

Water Relations of *Artemisia tridentata* ssp. *wyomingensis* and *Sarcobatus vermiculatus* in the Steppe of Southeastern Oregon

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ABSTRACT.—Xylem water potentials (ψ_x), stomatal conductance (g_s), transpiration rates (J), and osmotic potentials at full turgor (ψ^0) and incipient plasmolysis (ψ^p) of *Sarcobatus vermiculatus* (Hook.) Torr. and *Artemisia tridentata* Nutt. ssp. *wyomingensis* were examined during the growing season in southeastern Oregon. Predawn ψ_x ($B\psi_x$) declined 3.0 MPa through the summer for *Artemisia* and 2.0 MPa for *Sarcobatus*. The lowest $B\psi_x$ (-4.0 to -4.5 MPa for *Artemisia* and -3.5 to -3.8 MPa for *Sarcobatus*) were similar within species among years. Early in the summer g_s and J were similar for both shrubs, but in late summer they were two- to three-fold higher for *Sarcobatus*. Maximum g_s for *Artemisia* declined exponentially as $B\psi_x$ decreased, and it was lower than 0.20 cm sec^{-1} at $B\psi_x$ lower than -3.0 MPa. There was no significant relationship ($P \leq 0.05$) between $B\psi_x$ and g_s for *Sarcobatus*. *Artemisia* showed limited changes in ψ^0 (-2.0 to -3.2 MPa) and ψ^p (-1.1 to -1.8 MPa) through the summer; for *Sarcobatus* ψ^0 and ψ^p ranged from -1.9 to -3.8 MPa and -2.7 to -6.5 MPa, respectively. This reduction in osmotic potentials in *Sarcobatus* enables it to maintain turgor and high g_s , that is critical for completing its growth during a short period when environmental stresses are high. Conversely, *Artemisia* is evergreen, exploiting moisture that is available during spring and early summer when environmental stresses are typically low and minimizing water loss in summer through reduced g_s and leaf area adjustments.

INTRODUCTION

Sarcobatus vermiculatus (Hook.) Torr. and *Artemisia tridentata* Nutt. ssp. *wyomingensis* are morphologically, phenologically and ecologically distinct shrubs of the shrub steppe in North America. *Artemisia* is evergreen; *Sarcobatus* is winter deciduous, displaying leaves from late spring through early autumn. Both species possess the C_3 photosynthetic pathway (DePuit and Caldwell, 1973; Dina and Klikoff, 1973; Welkie and Caldwell, 1970). Because *Sarcobatus* is a halophytic phreatophyte (Robinson, 1958) and *Artemisia*, a xerophyte (Dietert, 1938; Rickard, 1982), we hypothesized their seasonal and diurnal water relations would be different.

Seasonal trends of water status in several shrubs of the shrub steppe have been reported (DePuit and Caldwell, 1973, 1975; Dina and Klikoff, 1973; Campbell and Harris, 1977; Black and Mack, 1986). In general, these studies have shown that leaf water potentials are highest in spring, decreasing as summer drought intensifies. Interspecies differences in water relations may be due to variation in morphology, physiology and root distribution (Moore *et al.*, 1972; DePuit and Caldwell, 1973, 1975).

Studies of gas exchange characteristics in shrubs have also demonstrated seasonal and species differences; gas exchange usually is highest in spring and early summer, and declines during midsummer (Moore *et al.*, 1972; DePuit and Caldwell, 1973). Peak physiological activity of *Artemisia* corresponds with favorable temperatures and moisture conditions of

drical cuvette, was used to measure g , and J , temperature (T) and relative humidity (RH). Vapor pressure deficit (VPD) was determined using T and RH . Photosynthetically active radiation (PAR) was measured with a LI-COR LI-109S quantum sensor. Wind speed at 80 cm above ground level was recorded with a Belfort anemometer. Leaves were removed from branches, and leaf area was determined with a LI-COR LI-3100 area meter; g , and J were corrected to this leaf area.

Osmotic potential determinations.—Beginning in mid-April 1985 and continuing at 3- to 4-week intervals through mid-October 1985, vegetative branches were collected from plants of both species and used to determine pressure-volume relations following the procedures of Kaplan and Gale (1974) and Richardson and McKell (1980). *Sarcobatus* was not sampled in October because several nights with freezing temperatures had occurred, causing its leaves to abscise. Before dawn on each day of collection, one terminal leader bearing several leaves was collected from at least 10 different plants of each species. After a leader was excised it was immediately placed in a jar with the cut end submerged in water, the sample was recut under water, and the jar was sealed and placed in a cooler containing ice. Samples were transported to the laboratory and allowed to rehydrate in darkness at approximately 5 C for 24–28 h. Five pressure-volume curves were determined for each species on all dates using a pressure chamber. Bulk-averaged osmotic potentials at full turgor (ψ_x^{100}) and incipient plasmolysis (ψ_x^0) were estimated as described by Roberts and Knoerr (1977) and Meinzer *et al.* (1983).

