

WATER RELATIONS OF HIGH-ELEVATION  
SALIX PHREATOPHYTES IN WYOMING

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## ABSTRACT

High-elevation phreatophytes were studied to identify environmental parameters influencing daily and seasonal water consumption. The water relations of Salix planifolia, S. wolfii, and Betula occidentalis at 2865 m were similar throughout the day. Transpiration was reduced before 1000 h as a result of dew on the leaves, but high stomatal conductances to water vapor diffusion ( $>15 \text{ mm s}^{-1}$ ) and transpiration flux densities ( $>100 \text{ mg m}^{-2} \text{ s}^{-1}$ ) occurred from 1000 to 1600 h, resulting in a daily water loss per unit leaf area of 4.5, 5.2, and 4.0  $\text{Kg m}^{-2}$ , respectively. Seasonal trends revealed a decrease in maximum stomatal conductance after 1 September, occurring in conjunction with minimum air temperatures consistently below  $0^{\circ}\text{C}$  and increased leaf senescence. The period of significant water consumption was from 10 July through 20 September.

For comparison, a site at lower elevation (2255 m) was examined. Diurnal variations of S. exigua and S. amygdaloides at this site were similar to the high-elevation site, but maximum stomatal conductances were only 51% of the high-elevation Salix species. However, transpiration occurred from sunrise to sunset at lower elevations, resulting in a daily water loss of 3.7 and 3.4  $\text{Kg m}^{-2}$  of leaf area, respectively. A midday depression in leaf conductance at the lower site may have been in response to xylem pressure potentials below  $-1.7 \text{ MPa}$ . Seasonally, conductances were constant until a decrease occurred after 15 September, probably due to low temperatures and the onset of senescence. The growth season at the low-elevation site was estimated to be from 15 June to 30 September.

Although differences between the two sites occurred with respect to maximum rates, microclimate and length of growth season, the data suggest that for both sites and all species examined, a stomatal conductance and seasonal water use were most influenced by solar irradiance, dew on leaves, minimum air temperatures in spring and fall, and phenology.

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## INTRODUCTION<sup>1/</sup>

At high elevations throughout the western United States, species of Salix often form dense thickets along streams. Although temperatures are relatively cool in these riparian communities, many high-elevation Salix species are very tolerant to low air (Sakai, 1970, 1974) and soil temperatures (Anderson and McNaughton, 1973), indicating a possibly prolonged growth season and continued water consumption when compared to other sympatric shrub species. Indeed, significant water consumption has been implied for Salix dominated communities based on estimates of evapotranspiration from environmental data (VanKlaveren et al., 1975). However, little information exists concerning the effects of environmental factors on the water relations of high-elevation phreatophytes, especially Salix.

Using potometers, Bliss (1960) compared transpiration rates of arctic and alpine Salix species, and found significantly greater rates in the alpine plants. Although transpiration was related to windspeed, air temperature, and water vapor deficit of the atmosphere, measurements were not conducted throughout the growth season. Stoner and Miller (1975) and Miller et al. (1978) provided more in-depth evaluations of the water relations of Salix species on a seasonal basis, but their research was restricted to species of the wet coastal tundra of Alaska. The objective of the present study was to examine daily and seasonal patterns in the water relations of high-elevation phreatophytes. We present data on factors affecting stomatal conductance and transpiration in five species of Salix and another common shrub, Betula occidentalis, that occur above 2200 m in southeastern Wyoming.

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<sup>1/</sup> This report has been reviewed and has been accepted for publication in the American Midland Naturalist.

## STUDY AREA AND METHODS

To quantify the water relations of high-elevation phreatophytes, intensive measurements were focused on a riparian shrub community at 2865 m elevation along Sally Creek in the Medicine Bow Mountains of southeastern Wyoming ( $41^{\circ} 21' N$   $106^{\circ} 11' W$ ). The site was  $\sim 2$  ha in area with no apparent slope and obviously poor drainage, and it was surrounded by a mesic forest of Pinus contorta, Abies lasiocarpa, and Picea engelmannii. Two species of Salix were selected for study, both being common throughout Wyoming (Dorn, 1977). Salix wolfii Bebb is a small shrub with relatively small leaves (Table 1), while Salix planifolia Pursh is much taller and has longer leaves. Betula occidentalis Michx. was included as it is also common throughout mountainous areas of Wyoming, being found in habitats similar to those of S. wolfii (Dorn, 1977). It is similar in stature to S. wolfii, but has almost circular leaves in comparison to the long, narrow leaves of the Salix species. These three species provided 70% of the total shrub cover (49%) at this site (Table 1).

