calibration was accomplished using standards of known reflectivity (Minnesota Mining and Manufacturing brand 202-A10 velvet white with mean reflectivity > 0.90 from 400 to 1000 nm and 101-A10 velvet black with reflectivity < 0.05 between 300 and 1000 nm). An intermediate reflectivity standard was made by using manufacturer-supplied reflectivity values for proportional volume mixtures of these two paints. Individual measurements included a calibration with higher and lower reflectivity standards immediately before and after each sample determination. Leaf absorptivity (a) was calculated by subtracting the sum of r and t from unity.

Water potentials

Stem water potentials (Ψ^{stem}) for detached stems were taken immediately after excision using a Scholander-type pressure bomb (PMS Instrument model 1000) with the aid of a 40× American Optical dissecting microscope to view the exudation of tissue fluid. Soil thermocouple psychrometers were used to measure soil water potentials (Ψ^{soil}) at 10, 20, and 40 cm below the soil surface (Wescor model MJ-55 or HR-33 microvoltmeters with model PT 51-05 sensors).

Gas exchange

The temperature influence on net photosynthesis was determined for *H. emoryi* sun and shade leaves on 15 October 1975 using the apparatus described in Nobel (1976). A flow-through infrared gas analyser system measured the net uptake of CO₂ for single excised leaves while in a leaf chamber submerged in a temperature-controlled water bath. Influences due to variations in R_{wv} were minimized by selecting leaves where the mean R_{wv} varied by less than ± 0.5 s cm⁻¹. Transpirational water loss (J_{wv}) and net photosynthesis (J_{CO_2}) equal a concentration difference (Δc_{wv} and Δc_{CO_2} , respectively) divided by the appropriate resistance (R_{wv} and R_{CO_2} , respectively). In turn R_{CO_2} is the sum of a gas phase resistance ($R_{CO_2}^{\text{gas}} = 1.56 R_{wv}$) and a liquid phase resistance ($R_{CO_2}^{\text{liq}}$). Details of these derivations and a discussion of their limitations are given in Nobel (1976).

Microclimate

Microclimatic measurements used for the energy balance calculations included direct, diffuse (sky), and reflected solar irradiation (measured individually with a Moll-Gorczynski pyranometer), upward and downward longwave radiation (Fritschen net radiometer modified to give unidirectional fluxes), and wind speed (Lambrecht model 641N hot-wire anemometer). All radiometric measurements were taken by placing the sensor at the actual leaf location and orientation, as were determinations of illumination (using a Photo Research model FC 200 TV-B illumination meter). Wind speeds were monitored approximately 3 cm upwind from a

leaf. Air temperatures (T_a) and air water vapour concentrations (c_{wv}) were measured approximately 10 cm above individual leaves with a ventilated thermocouple psychrometer calibrated against a dew-point hygrometer (Cambridge Systems EG and G model 880). All thermocouples used to measure wet- or dry-bulb air temperatures were shielded from direct solar irradiation. Rainfall was measured with a Meteorological Research model 384 tipping-bucket raingauge. Local times were converted to true solar time as described in List (1968).

Energy balance

Energy balance calculations were used to determine the quantitative importance of leaf size, absorptivity, and R_{wv} on leaf temperature. These quantities were individually varied in the energy balance equation while other microclimatic and leaf parameters were held constant. Leaf orientation problems were simplified by considering leaves whose surfaces were perpendicular to the sun's direct rays. Following the derivation given in Smith and Miller (1973), leaf temperature can be expressed as follows:

$$T_l = T_a + \left(\frac{E_i - \epsilon \sigma T_a^4 - \gamma[(c_{wv}^* - c_{wv})/R_{wv}]}{4\epsilon \sigma T_a^3 + h_c - \gamma \left[\frac{dc_{wv}^*}{dT_a} / R_{wv} \right]} \right) \quad (2)$$

where E_i is the total radiant energy absorbed by the leaf (longwave plus solar); ϵ is the leaf emissivity (considered to be 0.97); σ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ } ^\circ\text{K}^{-4}$); c_{wv}^* is the saturation water vapour concentration of ambient air; γ is the latent heat of vaporization of water at the leaf temperature; and h_c equals the thermal conductivity of still air divided by δ , where δ is calculated for the appropriate leaf shape given by Taylor (1975).

