Leaf Temperatures of Blackbrush: Relationships With Air and Soil Surface Temperatures

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Abstract: Comparative diurnal and seasonal leaf temperatures of blackbrush (*Coleogyne ramosissima* Torr.) plants were quantitatively examined in the Clark Mountain of southeastern California. Path analysis revealed that seasonality and diurnal period were significant positive predictors of air, soil surface, and blackbrush leaf temperatures. Path analysis also indicated that air temperature was a significant positive predictor of soil surface and blackbrush leaf temperatures. Blackbrush leaf temperatures consistently remained at or near air temperatures throughout the day and year. Sunlit leaf temperatures were significantly warmer than shade leaf temperatures during the summer season only, but not during rest of the seasons. Soil surface temperatures were significantly warmer than air and blackbrush leaf temperatures irrespective of seasonality and diurnal period. Significant interactions were detected between seasonality and diurnal period for air and blackbrush leaf temperatures in the Mojave Desert of southeastern California.

Introduction

Plant species have adapted to survive various environmental stresses in deserts such as low precipitation, low relative humidity, low soil moisture and nutrients, intense solar radiation, and high air and soil temperatures. Solar radiation on plants growing in warm, arid environments may cause their death if plant temperatures rise well above a critical level (Gates and others 1968). Leaf temperatures exceeding the air temperature by 10 °C are common in the Great Basin Desert of southern Utah (Gates and others 1968). Xerophytes must prevent sunlit leaves from becoming too warm when air temperature exceeds 50 °C or more. Leaf temperatures of many xerophytic species in southern Utah are very close to air temperatures (Gates and others 1968). Many warm desert plants have small leaves compared to their closely related species living in more mesic environments. There are ecomorphological reasons why the temperature of small leaves stay near air temperature. Large, thin leaves have a greater surface area, absorb heat, and lose water via transpiration more rapidly compared to small, thick leaves.

Temperatures of the sunlit soil surfaces ranged from 12 to 28 °C above air temperatures of the Great Basin Desert in southern Utah (Gates and others 1968). Summer seasons have the largest daily and annual range of soil surface temperatures of any season. However, any litter, debris, and vegetation covering the ground would substantially reduce the diurnal and annual range of soil surface temperatures in southern Nevada (Lei and Walker 1997b). Relative to open substrate temperatures, Suzan and others (1996) reported a 15 °C decrease in summer maximum temperatures and an increase in winter minimum temperatures of 3 °C under shrubs in the Sonoran Desert. During the winter when the ground is continuously covered with snow, soil surface temperatures remain at or a few degrees below freezing because the insulating capacity of the snow traps heat radiating from the earth, thus protecting plants from extreme cold (Barbour and others 1999).

Leaf temperatures of some desert plant species were quantified (Gates and others 1968; Gibbs and Patten 1970; Smith 1978). Yet, possible interactions and correlations between air and soil surface temperatures in determining leaf temperatures of blackbrush (*Coleogyne ramosissima*) shrubs in southeastern California of the Mojave Desert have not been documented.

Methods

Study Site

Field studies were conducted during four 3-month intervals from March through December 2001 at the Clark Mountain (roughly 35°41'N and 115°32'W; elevation 1,475 m) near the Nevada State border. The months of March, June, September, and December represented the four distinct seasons. Summers display warm, arid conditions, with maximum air temperatures in the 40 °C range. Winter air temperatures, on the contrary, are generally mild and pleasant. Winter rainfalls are mild and may last up to several days (Rowlands and others 1977). Monsoonal precipitation occurs from July through mid-September, as thunderstorms of high intensity and short duration. Soil erosion, especially along wash edges, is evidence of the intensity of some of the thunderstorm activity. The spring and fall seasons are generally considered most ideal for blackbrush growth and development, although sharp temperature changes can occur during these months. A relative humidity of 20 percent or less is common in summer seasons (Lei and Walker 1997a,b). A combination of high air temperatures and high evaporation, as well as low relative humidity, cloud cover,

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and low precipitation create a typical arid environment, with an average annual rainfall of less than 200 mm at midelevations of the Clark Mountain (Lei, personal observations, 2001).