### Water Relations Measurements

Water relations were monitored biweekly at 2 h intervals from dawn to dusk during the summer growth period of 1983. Diurnal variations in stomatal conductance to water vapor loss for sunlit and shaded leaves on 5 shrubs, considered representative in terms of location, size, and canopy structure, were measured with a diffusion porometer (Lambda Instruments Corporation model LI-700). Values for both adaxial and abaxial leaf surfaces were summed to determine total stomatal conductance for the leaf (Nobel, 1983). Corresponding leaf temperatures were measured with an infrared field thermometer (Barnes Engineering model 14-2204). Changes in xylem pressure potential



Table 1. Shrub and community characteristics at the high-elevation site. Values represent means  $\pm$  standard errors and different letters (a,b,c) indicate statistically significant differences ( $\alpha = 0.05$ ) between species.

<u>Parameter</u>	<u>Salix wolfii</u>	<u>Salix planifolia</u>	<u>Betula occidentalis</u>
Leaf length (cm)	3.5 $\pm$ 0.2 <sup>a</sup>	5.8 $\pm$ 0.4 <sup>b</sup>	1.5 $\pm$ 0.1 <sup>c</sup>
Leaf width (cm)	0.6 $\pm$ 0.1 <sup>a</sup>	0.8 $\pm$ 0.1 <sup>b</sup>	2.0 $\pm$ 0.1 <sup>c</sup>
Shrub height (m)	0.51 $\pm$ 0.03 <sup>a</sup>	2.04 $\pm$ 0.19 <sup>b</sup>	0.84 $\pm$ 0.08 <sup>c</sup>
Shrub diameter (m)	0.84 $\pm$ 0.05 <sup>a</sup>	1.62 $\pm$ 0.12 <sup>b</sup>	0.97 $\pm$ 0.11 <sup>a</sup>
Shrub projected area (m <sup>2</sup> )	0.57 $\pm$ 0.06 <sup>a</sup>	2.16 $\pm$ 0.32 <sup>b</sup>	0.82 $\pm$ 0.16 <sup>a</sup>
Shrub leaf area (m <sup>2</sup> )	1.10 $\pm$ 0.34 <sup>a</sup>	4.48 $\pm$ 0.12 <sup>b</sup>	1.33 $\pm$ 0.27 <sup>a</sup>
Shrub leaf area index	1.93 $\pm$ 0.40 <sup>a</sup>	2.07 $\pm$ 0.31 <sup>a</sup>	1.62 $\pm$ 0.32 <sup>a</sup>
Cover (%) <sup>*</sup>	14.1 $\pm$ 1.4 <sup>a</sup>	4.6 $\pm$ 2.7 <sup>b</sup>	14.9 $\pm$ 2.4 <sup>a</sup>
Leaf area/hectare (m <sup>2</sup> )	2721.3	952.2	2413.8

<sup>\*</sup> Other Salix species comprised an additional 15.7% cover such that total shrub cover was 49.3%.

throughout a day were monitored by periodically excising 5 branches (~10 cm in length) of each species, and placing them in a moist, opaque plastic bag until measurement (~10 min) with a pressure chamber (PMS model 1000). Transpiration flux density was calculated from measurements of water vapor deficits of the atmosphere, leaf temperature, and stomatal conductance.

Microclimatic measurements included the continuous recording of air temperature and relative humidity (Science Associates model 610 hygromograph) which were used to calculate the water vapor deficit of the atmosphere. In addition, incident solar irradiance was determined at the time of conductance measurements, using a pyranometer (Lambda Instruments LI-135A light meter equipped with a LI-200S sensor). Soil temperature and water potential at 20 cm depth were recorded biweekly at 5 locations (Wescor PT51-10 soil thermocouple psychrometers).

