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Water Relations of High-elevation 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 hr as a result of dew on the leaves, but high stomatal conductances to water vapor (>15 mm s^{-1}) and transpiration rates (>100 mg m^{-2} s^{-1}) occurred from 1000 to 1600 hr, resulting in daily water losses per unit leaf area of 4.5, 5.2 and 4.0 kg m^{-2}, respectively. Maximum stomatal conductances declined after 1 September in conjunction with minimum air temperatures consistently below 0 C and increased leaf senescence. The period of significant water consumption was from 10 July through 20 September.

Diurnal variations in stomatal conductance of *Salix exigua* and *S. amygdaloides* at 2255 m were similar to those at the high-elevation site, but maximum stomatal conductances were only 51% as great. However, transpiration occurred from sunrise to sunset at the lower elevation, resulting in daily water losses of 3.7 and 3.4 kg m^{-2} of leaf area, respectively. Midday depressions in leaf conductance at the lower site may have been in response to xylem pressure potentials below -1.7 MPa. Seasonally, conductances were constant until a decrease occurred after 15 September, probably due to low temperatures and leaf senescence. The growth season at the low-elevation site was estimated to be from 15 June-30 September.

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

INTRODUCTION

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 inferred 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*.

Bliss (1960) compared arctic and alpine *Salix* species with potometers, and found significantly greater transpiration rates in the alpine plants. Although he related transpiration to wind speed, 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

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data on factors affecting stomatal conductance and transpiration in four species of *Salix* and another common shrub, *Betula occidentalis,* that occur above 2200 m in southeastern Wyoming.

STUDY AREA AND METHODS

To quantify the water relations of high-elevation phreatophytes, intensive measurements were made in a riparian shrub community at 2865 m elevation along Sally Creek in the Medicine Bow Mountains of southeastern Wyoming (41° 21′ N 106° 11′ W). The site was ≈2 ha 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* common throughout Wyoming were selected for study (Dorn, 1977). *Salix wolfii* Bebb is a small shrub with relatively small leaves (Table 1), whereas *Salix planifolia* Pursh is much taller and has longer leaves. *Betula occidentalis* Michx. was included because it is also common throughout mountainous areas of Wyoming in habitats similar to those of *S. wolfii* (Dorn, 1977). It is similar in stature to *S. wolfii,* but has almost circular leaves in contrast 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-hr 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 five 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 adaxial and abaxial leaf surfaces were summed to determine total stomatal conductance (Nobel, 1983). Corresponding leaf temperatures were measured with an infrared thermometer (Barnes Engineering model 14-2204). Xylem pressure potentials were monitored throughout a day by periodically excising five 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 was calculated from measurements of water vapor deficits of the atmosphere, leaf temperature and stomatal conductance.

Air temperature and relative humidity were continuously recorded (Science Associates model 610 hygrothermograph) and 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-185A light meter equipped with a LI-200S sensor). Soil water potentials at 0.2-m depth were recorded biweekly at five 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 elevation, less intensive

TABLE 1. — Shrub and community characteristics at the high-elevation site. Values are means ±1 SE and different letters indicate statistically significant differences ($\alpha = 0.05$) between species as determined by single factor analysis of variance

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

*Other *Salix* species comprised an additional 15.7% cover such that total shrub cover was 49.3%

measurements were conducted at a 2255-m elevation 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 *S. 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±0.5 cm in length and 0.8±0.1 cm in width; leaves of *S. amygdaloides* averaged 9.1±0.3 cm long and 1.8±0.1 cm wide). Procedures described in Sokal and Rohlf (1969) were used for single factor analysis of variance and to calculate standard errors of data from both sites.

