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High Elevation Phreatophytes of Wyoming**

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Stomatal conductance patterns and environment in high elevation phreatophytes of Wyoming

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High-elevation (2305 m) phreatophytes (cottonwood, *Populus angustifolia* James, and willows, *Salix monticola* Nutt. and *Salix exigua* Bebb) in southeastern Wyoming commonly showed a pattern of increasing stomatal conductance (g_i) throughout the day, despite minimum leaf water potentials (ψ_l) as low as -2.7 MPa. Diurnally, light and leaf temperature were the most important variables influencing g_i , but there were also threshold values of ψ_l and leaf-to-air vapor pressure deficit for stomatal closure. Seasonally, maximum daily g_i (g_{max}) was similar between species, was positively related to minimum air temperature the previous night, and showed a threshold response to soil temperature. Two types of evidence existed for large soil-to-leaf conductances (g_{s-l}) and for liquid water being available to the roots. The first was no change in ψ_l despite increasing transpiration during the afternoon. The second was rapid evening recovery of ψ_l often to values higher than mean soil water potential to 60-cm depth. The combination of low atmospheric pressures at high elevation, large g_{s-l} and access to a water table may explain how these phreatophytes attained g_{max} of $0.8-0.9 \text{ mol m}^{-2} \text{ s}^{-1}$, much higher than g_{max} of low-elevation phreatophytes or high-elevation nonphreatophytes.

Key words: *Populus*, *Salix*, phreatophyte, stomatal conductance, xylem pressure potential.

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Dans le sud du Wyoming, des espèces phréatophytes telles que le *Populus angustifolia* James, *Salix monticola* Nutt. et *Salix exigua* Bebb présentent habituellement un patron d'augmentation de conductance stomatale (g_i) au cours de la journée, en dépit de potentiels hydriques foliaires minimum (ψ_l) aussi faibles que $-2,7$ MPa. Au cours de la journée, la lumière et la température foliaire sont les variables les plus importantes influençant la valeur g_i , mais on retrouve également des valeurs critiques de ψ_l et du déficit de pression de vapeur feuille-air pour la fermeture des stomates. Au cours de la saison, la valeur maximum de g_i (g_{max}) est identique entre les espèces, est positivement reliée avec la température minimum de l'air la nuit précédente, et montre un seuil de réaction par rapport à la température du sol. On retrouve deux types de preuve pour les conductances élevées sol-feuille (g_{s-l}) et pour disponibilité de l'eau aux racines. La première est liée à l'absence de changement dans la valeur ψ_l en dépit d'une augmentation de la transpiration pendant l'après-midi. La deuxième est une remontée rapide de la valeur ψ_l souvent à des valeurs plus élevées que le potentiel hydrique moyen du sol à 60 cm de profondeur. La combinaison entre les basses pressions atmosphériques à haute altitude, la forte valeur g_{s-l} , et l'accès à la nappe phréatique pourraient expliquer comment ces espèces phréatophytes peuvent atteindre des valeurs g_{max} de $0,8-0,9 \text{ mol m}^{-2} \text{ s}^{-1}$, largement supérieures à la g_{max} des phréatophytes de base altitude ou des non phréatophytes de haute altitude.

Mots clés: *Populus*, *Salix*, phréatophytes, conductance stomatale, pression potentielle du xylème.

[Traduit par la rédaction]

Introduction

In the semiarid, intermontane basins of southeastern Wyoming, arborescent vegetation is restricted to riparian zones and other areas where a permanent water table exists near the surface. This vegetation consists primarily of phreatophytes, woody perennials such as cottonwoods (*Populus* spp.), willows (*Salix* spp.), and alders (*Alnus* spp.), whose deep roots penetrate to water tables or to the capillary fringes above water tables throughout the growing season (Meinzer 1927).

Because of their reliable water supply, phreatophytes are traditionally viewed as avoiding water stress that often restricts growth of shallow-rooted nonphreatophytes. This stress is frequently manifested as low leaf water potentials (ψ_l) that may cause stomatal closure. Alternatively, roots in drying soils may send signals to stomata to close, preventing low ψ_l (Schulze 1986). By tapping deep sources of liquid water, phreatophytes may avoid low ψ_l and stomatal closure. Thus, diurnal and seasonal patterns of phreatophyte stomatal conductance (g_i) may be little affected by soil and plant water status.

For the high elevations (>1500 m) and cool, semiarid climate of Wyoming, solar radiation, low air (T_a) and soil (T_s) temperatures, high leaf-to-air vapor pressure differences (VPD), and low ψ_l (the latter correlated with soil water potential, ψ_s) have been repeatedly demonstrated to influence diurnal and seasonal patterns of conifer g_i in southeast Wyoming (Fahey 1979; Fahey and Young 1984; Smith 1984; Carter et al. 1988). Although one study found that solar radiation and T_a affected daily g_i of willows (Young et al. 1985), the potential effects of plant and soil water status and T_s on phreatophyte g_i remain unknown, especially for high-elevation species. The objectives of our research were (i) to measure diurnal and seasonal patterns of g_i and ψ_l for three high-elevation phreatophytes in southeastern Wyoming, (ii) to ascertain which environmental variables most strongly influenced diurnal and seasonal patterns of g_i and (iii) to interpret these g_i patterns and their controlling variables in terms of the phreatophytic growth habit.

Methods

Study site

Fieldwork was carried out during the growing season (mid-May to end of September) of 1986. A study site representative of riparian

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zones along natural, perennial streams was selected along the Little Laramie River at the foot of the Medicine Bow Mountains (41°20'N, 106°15'W) at an elevation of 2305 m. Narrowleaf cottonwood (*Populus angustifolia* James) formed small groves of one or more mature (15–25 m tall) trees surrounded by smaller trees and saplings. These groves were scattered throughout a mosaic of willow thickets, consisting primarily of 3–5 m tall sandbar willow (*Salix exigua* Bebb) and mountain willow (*Salix monticola* Nutt.) (nomenclature follows Nelson 1984). The largest of these groves and its adjacent willow thickets, located on a small terrace ≈2 m above the river, were chosen for intensive measurements.