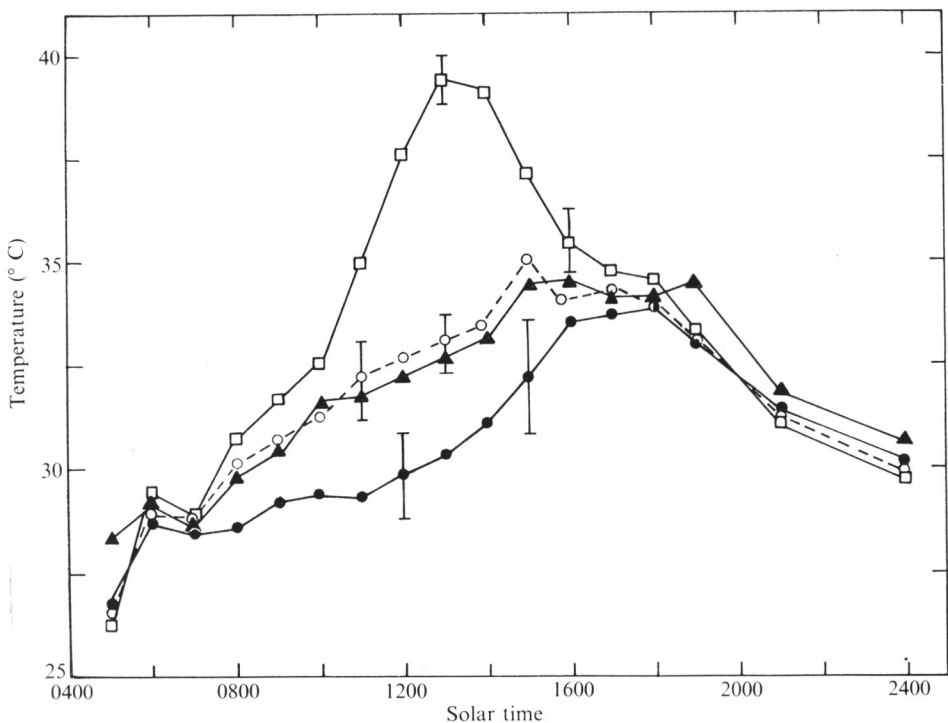


FIG. 1. Mean leaf temperatures for sun and shade leaves of *H. emoryi* determined on 9–10 September 1975. Final temperatures for shade leaves placed in the sun for 10 min are represented by □; ○ and ● are for sun and shade leaf temperatures, respectively, in their natural canopy positions; ▲ represents air temperatures. Vertical bars indicate maximum or minimum 95% confidence intervals for daytime measurements (night-time maximum confidence intervals were less than minimum daytime values).

RESULTS

Leaf temperature

Leaf temperature varied almost 9 °C throughout a day for both sun and shade leaves in their natural positions in the canopy (Fig. 1). Sun leaf temperatures (T_1^{sun}) were usually slightly above T_a during the daytime, while T_1^{shade} was often considerably below T_a . T_1^{sun} , T_1^{shade} , and T_a were maximum at about 1600. Shade leaves placed in the sun at 1300 were initially about 6 °C above T_a ; after 5 min, R_{wv} increased to over 30 s cm⁻¹ and T_1^{shade} rose an additional 1.6 to 3.1 °C (Fig. 1). At night, T_1 was generally 0.5 to 1.0 °C below T_a , reaching a minimum about one hour before sunrise (T_1^{shade} was then almost 2 °C below T_a).

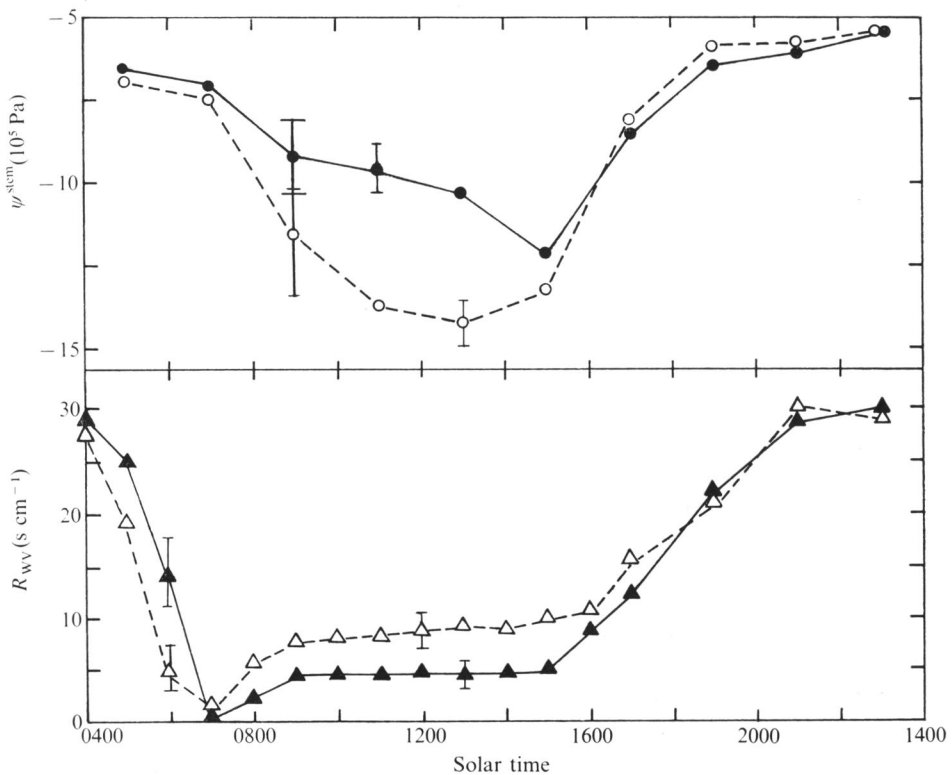


FIG. 2. Mean stem water potentials (Ψ^{stem}) and leaf resistances (R_{wv}) for sun (\circ , Δ) and shade (\bullet , \blacktriangle) leaves. Vertical bars represent 95% confidence limits as in Fig. 1.