RESULTS

High-elevation site. — Leaf expansion of all three species began the 1st 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 senescence was evident before 1 September. Stomatal conductance could not be measured on any day before 1000 hr because leaves of all species were consistently covered with dew until that time. Transpiration was considered to be at or near zero until after 0800 hr 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 greater than 20 C on 40% of the days (Fig. 2) and minima being below 0 C on 22% of the days (Fig. 1). However, throughout the entire month of August 1983 air temperatures never dropped below 0 C (Fig. 1). After the 1st 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 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 *Salix planifolia, Betula occidentalis* and *S. wolfii,* respectively (Fig. 1). 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 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 *Salix wolfii, S. planifolia* and *Betula occidentalis,* respectively (Table 2). 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 W m^{-2} at solar noon (Fig. 2). During that day air temperature rose from a low of 4 C at 0600 hr to a maximum of 22 C at 1300 hr (Fig. 2). At 1000 hr all three species exhibited similar stomatal conductances of ca. 21.5 mm s^{-1}, but maximum stomatal conductances for *Betula occidentalis, Salix planifolia* and *S. wolfii* were at 1000 hr (22 mm s^{-1}), 1400 hr (25 mm s^{-1}) and 1600 hr (28 mm s^{-1}), respectively (Fig. 2). Diurnal variations in transpiration for all three species followed changes in stomatal conductance, as leaf temperatures were within ±2 C of air temperature. Maximum transpiration occurred at 1400 hr for all species, when the vapor pressure deficit of the atmosphere was greatest, 1.2 kPa (Fig. 1). Total water losses for the day were 4.0, 4.5 and 5.2 kg m^{-2} of leaf area for *B. occidentalis*, *S. planifolia* and *S. wolfii*, 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

TABLE 2.—Comparison of stomatal conductances (mm s^{-1}) for sunlit (750 W m^{-2}), shaded (<100 W m^{-2}) and senescent leaves of three phreatophytic shrubs at the high-elevation site. Values were determined at 1400 hr 2 September 1983, and are means ±1 SE. For each species, all differences between means were statistically significant as determined by single factor analysis of variance with $\alpha = 0.05$

Species	*Sunlit*	*Shaded*	*Senescent*
Salix wolfii	10.7±0.5	7.7±1.2	0.4±0.1
S. planifolia	11.2±0.4	6.4±0.6	0.1
Betula occidentalis	7.7±0.2	6.9±0.5	0.8±0.4