Blackbrush shrublands often are considered a floristically simple community, consisting primarily of monospecific blackbrush stands with other woody species scattered throughout. Many common herbaceous plants are members of the Asteraceae, Agavaceae, Brassicaceae, Fabaceae, and Poaceae families. Blackbrush shrublands share a broad lower ecotone with creosote bush-white bursage (*Larrea tridentata-Ambrosia dumosa*) shrubland, and a broad upper ecotone with pinyon-Utah juniper (*Pinus monophylla-Juniperus osteosperma*) woodland (Lei and Walker 1997a,b).

Field Observations

Diurnal and seasonal air temperatures were measured concurrently with soil surface and blackbrush leaf temperatures to ensure comparability. Air temperatures were measured with a mercury-in-glass thermometer placing at 1.6 m above ground surface. Soil temperatures were measured with a metallic soil thermometer placed at the surface in open substrates and beneath shrub canopies.

Blackbrush shrubs were tagged with a brightly colored yarn prior to leaf temperature measurements to facilitate repeated sampling throughout the day. Air, leaf, and soil surface temperatures were measured at predawn (0600 hours), and then at 3-hour intervals through 1800 hours. Temperatures of 100 leaves from 50 blackbrush shrubs were taken with a fine-wire (0.02-mm) copper-constantan thermocouple inserted into leaf tissues. These 100 leaves were subdivided evenly between the top and bottom layers of canopy from the same plants to represent sunlit and shade leaves, respectively. Individual leaves within each layer of canopy were randomly selected to avoid biased sampling.

Statistical Analyses

Two-way Analysis of Variance (ANOVA; Analytical Software 1994) was performed to determine if air temperatures differed by seasonality (spring and summer) and/or by diurnal period (hour of day). Three-way Analysis of Variance (ANOVA; Analytical Software 1994) was conducted to detect significant effects of seasonality, diurnal period, and habitat type (open substrate and beneath shrub canopy) on soil temperatures. This three-way ANOVA was also used to detect significant effects of seasonality, diurnal period, and canopy position (top and bottom) on leaf temperatures. Path analysis, expressed as path coefficient or partial regression analysis (Analytical Software 1994), was performed to determine if diurnal period and seasonality had direct causal effects on air, soil surface, and blackbrush leaf temperatures. Path analysis was also performed to determine if air temperature had a causal effect on soil surface and blackbrush leaf temperatures. Linear regression analysis (Analytical Software 1994) was used to correlate soil surface temperatures with blackbrush leaf temperatures. Statistical significance was tested at the 5-percent level.

Results

Air, soil surface, and blackbrush leaf temperatures were significantly directly affected by seasonality and diurnal period ($P \leq 0.001$; fig. 1). Soil surface and blackbrush leaf temperatures were also significantly directly influenced by air temperatures ($P \leq 0.001$; fig. 2). Soil surface temperatures were significantly positively correlated with blackbrush leaf temperature, expressed as a curved, two-headed arrow ($P \leq 0.001$; figs. 1 and 2).

For ease of visualization, air, soil surface, and blackbrush leaf temperature patterns were extremely similar between the spring and fall seasons, and only the spring season values were included graphically. Blackbrush leaf temperatures consistently remained at or near air temperature throughout the day and year (fig. 3). The air-sunlit leaf temperature difference in magnitude became greater around noon hours during the summer season (fig. 3). Sunlit leaves located at the top of canopies were warmer relative to shade leaves located deep inside the canopies (fig. 4). Soil surface temperatures were significantly warmer than air ($P \leq 0.01$; fig. 5) and blackbrush leaf (fig. 3) temperatures irrespective of diurnal period and seasonality. A similar trend in temperature differences was also observed between air and soil beneath blackbrush shrub canopy, between air and shade leaves, as well as between shade leaves and soil beneath canopy (data not shown).