#### Low Elevation Comparison

To determine if measurements at the high-elevation site were representative of Salix communities at somewhat lower elevations, less intensive measurements were conducted at a 2255 m site (610 m lower). The site was located along the Little Laramie River (41° 18' N 105° 50' W), within a narrow riparian zone (~150 m wide) surrounded by a relatively arid short-grass prairie. In contrast to the high-elevation site, it was well drained and shrub cover was only ~20%. Salix exigua Nutt. and Salix amygdaloides Anderss were monitored as described previously, but community characteristics and daily microclimatic variations were not quantified. In comparison to the high-elevation species (Table 1), these shrubs were over 3 m tall and their leaves were larger (leaves of S. exigua averaged  $11.0 \pm 0.5$  cm in length and  $0.8 \pm 0.1$  cm in width; leaves of S. amygdaloides averaged  $9.1 \pm 0.3$  cm long and  $1.8 \pm 0.1$  cm wide).

## RESULTS

### High-Elevation Site

Leaf expansion for all three species began the first week of July at the high-elevation site, with senescence occurring by 20 September. Flowering and leaf expansion were completed in all three high-elevation species by 24 July and no senescence was evident before September 1. Stomatal conductance could not be measured on any day before 1000 h, as leaves of all species were consistently covered with dew until that time. Transpiration was considered to be at or near zero until after 0800 h because of the dew and a low atmospheric vapor pressure deficit (<0.3 KPa) (Larsson, 1981).

Maximum and minimum air temperatures were variable, with maxima being greater than 20°C on 40% of the days (Fig. 2) and minimum air temperatures being below 0°C on 22% of the days (Fig. 1). However, throughout the entire month of August air temperatures never dropped below 0°C in 1983 (Fig. 1). After the first week of September, and corresponding to the onset of senescence, maximum air temperatures were below 20°C consistently and minima were below 0°C with an absolute minimum of -10°C occurring on 19 September (Fig. 1). The maximum vapor pressure deficit of the atmosphere ranged from 0.3 KPa on 18 July to 1.8 KPa on 21 June (Fig. 1).

Maximum stomatal conductances of all three species increased during the summer until 16 August, with a gradual decrease thereafter to the lowest values measured on 15 September. The decreases in conductance coincided with lower air temperatures and increased senescence (Fig. 1). Early morning xylem pressure potentials of all three species remained above -0.3 MPa until after 1 September, and on 15 September minima of -0.6, -0.7, and -1.3 MPa were measured for S. planifolia, B. occidentalis, and S. wolfii, respectively (Fig. 1).