The terrace substrate was silty soil underlain by alluvial deposits of gravel and cobbles. Nearby vegetation outside the riparian zone was shortgrass prairie. Nine years of records (1977–1985) from a U.S. Forest Service weather station at Centennial, Wyoming, 10 km west of and 268 m higher than this site, showed a mean annual rainfall of 66 cm and a mean annual air temperature of 2.7°C.

Climate and soil variables

Rainfall in a nearby clearing and air temperature, relative humidity, and photosynthetic photon flux density (PPFD) 3 m above the willow thicket (8.8 m above ground) were continuously monitored during the growing season, using a tipping-bucket rain gauge (Rainwise model 111), a sun-shielded thermistor (Weathermeasure model 5123B), and a quantum sensor (Li-Cor model 190S) connected to a data logger (Campbell Scientific model CR21X). Soil temperature and water potential were measured weekly at 25- and 60-cm depths (three replicates per depth) using thermocouple psychrometers and a microvoltmeter (Wescor model HR-33T) operated in the dewpoint mode.

Stomatal conductances and leaf water potentials

Dawn-to-dusk variation in g_i and ψ_i was measured during five clear or mostly clear days, starting in early June when leaf expansion was approximately three-quarters complete. Cottonwood, mountain willow, and sandbar willow were sampled at roughly 3-week intervals. Measurements on sandbar willow were delayed until late June, when the lanceolate leaves were large enough to cover the porometer aperture.

Measurements were made on branches (cottonwood) or stems (willow) between 0.5 and 1.5 m height every 2 h on five separate plants of each species. The same plants were sampled throughout a given day, but not all the same plants were sampled on different days. If the plants were in direct sunlight, five sunlit and five shaded leaves were sampled on each plant. When there was no clear distinction between sunlit and shaded leaves, as at dawn and sunset or with overcast skies, five leaves per plant, regardless of exposure, were sampled.

Stomatal conductances were measured on the adaxial and abaxial leaf surfaces with a transient diffusion porometer (Li-Cor model Li-700) and summed to give total leaf conductance. The porometer cuvette was shaded from direct sunlight to maintain temperature differentials between leaves and the cuvette of less than 2°C. Calibrations were performed in the field before every set of measurements using the manufacturer's perforated plastic plate backed by wet filter paper. This plate was then calibrated in the laboratory against a precision-milled aluminum plate of the same dimensions. Conductances to water vapor for the various combinations of hole numbers and diameters were calculated from the theory for mass transfer through pores, assuming a single end-correction (Monteith 1973, p. 147). Ambient temperature (T) and pressure (P) were assumed to affect conductances through their influence on the diffusion coefficient of water vapor in air (D_{wv}):

$$[1] \quad D_{wv} = D_{wv}^{\circ} \left(\frac{T}{T^{\circ}} \right)^m \cdot \left(\frac{P^{\circ}}{P} \right)$$

where D_{wv}° is the diffusion coefficient at $T^{\circ} = 0^{\circ}\text{C}$ and $P^{\circ} = 101.3 \text{ kPa}$, and $m = 1.75$ (Smith and Geller 1979).

Natural leaf temperatures (T_l) were measured to $\pm 0.5^{\circ}\text{C}$ using an infrared thermometer (Barnes Engineering model 111). Air temper-

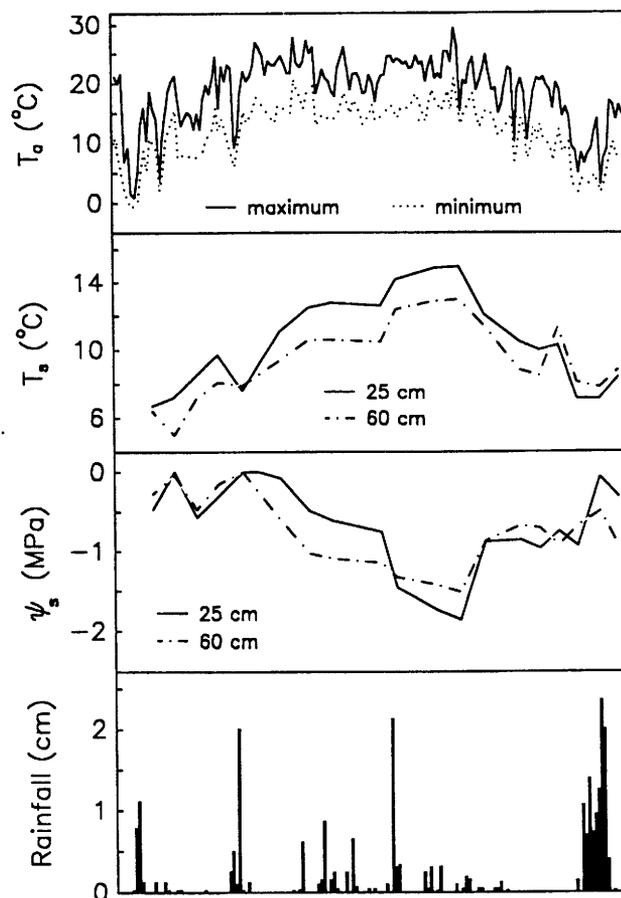


FIG. 1. Seasonal variation in environmental variables at the Little Laramie River study site. From top to bottom: maximum and minimum daily air temperature (T_a), mean soil temperature (T_s) at two depths, mean soil water potential (ψ_s) at two depths, and daily rainfall.

ature and relative humidity were measured at sample height with a copper-constantan thermocouple and a Vaisala sensor (Weathermeasure model 5121). Incident light, the sum of PPFD normal to the abaxial and adaxial surfaces of sample leaves, was measured on three of the sampling days using a quantum sensor.