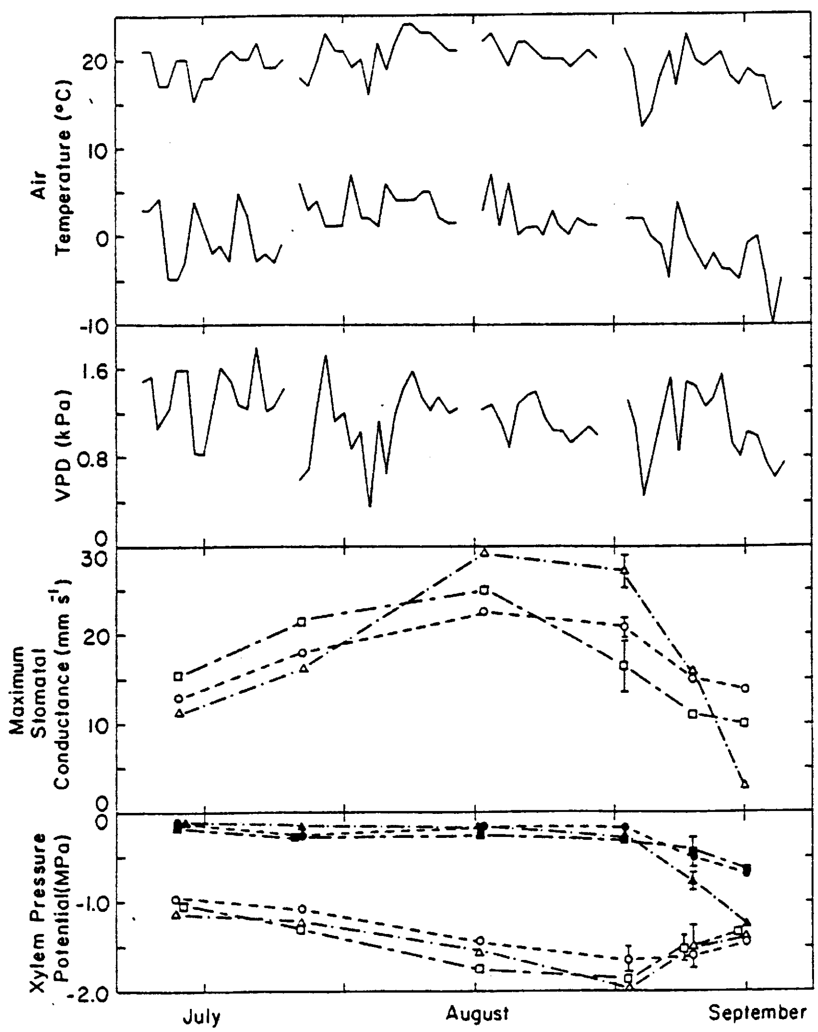

Fig. 1.—Seasonal variations in maximum and minimum air temperature, vapor pressure deficit of the atmosphere (VPD), maximum stomatal conductance, and maximum and minimum xylem pressure potential (shaded and open symbols, respectively) for *Salix planifolia* (□), *S. wolfii* (△) and *Betula occidentalis* (0) at the high-elevation site. Vertical bars indicate representative standard errors

hr. Xylem pressure potential remained relatively constant thereafter, with a gradual rise occurring in *B. occidentalis* (Fig. 2).

Low-elevation site. — At the low-elevation site, leaves were fully expanded in early July and were not senescent on 15 September (the last day of measurements). Solar irradiance at midday was 900 W m^{-2} and air temperature varied from 9 C at 0600 hr to 22 C at 1200 hr. For both species, stomatal conductance gradually decreased from ca. 10 mm s^{-1} at 1000 hr to 5 mm s^{-1} at 1400 hr; however, at 1600 hr *Salix exigua* attained a maximum of 16.2 mm s^{-1} and *S. amygdaloides* 10.9 mm s^{-1} (Fig. 3). Transpiration followed a similar pattern because leaf temperatures were consistently within ±2 C of air temper-

