SURFACE ENERGY BALANCE AFFECTS GAS EXCHANGE OF THREE SHRUB SPECIES

by Thayne Montague, Roger Kjelgren, and Larry Rupp

Abstract. We investigated the energy balance of vegetative and nonvegetative surfaces and gas exchange for 3 shrub species growing over each surface. During a 1-week period, incoming short-wave radiation, surface and soil temperature, and soil heat flux for turf and pine-bark mulch surfaces were gathered. Air temperature and relative humidity at 2 heights over each surface were also measured. Mulch surface and air temperatures were warmer and soil temperature below mulch was cooler than turf throughout each day. Relative humidity varied with height above turf, but each height was comparable over mulch. For the majority of each day, soil heat flux below turf was greater than mulch. Dawn-to-dusk measurements of stomatal conductance, leaf temperature, and water loss for containerized skunkbush sumac (Rhus trilobata), spreading euonymus (Euonymus klatschmovicus 'Manhattan'), and redosier dogwood (Cornus sericea) were measured. Shrubs in mulch had higher leaf temperatures and greater leaf-to-air vapor pressure differences than shrubs in turf. Rhus trilobata had greater stomatal conductance and water loss in turf than mulch. However, for E. klatschmovicus and C. sericea, there were no differences in stomatal conductance or water loss between surface treatments. Midday photosynthetic rate was generally greatest for shrubs over turf. Shrub gas exchange differed according to how stomata responded to the leaf-to-air vapor pressure difference over each surface.

Keywords. Rhus trilobata; Euonymus klatschmovicus 'Manhattan'; Cornus sericea; microclimates; gas exchange; leaf-to-air vapor pressure difference; water loss; urban landscape

Nonvegetative and vegetative urban landscape surfaces create distinctive microclimates (Whitlow and Bassuk 1987; Kjelgren and Clark 1992). A surface receiving solar radiation can disperse energy in different ways: warm the air above it by convection, conduct energy into the soil, convert energy to latent heat during transpiration, or re-radiate energy as long-wave radiation (Doll et al. 1985). Because of the lack of transpirational cooling, heat convection and long-wave radiation from nonvegetative surfaces releases large amounts of energy into the air (Whitlow and Bassuk 1987). These factors have been found to increase air temperature and decrease relative humidity in urban areas (Miller 1980; Whitlow and Bassuk 1988; Kim 1992; Kjelgren and Clark 1992). Leaves of woody plants placed over nonvegetative surfaces intercept more convected and long-wave energy than plants over a vegetative surface (Whitlow and Bassuk 1987). Consequently, plants over nonvegetative surfaces have higher leaf temperatures (Whitlow and Bassuk 1988) and are exposed to greater evaporative demand (high leaf-to-air vapor pressure difference) than plants over vegetative surfaces (Kim 1992; Whitlow and Bassuk 1987). How transpiration is influenced by this increased evaporative demand depends on the extent to which a plant regulates stomatal opening (Farquhar 1978; Turner et al. 1984; Choudhury and Monteith 1986; Jarvis and Mcnaughton 1986). To regulate transpiration, stomata of many woody plants close when leaf-to-air vapor pressure differences (LVPD) are high (Turner et al. 1984; Choudhury and Monteith 1986). Plants that maintain open stomata dissipate more energy through transpirational evaporative cooling but use more soil water. Plants that close their stomata lose less water, but limit photosynthesis and increase respiration due to higher leaf temperatures (Kartusch 1983; Kjelgren and Clark 1993).

Depending upon species and location, woody landscape plants in urban environments may have increased (Miller 1980; Halverson and Potts 1981; Potts and Herrington 1982; Zajicek and Heilman 1991) or decreased (Kjelgren and Clark 1993) water loss. Dawn-to-dusk stomatal conductance and transpiration for sweetgum (Liquidambar styraciflua) trees in an urban plaza in Seattle, Washington, were lower than sweetgum trees in a nearby park (Kjelgren and Clark 1993). Zajicek and Heilman (1991) reported that crape myrtle (Lagerstroemia indica) cultivars placed over pine-bark mulch had higher stomatal conductance during the morning when compared to plants over turf or bare soil. However, as LVPD increased in
the afternoon, stomatal conductance for plants over mulch was comparable to plants over turf and bare soil. Because of greater morning stomatal conductance, daily water use was greater for plants over mulch when compared to plants over turf and bare soil (Zajicek and Heilman 1991). Transpiration rates for honeylocust (*Gleditsia triacanthos* inermis) and green ash (*Fraxinus pennsylvanica*) trees in urban settings also increased when compared to trees in rural sites (Halverson and Potts 1981; Potts and Herrington 1982; Whitlow and Bassuk 1988).