Following measurements, the shoots to which the sample leaves were attached were excised and placed in plastic bags over ice in the dark for determination of shoot xylem pressure potentials (assumed = ψ_i) within 30 min using a pressure bomb (PMS Instruments model 1000). When both sunlit and shaded leaves were measured, ψ_i was measured only on the shoots bearing sunlit leaves.

Five days' additional g_i measurements near the beginning and end of the growing season, and one extra day's measurement of early morning ψ_i , were performed at noon on clear days for each of the above species. These data were intended to clarify the seasonal pattern of maximum daily g_i ($= g_{max}$) and early morning ψ_i ($= \psi_{max}$).

Results

Climate and soil variables

Maximum and minimum T_a fluctuated substantially from day to day, but averaged about 15°C higher in midsummer than in late spring and early fall (Fig. 1). Soil temperature at 25-cm depth increased from 7°C in early May to about 15°C in August, while T_s at 60 cm was 1–2°C less than at 25 cm, except in September (Fig. 1).

Soil water potential remained above -0.5 MPa from early May to mid-June (Fig. 1). Rainfall occurred repeatedly from late June to mid-August, yet a decrease in ψ_s of 1.4 to 1.8 MPa

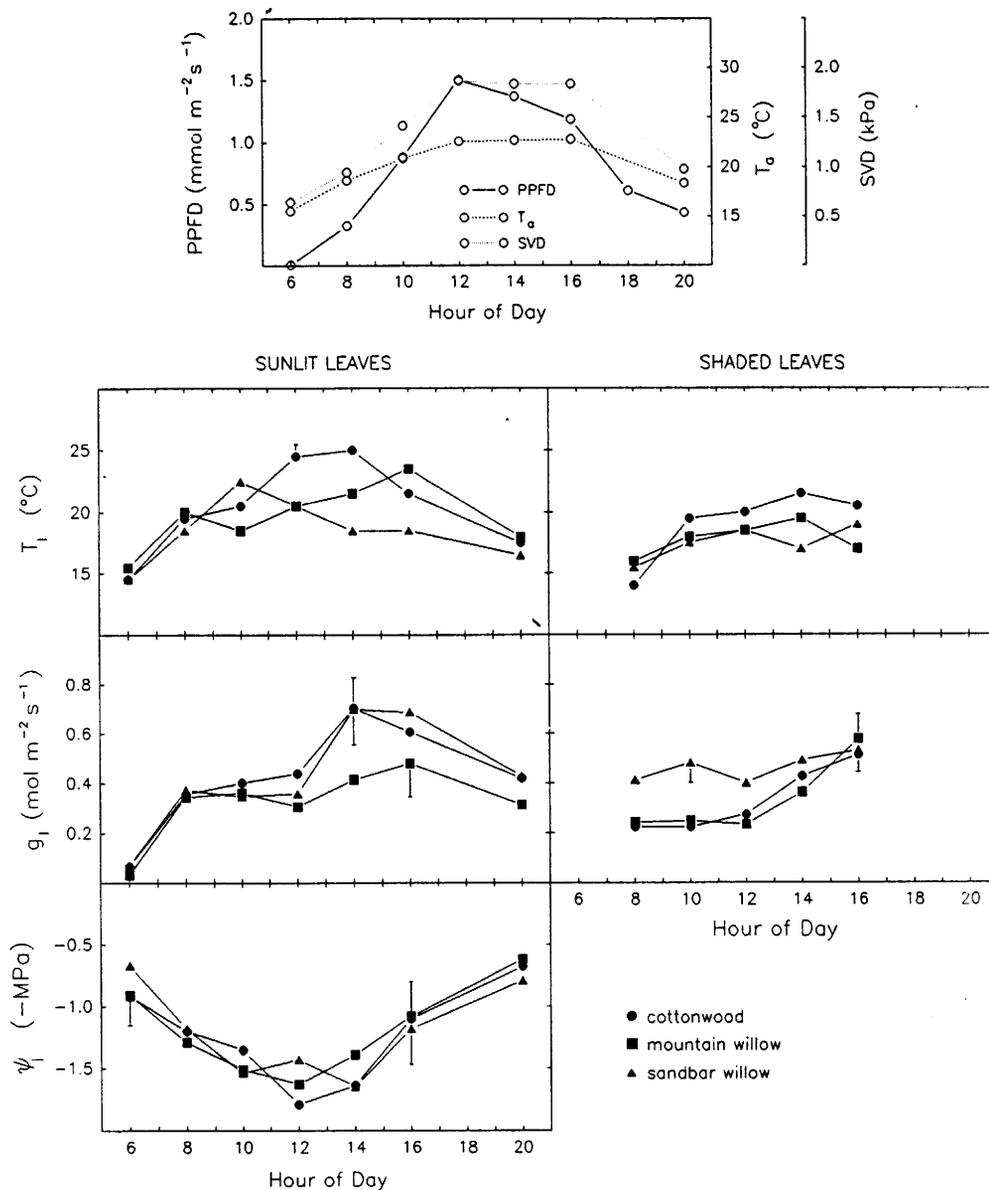


FIG. 2. Daily patterns of climatic (top) and plant variables (bottom) in high-elevation Wyoming phreatophytes on June 29. The largest standard error ($n = 5$), if larger than the data symbols, and its time of occurrence are shown separately for each species. Light rain prevented porometry at 18:00 h. PPFD, photosynthetic photon flux density; T_a , air temperature; SVD, atmospheric saturation vapor pressure deficit; T_l , leaf temperature; g_l , stomatal conductance; ψ_l , leaf water potential.

occurred at both depths over the same period. This could be the result of dropping water tables and increasing soil water depletion by phreatophyte transpiration. During the next 2 weeks, ψ_s increased by about 1 MPa at both depths, despite little rainfall, for unknown reasons. A further increase in ψ_s accompanied heavy rains in late September.