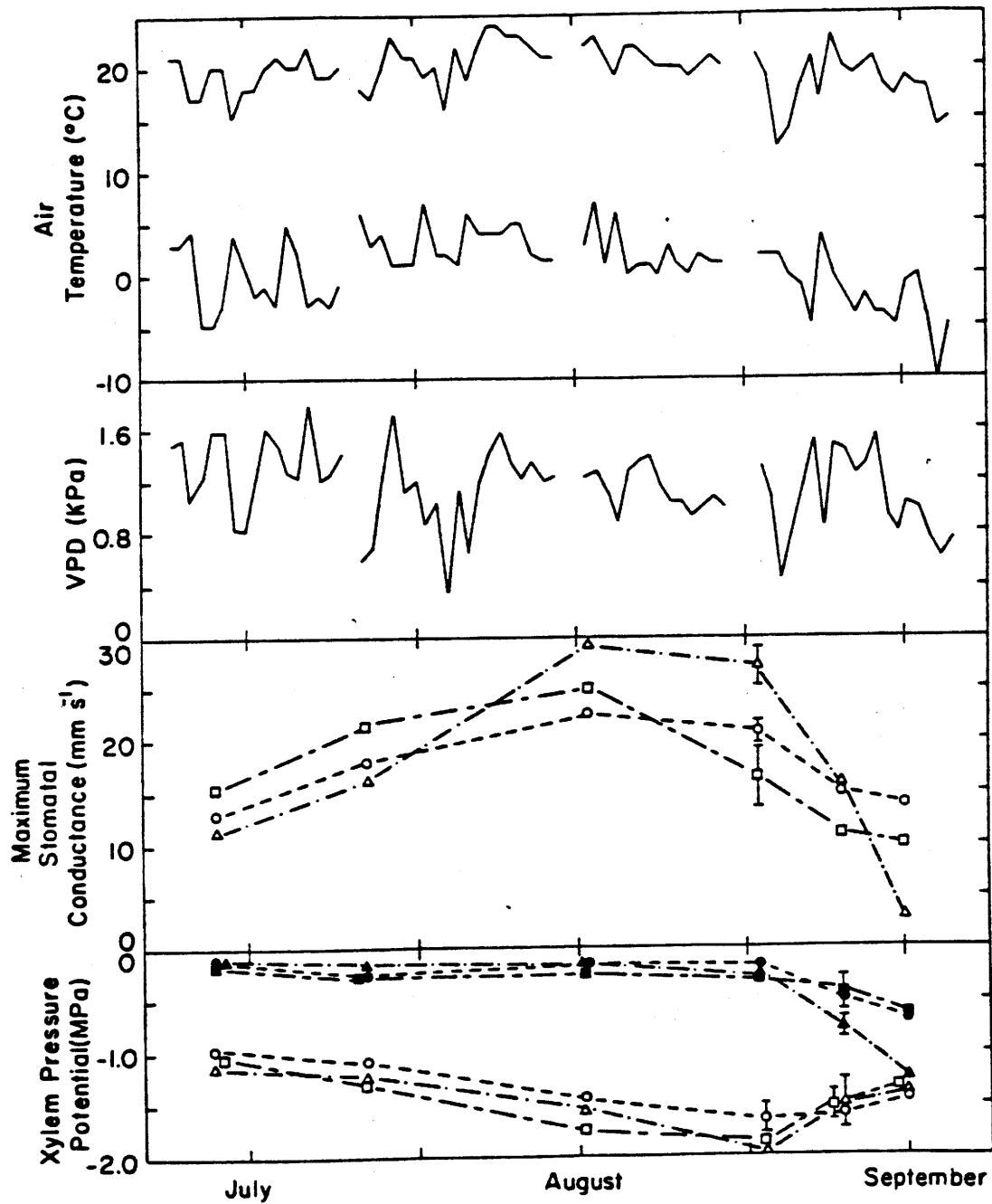


Figure 1. Seasonal variations in maximum and minimum air temperature, vapor pressure deficit of the atmosphere (VPD), maximum stomatal conductance, and maximum and minimum xylem pressure potential (shaded and open symbols, respectively) for *Salix planifolia* ( $\square$ ), *S. wolfii* ( $\Delta$ ), and *Betula occidentalis* ( $\circ$ ) at the high-elevation site. Vertical bars indicate representative standard errors.