Past research has primarily been conducted in regions of high relative humidity. In such regions, LVPD (evaporative demand) is generally lower than LVPD in regions of low relative humidity. There is little information on how woody landscape plants respond to high energy loads in arid regions. This study investigated energy balance between 2 common landscape surfaces in an arid climate and how surface energy balance influenced gas exchange and water use of 3 ornamental shrub species in each surface.

**Materials and Methods**

This experiment was conducted at a Utah State University research farm in Logan, Utah (41°45'N, 111°49'W; elevation 1,341 m [4,400 ft]). To represent a nonvegetative, urban surface, soil in a 9.1 x 18.3 m (30 x 60 ft) area was covered with 0.15 m (6 in.) of coarse pine-bark mulch. Bare soil surrounded the mulch for at least 9.1 m (30 ft) on each side. Twenty-four m (80 ft) north of the mulch site was an area of established Kentucky bluegrass (*Poa pratensis*) that was used to represent a vegetative surface. The vegetative surface was 30.5 x 30.5 m (100 x 100 ft) with several large trees and small shrubs on the perimeter. Between these 2 surfaces was a 6.0 x 30.5 m (20 x 100 ft) section of Kentucky bluegrass and a 6-m (20-ft)-wide asphalt road. In May 1995, established skunkbush sumac (*Rhus trilobata*), spreading euonymus (*Euonymus kiautschovicus* 'Manhattan'), and redosier dogwood (*Cornus sericea*) in 7.5 L (2 gal) containers were purchased from a local nursery. All shrubs were held under standard nursery practices in a common area for 2 weeks until placed into treatment areas.

Throughout the growing season, all shrubs remained in their containers. To moderate root-zone temperature, holes were dug in each surface treatment area such that the top of each container would be slightly below grade. Holes in each surface treatment plot were centrally located such that each hole was at least 4.5 m (15 ft) from the outer edge of the treatment surface and 3 m (10 ft) from another hole. In mid-May 1995, 4 shrubs of each species were randomly placed in each surface treatment. Single shrubs of each species were grouped together to form a replicate, with 4 replicates for each treatment. Throughout the growing season, all shrubs were well watered to avoid drought stress.

A weather station was placed over each surface and programmed to continuously collect data from mid-June until late August 1995. Incoming short-wave radiation was measured with a pyranometer sensor (Model LI-200SZ, LI-COR, Inc., Lincoln, Nebraska). Soil heat flux ($S_F$) and soil temperature ($T_o$) were measured with a heat-flow transducer (Radiation-Energy Balance Systems Inc., Seattle, Washington) and a 0.38 mm (0.014 in.) diameter copper-constantan thermocouple (Omega Engineering Inc., Stamford, Connecticut), respectively. Sensors were placed 1 cm (0.4 in.) below the soil for mulch and immediately below the thatch layer for turf. At the time of installation, soil surrounding the mulch sensors was saturated with water and allowed to drain to field capacity. Temperature of each surface ($T_s$) was measured with an infrared thermometer (Everest InterScience Inc., Fullerton, California) placed 0.5 m (1.6 ft) above each surface. Air temperature ($T_A$) and relative humidity ($R_H$) were measured with a combination temperature and humidity probe placed 2 m (6.5 ft) (Model CR500, Campbell Scientific Inc., Logan, Utah) and 0.3 m (1 ft) (Model HMP-35A, Vaisala Inc., Helsinki, Finland) above each surface. All sensors were scanned every 10 seconds and averages were recorded every 30 minutes with a data logger (Model CR10, Campbell Scientific Inc., Logan, Utah).