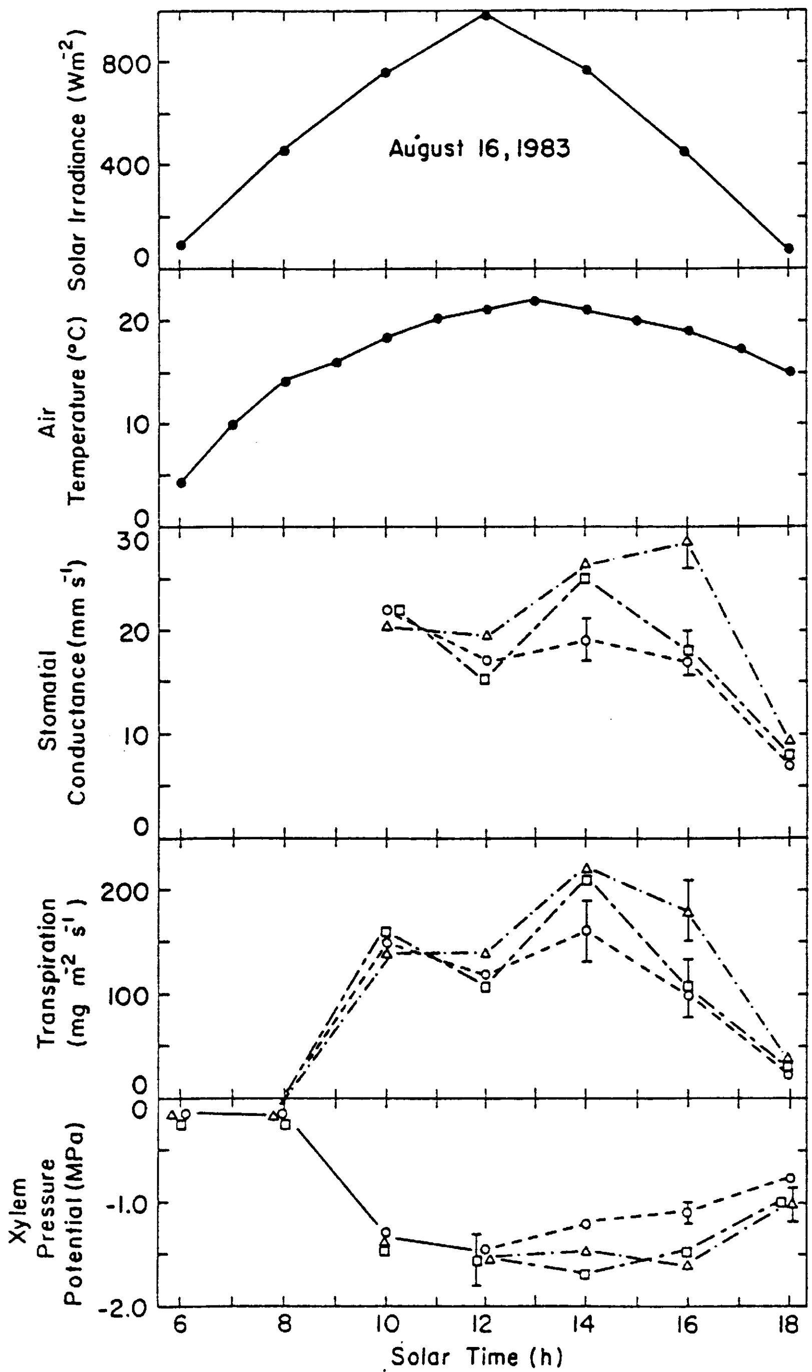

Fig. 2. — Clear day (16 August 1983) values of solar irradiance, air temperature, stomatal conductance to water vapor, transpiration and xylem pressure potential for *Salix planifolia* (□), *S. wolfii* (△) and *Betula occidentalis* (0) at the high-elevation site. Vertical bars indicate representative standard errors

ature and there was only slight change in the vapor pressure deficit. Water losses for the entire day were 3.7 and 3.4 kg m^{-2} of leaf area for *S. amygdaloides,* respectively. Xylem pressure potentials of both species were very similar throughout the day, being −0.5 MPa at 0600 hr and decreasing to < −1.5 MPa throughout the rest of the day until after 1600 hr when a slight increase occurred (Fig. 3).

Seasonally, air temperatures were near 21 C on measurement days and the maximum vapor pressure deficits of the atmosphere were above 1 kPa (Table 3). 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 from 1000 to 1600 hr, 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 night time air temperatures and the onset of senescence (Fig. 1).

In contrast to species at the high-elevation site, stomatal conductance of *Salix exigua* and *S. amygdaloides* declined 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 the 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 that for the high-elevation *Salix* species, 13.6 and 26.5 mm s^{-1}, 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

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 ±1 SE

	Date			
Parameter	8/1	8/18	9/5	9/15
Maximum air temperature (°C)	22	19	22	21
Maximum VPD (kPa)	1.33	1.08	1.94	1.92
Maximum stomatal conductance (mm s^{-1})	10.1±0.9	17.2±1.1	16.2±0.9	4.8±0.5
	9.0±0.7	12.5±0.9	10.9±0.8	4.5±0.4
Maximum xylem pressure potential (MPa)	−0.30±0.03	−0.44±0.10	−0.62±0.07	−0.28±0.03
	−0.32±0.05	−0.35±0.10	−0.52±0.08	−0.32±0.02
Minimum xylem pressure potential (MPa)	−1.32±0.06	−2.01±0.04	−1.95±0.10	−2.00±0.03
	−1.18±0.06	−1.73±0.05	−2.05±0.08	−2.05±0.18

site, maximum transpiration rates were only reduced by 31% on the average, due probably to a greater vapor pressure deficit throughout the day at the low-elevation site (1.92 vs. 1.22 kPa). On a daily basis, water loss from the *Salix* phreatophytes at the low-elevation site averaged 3.6 kg m^{-2} of leaf area, compared to 4.8 kg m^{-2} 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 daily water consumption when compared to the low-elevation species.