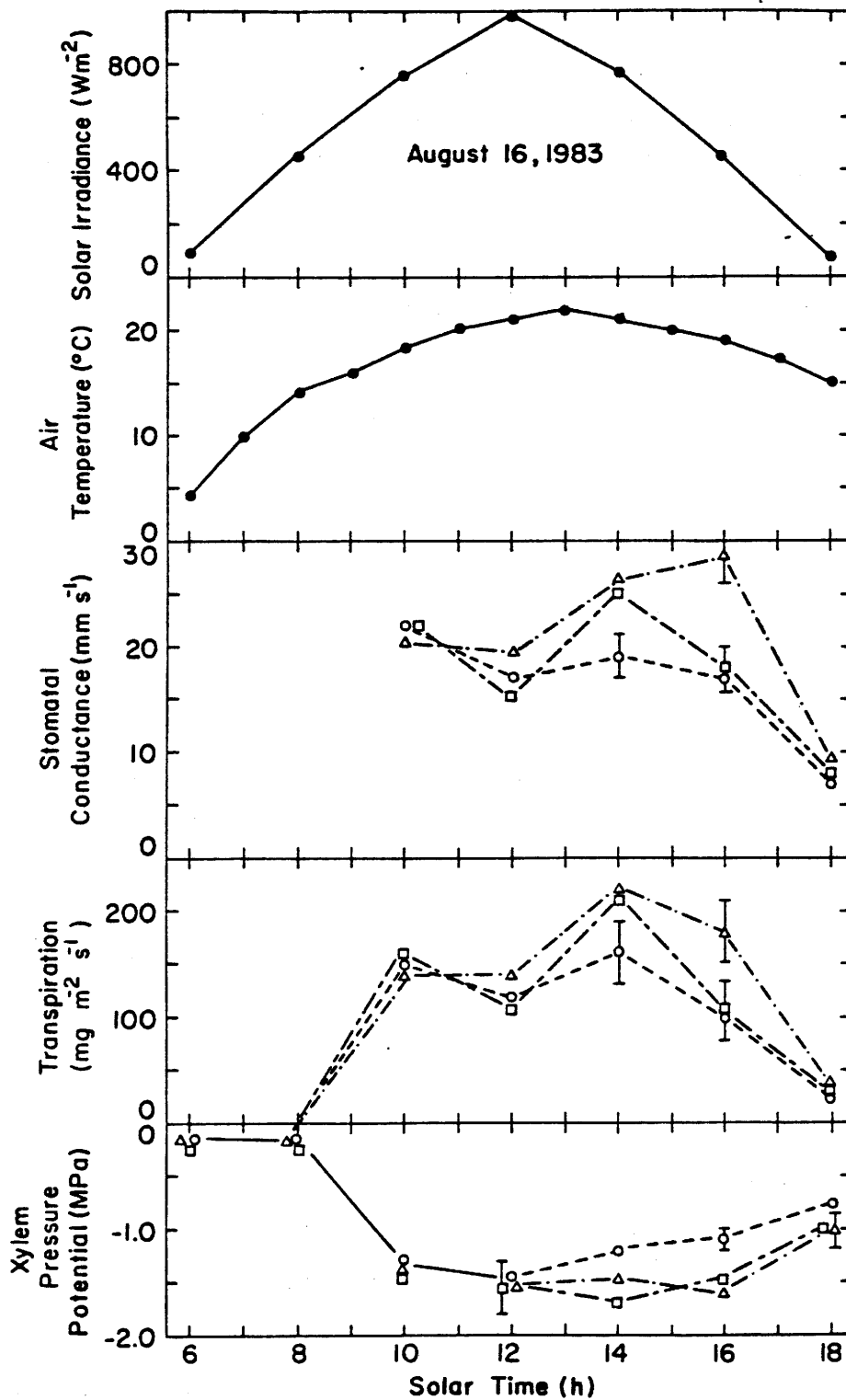


Figure 2. Clear day changes (August 16, 1983) in solar irradiance, air temperature, stomatal conductance to water vapor, transpiration flux density, and xylem pressure potential for *Salix planifolia* (□), *S. wolfii* (Δ), and *Betula occidentalis* (○) at the high-elevation site. Vertical bars indicate representative standard errors.

By comparison, soil water potential remained  $>-0.2$  MPa during the entire measurement period from early July till late September. Midday xylem pressure potentials decreased during the summer from near  $-1.0$  MPa on 12 July to  $<-1.5$  MPa on 16 August. After this date, the minimum xylem pressure potential increased in all three species and approached early morning maxima (15 September) as the leaves of the species senesced (Fig. 1).

Stomatal conductance varied seasonally as well as with time of day for each of the three species. For all three species maximum conductance occurred for sunlit leaves, with reductions due to shading being 28%, 43%, and 10% for S. wolfii, S. planifolia, and B. occidentalis, respectively (Table 2). Further, senescent leaves (i.e., leaves differing in color from healthy green leaves), when compared to healthy sunlit leaves, showed reductions in stomatal conductance of  $>90\%$  for all three species (Table 2).

Maximum stomatal conductances were recorded on 16 August, when skies were clear throughout the day and the solar irradiance was  $1050 \text{ W m}^{-2}$  at solar noon (Fig. 2). During that day air temperature rose from a low of  $4^{\circ}\text{C}$  at 0600 h to a maximum of  $22^{\circ}\text{C}$  at 1300 h (Fig. 2). At 1000 h all three species exhibited similar stomatal conductances of about  $21.5 \text{ mm s}^{-1}$ , but maximum stomatal conductances for Betula occidentalis, S. planifolia and S. wolfii were at 1000 h ( $22 \text{ mm s}^{-1}$ ), 1400 h ( $25 \text{ mm s}^{-1}$ ), and 1600 h ( $28 \text{ mm s}^{-1}$ ), respectively (Fig. 2). Diurnal variations in transpiration for all three species followed changes in stomatal conductance, as leaf temperatures were within  $\pm 2$  degrees of air temperature. Maximum transpiration flux densities occurred at 1400 h for all species, when the vapor pressure deficit of the atmosphere was greatest, being 1.2 KPa (Fig. 1). Total water losses for the day were 4.0, 4.5, and  $5.2 \text{ Kg m}^{-2}$  of leaf area for B. occidentalis, S. planifolia, and S. wolfii,

Table 2. Comparison of stomatal conductances ( $\text{mm s}^{-1}$ ) for sunlit ( $750 \text{ W m}^{-2}$ ), shaded ( $<100 \text{ W m}^{-2}$ ), and senescent leaves of three phreatophytic shrubs at the high-elevation site. Values were determined at 1400 h, 1 September 1983, and are means  $\pm$  standard errors. For each species, differences among values were statistically significant with  $\alpha = 0.05$ .