Dawn-to-dusk measurements of leaf temperature ($T_L$), stomatal conductance ($G_s$), and shrub water loss were performed on June 22 and 29, and August 8 and 27, 1995. On the evening be-
fore measurements were taken, all shrubs were removed from treatments and irrigated until water drained from the bottom of the container. All containers were allowed to drain until the next morning when containers were enclosed within 2 plastic bags and sealed with duct tape. Each shrub was weighed before and after all measurements were taken, and gravimetric water loss was calculated as the difference between before and after weights. Leaf temperature was measured with a handheld infrared thermometer (Everest InterScience Inc., Fullerton, California), and $G_s$ was measured with a steady-state porometer (Model 1600, LI-COR Inc., Lincoln, Nebraska). Measurements began near 9:00 A.M. (Mountain Daylight Time) on each study day. Four sun and 2 shade leaves on each shrub were measured. Measurements began on the first replicated species group in mulch and then continued in turf. This cycle was repeated until all 4 species replicates were measured. Following the measurement of the fourth shrub group, the cycle was repeated after about an hour break. Data collection ceased about 6:00 P.M. Throughout each study day, each shrub was measured 5 or 6 times. After all experiments ended, each shrub was defoliated and total leaf area was measured with a leaf area meter (Model CI-203, CID Inc., Vancouver, Washington). Daily shrub water loss for each study day was calculated by dividing gravimetric water loss ($cm^3$) by total leaf area ($cm^2$) and expressing in mm (in.).

On 3 dates (August 9, 25, and 31, 1995), between 1:00 and 3:00 P.M., midday photosynthetic rate ($P_N$) was measured with a portable photosynthesis system (Model 6200, LI-COR Inc., Lincoln, Nebraska) in closed mode (Mitchell 1992). Measurements began on the first replicated species group in mulch and then continued in turf. This cycle was repeated until all 4 species replicates were measured. For each shrub, 3 fully expanded, full-sun leaves were measured and 3 observations were taken per leaf.

Typical surface energy balance was calculated using weather data from a 5-day period (July 17 to 21, 1995). Thirty-minute means for short-wave radiation, and $S_F$, $T_A$, $T_0$, and $R_h$ for each surface were averaged and plotted against time of day. Standard errors (SE) of the means of 2:00 P.M. observations (time of average greatest short-wave radiation) were calculated for each climatic variable. Due to similarities of results among the 4 sample dates, only dawn-to-dusk data from August 27 will be discussed. Leaf-to-air vapor pressure difference was calculated using saturated vapor pressure at leaf temperature and ambient vapor pressure (Jones 1992). Stomatal conductance, $T_L$, and LVPD were plotted against time of day. Cycle means were exposed to analysis of variance appropriate for a split-plot design (SAS 1989). If significant differences were found, means were separated by Fisher’s Least Significance Difference Procedure ($\alpha = 0.10$). Stomatal conductance and LVPD data were analyzed by regression analysis and linear curves were fitted to the data (SAS 1989). Midday $P_N$ results were similar on each day; therefore, only data from August 31 will be discussed. Gravimetric water-loss means for August 27 and midday $P_N$ for August 31 were exposed to analysis of variance appropriate for a split-plot design (SAS 1989). If significant differences were found, means were separated by Fisher’s Least Significance Difference Procedure ($\alpha = 0.10$).

Results

Climate conditions over the course of the 5-day weather sample period (July 17 to 21, 1995) were characterized by sunny and clear skies (Figure 1a). Surface properties of turf and mulch affected microclimates and soil energy balance. Soil heat flux below turf peaked at 59.5 watts m$^{-2}$, while $S_F$ for mulch peaked at 36.6 watts m$^{-2}$ (Figure 1a). Soil temperature for turf was also greater than $T_0$ for mulch (Figure 1b). Soil temperature below turf was 11% to 35% greater than $T_0$ below mulch. Surface temperatures of turf and mulch were also different (Figure 1b). Maximum mulch $T_S$ reached 62.6°C (144.6°F), while maximum turf $T_S$ was 31.7°C (89.1°F).

Above each surface, the microclimate differed more at 0.3 m than at 2.0 m (Figure 1c, d). Air temperature over each surface at 2 m was nearly the same until about 4:00 P.M. After that time, $T_A$ at 2 m over turf was cooler than $T_A$ over mulch (Figure 1c). At the 0.3 m height, $T_A$ over mulch
was greater than $T_A$ over turf throughout each day (Figure 1c). Except over turf at 0.3 m, $R_H$ over each surface was similar at each height (Figure 1d). Throughout the day, $R_H$ over turf at 0.3 m was up to 120% greater than $R_H$ at the other 3 recording locations.