On a daily basis, T_a and atmospheric saturation vapor pressure deficit (SVD) were maximal between noon and midafternoon, but afternoon cloudiness often reduced PPFD (e.g., Fig. 2). Most rainfall occurred as afternoon and evening thunderstorms.

Daily patterns of g_l and ψ_l

An example of the most commonly observed, diurnal pattern of g_l , an increase throughout the day to a maximum in the afternoon, is shown in Fig. 2. Both sunlit and shaded leaves exhibited this behavior. The only exceptions to the pattern were

an extended midday (1200–1600 h) maximum in cottonwood g_l on June 2 and August 3, and partial afternoon stomatal closure in mountain willow on July 17 and August 3 (data not shown).

On the particular day shown in Fig. 2, g_l of sunlit mountain willow leaves was less than that of sunlit cottonwood and sandbar willow leaves during the afternoon, while g_l of shaded sandbar willow leaves was greater than that of shaded cottonwood and mountain willow leaves in the morning. During other days, sunlit and shaded g_l of the three species were fairly similar throughout the day.

On all days and for all species, ψ_l declined from its early-morning value to a midday minimum, followed by a late afternoon and evening increase (e.g., Fig. 2). Sunset values of ψ_l ranged from -0.3 MPa below to -0.3 MPa above early-morning values, indicating complete or near-complete recovery of ψ_l on a daily basis.

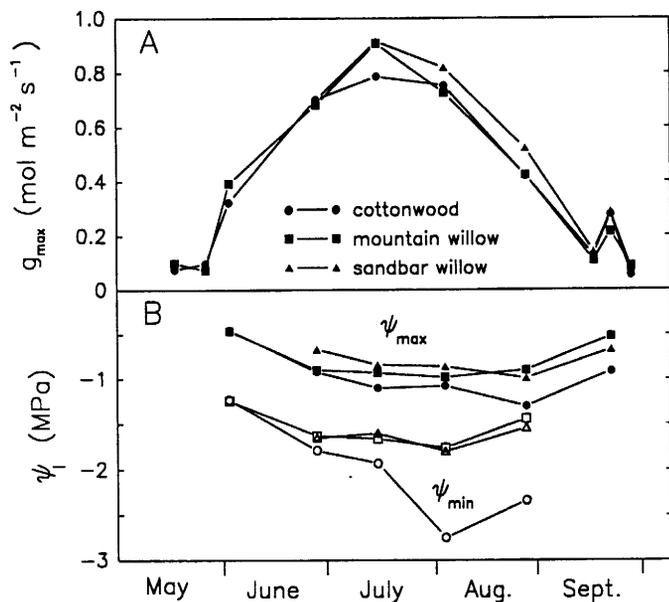


FIG. 3. Seasonal variation in (A) maximum daily stomatal conductance (g_{\max}) and (B) early morning (ψ_{\max}) and minimum midday (ψ_{\min}) leaf water potential (ψ) in three phreatophyte species. Each point is the mean of five measurements on separate plants.

Incident PPFD on sunlit leaves reached values exceeding $1.5 \text{ mmol m}^{-2} \text{ s}^{-1}$ at midday, while PPFD on shaded leaves never exceeded $0.6 \text{ mmol m}^{-2} \text{ s}^{-1}$ (data not shown). Sunlit T_1 varied between 4°C below and 6°C above T_a , while shaded T_1 lay between T_a and 6°C less than T_a (e.g., Fig. 2). On individual days, sunlit and shaded VPD (data not shown) displayed similar temporal variation to sunlit and shaded T_1 .

Seasonal patterns of g_i and ψ_i

Seasonal variation in g_{\max} , ψ_{\max} , and midday minimum ψ (ψ_{\min}) is shown in Fig. 3. Values of g_{\max} early and late in the growing season may be underestimates because g_{\max} usually occurred in the midafternoon to late afternoon during the five dawn-to-dusk measurement days (e.g., Fig. 2). Given this caveat, the general pattern for all three species was a rapid increase in g_{\max} between late May and midsummer, followed by a decline into mid-September (Fig. 3A). The seasonally largest value of g_{\max} was $\approx 0.8 \text{ mol m}^{-2} \text{ s}^{-1}$ in cottonwood and $\approx 0.9 \text{ mol m}^{-2} \text{ s}^{-1}$ in the two willow species. At any given time during the year, g_{\max} was quite similar among species.

All species had similar declines in ψ_{\max} and ψ_{\min} until August, when ψ_{\min} of cottonwood became substantially less than ψ_{\min} of the willow species (Fig. 3B). The greatest leaf water stress experienced during the summer was -2.7 MPa for cottonwood and -1.8 MPa for the willows. All species showed increases of ψ_{\min} in August and of ψ_{\max} in September.

Environmental variables and g_i

Two approaches were used to try to separate the influences of various environmental and plant variables on diurnal and seasonal patterns of g_i in each species. In the first approach, individual g_i measurements were plotted against concurrently measured environmental variables and ψ_i , using data from the five dawn-to-dusk measurement days, to determine if relationships between g_i and these variables could be elucidated by boundary-line analysis. It was assumed that points lying below

TABLE 1. The percentage of total variance in daily stomatal conductance of each species explained by several independent variables in multiple linear regressions ($n = 129\text{--}224$)

Variable ^a	Species		
	Cottonwood	Mountain willow	Sandbar willow
PPFD	2.5	2.2	2.2
T_a	33.3	ns	24.0
VPD	ns	ns	2.0
ψ_i	ns	21.2	ns
Total	35.8	23.4	28.2

^a PPFD, photosynthetic photon flux density; T_a , air temperature; VPD, leaf-to-air vapor pressure difference; ψ_i , leaf water potential; ns, nonsignificant at $P = 0.15$.

each boundary line were limited by some other variable than that used as the independent variable in a particular plot (Jarvis 1976; Chambers et al. 1985). Boundary-line plots for cottonwood are shown in Fig. 4. Plots for the two willow species (not shown) were generally similar.