<u>Species</u>	<u>Sunlit</u>	<u>Shaded</u>	<u>Senescent</u>
<u>Salix wolfii</u>	10.7 $\pm$ 0.5	7.7 $\pm$ 1.2	0.4 $\pm$ 0.1
<u>Salix planifolia</u>	11.2 $\pm$ 0.4	6.4 $\pm$ 0.6	< 0.1
<u>Betula occidentalis</u>	7.7 $\pm$ 0.2	6.9 $\pm$ 0.7	0.8 $\pm$ 0.4

respectively. The xylem pressure potentials of all three phreatophytes were similar throughout the day (Fig. 2). Early morning values of  $>-0.3$  MPa reflected the moisture available in the saturated soils; however, when stomatal conductance and transpiration increased, xylem pressure potential quickly dropped to  $<-1.3$  MPa at 1000 h. Xylem pressure potential remained relatively constant thereafter, with a gradual rise occurring for B. occidentalis (Fig. 2).

#### Low-Elevation Site

At the low-elevation site, leaves were fully expanded in early July and were not yet senescent on 15 September (the last day of measurements). Figure 3 illustrates diurnal variations in microclimate and water relations for S. exigua and S. amygdaloides at the low-elevation site, on a clear day. Solar irradiance at midday was  $900 \text{ W m}^{-2}$  and air temperature varied from  $9^{\circ}\text{C}$  at 0600 h to  $22^{\circ}\text{C}$  at 1200 h. For both species, stomatal conductance gradually decreased from about  $10 \text{ mm s}^{-1}$  at 1000 h to  $5 \text{ mm s}^{-1}$  at 1400 h; however, at 1600 h S. exigua attained a maximum of  $16.2 \text{ mm s}^{-1}$  and S. amygdaloides  $10.9 \text{ mm s}^{-1}$  (Fig. 3). Transpiration followed a similar pattern since leaf temperatures were consistently within  $\pm 2^{\circ}\text{C}$  of air temperature and the vapor pressure deficit changed gradually as well. Water losses for the entire day were  $3.7$  and  $3.4 \text{ Kg m}^{-2}$  of leaf area for S. exigua and S. amygdaloides, respectively. Xylem pressure potentials of both species were very similar throughout the day, being  $-0.5$  MPa at 0600 h and decreasing to  $<-1.5$  MPa throughout the rest of the day until after 1600 h when a slight increase occurred (Fig. 3).

Seasonally, air temperatures were near  $21^{\circ}\text{C}$  on measurement days and the maximum vapor pressure deficit of the atmosphere was above 1 KPa (Table 3).



