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ECOPHYSIOLOGY OF THE TEMPERATE DESERT HALOPHYTES: ALLENROLFEA OCCIDENTALIS AND SARCOBATUS VERMICULATUS

James D. Trent¹, Robert R. Blank¹,², and James A. Young¹

ABSTRACT.—Numerous basins of the intermountain area often have extensive playa surfaces that are nearly devoid of vegetation. Margins of these playas support sparse communities dominated by the chenopod shrubs Allenrolfea occidentalis (iodine bush) and Sarcobatus vermiculatus (black greasewood). These plants establish and persist in an environment where halomorphic soils induce extreme osmotic stress and atmospheric precipitation is very low and erratic and occurs largely during the winter when temperatures are too low for growth. We measured net CO₂ assimilation rates, leaf conductances, transpiration rates, water-use efficiencies, and stem xylem potentials for these two C₃ species. Data were collected in above-average (1991) and below-average (1992) precipitation years. Net CO₂ assimilation rates for Allenrollea were statistically similar in 1991 and 1992 but in general declined for Sarcobatus in 1992. For both species, leaf conductances and leaf transpiration rates declined significantly from 1991 to 1992, with the decline significantly greater for Sarcobatus. Water-use efficiencies doubled from 1991 to 1992 for both plant species. Predawn xylem water potentials were -2.2 and -3.3 MPa for Allenrollea and -1.8 and -2.6 MPa for Sarcobatus beginning in May 1991 and 1992, respectively, and dropped to -3.8 and -4.2 MPa for Allenrollea and -1.8 and -2.8 MPa for Sarcobatus by September 1991 and 1992, respectively. Afternoon xylem water potentials were -3.1 and -2.0 MPa for Allenrollea and -2.6 and -2.2 MPa for Sarcobatus beginning in May 1991 and 1992, respectively. Xylem water potentials dropped to -5.0 MPa for Allenrollea and -3.4 MPa for Sarcobatus by September of both 1991 and 1992. For Allenrollea, in general, the total soil water potential within the zone of maximum root activity is more negative than the plant's predawn xylem potential, which suggests that the plant is partially phreatophytic and/or has a large capacitance due to its extensive woody root system.

Key words: iodine bush, black greasewood, photosynthesis, conductance, transpiration, water potential, water-use efficiency, salt desert.

The vast pluvial lakes that occupied the basin of the intermountain area during the Pleistocene (Russell 1885) exposed extensive lake plains to colonization by plants as the waters evaporated during the late Pleistocene. Halomorphic soils, wind erosion, and atmospheric aridity hindered colonization of these environments (Billings 1945, 1949, West 1983). Lower portions of these basins remain nearly free of vegetation as barren playa surfaces. Margins of these playas currently limit plant colonization. Communities of shrubs dominated by Chenopodiaceae characterize much of the pluvial lake plain environment (Billings 1949). Apparently, these shrubs and half-shrubs have undergone explosive evolution in successfully exploiting the lake plain environments (Stutz 1978). The North American endemic chenopods Sarcobatus vermiculatus (Hook.) Torr. (black greasewood) and the monospecific Allenrollea occidentalis (S. Wats) Kuntz (iodine bush) have colonized extremely saline habitats of these temperate desert basins (Young et al. 1995).

Sarcobatus, found in numerous plant communities in temperate deserts (e.g., Billings 1945), is moderately salt tolerant and can survive at the low end of the moisture gradient in salt desert communities (Skougard and Brotherson 1979). Sarcobatus, which employs the C₃ photosynthetic carbon reduction pathway, can be phreatophytic if the groundwater table is high enough (Robinson 1958, Rickard 1965, Groeneweld 1990). Allenrollea, also a C₃ (scanning electron microscopy of leaf section did not show structures indicative of C₄ pathways), is much more restricted in ecological amplitude, being limited to a few communities directly at the margin of playas where soils are often poorly drained, have high surface soil salinity, but are non-sodic (Shantz 1940, Skougard and Brotherson 1979).

The purpose of this study was to determine plant strategies that allow Allenrollea and Sarcobatus to survive, indeed flourish, in this harsh, extremely saline playa margin environment. Our working hypothesis postulated that

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roots of *Sarcobatus* tap shallow, lower osmotic potential groundwater, while roots of *Allen­rolfea* primarily seek moisture from the eolian mounds on which they are found. This hypothe­sis was tested by studying plant-soil relations­hips and measuring plant ecophysiological attributes for *Allenrolfea* and *Sarcobatus* over 2 yr. Fortuitously, the years differed markedly in precipitation, which provided insight into water acquisition.