Stomata of cottonwood were fully open at PPFD exceeding $0.15 \text{ mmol m}^{-2} \text{ s}^{-1}$ and often were partially open in the dark (Fig. 4A). The same behavior was exhibited by the willow species. There was an apparent optimum T_1 of about $20\text{--}25^\circ\text{C}$, below and above which cottonwood g_i declined markedly (Fig. 4B). Slightly lower optima were displayed by the willow species. Stomatal closure in cottonwood occurred when VPD exceeded a threshold value of $\approx 2 \text{ kPa}$ in sunlit leaves (Fig. 4C). A separate, lower threshold for shaded leaves was suggested, but this may have been an artifact, since shaded leaves never attained as high a VPD as occurred in sunlit leaves. In mountain willow, the VPD threshold for stomatal closure was also 2 kPa , while in sandbar willow the data did not show an obvious threshold. Cottonwood also exhibited stomatal closure when ψ_i declined below -1.7 MPa (Fig. 4D). Sandbar willow had a threshold ψ_i of about -1.4 MPa , while the data for mountain willow indicated that a threshold ψ_i , if present, was less than -2.0 MPa .

Table 1 shows the results of stepwise, multiple linear regressions between individual g_i measurements and concurrently measured environmental and plant variables on the five dawn-to-dusk measurement days. Using a generous $\alpha = 0.15$ for variable entry and removal, the variable explaining the highest proportion (21% to 33%) of the daily variation in g_i for each species was T_a for cottonwood and sandbar willow and ψ_i for mountain willow. VPD also entered for sandbar willow and PPFD for all three species, but these additional variables accounted for less than a few percent of the variance in daily g_i of each species (Table 1). The overall coefficient of determination for each species' model was low ($r^2 = 0.23\text{--}0.36$).

Minimum T_a the previous night (as measured above the willow thickets) explained a high proportion of the variance (85–87%) in seasonal g_{\max} of each species, according to stepwise, multiple linear regressions. All species responded similarly to this variable (Fig. 5A) because seasonal changes in absolute values of g_{\max} differed little between species (Fig. 3A). Although no other variable entered the regressions for cottonwood and mountain willow, ψ_s at 60 cm and T_s at 25 cm together explained an additional 12% of the variance in g_{\max} of sandbar willow. The response to T_s appeared nonlinear, with much reduced g_{\max} below a threshold of $8\text{--}10^\circ\text{C}$ (Fig. 5B).

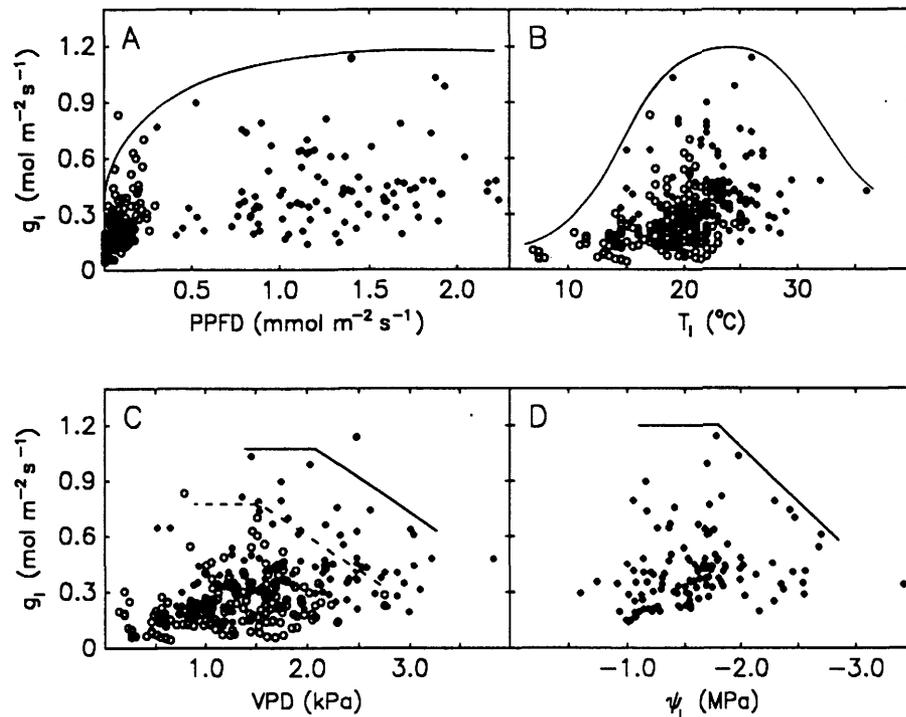


FIG. 4. Boundary-line analysis of stomatal conductance (g_l) of cottonwood leaves in relation to concurrent photosynthetic photon flux density (PPFD), leaf temperature (T_l), leaf-to-air vapor pressure deficit (VPD), and leaf water potential (ψ_l). Each point is an individual measurement made between dawn and dusk from June 3 to August 30. There were several zero g_l values at zero PPFD. ●, sunlit leaves; ○, shaded leaves.

Discussion

Comparisons with other phreatophyte species

Phreatophyte g_l in this study generally increased throughout the day. Similarly, Young et al. (1985) observed maximum g_l in late afternoon for four *Salix* species growing in riparian zones in the Medicine Bow Mountains. In contrast to these Wyoming studies, desert phreatophytes showed one of three diurnal patterns of g_l : (i) extended midday maximum, (ii) afternoon partial stomatal closure, or (iii) midmorning maximum, followed by a decline the rest of the day (Hanson 1979; Szarek and Woodhouse 1976; Nilsen et al. 1981, 1983, 1984). One or more of the three desert patterns, but not the pattern we found, were observed in the field for other phreatophytic cottonwood and willow species (Pallardy and Kozlowski 1981; Pezeshki and Hinckley 1982, 1988; Ceulemans et al. 1988; Dawson and Bliss 1989a, 1989b). Unlike g_l , the daily patterns of ψ_l measured in this study were similar to those exhibited in the field by both desert phreatophytes (Haas and Dodd 1972; Hanson 1979; Mooney et al. 1980; Anderson 1982; Nilsen et al. 1981, 1983) and other phreatophytic cottonwood and willow species (Small 1972; Stoner and Miller 1975; Pallardy and Kozlowski 1981; Young et al. 1985; Pezeshki and Hinckley 1988; Dawson and Bliss 1989b).