Soil surface temperatures ranged from slightly below air temperature in December to nearly 16 °C above air temperatures in June (fig. 6). Within a single day, the soil-air

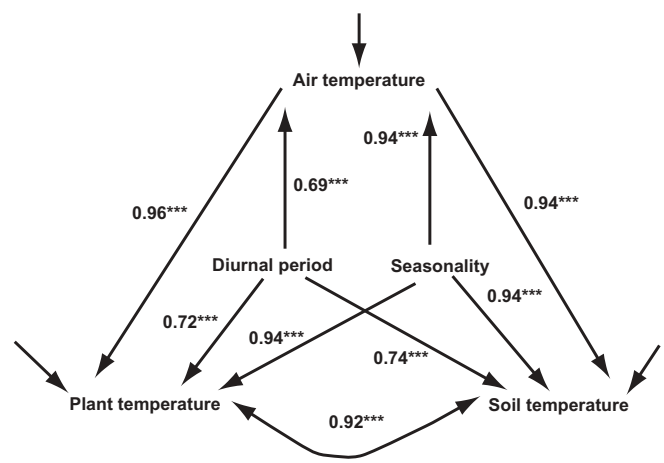

Figure 1—Path diagram depicting hypothesized relationships between blackbrush leaf temperatures and various environmental attributes. The direct causal effect of each attribute (straight, one-headed arrows) on blackbrush leaf temperature is the standardized partial regression coefficient (path coefficient). A short, unlabeled (residual) arrow is shown to indicate that additional biotic and abiotic factors may play a role in determining the overall leaf temperature. Soil temperatures were measured in open substrates, while leaf temperatures were measured at the top of the canopy exposed to prolonged direct sunlight. *** = P values less than 0.001.

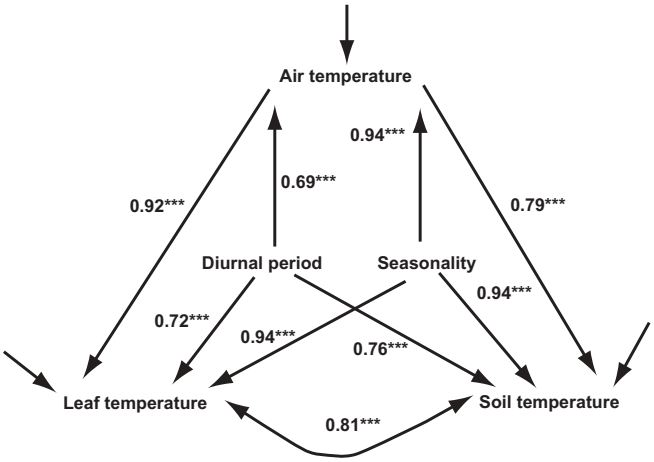

Figure 2—Path diagram depicting hypothesized relationships between blackbrush leaf temperatures and various environmental attributes. The direct causal effect of each attribute (straight, one-headed arrows) on blackbrush leaf temperature is the standardized partial regression coefficient (path coefficient). A short, unlabeled (residual) arrow is shown to indicate that additional biotic and abiotic factors may play a role in determining the overall leaf temperature. Soil temperatures were measured under shrub canopies. Leaf temperatures were measured at the bottom of the canopy, and leaves were shaded throughout much of the day. *** = P values less than 0.001.