Leaf resistance and stem water potential

R_{wv} for sun and shade leaves sharply decreased shortly after sunrise (0500), reached a minimum near 0700 (1.2 s cm⁻¹ for sun leaves and 1.5 s cm⁻¹ for shade ones), rose gradually through the day-time, and then increased more rapidly from just before sunset (1645, when the bush became entirely shaded) to 2200 (Fig. 2). R_{wv} for shade leaves was greater until 0800, after which R_{wv} for sun leaves was nearly 4 s cm⁻¹ higher until appreciable stomatal closure at 1700. At night R_{wv} was about 30 s cm⁻¹ for both sun and shade leaves.

Ψ^{stem} was initially the same near sun and shade leaves (about -7×10^5 Pa); it decreased more rapidly for stems with sun leaves, which became 4×10^5 Pa lower in water potential than near shade leaves from 1100 to 1300, Ψ^{stem} becoming similar again after 1800 (Fig. 2). Minimum Ψ^{stem} near sun leaves (-14×10^5 Pa) occurred at 1300, while Ψ^{stem} for shade leaves was minimal at 1700 (-12×10^5 Pa).

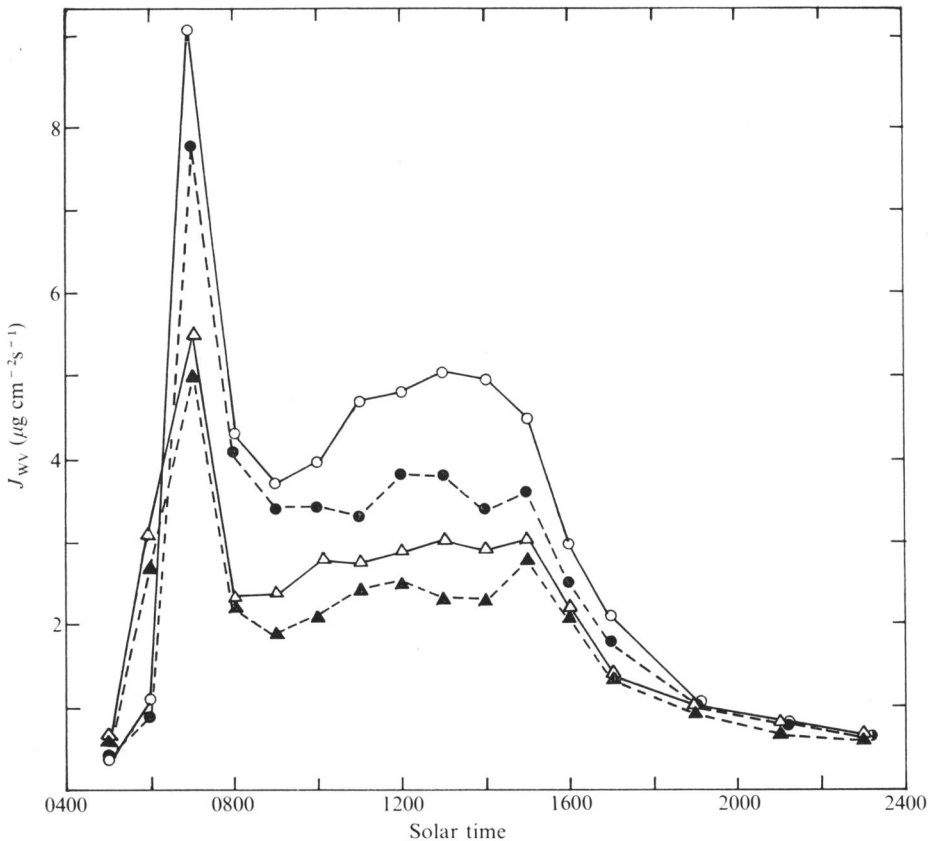


FIG. 3. Initial transpiration rates (J_{wv}) calculated for sun (Δ) and shade (\bullet) leaves in natural canopy positions, sun leaves in shade (\blacktriangle), and shade leaves in sun (\circ).

Transpiration

Except during the early morning, J_{wv} calculated for shade leaves was about 20% greater than for sun leaves in their natural canopy positions (Fig. 3). Maximum J_{wv} occurred at 0700, when both sun and shade leaves were transpiring at more than twice the rates typical for the remainder of the day. Using the T_1 measured immediately after placing shade leaves in the sun, J_{wv} from 1100 to 1600 was about 25% greater than for naturally positioned shade leaves (Fig. 3); however, after 5 to 10 min, R_{wv} increased to over 20 s cm^{-1} and the calculated transpiration became less than $1 \mu\text{g cm}^{-2} \text{ s}^{-1}$. J_{wv} for sun leaves placed in the shade was initially less than for natural shade leaves (Fig. 3), but ensuing decreases in R_{wv} led after 10 min to similar J_{wv} 's as for shade leaves in the shade.