The seasonally highest g_{\max} values observed in this study, 0.8–0.9 mol m⁻² s⁻¹, were substantially larger than the 0.1–0.3 mol m⁻² s⁻¹ reported for naturally growing desert, temperate, and arctic phreatophytes from low elevations (Small 1972; Stoner and Miller 1975; Hanson 1979; Anderson 1982; Nilsen et al. 1983; Kowalik and Eckersten 1984). Maximum g_l for planted, low-elevation *Populus* and *Alnus*, up to 0.6 mol m⁻² s⁻¹, were somewhat lower than our observed

values (Pallardy and Kozlowski 1981; Pezeshki and Hinckley 1982, 1988; Schulte et al. 1987; Ceulemans et al. 1988). Körner and Mayr (1981) observed seasonal maximum g_{\max} of 0.1–0.2 mol m⁻² s⁻¹, much lower than in our Wyoming phreatophytes, for two wet-meadow willow species at 2530 m elevation in the Austrian Alps. In the Medicine Bow Mountains, seasonal maximum g_{\max} (mol m⁻² s⁻¹) was 0.4–0.6 for riparian *S. exigua* and *Salix amygdaloides* Anderss at 2255 m elevation, 0.7–0.9 for riparian *Salix planifolia* Pursh, *Salix wolfii* Bebb, and *Betula occidentalis* Hook. at 2865 m, and 0.6 for wet-meadow *Salix brachycarpa* Nutt. at 3300 m, values similar to or somewhat lower than our observations at 2305 m (Oberbauer and Billings 1981; Young et al. 1985). In comparison, nonphreatophytic conifers and alpine tundra plants growing in the Medicine Bow Mountains had maximum g_{\max} of 0.1–0.3 and 0.1–0.6 mol m⁻² s⁻¹, respectively (Oberbauer and Billings 1981; McNaughton 1984; Smith 1984; Carter et al. 1988). Higher values of g_{\max} occurred in *Salix arctica* Pall. growing at 2030-m elevation than in the same species growing near sea level (0.20 vs. 0.13 mol m⁻² s⁻¹) (Dawson and Bliss 1989a).

Seasonal minimum ψ_{\min} values recorded in this study (–1.8 to –2.7 MPa; Fig. 3B) were generally lower than those reported in the field for temperate, arctic, and alpine cottonwood and willow species (–0.8 to –2.0 MPa) (Small 1972; Stoner and Miller 1975; Körner and de Moraes 1979; Oberbauer and Billings 1981; Young et al. 1985), but higher than those observed in desert phreatophytes (< –3.0 MPa) (Haas and Dodd 1972; Hanson 1979; Mooney et al. 1977, 1980; Nilsen et al. 1981, 1983, 1984).

Except when low light was limiting (Fig. 4A), the strongest association between daily changes in Wyoming phreatophyte g_l and environmental variables was that with T_l , with an appar-

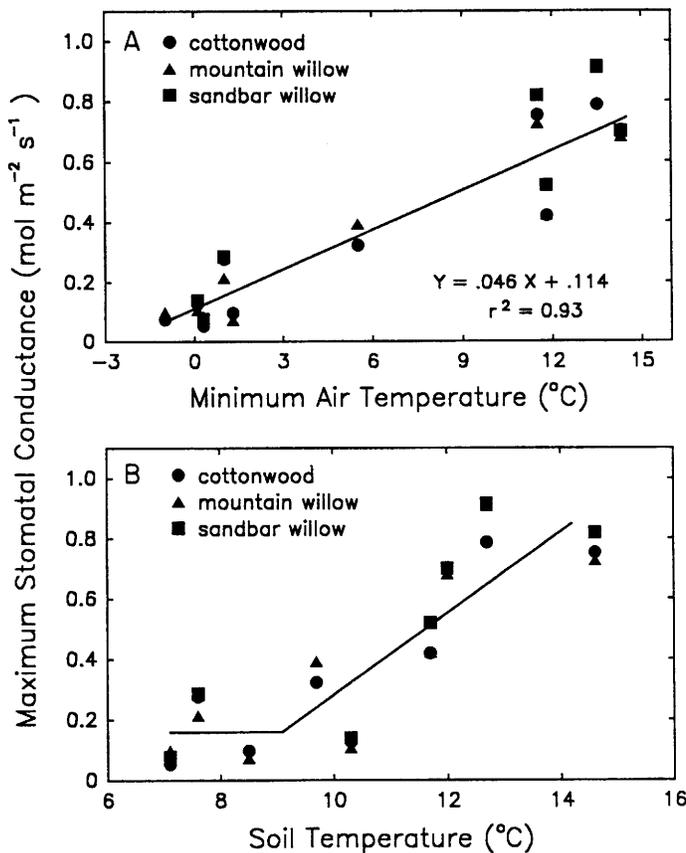


FIG. 5. The influences on mean maximum daily stomatal conductance (g_{\max} ; $n = 5$) of each species due to (A) minimum air temperature (T_a) the preceding night and (B) mean soil temperature (T_s) at 25-cm depth. Data were collected between May 18 and September 30. The regression line for all plants is shown in (A), a hand-drawn line in (B).

ent optimum of 20–25°C (Fig. 4B). This same optimum was found in potted *Populus deltoides* Bartr. ex Marsh. by Regehr et al. (1975). Temperature also exerted a major influence on seasonal patterns of g_{\max} in our species. Extrapolation of the relationship in Fig. 5A indicated minimum T_a for stomatal opening of -2 to -3 °C, while the T_s threshold was ≈ 8 – 10 °C. Drew and Bazzaz (1979) found that nighttime T_a of 4 to 10°C slowed stomatal opening the next morning in potted *P. deltoides*. Dawson and Bliss (1989a) observed reductions of g_{\max} in arctic and alpine *S. arctica* as T_s at 10-cm depth decreased below 10°C. However, Anderson and McNaughton (1973) found that chilling roots of alpine willow species to 3°C did not affect transpiration.