**METHODS**

The study site is in Eagle Valley, an embay­ment of pluvial Lake Lahontan, near the Hot Springs Mountain Range about 80 km north­east of Reno, Nevada (119°15'W, 39°45'N, 1234 m). The landscape consists of a lake plain rising in a series of small (>1 m) escarpments bordering a large playa. A band of large (>10 m) sand dunes forms a disjunct are across the lake plain. *Allenrolfea* forms a very sparse com­munity, with plants located on low mounds (0.1–0.5 m high) on a former playa surface. Occasional *Sarcobatus* and/or *Atriplex lentiformis* ssp. *torreyi* (Torrey saltbush) share mounds with the smaller *Allenrolfea*. Discontin­uous colonies of *Distichlis spicata* (desert salt­grass) are the only herbaceous vegetation found in the communities. Mounds and intermound soils are extremely saline (Tables 1, 2) and consist of coarse-textured eolian material over­lying clay- and silt-rich lacustrine sediments remnant of pluvial periods of Lake Lahontan (Blank et al. 1992). The high osmotic potential of the soil seedbed limits new plant recruit­ment (Blank et al. 1994).

Prior to the studies, 8 perforated PVC tubes were installed throughout the study area to monitor the water table. The tubes extended to a depth of 3 m. Measurements were taken monthly throughout 1991 and 1992. A sample of the groundwater was returned to the labora­tory and electrical conductivity (EC) deter­mined using a salinity drop tester; total water potential was measured on selected samples using a Decagon DC-10 thermocouple psy­chrometer (mention of trade names does not imply endorsement by the USDA).

Separate studies were conducted in 1991 and 1992. The 30-yr average annual precipita­tion for this region is 11.5 cm (Reed 1941). In 1991 and 1992 the study area received 14.6 cm and 9.6 cm of precipitation, respectively (based on rain gauges at the study site). Thus, plant-water relations and carbon exchange were measured in above-average and below-average precipitation years. In the 1st study diurnal measurements (6–8 measurements from sunrise to sunset) of net photosynthesis, leaf conductance, transpiration, relative humidity, leaf temperature, and photosynthetically active radiation (PAR) were taken with an LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE) equipped with a 0.25-L leaf cham­ber. Plots (4 blocks) were randomly selected that contained both *Allenrolfea* and *Sarcobatus*, and ecophysiology measurements were taken by block on 10 July, 2 August, and 25 September 1991 and on 10 July, 8 August, and 23 Septem­ber 1992. To facilitate measurements, stems containing several leaves were inserted into the chamber. After measurement stems were har­vested and returned on ice to the laboratory where leaf areas were measured. *Allenrolfea* ecophysiological measurements were based on cylindrical leaf area, as stomata appeared to cover the entire leaf. *Sarcobatus* measurements were based on a 1-sided flat leaf because in the samples we examined stomata occurred only on the hairy and flattened leaf surface.

In the 2nd study more intensive afternoon ecophysiology measurements were taken. Mea­surements were taken as mentioned above in the diurnal study; however, we measured pre­dawn and afternoon stem xylem potentials with a Scholander-type pressure chamber. Measure­ments were taken on 30 April, 10 June, 8 July, 30 July, and 23 September 1991 and 20 April, 27 May, 26 June, 16 July, 7 August, and 23 September 1992.

In August 1991 we determined rooting depth and root length density for *Allenrolfea* by digging into 4 mounds occupied exclusively by *Allenrolfea*. Roots were collected at depths of 0–30, 30–60, 60–90, 90–120, and 120–150 cm. The volume of soil taken was 3780 cm³. Soil was washed from roots in tubs and organic debris was picked from the roots. Root length was determined using a Comair root length scanner (Hawker de Havilland, Salisbury, South Australia). A subsample of roots were stained with a congo red solution (congo red stains dead roots) and examined with a light micro­scope to determine the proportion of dead roots, which was then used to correct root length density.

To prepare samples of *Allenrolfea* for scan­ning electron microscopy, we immediately
placed freshly excised leaves in a solution of 5% glutaraldehyde, 25% polyethylene glycol, and 10% acetone. After 1 wk we dehydrated the leaves using a graded series of alcohol and then critical-point-dried them prior to observation.

Near the time diurnal and afternoon measurements were taken, we collected soil at depths of 20, 40, and 60 cm from mounds (6 replicates) near where plant measurements were taken. Though the mounds were largely occupied by Allenrollea, some samples were taken from mounds occupied by both species. We immediately placed the soil in a sealed glass vial and returned it to the laboratory. In the laboratory the samples were homogenized and total soil water potential was determined with a Decagon SC-10 thermocouple psychrometer. The extreme salinity of samples required instrument calibration using a series of saturated salt solutions.