Responses of plants were compared after constructing 95% confidence limits for the means (Snedecor and Cochran, 1980).

RESULTS

Seasonal changes in predawn xylem water potentials and soil moisture.—As soil moisture declined over the growing season in 1982 and 1983, $B\psi_x$ for *Artemisia* decreased more than that for *Sarcobatus* (Fig. 1). In 1982, $B\psi_x$ of both shrubs declined from mid-July until mid-September, increasing in early October when soil moisture increased. In 1983, $B\psi_x$ for *Artemisia* and *Sarcobatus* declined through June and July, rose after soil moisture increased in August, and decreased to the seasonal low in early October. Predawn xylem water potentials for *Artemisia* dropped from -1.5 to -4.5 MPa in 1982 and from -1.0 to -4.0 MPa in 1983. *Sarcobatus* $B\psi_x$ declined from -1.8 to -3.8 MPa and from -1.4 to -3.5 MPa in 1982 and 1983, respectively.

Diurnal cycles.—Temperatures were below normal and precipitation was above normal in 1982 and 1983. There was a pronounced peak in autumn–spring precipitation followed by a characteristic summer drought and high temperatures in July and August. Diurnal measurements of PAR , T , VPD and wind speeds determined in 1983 are representative of the aerial environmental conditions during the growing season in the shrub steppe (Fig. 2). Temperatures and evaporative demand increased through the summer to a high in August, declining in September.

Diurnal xylem water potentials, stomatal conductance and transpiration rates.—In June, July and August ψ_x were similar for both shrubs, but in September ψ_x were lower for *Artemisia* (Fig. 3). Diurnal fluctuation in ψ_x ($\Delta\psi_x$) increased for both species as the growing season progressed with *Artemisia* exhibiting the greatest variation. *Artemisia* $\Delta\psi_x$ increased from 1.4 MPa early in the summer to 2.4 MPa in late September. For *Sarcobatus*, $\Delta\psi_x$ increased from 1.6 MPa in June and July to 2.2 MPa in August, declining to 0.8 MPa in late September.

In June and July, g , and J were similar for *Artemisia* and *Sarcobatus*, but in August and September they were significantly lower ($P \leq 0.05$) for *Artemisia* (Fig. 3). Clear single

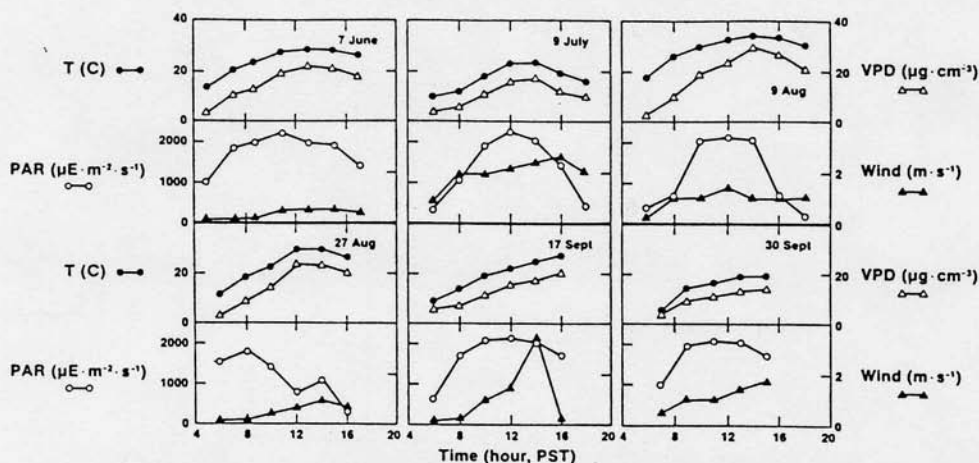


FIG. 2.—Temperatures (T), photosynthetically active radiation (PAR), vapor pressure deficit (VPD) and wind speeds during diurnal measurements in 1983. Each point represents the mean of eight measurements except for wind speeds which were a single measurement

lower than *Artemisia* with differences most pronounced after May. *Artemisia* ψ_r^0 decreased from a high in April to a seasonal low of -3.2 MPa in late August. *Sarcobatus* ψ_r^0 declined from a maximum in April to a minimum, averaging -6.5 MPa in late July, the warmest month of the year.