During the growing 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

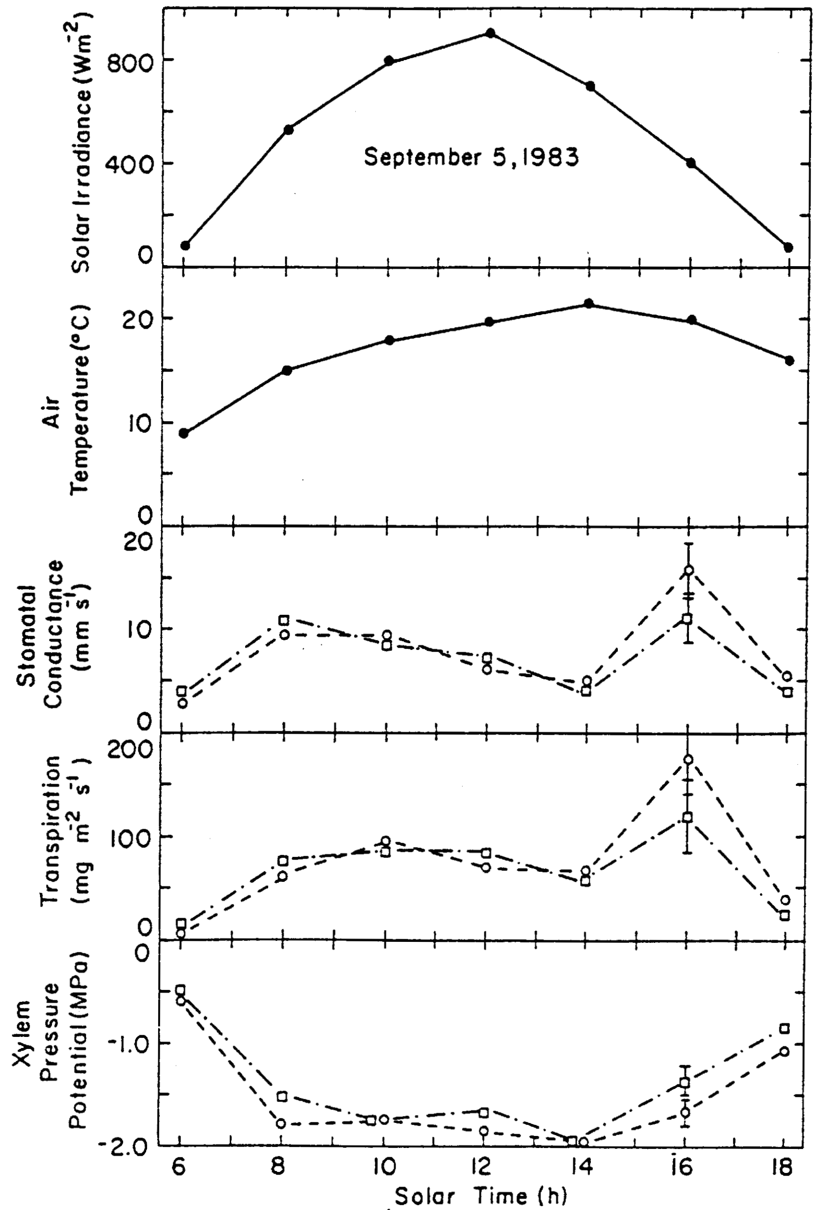

Fig. 3.—Clear day (5 September 1983) values of solar irradiance, air temperature, stomatal conductance to water vapor, transpiration and xylem pressure potential for *Salix exigua* (0) and *S. amygdaloides* (□) at the low-elevation site. Vertical bars indicate representative standard errors

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 resulted from 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 1 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 growing season (≈10 weeks). 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 shrubs most tolerant to freezing temperatures, with leaves capable of surviving −20 C and dormant plants withstanding −70 C. 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, 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 autumn, and phenology. However, stomatal conductances and transpiration rates were notably higher at the high-elevation site. The data presented in this study indicate phreatophytes may be an important component in high-elevation riparian communities throughout the western United States. In areas where dense thickets of these shrubs occur, they may significantly influence stream flow characteristics, drainage from surrounding meadows, and the availability of water to other riparian species.