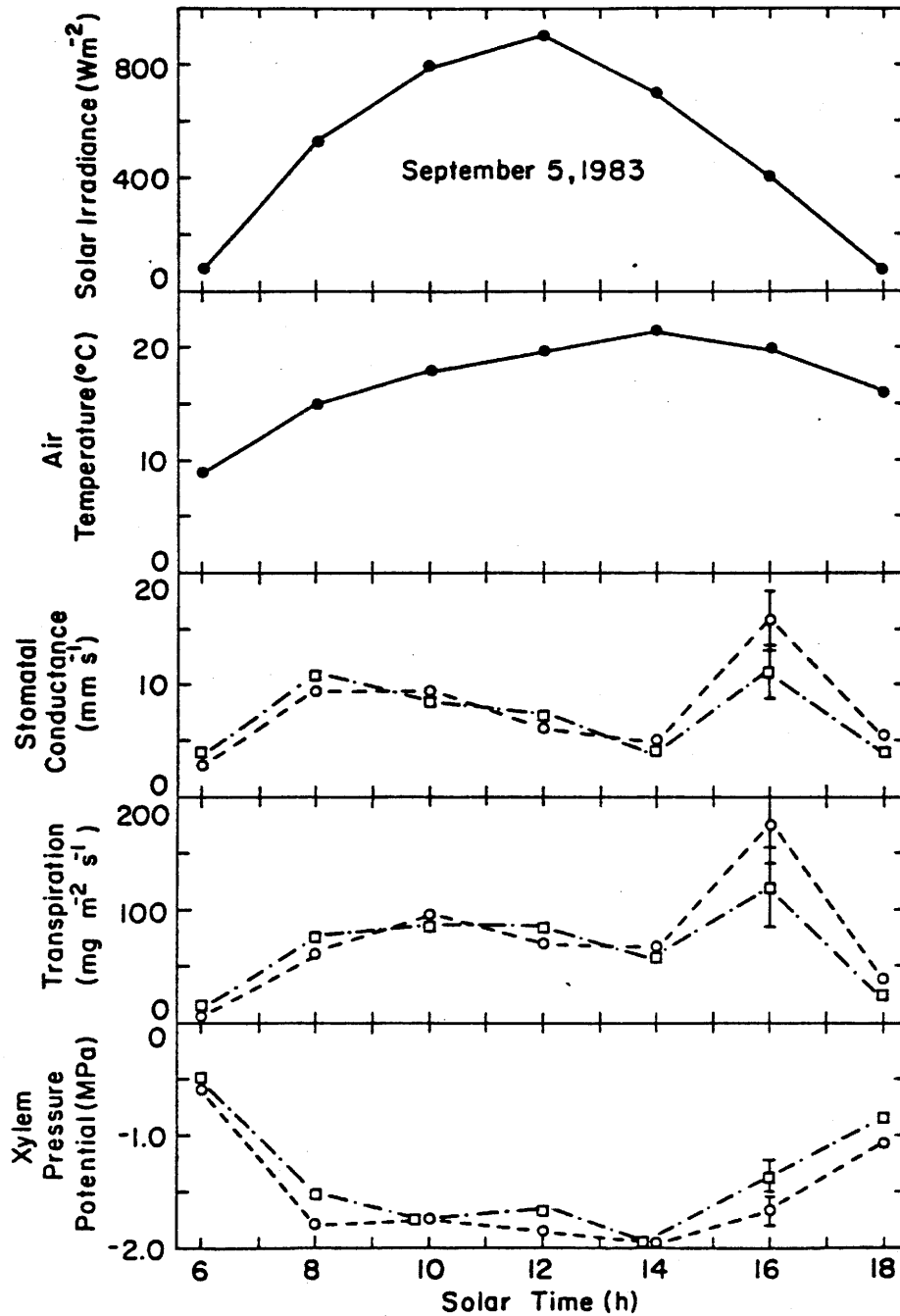


Figure 3. Clear day changes (September 5, 1983) in solar irradiance, air temperature, stomatal conductance to water vapor, transpiration flux density, and xylem pressure potential for *Salix exigua* (O) and *S. amygdaloides* (□) at the low-elevation site. Vertical bars indicate representative standard errors.

Table 3. Seasonal variations in environmental and water relations parameters at the low-elevation site. For plant data, upper and lower values are for Salix exigua and S. amygdaloides, respectively, and are means  $\pm$  standard errors.

Parameter	Date			
	8/1	8/18	9/5	9/15
Maximum Air Temperature ( $^{\circ}\text{C}$ )	22	19	22	21
Maximum VPD (KPa)	1.33	1.08	1.94	1.92
Maximum Stomatal Conductance ( $\text{mm s}^{-1}$ )	10.1 $\pm$ 0.9 9.0 $\pm$ 0.7	17.2 $\pm$ 1.1 12.5 $\pm$ 0.9	16.2 $\pm$ 0.9 10.9 $\pm$ 0.8	4.8 $\pm$ 0.5 4.5 $\pm$ 0.4
Maximum Xylem Pressure Potential (MPa)	-3.0 $\pm$ 0.3 -3.2 $\pm$ 0.5	-4.4 $\pm$ 1.0 -3.5 $\pm$ 1.0	-6.2 $\pm$ 0.7 -5.2 $\pm$ 0.8	-2.8 $\pm$ 0.3 -3.2 $\pm$ 0.2
Minimum Xylem Pressure Potential (MPa)	-13.2 $\pm$ 0.6 -11.8 $\pm$ 0.6	-20.1 $\pm$ 0.4 -17.3 $\pm$ 0.5	-19.5 $\pm$ 1.0 -20.5 $\pm$ 0.8	-20.0 $\pm$ 0.3 -20.5 $\pm$ 1.8

Maximum observed stomatal conductance for both species occurred on 18 August and minima on 15 September (Table 3). Maximum xylem pressure potentials for the Salix species were between -0.2 and -0.7 MPa, and minima varied from -1.1 to -2.1 MPa (Table 3).