R_{wv} responses

Stomatal responses to illumination, Δc_{wv} , Ψ^{stem} , and T_1 were considered. From 0500 to 0700, illumination on a horizontal plane increased from 90 lx to 60 klx, leading to the marked decreases in R_{wv} noted in Fig. 2. From 0800 to 1500, the illumination was fairly constant (90 ± 15 klx), while it decreased below 2 klx at 1645 and stomatal closure occurred (Fig. 2). Fig. 4 also indicates the diurnal opening and closing responses of stomata, plus the response to Δc_{wv} occurring during the day-time. From 0800 to 1500 R_{wv} for sun leaves increased linearly with Δc_{wv} [R_{wv} in $s\ cm^{-1} = 0.49 (\Delta c_{wv} \text{ in } g\ m^{-3}) - 2.6$, $r = 0.93$]. A similar linear correlation between R_{wv} and Δc_{wv} existed for shade leaves ($R_{wv} = 0.51 \Delta c_{wv} - 4.0$, $r = 0.82$).

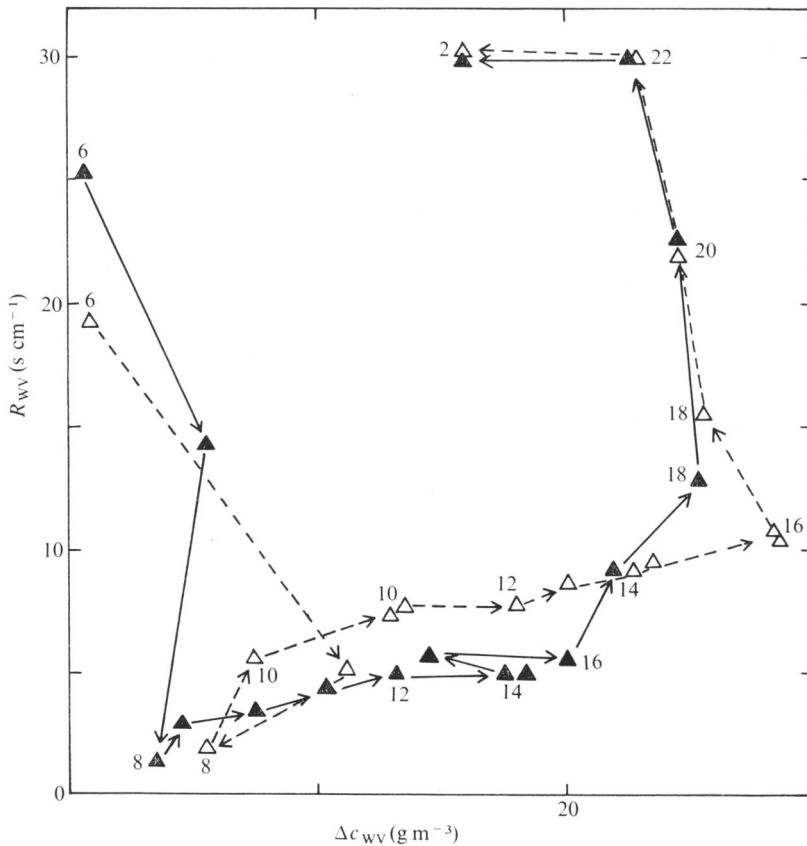


FIG. 4. Diurnal relationship between R_{wv} and Δc_{wv} for sun (Δ) and shade (\blacktriangle) leaves. Arrows show the temporal progression with solar time indicated in hours.

Both correlations were statistically significant using Student's t -test at $P < 0.01$ (Snedecor, 1955). Using the data in Figs 1 and 2 for 0800 to 1500, linear regressions of R_{wv} on T_1 and on Ψ^{stem} for sun leaves [R_{wv} in $s\ cm^{-1} = 0.99 (T_1^{sun} \text{ in } ^\circ C) - 19.1$, $r = 0.75$; R_{wv} in $s\ cm^{-1} = -0.97 (\Psi^{stem} \text{ in } 10^5\ Pa) - 5.2$, $r = -0.72$] and for shade leaves ($R_{wv} = 0.81 T_1^{shade} - 19.8$, $r = 0.73$; $R_{wv} = -1.33 \Psi^{stem} - 8.1$, $r = -0.75$) were statistically significant at $P < 0.01$, but had lower degrees of correlation than for Δc_{wv} .

Energy balance

Mean leaf reflectivity (r) to solar irradiation was 35% greater for sun leaves (0.54 ± 0.03) from 1.1 to 1.9 cm in length than for shade leaves (0.40 ± 0.04) from 4.1 to 5.8 cm in length. Student's t -test (Snedecor, 1955) indicated statistically significant differences between these means at $P < 0.01$. Reflectivities between abaxial and adaxial surfaces were within ± 0.04 (eight measurements) and were not statistically significant at $P < 0.01$. Transmissivity (t) was less than 0.05 for 20 sun and shade leaves, corresponding to similar data reported by Nobel (1976). Subtracting the sum of t and r from unity gave a mean absorptivity of 0.44 for sun leaves and 0.56 for shade leaves.