During August 27, 1995, dawn-to-dusk measurements, climatic conditions were typical for a summer day in the Intermountain West. Skies were clear and sunny (total short-wave irradiance of 24.1 MJ m$^{-2}$), $T_A$ was warm (32.6°C [(90.6°F) maximum and 11.9°C (53.4°F)] minimum), wind speed was moderate (1 to 4.4 m s$^{-1}$ [2.2 to 9.8 mph]), and $R_H$ was low (15.4% minimum and 66.6% maximum). For each species, $T_L$ and evaporative demand (LVPD) were generally higher over mulch (Figure 2d–i). Highest $T_L$ for plants in mulch was 33.3°C (92°F) versus 30.8°C (87.4°F) for those in turf (Figure 2d–f). Leaf-to-air vapor pressure differences for shrubs in mulch were 13% to 40% greater than LVPD for shrubs in turf (Figure 2g–i).

Stomatal conductance did not differ greatly between surfaces for *E. kiautschovicus* and *C. sericea* but did for *R. trilobata*. In general, $G_s$ for *E. kiautschovicus* and *C. sericea* over turf and mulch were not different throughout the day (Figure 2b, c). However, $G_s$ for *R. trilobata* shrubs over turf was up to 32% greater than $G_s$ for *R. trilobata* over mulch (Figure 2a). Throughout the day, $G_s$ for *R. trilobata* was greater than $G_s$ of the other species, regardless of surface treatment (Figure 2a–c). For each species, $G_s$ decreased as LVPD increased (Figure 3a–b). This inverse relationship was found for each surface treatment.
Treatment effects on water loss for each species were not evident except for *R. trilobata* (Table 1). Water loss for *R. trilobata* in turf was 16% greater than water loss in mulch. *Rhus trilobata* had greater $G_s$ (Figure 2a–c), and water loss was approximately 50% greater than *E. kiautschovicus* or *C. sericea* (Table 1), regardless of surface.

Shrub midday $P_N$ differed between surfaces and species. August 31, 1995, data show that *R. trilobata* and *E. kiautschovicus* over turf had higher $P_N$ than shrubs over mulch (Table 1). Photosynthetic rates for *R. trilobata* and *E. kiautschovicus* over turf were 54% and 75% greater, respectively, than $P_N$ over mulch. However, for *C. sericea* there was no difference in $P_N$ between surface treatments (Table 1).

**Discussion**

Increased heating of the mulch surface compared to the turf surface was due to the lack of evaporative cooling and the partitioning of absorbed solar radiation. Solar radiation reaching turf was dissipated as latent heat via turf transpiration, which reduced $T_S$ when compared to mulch (Figure 1b). Zajicek and Heilman (1991) found relative and absolute differences in $T_S$ for turf and pine-bark mulch that were similar to those in our study. Soil heat flux and $T_o$ below mulch were lower when compared to turf (Figure 1a, b) indicating that solar radiation reaching the mulch surface was not conducted into the soil. Mulch acted as insulation and prevented energy from penetrating into the soil. Instead, radiation reaching the mulch surface was re-radiated as long-wave radiation.
Higher sensible heat flux from the mulch surface was evident since $T_A$ and $R_H$ at 0.3 m were different than those recorded at 2 m (Figure 1c, d). Some researchers have recorded weather data at the height of approximately 2 m (Miller 1980; Zajicek and Hellman 1991; Kjelgren and Clark 1992), while others have not specified a recording height (Halverson and Potts 1981; Whitlow and Bassuk 1987, 1988). Our research indicates that microclimates at 0.3 m can be substantially different than microclimates at 2 m. At 0.3 m there would be less air mixing than at 2 m (Monteith and Unsworth 1990); therefore, $T_A$ and $R_H$ would be more closely linked to the surface than $T_A$ and $R_H$ at 2 m. Differences between

![Figure 3. Actual and predicted values for effect of leaf-to-air vapor pressure difference (LVPD) on stomatal conductance ($G_s$) for 3 containerized shrub species growing over turf and pine-bark mulch (August 27, 1995). Predicted regression line equations are followed by $r^2$ values and significance for the equation.](image-url)

$R. trilobata$ over turf (a): $G_s = 107.1085 - 13.9866x$, $r^2 = 0.0610$, $P = 0.0081$