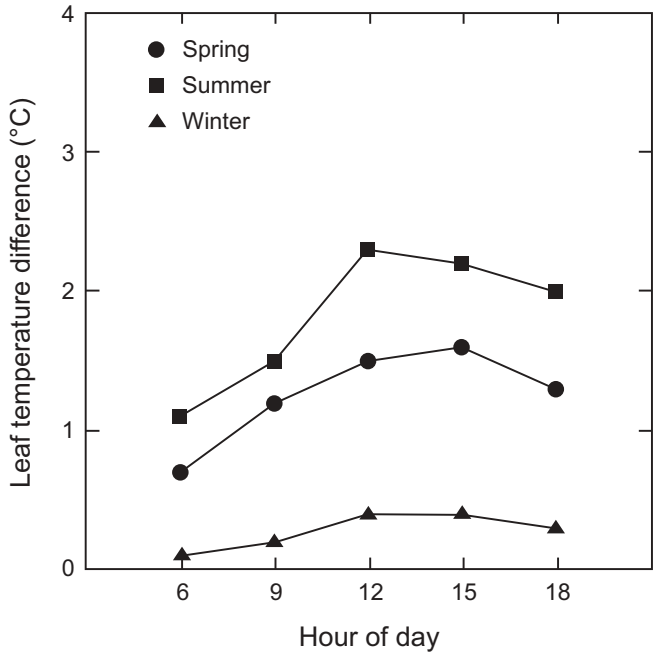

Figure 4—Temperature difference (n = 100 per diurnal period per season) between sunlit and shade leaves in the Clark Mountain of southeastern California. Shade leaves were located deep inside the canopy, and leaves were shaded throughout much of the day.

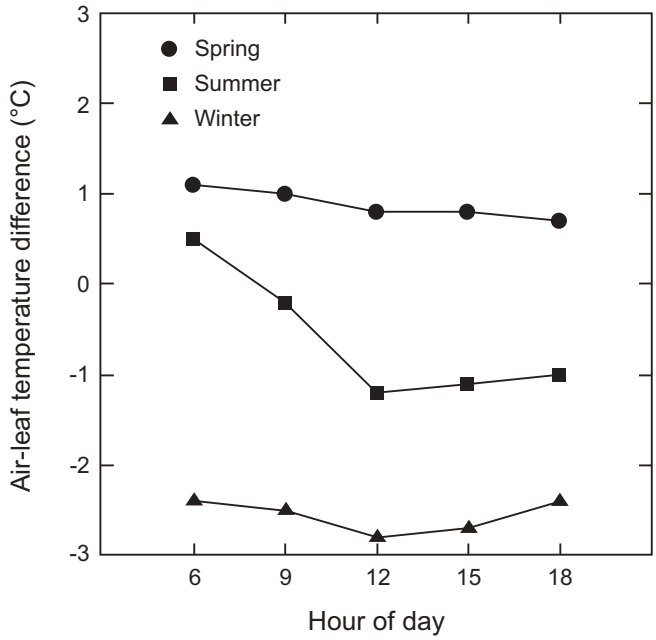

Figure 3—Temperature difference (n = 100 per diurnal period per season) between air and sunlit leaf exposed to prolonged, direct sunlight in the Clark Mountain of southeastern California.

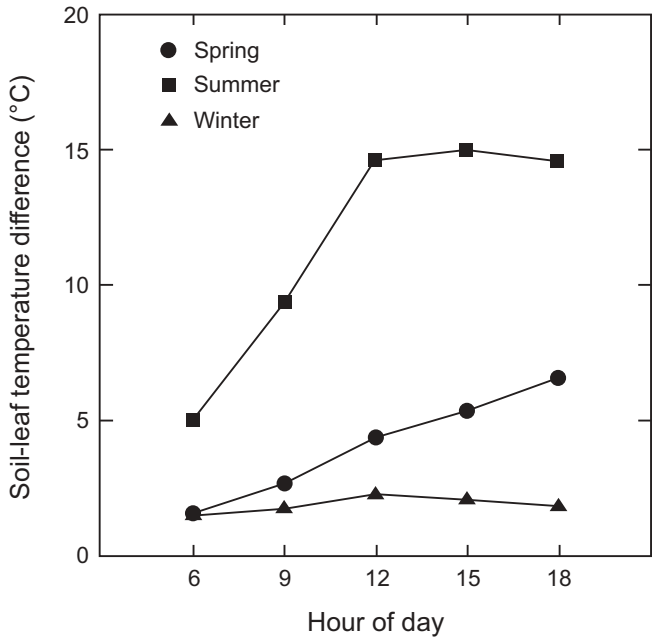

Figure 5—Temperature difference (n = 100 per diurnal period per season) between sunlit soil surface (open substrate) and sunlit leaves in the Clark Mountain of southeastern California.