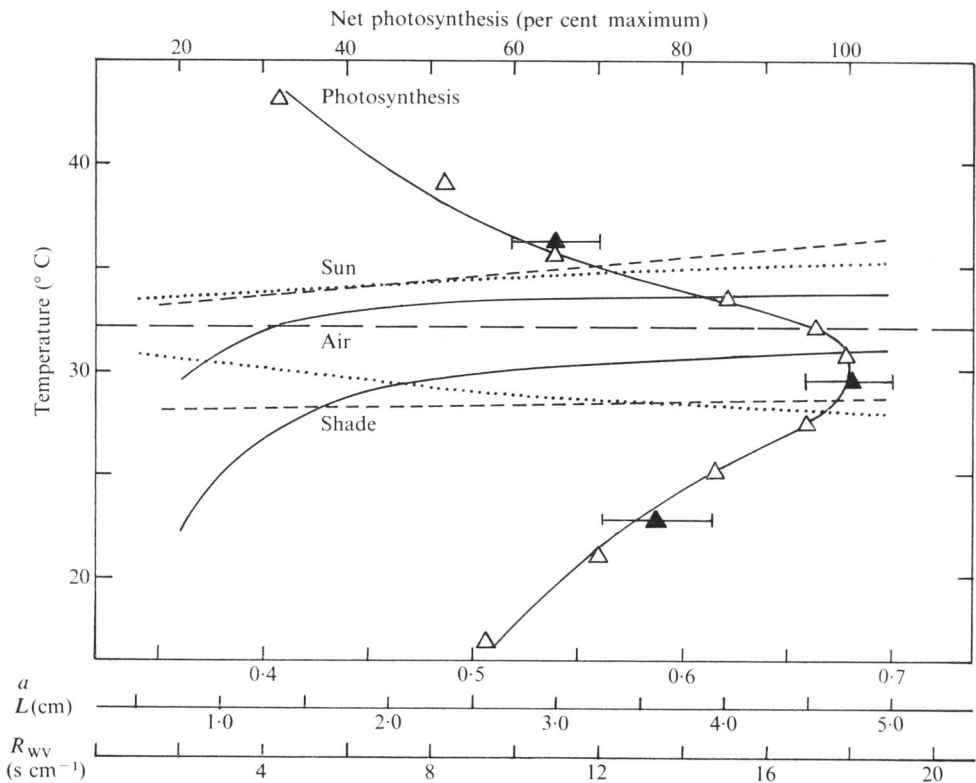


FIG. 5. The influence of leaf size (L) (\cdots), absorptivity (a) ($----$), and leaf resistance (R_{wv}) ($—$) on calculated leaf temperatures for sun and shade leaves at solar noon on 10 September 1975. Photosynthetic rates are from Nobel (1976) (Δ) plus additional measurements on 15 October (\blacktriangle), assuming that maximum photosynthesis occurred at about 30 °C. Microclimate parameters for sun and shade leaves, respectively, were as follows: E_i of 1088 and 495 $W\ m^{-2}$; a of 0.44 and 0.56; R_{wv} of 5.0 and 9.0 $s\ cm^{-1}$; l of 1.5 and 4.0 cm; v of 46 and 32 $cm\ s^{-1}$.

Calculated T_1 (equation 2) for sun leaves oriented normal to the sun's rays at 1200 on 10 September 1975 decreased almost 2 °C for a decrease in absorptivity of 0.25 (Fig. 5), corresponding to an approximate 20% increase in photosynthesis. Increasing sun leaf length by 2.0 cm resulted in a 1 °C rise in T_1 and a decrease in photosynthesis of about 10%. Simulations varying R_{wv} did not show significant

influences on T_1 until R_{wv} was reduced below 9 s cm^{-1} . A change in R_{wv} from 9 to 4 s cm^{-1} increased predicted photosynthesis about 15%. Calculated T_1^{sun} at solar noon was above T_a and optimal photosynthetic temperatures at all R_{wv} values except those below 4 s cm^{-1} , while T_1^{shade} was always below T_a . Varying shade leaf absorptivity caused negligible changes in T_1^{shade} (Fig. 5). Increasing shade leaf length from 1.0 to 4.0 cm caused predicted T_1^{shade} to decrease 1.5°C , corresponding to a relatively small decrease in photosynthesis (2%). Simulated decreases in R_{wv} when it was below 5 s cm^{-1} created substantial reductions in T_1^{shade} and predicted photosynthesis.

Leaf size variation

The quantitative importance of sun versus shade leaf morphology on whole plant transpiration and photosynthesis depends upon the relative percentages of these leaves on individual plants. *H. emoryi* bushes with more and larger shade leaves were found adjacent to north-facing slopes (e.g., canyon walls) where much of the plant was shaded during the day. In general plants with greater numbers of leaves tended to have a higher proportion of shade leaves. Leaves tended to be larger and more abundant in the spring than in late summer, e.g., the leaf area index (LAI) for five plants was 3.0 to 5.6 in May and 0.9 to 2.1 in September. The leaf length for fully exposed sun leaves on non-irrigated bushes was $0.83 \pm 0.06 \text{ cm}$ on 8 September 1975 and $1.63 \pm 0.11 \text{ cm}$ on 9 March 1976. Also, sun leaf length on 7 July 1975 for exposed leaves was $1.51 \pm 0.08 \text{ cm}$ on an irrigated bush and $1.04 \pm 0.05 \text{ cm}$ on a non-irrigated bush. Both of these comparisons were statistically significant ($P < 0.01$) using Student's *t*-test. Growth measurements on the irrigated *H. emoryi* for two 3-week intervals (4–26 September 1975 and 8–29 October 1975) showed that the increase in leaf surface area per tertiary branch was nearly equal for sun and

TABLE 1. *Seasonal changes in percentage of total leaf area on a plant for leaves greater than 2.0 cm in length*

Plus or minus values represent ranges for three repeated estimates. Leaf area equalled $0.68 (\text{leaf length})^2$.