The data were analyzed as a split-block in time using SAS analysis of variance (ANOVA) models. In the 1st experiment the data were analyzed by year and month to determine species and diurnal effects on physiological parameters. The species effect was tested by the species × block interaction term while the diurnal effect was tested by the overall error mean square. In the 2nd experiment, data were analyzed by year to determine the species and monthly effect on physiological parameters. Similar error terms were selected as in the 1st experiment. A probability value of $P < 0.05$ was used throughout the analyses to test significance of F values. Only significant differences are reported in the text. When significant interactions occurred between main effect means, only those judged to have ecological significance were interpreted.

**RESULTS**

Measurements were taken on cloudless days, so the PAR perpendicular to the sun reached approximately 2000 $\mu$mol m$^{-2}$ s$^{-1}$ by about 1030 h for all measurement dates. Values of net CO$_2$ assimilation, leaf conductance, and leaf transpiration depend on leaf area, which for these 2 species is difficult to unambiguously define. For this reason we will concentrate on diurnal, seasonal, and yearly changes by species in these values.

Net CO$_2$ assimilation rates were generally highest in the late morning and decreased slightly through the rest of the day (Fig. 1). In general, for equivalent diurnal seasonal
measurement dates, rates were significantly higher for both plant species in 1991 (wet) than in 1992 (dry); however, a similar pattern was not evident in the more comprehensive afternoon data set (Fig. 2). In 1991 net CO₂ assimilation was highest in midsummer, whereas in 1992 there was no significant trend with season (Fig. 2).

For the first 2 dates in 1991, leaf conductance was generally highest in the morning and decreased in the afternoon, with a slight increase again by late afternoon (Fig. 1). This pattern was not evident in the 25 September 1991 diurnal measurement. Leaf conductance for both Sarcobatus and Allenrolfea was significantly less in 1992 than in 1991 (Figs. 1, 2). Moreover, the differences in leaf conductance between Allenrolfea and Sarcobatus were significantly less in 1992 than in 1991 (Figs. 1, 2). In 1991 leaf conductance varied significantly by time of day for Sarcobatus, but a diurnal pattern was more mute in 1992 (Fig. 1). Leaf transpiration rates followed the same trends as leaf conductance (Figs. 1, 2).

Water-use efficiency of Allenrolfea was significantly greater than Sarcobatus for all measurement dates in 1991 and 1992, with the exception of the 25 September 1991 measurement (Fig. 1). Water-use efficiencies in 1991 for both plants were significantly less than in 1992.
In 1991 and 1992, *Allenrolfea* had significantly more negative afternoon and predawn stem xylem potentials than *Sarcobatus* (Fig. 3). Soil water potentials remained between −15 and −20 MPa at the 20-cm depth for 1991 and until August 1992 when they dropped to −40 to −50 MPa (Fig. 3). In 1991 soil water potentials at 40 cm actually increased from about −11 MPa to −7 MPa from May to July and decreased to −5 MPa by late September. In 1992, however, the soil water potential at 40 cm was about −6 MPa from April to July and then dropped to −20 MPa by August. There were no significant differences in leaf temperature between plant species for 1991, the above-average precipitation year (Fig. 3). In 1992, the dry year, afternoon leaf temperatures of *Sarcobatus* were consistently higher than those of *Allenrolfea*.

*Allenrolfea* produces the greatest quantity of its roots at 30–60 cm in the hummock, with a small quantity of its roots occurring down to 120–150 cm (Fig. 4). Studies of the rooting density of *Sarcobatus* indicate it exponentially declines with depth (Groeneveld 1990).

Changes from an above-normal precipitation year (1991) to a below-normal precipitation year (1992) are reflected in the depth to the water table (Table 3). By summer 1992 the water table had dropped below 3 m for all access tubes. The EC data also show that groundwater is much less saline than is the soil solution in the soil above (see Tables 1, 2).

**DISCUSSION**

Leaf conductance and transpiration of the chenopod shrubs *Sarcobatus vermiculatus* and
Allenrolfea occidentalis declined to a greater extent than net assimilation of CO₂ from the above-average precipitation year (1991) to the below-average precipitation year (1992). These data indicate that stomatal conductance does not directly correlate with net photosynthesis in these species. The decrease in transpiration and conductance from the wetter to the drier year is in support of Antlfinger and Dunn (1983), who stated that high transpiration rates and conductances in an environment of low water potential and high salinity would have a great impact on salt balance and tissue hydration of the plant species. In this study reduced conductance and transpiration in the dry year may have been fundamental to maintaining tissue hydration of these salt desert plant species. Although we did not measure the water potential of the protoplast compartment, osmoregulation is important in maintaining cell hydration for halophytic species in wet or dry years (Kramer and Boyer 1995).