Stomatal responses to VPD have been reported in a number of phreatophyte species. In the arctic tundra willow (*S. arctica* Pall.), g_1 decreased as VPD increased or decreased away from an optimum value (Dawson and Bliss 1989b). Desert phreatophytes showed sharp declines in g_1 as VPD rose above threshold values during the summer months, but during winter this response was sometimes reversed (Mooney et al. 1977; Anderson 1982; Nilsen et al. 1983). VPD thresholds were also observed in naturally growing and potted *Populus trichocarpa* Torr. & Gray by Pezeshki and Hinckley (1982, 1988); these thresholds decreased from > 2 kPa in early summer to near 1 kPa in late summer following drought. However, neither Sheriff (1977) nor Schulte et al. (1987) found a g_1 vs. VPD

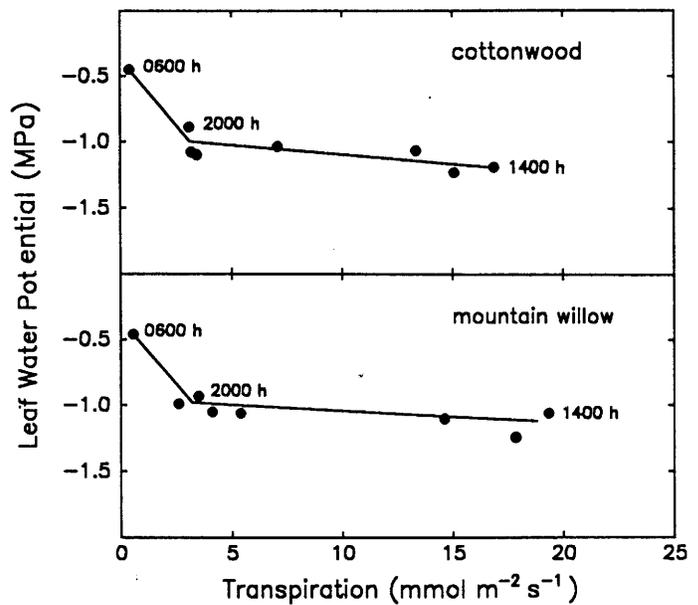


FIG. 6. The relationship between leaf water potential (ψ_l) and transpiration (the product of stomatal conductance and leaf-to-air vapor pressure deficit) in cottonwood and mountain willow on June 3. Each point is the mean of five measurements on separate plants. Hand-drawn lines are used to estimate g_{s-1} , not to represent time courses, but the time of day is indicated for several points.

relationship in excised, well-watered *Populus alba* L. or *P. trichocarpa* shoots, respectively.

Stomatal closure in Wyoming phreatophytes did not occur until ψ_l declined to -1.7 MPa or lower (Fig. 4D). In contrast, desert phreatophytes can be quite sensitive to ψ_l . For example, g_1 of *Olneya tesota* Gray declined below ψ_l of about -0.6 MPa (Szarek and Woodhouse 1976). A threshold ψ_l for stomatal closure of -0.6 to -2.0 MPa was noted in other phreatophytic cottonwood and willow species (Regehr et al. 1975; Pallardy and Kozlowski 1981; Pezeshki and Hinckley 1982; Ceulemans et al. 1988).

Effects of the soil–plant–atmosphere pathway

Despite the threshold response of g_1 to ψ_l shown by boundary-line analysis (Fig. 4D), ψ_l was a poor predictor of g_1 both during the day (Table 1) and seasonally (Fig. 3). This was not surprising, since ψ_l and g_1 interact not only with each other, but also with the water fluxes and conductances to liquid water flow in the soil–plant–atmosphere pathway (Elfving et al. 1972). Numerous examples have been reported of changes in g_1 independent of ψ_l (e.g., Teskey et al. 1983; Schulte 1986; Schulte et al. 1987). In some cases, ψ_{\max} is correlated with g_{\max} ; in other cases, it is not (Reich and Hinckley 1989 and references therein). Reich and Hinckley (1989) suggested that strong correlations between ψ_{\max} and g_{\max} should be expected when soil-to-leaf hydraulic conductance (g_{s-1}) is constant during the day and ψ_l comes into equilibrium with ψ_s during the night. In this situation, decreased g_{s-1} during soil drying should reduce ψ_{\max} and hence g_{\max} (Running 1980).

Were the above preconditions satisfied in the species we studied? To answer this, we examined the relationship between ψ_l and transpiration, the product of g_1 and VPD, where the slope of the line represents g_{s-1} (Landsberg 1986). In early June, ψ_l fell rapidly in the early morning as transpiration