Bush location	Height (m)	Percentage of total leaf area for leaves > 2.0 cm				
		23 May 1975	7 July 1975	8 Sept. 1975	11 Dec. 1975	9 March 1976
Adjacent to north-facing canyon wall	2.4	84	36	27	33	71 ± 9
Adjacent to north-facing wash bank	1.6	50 ± 8	29 ± 5	—	22	42
Adjacent to north-facing side of large rock formation	1.8	66	36	20	24	40 ± 3
Exposed plant in wash	1.3	44	17	—	18	41
Exposed plant in canyon	1.4	38	20 ± 2	16	16	42

shade leaves. Specifically, the mean area added per branch for 15 tertiary branches at the appropriate canopy positions was $44.5 \pm 5.9 \text{ cm}^2$ for sun leaves (mean length = $1.31 \pm 0.23 \text{ cm}$) and $43.8 \pm 6.7 \text{ cm}^2$ for shade leaves ($2.74 \pm 0.33 \text{ cm}$).

To determine the influences of season and microclimate on the relative percentages of shade leaves, five plants from representative microhabitats were monitored from May 1975 to March 1976 (Table 1). Leaves greater than 2 cm in length accounted for a maximum percentage of the total leaf area (84%) in May for a plant located alongside a canyon wall, while the maximum concurrently recorded for a bush not shaded by the surroundings was 44%. These percentages decreased sharply through the summer, remained low during winter, but increased to comparatively high values in early March 1976 following substantial rainfall during the first 2 weeks in February (65 mm) and 7 mm during the first week in March 1976.

DISCUSSION

Individual *H. emoryi* bushes can have varying percentages of sun and shade leaves depending on season and microhabitat. Leaf size appears to be inversely related to the daily integrated illumination received by the leaf (Nobel, 1976), and thus would be strongly influenced by canopy structure and by shading from the surroundings. During periods of rapid growth following rainfall, a greater number of large leaves developed, primarily in the interior and north-facing sides of bushes. Consequently, considerable portions of the total leaf area consisted of the larger shade-type leaves during the spring when flowering occurred. In the following paragraphs the physiological and morphological differences measured for sun versus shade leaves are discussed in terms of their quantitative influence on whole plant transpiration and photosynthesis, paying particular attention to leaf temperatures and energy balance.

Stomatal responses

The early morning decrease in leaf resistance (R_{wv}) to below 2 s cm^{-1} for all leaves was correlated with rapidly increasing illumination from 0500 to 0700 (Fig. 2). The minimum R_{wv} at 0700 created a short-term increase in transpiration (J_{wv}) that was the maximum rate occurring for the day (Fig. 3). Immediately following this transient rise in J_{wv} with its substantial rate of water loss, a partial stomatal closing occurred, indicated by higher R_{wv} values. Although R_{wv} for sun leaves was almost twice that for shade leaves during most of the day (Fig. 2), $J_{\text{wv}}^{\text{shade}}$ was less than 20% greater than $J_{\text{wv}}^{\text{sun}}$. This disproportionate effect on J_{wv} compared to the increase in R_{wv} for sun leaves was due to the greater sun leaf temperatures, which increases the water vapour concentration (c_{wv}^*) inside a leaf and leads to a greater Δc_{wv} from leaf to air. This influence on J_{wv} becomes more pronounced at higher leaf temperatures due to the nearly exponential increase of c_{wv}^* with temperature.

R_{wv} for sun and shade leaves gradually increased throughout the day (Figs 2, 4), while J_{wv} remained relatively constant. This can be attributed to the linear increase in R_{wv} with increasing Δc_{wv} ($r = 0.93$ for sun leaves and $r = 0.82$ for shade

leaves) (Fig. 4). Similar linear responses of R_{wv} to T_1 and Ψ^{stem} were not as strongly correlated and, in the case of T_1 , were due mainly to the influence of T_1 on Δc_{wv} . Although stem water potentials were initially the same, Ψ^{stem} during the day became lower for sun leaves than shade leaves, possibly reflecting the greater distance along the major branches where the tertiary branches for sun leaves occur. This 4×10^5 Pa difference, similar to values reported for sun and shade leaves on *Picea engelmannii* by Kaufmann (1975), would have been even greater were it not for the partial stomatal closure which reduced J_{wv} for the sun leaves. Shade leaves were transpiring about the same per unit area as sun leaves, but several times more per leaf due to the much greater surface area of shade leaves. In this regard, growth measurements during September and October showed that the leaf area added on tertiary branches in the sun or shade was very nearly equal, and so the total transpirational water loss per tertiary branch would actually be about the same for sun and shade leaves. This approximate constancy of water loss may indicate a physiological limitation controlling the total leaf area produced per tertiary branch. In turn the amount of water that could be transpired and hence the leaf area produced per branch would depend on the availability of water to the plant.