DISCUSSION

Although *Sarcobatus* is a phreatophyte and *Artemisia* is a xerophyte, some aspects of their water relations were similar. The most obvious distinctions between these shrubs were in g_s , ψ_r^{100} and ψ_r^0 , and these differences were accentuated by summer drought. Early in the summer g_s , J , ψ_x , ψ_r^{100} and ψ_r^0 were similar for both shrubs. With the progression of summer drought g_s , J and ψ_x decreased more in *Artemisia*, and ψ_r^{100} and ψ_r^0 declined more in *Sarcobatus*.

The seasonal decline of ψ_x for *Artemisia* is consistent with other studies (DePuit and Caldwell, 1973; Branson and Shown, 1975; Campbell and Harris, 1977; Black and Mack, 1986), and trends in ψ_x for *Sarcobatus* are similar to the results reported by Detling and Klikoff (1973). The lower $B\psi_x$ exhibited by *Artemisia*, compared to *Sarcobatus*, apparently reflects differences in soil moisture status in their rooting zones.

Water deficits and temperature extremes limit gas exchange of most shrubs of the shrub steppe during the later part of the growing season (Moore *et al.*, 1972; DePuit and Caldwell, 1973, 1975; Campbell and Harris, 1977; Miller, 1988). The decrease of g_s and J exhibited by *Artemisia* in response to summer drought is similar to other species in the shrub steppe. The relatively high g_s and J exhibited by *Sarcobatus* throughout the summer is unlike gas exchange in other shrubs of the shrub steppe.

The relationship between $B\psi_x$ and g_s shows that maximum g_s for *Artemisia* was less than 0.20 cm sec^{-1} , varying little during the growing season when $B\psi_x$ was lower than approximately -3.0 MPa. Black and Mack's (1986) data also show that g_s was lower than 0.20 cm sec^{-1} when $B\psi_x$ for *Artemisia* was below -3.0 MPa. These results parallel those of Dina and Klikoff (1973), who reported positive net photosynthesis for *Artemisia* at ψ_x higher than -3.0 MPa. Therefore, in addition to changes in leaf morphology, leaf aging and advancing

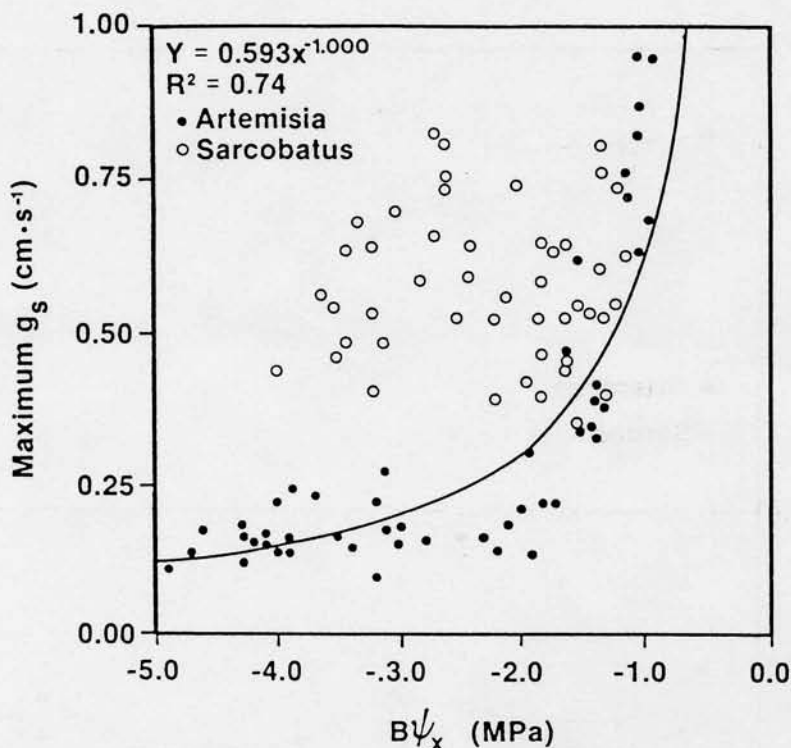


FIG. 4.—Relationships between predawn xylem water potentials ($B\psi_x$) and maximum stomatal conductance (g_s) for *Artemisia* and *Sarcobatus* in 1983. The regression equation and coefficient of determination are indicated for *Artemisia*