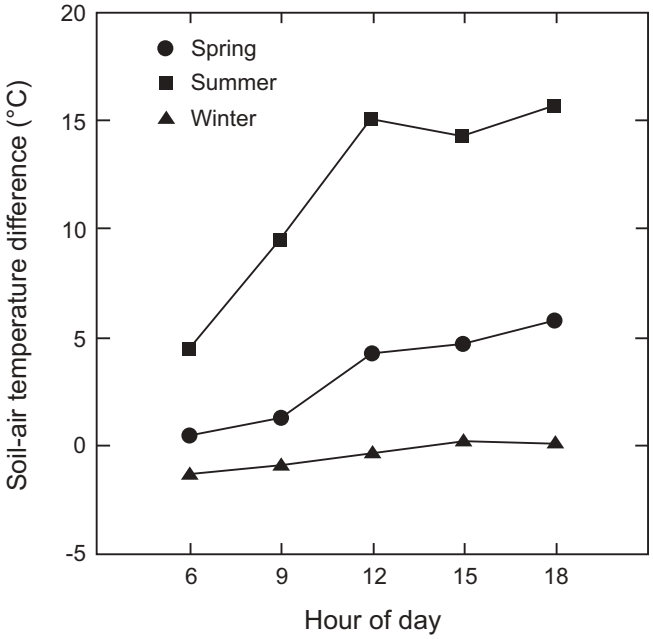

Figure 6—Temperature difference (n = 100 per diurnal period per season) between air and sunlit soil surface (open substrate) in the Clark Mountain of southeastern California.

temperature differences in magnitude became greater around midafternoon hours irrespective of seasonality (fig. 6). Soil surface temperatures in open substrate were significantly warmer ($P \leq 0.01$) than soil temperature under shrub canopies during the dry summer season, but were not significantly different during the snowy winter season (fig. 7).

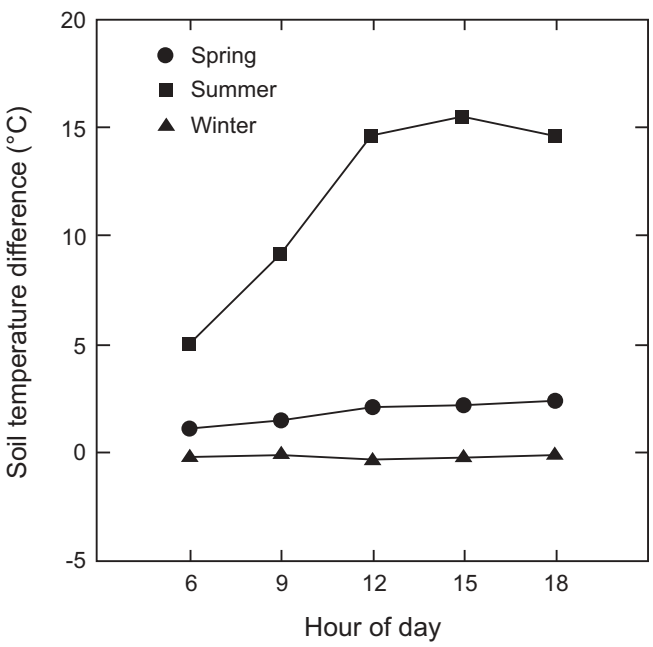

Figure 7—Temperature difference (n = 100 per diurnal period per season) between sunlit soil surface (open substrates) and soil beneath shrub canopies in the Clark Mountain of southeastern California.

Significant interactions were detected between seasonality and diurnal period for air and blackbrush leaf temperatures (table 1). Sunlit leaf temperatures were significantly warmer ($P \leq 0.05$; table 1) relative to shade leaf temperatures. All possible interactions (seasonality, diurnal period, and habitat type) were found to be significant for soil surface temperatures (table 1).