A close coupling of R_{wv} to Δc_{wv} would be especially adaptive in situations where water is limiting. If stomatal opening is curtailed on days with an unusually high Δc_{wv} , considerable transpirational water savings could result. Also, avoiding stomatal opening when Δc_{wv} is large would conserve soil water, important even when Ψ^{soil} is high. For instance, Ψ^{soil} following rainfall in February (65 mm) remained above -3.0×10^5 Pa at depths below 10 cm until mid-April, but stomatal responses to Δc_{wv} still occurred. By selectivity opening stomata during periods of low Δc_{wv} , the total water lost per CO_2 fixed would be less. Such improved water use efficiency for plants with stomata sensitive to Δc_{wv} has been discussed elsewhere (Hall and Kaufmann, 1975; Schulze, Lange, Kappen, Evenari, and Buschbom, 1975).

Leaf transpiration and photosynthesis

Mean sun leaf temperatures (T_1^{sun}) during the day were considerably above optimal photosynthetic temperatures. Using energy balance relations (equation 2) to predict T_1^{sun} as a function of R_{wv} shows that R_{wv} would have to decrease from about 9.0 to 3.0 s cm⁻¹ to reduce leaf temperatures at 1200 on 10 September to 31.0 °C, very close to the optimal photosynthetic temperature (Fig. 5). This 2.6 °C decrease in T_1^{sun} would create a 20% increase in photosynthesis due to temperature effects alone. In addition, using the data provided by Nobel (1976), a reduction in R_{wv} from 9.0 to 3.0 s cm⁻¹ would cause a 46 per cent decrease in R_{CO_2} (from 20.4 to 11.1 s cm⁻¹) for *H. emoryi*, and thus an 85% increase in J_{CO_2} at light saturation. Transpirational water losses would increase almost three-fold after correcting for a 17% savings due to the decrease in Δc_{wv} at these lower leaf temperatures. Thus, for these simulated conditions, a three-fold reduction in R_{wv} for sun leaves would increase J_{wv} by 183% for an increase in J_{CO_2} of 122%.

Temperature influences on J_{CO_2} are also brought about via changes in leaf absorptivity and leaf size. A change in absorptivity from 0.44 to the 0.56 measured for a shade leaf would cause T_1^{sun} to increase from 33.6 to 35.6 °C (Fig. 5), while an

accompanying change to a shade leaf size (from 1.5 to 4.0 cm long) would further raise T_1^{sun} to 36.6 °C. These changes would decrease photosynthesis by 28%, but would increase transpiration 27%, and would be of no obvious adaptive value. On the other hand, reducing absorptivity could advantageously lower T_1^{sun} , while decreases in size for the already small sun leaves would be less important, since convective cooling cannot decrease T_1^{sun} below T_a .

Another morphological influence on J_{CO_2} is the reduction in the CO_2 liquid phase resistance ($R_{\text{CO}_2}^{\text{liq}}$) when the available internal surface area per unit leaf area (A^{mes}/A) is higher (Nobel *et al.*, 1975; Nobel, 1976), which is accomplished without any significant influence on J_{wv} (Tanton and Crowdy, 1972; Meidner, 1976). For example, a 1.5-cm sun leaf would have an A^{mes}/A 47% higher than a 4.0-cm shade leaf (36.2 versus 24.7, Nobel, 1976). For an R_{wv} of 9.0 s cm⁻¹ appropriate for 1200 (Fig. 2), J_{CO_2} would correspondingly be 15% higher for the sun leaf, while at 0700 it would be 37% higher due to the much lower R_{wv} (1.2 s cm⁻¹) at that time. In summary, for 9–10 September 1975, the lower absorptivity, shorter length, and higher A^{mes}/A would all contribute to a greater J_{CO_2} for a sun leaf without increasing J_{wv} . Alternatively, decreasing R_{wv} to reduce T_1^{sun} toward the optimal photosynthetic temperature would cause considerable water loss, although a compensatory gain in J_{CO_2} occurs.

For naturally positioned shade leaves R_{wv} was lower than for sun leaves during the day and T_1^{shade} was closer to that optimal for photosynthesis (Figs 1, 2, 5). Due to their high absorptivity and large size, exposing shade leaves to direct solar irradiation caused T_1^{shade} to increase rapidly above photosynthetically optimal levels, consequently Δc_{wv} increased leading to partial stomatal closure, and hence leaf temperature rose even further. The physiological advantage of having larger leaves in the shade could be related to increased light interception as well as optimizing temperatures for photosynthesis. Because of the predominant influence of the latent heat term (equation 2), T_1^{shade} can be well below T_a (Figs 1, 5). Considering that the optimal temperature for photosynthesis in May and October was about 30 °C (Fig. 5), the importance of having T_1 below T_a can be ascertained from available weather records at the study site. From 1960 to 1975, average daily mean temperatures for May through September were about 31 °C, maximum temperatures averaged 35.2 °C, and the absolute maxima were near or above 30 °C for every month except December (26.7 °C). Thus for *H. emoryi* T_1^{shade} being below T_a can be an advantage throughout most of the year.