#### DISCUSSION

Despite differences in growth form, the water relations of Salix planifolia, S. wolfii, and Betula occidentalis were similar throughout a day, as well as seasonally, at the high-elevation site. On clear days all three phreatophytes maintained relatively high stomatal conductance and transpiration flux density from 1000 to 1600 h, even though xylem pressure potentials were lowest during this same time period (Fig. 1). Seasonal trends in conductance for the three shrub species were similar as well, with a decrease occurring in conjunction with lower nighttime air temperatures and the onset of senescence (Fig. 1).

In contrast to species at the high-elevation site, S. exigua and S. amygdaloides exhibited a decline in stomatal conductance throughout a day at the low-elevation site (Fig. 3). This may have been due to drier soils and, consequently, lower minimum xylem pressure potentials throughout a day for the low-elevation species. Although minimum values were only -0.4 MPa lower, this may have been below the xylem pressure potential that initiates stomatal closure, a threshold observed in several phreatophytes (Nilsen et al., 1981; Anderson, 1982). Stoner and Miller (1975) found reductions in arctic Salix stomatal conductance when xylem pressure potentials dropped below -1.4 MPa. Assuming -1.4 MPa is appropriate for species investigated in the present study, the minimum xylem pressure potentials for species at the high-elevation site were near or slightly above this value, while the minimum xylem pressure potentials of the low-elevation phreatophytes were below, resulting in decreased

stomatal conductances. Furthermore, on clear days when leaves were fully expanded, the average minimum stomatal conductance for the low-elevation species was only 51% of the high-elevation Salix species, being 13.6 and 26.5 mm s<sup>-1</sup>, respectively.

Consistent with predictions of Smith and Geller (1979) based on biophysical differences with elevation, stomatal conductances and transpiration rates were greater at the high-elevation site. However, despite the much lower conductances at the low-elevation site, maximum transpiration rates were only reduced by 31% on the average, due probably to a greater vapor deficit throughout the day at the low-elevation site (1.92 versus 1.22 KPa). On a daily basis, water loss from the Salix phreatophytes at the low-elevation site averaged 3.6 Kg m<sup>-2</sup> of leaf area, compared to 4.8 Kg m<sup>-2</sup> for the high-elevation species. Thus, although transpiration may have been substantially reduced during the morning as a result of dew (Larsson, 1981), the greater stomatal conductances during the day led to greater water consumption on a daily basis when compared to the low-elevation.

During the growth season, stomatal conductances were greatest at the high-elevation site after leaf expansion and before the onset of senescence. Similar to other studies (Raschke, 1975; Thimann and Satler, 1979a, b; Kaufmann, 1982 b; Wardle and Short, 1983), leaf senescence resulted in more than a 90% reduction in stomatal conductance as compared to healthy sunlit leaves (Table 2). A decrease in maximum xylem pressure potential for the three species coincided with the increase in senescence, even though soil water potentials remained >-0.2 MPa. This may have reflected possible increases in root resistance to water uptake during cold hardening and the onset of dormancy (Larcher, 1980). In addition to senescence, maximum conductances may have been reduced as a

result of previous night minimum air temperatures, which in September were at or below 0°C on all but one night. Reductions in stomatal opening in response to low night air temperatures have been demonstrated for Pinus contorta (Fahey, 1979) as well as other possible phreatophytes, including Populus deltoides (Drew and Bazzaz, 1979) and P. tremuloides (Kaufmann, 1982a). Late-season reductions in maximum stomatal conductances were also measured at the low-elevation site, where low night temperatures in September may have contributed to the decline.

Although low night temperature may have contributed to senescence and declines in maximum conductance, the three high-elevation species apparently tolerate a low temperature environment and a short growth season (~10 weeks). Indeed, throughout the summer air temperatures were at or below 0°C on 22% of the nights. Sakai (1970, 1974) demonstrated that Salix species are among the most tolerant to freezing temperatures of all shrubs, with leaves capable of surviving -20°C and dormant plants withstanding -70°C, and Anderson and McNaughton (1973) found no significant reductions in either transpiration or photosynthesis when roots of alpine Salix species were chilled to 3°C. Thus, even though the growth season is relatively cool and short, these species may transpire appreciable amounts of water.

In summary, stomatal conductance and transpiration rates were notably higher at the high-elevation site; however, other differences between species at the two sites were minor. For both sites and all species examined, stomatal conductance and water use were most influenced by solar irradiance, dew on leaves, minimum air temperatures in spring and fall, and phenology.

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