Discussion

Diurnal and seasonal temperature profiles were used to compare differences in magnitude of air, soil surface, and blackbrush leaves. Moreover, habitat type and canopy position are included as an additional variable for measuring soil surface temperatures and blackbrush leaf temperatures, respectively. The connections among environmental variables are represented in path diagrams by two types of arrows: a straight, one-headed arrow signifies a causal relationship between two variables, and a curved, two-headed arrow signifies a simple correlation between them (Loehlin 1998).

In this study, path analysis indicated that seasonality and diurnal period were significant positive predictors of air, soil surface, and blackbrush leaf temperatures. This analysis also revealed that air temperature was a significant positive predictor of soil surface and blackbrush leaf temperatures. Comparing to other seasons, the air-soil surface temperature difference in magnitude became substantially greater around midafternoon hours in open substrates during the dry summer season. Among all measured temperatures, the hottest temperatures were observed on soil surfaces in open substrates, exceeding both air and blackbrush leaf temperatures by as much as 15.8 °C in the summer season. Temperatures at soil surface in open substrates were significantly warmer, and experienced more seasonal extremes than temperatures at soil surface beneath shrub canopies in southern Nevada (Lei 1995; Lei and Walker 1997b) because the bare soil is a good heat absorber and it heats up much more rapidly.

According to the path diagram, a short, unlabeled (residual) arrow is pointed at air temperature, implying that variation in air temperature is subject to additional influences besides seasonality and diurnal period. Air and soil temperatures vary in a fairly parallel manner. Since air temperature is chiefly dependent on radiation and conduction from and to the ground, it follows that the diurnal and annual courses of the air temperatures and the ground temperatures should be similar (Shanks 1956).

A residual arrow is also pointed at soil surface temperatures in the path diagram. Soil surface temperatures are largely determined by a combination of air temperature, the presence of soil moisture and resulting evaporation, the presence of litter, debris, and/or vegetation cover, as well as the radiation regime incident upon the soil surface. During winter seasons, the presence of moisture at the soil surface and the resulting evaporation tends to give a low and uniform soil temperature (Shanks 1956). A persistent snow cover maintains the soil temperatures at or near 0 °C regardless of the air temperature, and even insulates the soil sufficiently to allow warmth from below to cause a slight rise in soil temperature. Conversely, a lack of snow cover allows

Table 1—Summary of two-way ANOVA showing the effects of seasonality, dirunal period, and their interactions on air temperatures. Summary of three-way ANOVA showing the effects of seasonality, diurnal period, habitat type or canopy position, and their interactions on soil surface and blackbrush leaf temperatures, respectively. df = 1 for seasonality, habitat type, and canopy position; df = 4 for diurnal period.

	Air temperature		Soil temperature		Leaf temperature	
Variable	F	P	F	P	F	P
Seasonality (A)	7,512.80	0.0000	14,668.39	0.0000	14,423.44	0.0000
Diurnal period (B)	347.71	.0000	775.93	.0000	560.71	.0000
Habitat type (C)	—	—	655.16	.0000	—	—
Canopy position (C)	—	—	—	29.88	.0000	—
A, B	13.17	0.0008	72.74	0.0000	24.41	0.0000
B, C	—	—	12.33	.0000	.12	.97
A, C	—	—	76.39	.0000	1.98	.18
A, B, C	—	—	3.07	0.0415	.51	.73

the soil temperature to average lower than the freezing point under frigid winter conditions (Shanks 1956).

Soil surface and blackbrush leaf temperature were significantly correlated with, and have a significant direct effect on, each other in this study. A dense vegetation cover or any covering on the soil considerably lessens the diurnal and annual surface temperature ranges. Due to the presence of dense blackbrush shrub canopies, soil surface temperatures under prolonged shade consistently remained at or near the air temperatures, with relatively little direct radiation reaching the ground. A large amount of solar radiation is absorbed by the vegetation rather than by the soil (Suzan and others 1996). In this study, soil temperatures beneath shrub canopies were 2.2 to 15.7 °C cooler than soil temperatures in adjacent open substrates during the summer month, but were only 0.9 to 2.4 °C warmer during the winter month. Shade decreases soil surface temperatures by 13.5 C to 15 °C in summer seasons, but increases soil temperatures by 1.2 to 3 °C in winter seasons in the Sonoran Desert (Franco and Nobel 1989; Suzan and others 1996). Shade is normally considered advantageous to seedling establishment in deserts of southeastern California because it moderates temperature extremes and water loss in microhabitats beneath shrub canopies (Walker and others 2001). Hence, shade creates cooler microhabitat temperatures and higher moisture regimes compared to adjacent open substrates.