$R. trilobata$ over mulch (a): $G_s = 67.0408 - 4.7672x$, $r^2 = 0.0371$, $P = 0.0512$

$E. kiautschovicus$ over turf (b): $G_s = 58.5610 - 7.2548x$, $r^2 = 0.1211$, $P = 0.0001$

$E. kiautschovicus$ over mulch (b): $G_s = 42.4121 - 4.6014x$, $r^2 = 0.0762$, $P = 0.0037$

$C. sericea$ over turf (c): $G_s = 47.1067 - 5.619x$, $r^2 = 0.0595$, $P = 0.0122$

$C. sericea$ over mulch (c): $G_s = 43.3024 - 4.3090x$, $r^2 = 0.0680$, $P = 0.0059$

Surface climatic variables at 2 m may also be minimized by the size and spacing of the surfaces. A larger surface area and greater distance between surfaces may have resulted in climatic variables that were less of a mixture of the 2 surfaces (Oke 1983; Monteith and Unsworth 1990). Because mulch $T_A$ was higher and $R_H$ was lower at 0.3 m than at 2 m, shrubs growing over the mulch surface were exposed to greater evaporative demand (higher LVPD) than shrubs growing over the turf surface.

High LVPD for shrubs over turf and mulch surfaces resulted in partial stomatal closure (Farquhar 1978; Turner et al. 1984) for shrubs over each surface (Figure 3a–c). Greater heating of the mulch
Surface properties also appear to influence midday $P_N$ of *R. trilobata* and *E. kiautschovicus* but not *C. sericea* (Table 1). Because a decrease in $P_N$ is expected with a decrease in $G_s$ (Hinckley et al. 1978), reduced $P_N$ was anticipated for *R. trilobata* over mulch compared to *R. trilobata* over turf (Table 1). However, because $G_s$ for *E. kiautschovicus* over mulch and turf is similar (Figure 2b), greater $P_N$ for *E. kiautschovicus* over turf was unexpected. High leaf temperature, high LVPD, and stomatal closure can limit photosynthetic rate in woody plants (Hinckley et al. 1978; Kartusch 1983; Turner et al. 1984), and this appears to be the case for *R. trilobata* and *E. kiautschovicus* over mulch and for *C. sericea* over turf and mulch. Why midday $P_N$ for *E. kiautschovicus* over turf and mulch were similar, despite lower $G_s$ rates for *E. kiautschovicus* over mulch, is unknown.

Our results differ from those found by Zajicek and Heilman (1991), who report greater water loss for containerized crape myrtle (*Lagerstroemia indica*) cultivars over pine-bark mulch compared to cultivars over turf. Increased water loss for crape myrtle over pine-bark mulch may be the result of factors not found in our study. Weather conditions in their study were similar to those during our study except that $R_H$ was greater during their experiment than $R_H$ during ours (Zajicek and Heilman 1991; Figure 1d). Therefore, plants in their study were subjected to lower LVPD through more of the day than we observed. This allowed crape myrtle stomata to remain open longer and increased water loss. Another factor could be that stomata of crape myrtle are less sensitive to LVPD than species used in our study (Turner et al. 1984).

**Conclusions**

Microclimates over turf and pine-bark mulch surfaces were different because of dissimilar surface properties. Mulch acted as insulation and prevented energy from reaching the soil. Consequently, the mulch surface was hotter and re-radiated more energy than the turf surface. The increase in available energy increased $T_A$ and decreased $R_H$ over the mulch surface. In contrast, turf dissipated energy through transpirational

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**Table 1. Water loss and midday photosynthetic rate for containerized *R. trilobata*, *E. kiautschovicus*, and *C. sericea* growing over turf and pine-bark mulch.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Water loss Aug. 27, 1995 mm (in.)</th>
<th>Photosyn. rate Aug. 31, 1995 umole m⁻² s⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Turf</td>
<td>Mulch</td>
</tr>
<tr>
<td><em>R. trilobata</em></td>
<td>3.3 (0.13) a</td>
<td>2.8 (0.11) b</td>
</tr>
<tr>
<td><em>E. kiautschovicus</em></td>
<td>1.5 (0.06)</td>
<td>1.3 (0.05)</td>
</tr>
<tr>
<td><em>C. sericea</em></td>
<td>1.5 (0.06)</td>
<td>1.2 (0.05)</td>
</tr>
</tbody>
</table>

**Significance**

| Species x treatment | NS | *** |
| Treatment          | *** | *** |

*NS, **, ***: Nonsignificant or significant at the 5% or 1% level by F-test, respectively.