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LITERATURE CITED

ANDERSON, J.E. 1982. Factors controlling transpiration and photosynthesis in *Tamarix chinensis* lour. *Ecology*, 63:48-56.

_______ AND S.J. MCNAUGHTON. 1973. Effects of low soil temperature on transpiration, photosynthesis, leaf relative water content, and growth among elevationally diverse plant populations. *Ibid.*, 54:1220-1233.

BLISS, L.C. 1960. Transpiration rates of arctic and alpine shrubs. *Ibid.*, 41: 386-388.

DREW, A.P. AND F.A. BAZZAZ. 1979. Response of stomatal resistance and photosynthesis to night temperature in *Populus deltoides*. *Oecologia*, 41:89-98.

DORN, R.S. 1977. A manual of the vascular plants of Wyoming. Garland Publishing, Inc., New York. 1498 p.

FAHEY, T.J. 1979. The effect of night frost on the transpiration of *Pinus contorta* ssp. *latifolia*. *Oecol. Plant.*, 14:483-490.

KAUFMANN, M.R. 1982a. Evaluation of season, temperature, and water stress effects on stomata using a leaf conductance model. *Plant Physiol.*, 69:1023-1026.

_______. 1982b. Leaf conductance during the final season of a senescing aspen branch. *Ibid.*, 70:655-657.

LARCHER, W. 1980. Physiological plant ecology. Springer-Verlag, New York. 303 p.

LARSSON, S. 1981. Influence of intercepted water on transpiration and evaporation of *Salix*. *Agric. Meteorol.*, 23:331-338.

MILLER, P.C., W.A. STONER AND J.R. EHLERINGER. 1978. Some aspects of water relations of arctic and alpine regions, p. 343-357. *In*: L.L. Tieszen (ed.). Vegetation and production ecology of Alaskan arctic tundra. Springer-Verlag, New York.

NILSEN, E.T., P.W. RUNDEL AND M.R. SHARIFI. 1981. Summer water relations of the desert phreatophyte *Prosopis glandulosa* in the Sonoran desert of Southern California. *Oecologia*, **50**:271-276.

NOBEL, P.S. 1983. Biophysical plant physiology and ecology. W.H. Freeman and Co., New York. 608 p.

RASCHKE, K. 1975. Stomatal action. *Annu. Rev. Plant Physiol.*, **26**:309-340.

SAKAI, A. 1970. Freezing resistance in willows from different climates. *Ecology*, **51**:485-491.

———. 1974. Mechanism of frost resistance in highly resistant shoots (*Salix sachalinesis, Populus gelrica, Betula pubescens*). *Sov. Plant Physiol. (Engl. Transl. Fitziol. Rast.)*, **21**:113-117.

SMITH, W.K. AND G.N. GELLER. 1979. Plant transpiration at high elevations: theory, field measurements, and comparisons with desert plants. *Oecologia*, **41**:109-122.

SOKAL, R.R. AND F.J. ROHLF. 1969. Biometry. W.H. Freeman and Co., New York. 776 p.

STONER, W.A. AND P.C. MILLER. 1975. Water relations of plant species in the wet coastal tundra at Barrow, Alaska. *Arct. Alp. Res.*, **7**:109-124.

THIMANN, K.V. AND S.O. SATLER. 1979a. Relation between leaf senescence and stomatal closure: senescence in light. *Proc. Natl. Acad. Sci. USA*, **76**:2295-2298.

——— AND ———. 1979b. Relations between leaf senescence and stomatal closure: senescence in darkness. *Ibid.*, **76**:2270-2273.

VANKLAVEREN, R.W., L.O. POCHOP AND W.E. HEDSTROM. 1975. Evapotranspiration by phreatophytes in the North Platte Basin of Wyoming. Water Resources Series #56, Water Resources Research Institute, University of Wyoming, Laramie. 27 p.

WARDLE, K. AND K.C. SHORT. 1983. Stomatal responses and the senescence of leaves. *Ann. Bot.*, **52**:411-412.

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