Direct heating of the soil surface by solar radiation is important in considering the total heat load in the environment (Gibbs and Patten 1970). Heat is transferred from the soil to the plants by reradiation, convective air currents, and conduction by direct physical contact with the plants. Heat is also conducted from the soil surface to lower portions of plants where roots and soil exchange heat (Gibbs and Patten 1970). The tendency for canopies of blackbrush to occur near the ground surfaces allows the leaves to approach high temperature extremes. A combination of high leaf temperatures, low soil moisture, and low plant water content may play a vital role in determining the lower elevational limit of blackbursh in southeastern California of the Mojave Desert.

In this study, leaf temperatures of blackbrush consistently remained at or near air temperatures throughout the day and year because the leaves are small and dissipate heat primarily by convection. The dimensions of blackbrush leaves ranged from 0.5 to 1.4 cm in length, and were less than 1 cm in width. Temperatures of a leaf measuring 1 by 1 cm or less remain close to air temperatures (Gates and others 1968). They (1968) also discovered that temperatures of small leaves in shrubs and trees (*Artemisia*, *Ephedra*, *Juniperus*, and so forth) were within 3 °C of air temperatures in southern Utah, which is in agreement with this study.

Significant interactions were observed between seasonality and diurnal period for leaf temperatures. When evaluating individual variables alone, significant differences were observed in seasonality, diurnal period, and canopy position for blackbrush leaf temperatures. The coolest leaves were found within the leaf canopy, and were shaded from direct sunlight throughout much of the day. Early morning and late afternoon sunlight produces relatively less heat stress in plant tissues than midday sunlight in southern Nevada (Brittingham and Walker 2000). Reduced leaf temperature decreases heat damage to tissues, enhances stomatal functioning, maintains protein and membrane integrity, and lessens photoinhibition in summer dry seasons (Brittingham and Walker 2000; Singla and others 1997). Shading also decreases leaf temperature, thereby reducing water vapor concentration within intercellular air spaces, and reducing water vapor concentration gradient between intercellular air spaces and ambient air (Brittingham and Walker 2000).

In this study, leaf temperatures ranged from 2.8 °C below to 1.2 °C above air temperatures depending on seasonality, diurnal period, and canopy position, as well as on the intensity, duration, and frequency of direct sunlight. Sun leaves were considered those that were fully exposed to sunlight for most of the day. Conversely, shade leaves were located deeply inside the leaf canopy, mostly shaded during the day. Shade leaves ranged from 0.5 to 2.3 °C cooler than sun leaves of the same plants in this study.

Ecological Implications

The diurnal and seasonal fluctuations of air temperatures largely determined the fluctuations of soil surface and blackbrush leaf temperatures. Small leaves found in many desert plant species are important morphological adaptations in the regulation of leaf temperature. Due to high transpiration rates and high stomatal conductance, small leaves may act to reduce leaf temperatures to more optimal photosynthetic levels, particularly for rapid growth periods

when water is abundant (Smith 1978). Without ample water supply and high transpiration rates, a larger leaf size that orients horizontally, exposed to prolonged sunlight and without pubescent layers, can contribute to warmer leaf temperatures, often well above air temperatures. Blackbrush is a typical microphyllous desert shrub species, so it is not surprising that leaf temperatures stay close to air temperatures. This phenomenon has been shown many times for microphyllous desert species. Thus, unusually high leaf temperatures for extensive periods can cause long-term or even permanent (irreversible) plant tissue damage in frequently stressful desert environments.

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