We suspect that the plant physiological changes from the wet to dry year may be partially explained by an increase in soil salinity. Flanagan and Jelleries (1988) reported that as salinity increased, photosynthesis in Plantago maritima declined from 17 to 14 µmol m⁻² s⁻¹ while leaf conductance dropped markedly from 370 to 172 mmol m⁻² s⁻¹. In their study water-
use efficiency increased from 5.7 to 8.5 mmol CO₂ mol⁻¹ H₂O, similar to our trend from a wet to a dry year.

Increased soil salinity cannot fully explain the dramatic decreases in leaf conductance from a wet to a dry year. Kleinkopf and Wallace (1974) showed that net assimilation rates and transpiration were not reduced for the salt-tolerant species Tamarix ramosissima when salinity increased from 10 to 200 mmol. Pearcy and Ustin (1984) suggested that increased salinity primarily reduced photosynthesis within the mesophyll and secondarily as a result of reduced leaf conductance. Our data show a slight reduction in photosynthesis with a much larger reduction in leaf conductance.

The effect of soil water potential on photosynthesis, conductance, and transpiration from the 1st (wet) and the 2nd (dry) year is inconclusive. Based on monitor wells at the study site, the water table dropped significantly from 1991 to 1992 and was below 3 m for much of the 1992 season. Since Sarcobatus is a facultative phreatophyte (Romo and Haferkamp 1989), and it likely extends roots to at least this depth (Groeneveld 1990), a drop in the water table could explain its reduced transpiration and conductance in 1992. The decline in transpiration and conductance from 1991 to 1992 for Allenrolfea is perplexing. Root distribution of Allenrolfea suggests it obtains most of its water from within the mound it grows on; yet, the total soil water potential within the mound did not change appreciably during the growing seasons from 1991 to 1992. Indeed, even during the wet year the total soil water potential measured in mounds where maximum root length of Allenrolfea occurs was generally more negative than the midday xylem water potential. One possibility is that a small number of Allenrolfea roots have tapped into the lowering water table; it is probably a facultative phreatophyte like Sarcobatus. During the course of this study, several Allenrolfea mounds and adjacent interspaces were excavated. From these excavations it is evident that there is an extensive network of coarse, woody roots of Allenrolfea. Samples of large roots have nearly 120 rings, which may constitute annual rings. The moisture content of coarse, woody roots averaged 67% by weight when measured in the spring before appreciable plant growth. These findings suggest that the water relations of Allenrolfea may involve a large root capacitance factor.

An alternative explanation of reduced CO₂ assimilation, conductance, and transpiration rates and more efficient water use from 1991 to 1992 involves nitrogen. When moisture is available in surface soil horizons, plants can uptake sufficient, likely luxuriant, inorganic nitrogen owing to plentiful levels in the soil (Tables 1, 2). However, as available moisture in the upper soil profile declines as it did during the dry year of 1992, a plant obtains a

Allenrolfea occidentalis live root length density by depth below top of hummock.

![Fig. 4. Allenrolfea occidentalis live root length density by depth below top of hummock.](image)
greater fraction of water needed from lower soil horizons closer to or within the water table. Inorganic nitrogen levels decline as the water table is approached, which suggests that plants may become deficient in nitrogen (Table 2). Khan et al. (1994) determined that additions of nitrate-N to saline substrates significantly increased carbon assimilation, transpiration, stomatal conductance, and water-use efficiency in alfalfa.

As compared to Sarcobatus, Allenrolfea exhibited significantly lower stomatal conductance in the wet year 1991 in addition to having, in general, higher water-use efficiency in 1991 and 1992. High water-use efficiency in Allenrolfea is partly a function of an extremely rugose epidermal layer in which the stomata are recessed (Fig. 5). The thick boundary layer caused by the rugose surface contributes to lowered stomatal conductance and higher water-use efficiencies (Kramer and Boyer 1995).

Allenrolfea and Sarcobatus maintain similar leaf xylem potentials from a low-precipitation year with a water table depth remaining above 3 m to a dry year when the water table drops below 3 m. A decrease in leaf conductance best explains the maintenance of leaf xylem potentials in the dry 2nd year. Decreased water loss as a result of lowered stomatal resistance should maintain xylem potentials.

In conclusion, Allenrolfea and Sarcobatus have reduced net assimilation rates, conductances, and transpiration rates during a low-precipitation year. A drop in water table depth, possibly in combination with reduced nitrogen uptake by the plants, explains these results. In high-precipitation years, abundant soil moisture results in high net assimilation rates, high conductance, and high transpiration rates. These years of high soil moisture result in low water-use efficiencies. In contrast to this, plants have the ability to reduce leaf conductance and increase water-use efficiencies in low-precipitation years. This allows the plants to maintain predawn and afternoon water potentials, which vary little from high- to low-precipitation years in these saline environments.

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