Means between columns having the same letter are not different (LSD, α = 0.10).
cooling and allowed more energy to reach the soil. Therefore, $T_A$ was lower and $R_n$ was greater over the turf surface. These data show that at 0.3 m, the microclimate over a pine-bark mulch surface is more extreme than the microclimate over turf. These data also demonstrate that plant canopies 2 m above a surface (such as trees) would be exposed to a mix of the surrounding microclimate variables and not just the microclimate produced by the surface below.

In an arid climate, gas exchange and water loss by containerized $R.\text{trilobata}$, $E.\text{kiautschovicus}$, and $C.\text{sericea}$ were influenced differently by each surface. $Rhus\text{trilobata}$ was less sensitive to LVPD than $E.\text{kiautschovicus}$ or $C.\text{sericea}$. This was indicated by higher $G_s$ and water loss for $R.\text{trilobata}$ than $E.\text{kiautschovicus}$ and $C.\text{sericea}$ under similar climatic conditions. Both $R.\text{trilobata}$ and $C.\text{sericea}$ are native Utah species. Each can be found in moist sites; however, $R.\text{trilobata}$ can also be found in very dry sites (Welsh et al. 1987). Euonymus kiautschovicus is similar to $C.\text{sericea}$ in that it is native to humid, understory sites in China (Steward 1950; Dirr 1990). Although $R.\text{trilobata}$ is native to arid habitats and is considered drought tolerant (Taylor’s Guide to Water-Saving Gardening 1990), under nonlimiting soil water conditions $R.\text{trilobata}$ used more water than $E.\text{kiautschovicus}$ and $C.\text{sericea}$, species considered less drought tolerant. Similar results with mesquite ($Prosopis\text{alba}$) and live oak ($Quercus\text{virginiana}$) trees, considered drought tolerant and nondrought tolerant, respectively, have also been reported (Levitt et al. 1995). Greater water loss from $R.\text{trilobata}$ indicates that a drought-tolerant shrub species can use more water than nondrought tolerant species if soil water is plentiful. Our research indicates that under nonlimiting soil water conditions, $R.\text{trilobata}$ may be better suited than $E.\text{kiautschovicus}$ and $C.\text{sericea}$ to sustain growth under the high $T_A$ and low $R_n$ found in urban climates throughout the Intermountain West.

**Literature Cited**


Resumen. Se investigó el balance de energía de superficies vegetativas y no vegetativas y el intercambio de gases para tres especies de arbustos en cada superficie. Durante un periodo de una semana, a mediados de Julio, se registraron las entradas de radiaición de onda corta, la temperatura de la superficie y del suelo, y el flujo de calor del suelo para superficies de pasto y mulch de corteza de pino. También se midieron la temperatura del aire y la humedad relativa a dos alturas sobre cada superficie. A través de cada día, las temperaturas del mulch superficial y del aire fueron más calientes y la temperatura del suelo debajo del mulch fue más fría, que las del pasto. La humedad relativa varió con la altura arriba del pasto, pero esto fue comparable con el mulch. Para la mayor parte del día, el flujo de calor del suelo debajo del pasto fue mayor que el del mulch. Se hicieron mediciones de la mañana a la tarde del comportamiento estomatal, temperatura de la hoja y pérdida de agua en contenedor para el zumaque de zorrillo (Rhus trilobata), euonymus disperso (Euonymus kiautschovicus "Manhattan") y comejo (Cornus sericea). Los arbustos en mulch tuvieron mayores temperaturas de la hoja y mayores diferencias de presión de vapor de la hoja al aire que los arbustos con pasto. Rhus trilobata tuvo mayor respuesta estomatal y pérdida de agua en pasto que en mulch. Sin embargo, para E. kiautschovicus y C.sericea, no hubo diferencias en respuesta estomatal o pérdida de agua entre los tratamientos superficiales. La tasa fotosintética de mediodía fue generalmente mayor para los arbustos sobre pasto. El intercambio de gas de los arbustos difirió de acuerdo a como los estomates respondieron a la diferencia de presión de vapor de la hoja sobre cada superficie.