Changes in osmotic potentials for *Artemisia* in the present study were not as great as those reported by Campbell and Harris (1977). Using psychrometric procedures, they determined osmotic potentials near -2.0 and -6.0 MPa in wet and dry years, respectively. The procedure of hydrating tissue in the present study and deriving ψ_x^0 and ψ_x^{100} from pressure-volume relations may introduce errors in these parameters. Meinzer *et al.* (1986) reported that ψ_x^0 increased up to 3.0 MPa during rehydration of tissues in the desert shrub *Larrea tridentata*. They attributed this change to irreversible alteration of cell wall characteristics. The measurements of ψ_x in 1982 and 1983 and osmotic potentials in 1985 suggest that *Artemisia* would experience negative turgor throughout much of the summer. The actual occurrence of negative turgor under field conditions has been scrutinized and is still open to debate (Tyree, 1976; Tyree and Jarvis, 1982). Measurements of g_s and ψ_x however, showed that stomatal opening was small at $B\psi_x$ readings lower than about -3.0 MPa, which is in close agreement with the minimum of -3.2 MPa determined for ψ_x^0 in *Artemisia*. This provides another line of evidence that *Artemisia* ψ_x were probably near ψ_x^0 for much of the summer.

The lack of a relationship between $B\psi_x$ and maximum g_s for *Sarcobatus* is attributed to reduction in osmotic potentials facilitating turgor maintenance and stomatal opening. The decline in ψ_x^0 indicates that *Sarcobatus* was able to maintain turgor and open stomata as ψ_x declined. This was supported by measurements of ψ_x and g_s . Rickard (1965) found that ion concentrations increased in leaves of *Sarcobatus* throughout the growing season. Others have

$B\psi_x$ were still responsive to changes in soil moisture in the upper 60 cm of the profile. Exploitation of a permanent water supply, utilization of soil moisture in the upper profile, and reducing osmotic potentials represent structural and functional adaptations enabling *Sarcobatus* to maintain a favorable water balance and function over a wide range of environmental conditions. Similar characteristics in g_s have also been reported for other deciduous shrubs of the shrub steppe (DePuit and Caldwell, 1975; Miller, 1988). The adaptive significance of this high g_s is that it allows *Sarcobatus* to complete its annual growth during a relatively short period in the summer when environmental stresses are typically high, yet produce larger amounts of phytomass than several shrub communities in the shrub steppe (Branson *et al.*, 1976).

Artemisia relies on soil moisture that is seasonally available in the upper soil profile (Fernandez and Caldwell, 1975; Sturges, 1977). It avoids drought by growing when soil moisture is typically high and environmental stresses are low (DePuit and Caldwell, 1973, 1975; Miller, 1988). Transpiration-retarding mechanisms, including leaf shedding (Diettert, 1938) and stomatal responsiveness to declining $B\psi_x$, enable *Artemisia* to limit transpiration as environmental stresses increase. Displaying leaves throughout the year may enable *Artemisia* to be opportunistic, exploiting moisture and temperature conditions that are temporarily favorable early in the growing season (DePuit and Caldwell, 1973, 1975).

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LITERATURE CITED

- BLACK, R. A. AND R. N. MACK. 1986. Mount St. Helens ash: recreating its effects on the steppe environment and ecophysiology. *Ecology*, 67:1289-1302.
- BRANSON, F. A. AND L. M. SHOWN. 1975. Soil moisture stress as related to plant-moisture stress in big sagebrush (*Artemisia tridentata* Nutt.). *J. Range Manage.*, 28:212-215.
- , R. F. MILLER AND I. S. MCQUEEN. 1976. Moisture relationships in twelve northern desert shrub communities near Grand Junction, Colorado. *Ecology*, 57:1104-1124.
- CAMPBELL, G. S. AND G. A. HARRIS. 1977. Water relations and water use patterns for *Artemisia tridentata* Nutt. in wet and dry years. *Ecology*, 58:652-659.
- DEPUIT, E. J. AND M. M. CALDWELL. 1973. Seasonal pattern of net photosynthesis of *Artemisia tridentata*. *Am. J. Bot.*, 60:426-435.
- AND ———. 1975. Gas exchange of three cool-desert species in relation to temperature and water stress. *J. Ecol.*, 63:835-858.
- DETLING, J. K. AND L. G. KLIKOFF. 1973. Physiological response to moisture stress as a factor in halophyte distribution. *Am. Midl. Nat.*, 90:307-318.
- DIETTERT, R. A. 1938. The morphology of *Artemisia tridentata* Nutt. *Lloydia*, 1:3-74.
- DINA, S. J. AND L. G. KLIKOFF. 1973. Effect of plant moisture stress on carbohydrate and nitrogen content of big sagebrush. *J. Range Manage.*, 26:207-209.
- FERNANDEZ, O. A. AND M. M. CALDWELL. 1975. Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. *J. Ecol.*, 63:703-714.
- GLENN, E. P. AND J. W. O'LEARY. 1984. Relationship between salt accumulation and water content of dicotyledonous halophytes. *Plant, Cell, Environ.*, 7:253-261.