Whole plant aspects

To evaluate the adaptive significance of sun/shade leaf dimorphism, the influence on total plant water economy and photosynthesis should be determined. One extreme could be a porous exposed bush with only sun leaves, all 1.5 cm in length. As shown in Table 2, total net photosynthesis would be slightly more than double that for an exposed bush with 4.0 cm shade leaves. Moreover, comparing relative water use efficiencies, the transpiration ratio (mass of H₂O lost/mass of CO₂ fixed) for the bush with sun leaves would be less than half that of the bush with only shade leaves. This transpiration ratio of 104 calculated for a bush with only

sun leaves is considerably lower than minimum values generally reported for C₃ and C₄ plants (450–600 and 250–350, respectively; Szarek and Ting, 1975), and is primarily a consequence of the relatively high R_{wv} for leaves in the sun maintained by this xeric plant during the day. When sun leaves were placed in the shade, their predicted daily photosynthesis was lower than that for shade leaves, since T_1^{sun} tended to be above that optimal for photosynthesis. This helps cause the transpiration ratio calculated for sun leaves in the shade to be the highest (249) of the four combinations of sun and shade leaf exposures simulated in Table 2. Both in terms of total net photosynthesis and the transpiration ratio, sun-type leaves perform better in the sun and shade-type leaves in the shade, a situation insured during leaf development by the inverse response of leaf size to total integrated illumination (Nobel, 1976).

TABLE 2. *Total daily photosynthesis and transpiration predicted for H. emoryi with various percentages of 1.5-cm sun leaves and 4.0-cm shade leaves*

The total transpiration for sun leaves in the sun and shade leaves in the shade was obtained from the areas under the curves in Fig. 3; transpiration for sun leaves in the shade and shade leaves in the sun was calculated from the steady-state T_1 in Fig. 1 and the appropriate R_{wv} 's. Total photosynthesis was calculated assuming light saturation from 0700 to 1600 for sunlit leaves, 15 klx in the shade (appropriate for a 4.0-cm leaf; Nobel, 1976), and using measured illuminations at other times (0500 to 0700, 1600 to 1800). The quantitative influence of illumination on photosynthesis was determined from measurements taken by Nobel (1976). Transpiration and photosynthesis are expressed per unit leaf area, while the transpiration ratio is on a mass H₂O/mass CO₂ basis.

Condition	Transpiration (mg cm ⁻²)	Photosynthesis (μmol cm ⁻²)	Transpiration ratio
Sun leaves in sun	120	26.2	104
Shade leaves in sun	125	12.6	226
Sun leaves in shade	154	14.0	249
Shade leaves in shade	146	16.9	196
50% sun leaves in sun, 50% shade leaves in shade	133	21.6	140
33% sun leaves in sun, 67% shade leaves in shade	137	20.0	156

Table 2 shows that the daily water loss per unit area is rather uniform for plants with the four combinations of single leaf types considered (120 to 154 mg cm⁻²), with the higher rates predicted for leaves in the shade. Moreover, the availability of water necessary for leaf initiation leads to increased shading caused by having more leaves. Assuming equal integrated illumination for exposed sun leaves in March and September, the two-fold greater leaf length in March indicates that leaf length is also influenced by water availability (the February rainfall caused Ψ_{soil} to be about -10^4 Pa in March, whereas it was $<9 \times 10^6$ Pa in September). This effect of water is supported by the measurements on irrigated and non-irrigated *H. emoryi* in July where a 50% greater length was observed for exposed sun leaves on the irrigated versus the non-irrigated bush. Thus not only does water availability directly influence the ultimate size of individual leaves, but it indirectly

influences shade leaf growth by providing shade. However, the relative size differences between sun and shade leaves on the same plant appears to depend on the daily integrated illumination received by individual leaves (Nobel, 1976), regardless of the availability of water.

The presence of both sun and shade leaves affects the transpiration and photosynthesis of the whole plant. Non-overlapping sun leaves in the sun, which would ensure light saturation of photosynthesis during most of the day, can be considered to represent a LAI of 1. If water becomes available and a second layer of shade leaves in the shade develops, the transpiration ratio could increase from 104 to 140 (Table 2). If a third layer of shade leaves is now added, the transpiration ratio becomes 156, indicating an even lower water use efficiency. However, the total photosynthesis per cm² of ground area would go from 26.2 to 43.2 to 60.0 μ moles of CO₂ fixed (Table 2). A strategy for maximizing photosynthesis per leaf when water is not available is reflected in the low LAI (0.9 to 2.1) and a high percentage of sun leaves in the drier part of the year, creating a more porous or open canopy. During periods when water is available and rapid growth ensues (LAI of 3.0 to 5.6), the total photosynthesis of the plant is enhanced by the addition of more shade leaves, although the transpiration ratio becomes higher. Thus, although small sun leaves are advantageous when the canopy is porous (low LAI), increased shade leaf growth when water is available increases CO₂ uptake for the plant as a whole. In summary, the usual adaptive strategy of water conservation by this desert plant appears to be relinquished in favour of greater growth and photosynthesis per plant with accompanying higher transpiration ratios during periods when water is plentiful. This could be especially advantageous during the spring considering the metabolic cost of producing flowers.

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