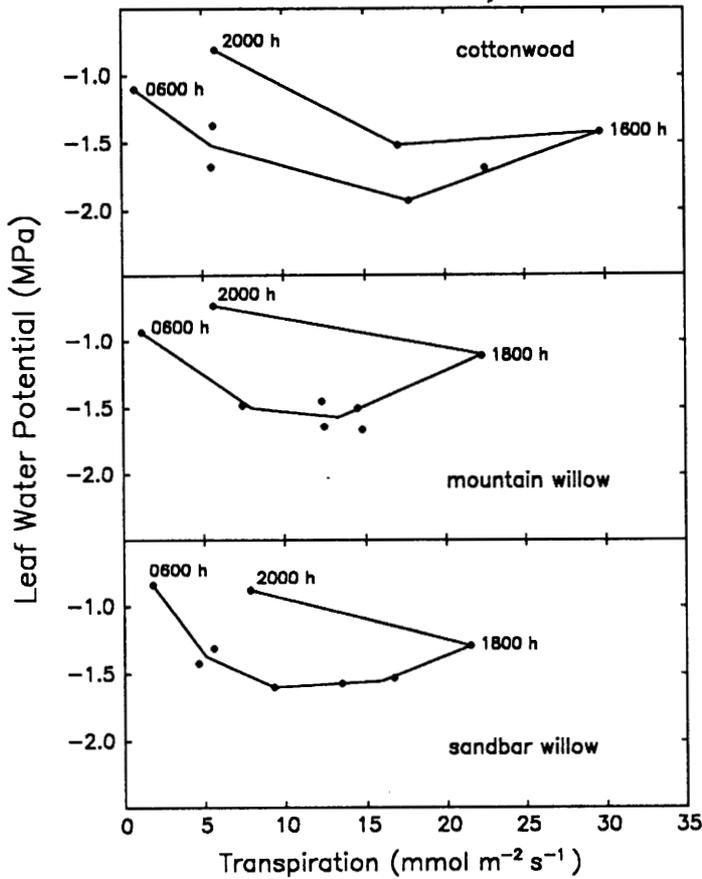


FIG. 7. The relationship between leaf water potential (ψ_l) and transpiration in cottonwood, mountain willow, and sandbar willow on July 17. Similar patterns were displayed by each species on June 29, August 3, and August 30. Each point is the mean of five measurements on separate plants. Hand-drawn lines are used to estimate g_{s-1} , not to represent time courses, but the time of day is indicated for several points.

increased, at a similar g_{s-1} in both cottonwood and mountain willow of $\approx 5 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ (Fig. 6). This may have represented depletion of twig sapwood water, with g_{s-1} representing a conductance between storage tissues and the xylem (Schulze et al. 1985). Thereafter, transpiration continued to increase without a further decline in ψ_l , as g_{s-1} increased to a very high value of $\approx 90 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$, presumably representing xylem liquid flow conductance below the crown. Transpiration declined later in the day at the same high g_{s-1} , but there was little recovery of ψ_l .

During the remaining four measurement days, a different pattern was evident (Fig. 7). After an early morning decline in ψ_l as transpiration increased, at a g_{s-1} of $\approx 8\text{--}11 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ (depending on species), g_{s-1} again became very large and ψ_l remained constant or even increased slightly despite continued increases in transpiration. During the evening, ψ_l at a given value of transpiration was higher than earlier in the day, i.e., a hysteresis loop existed. This pattern suggested that the water potential gradient between the soil and the leaves increased despite no change or an increase in ψ_l . This could only come about if liquid water became available to the roots, as would presumably be the case in phreatophytes and other species with roots in saturated soil (Schulze et al. 1985).

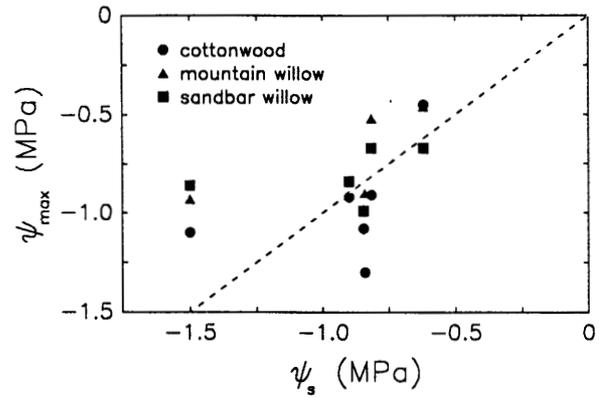


FIG. 8. The relationship between mean early morning leaf water potential (ψ_{\max} ; $n = 5$) and the mean of soil water potential (ψ_s) at 25- and 60-cm depths. The broken line shows a 1:1 correspondence.

In nonphreatophytic trees, overnight recovery of ψ_l does not exceed ψ_s integrated over the rooting depth (e.g., Dougherty and Hinckley 1981). However, ψ_{\max} of cottonwood and willows in midsummer to late summer in this study sometimes was higher than the mean of ψ_s at 25- and 60-cm depths (Fig. 8), suggesting that these species were relying on a source of water deeper than 60 cm. A similar conclusion was reached by Ginter-Whitehouse et al. (1983) for black walnut (*Juglans nigra* L.) because ψ_{\max} in midsummer remained above ψ_s to measured to 105-cm depth. Using tritiated water as a tracer, Stringer et al. (1989) found that ψ_{\max} was higher in white oak (*Quercus alba* L.) trees whose roots tapped deep (>2 m) soil water than in trees with shallower root systems.

Figures 6–8 suggest that although equilibrium between ψ_l and ψ_s apparently occurred rapidly in our species, g_{s-1} was not constant during the day. This may explain why ψ_{\max} and g_{\max} were not correlated in our species. There was no evidence for significant use of stem sapwood water for transpiration, which should have produced a ψ_l -transpiration hysteresis loop in the reverse direction to that observed (e.g., Fig. 7) (Landsberg 1986).

Because of the development of the diurnal ψ_l -transpiration hysteresis loop after early June (e.g., Fig. 7), it was not possible to determine if daily mean g_{s-1} (following the early morning decline in ψ_l) changed during the summer, as was reported in other woody species (Küppers 1984; Reich and Hinckley 1989). A positive relationship between g_{s-1} and T_s might explain how cold soils could limit g_{\max} (Fig. 5B). Low T_s has been repeatedly shown to reduce hydraulic conductances of tree roots to a degree much greater than increased viscosity of water (Elfving et al. 1972; Kaufmann 1975, 1977; Running and Reid 1980; Teskey et al. 1984).

There are other influences on g_l that operate independently of the soil-to-leaf hydraulic pathway. For example, as previously discussed, both T_l and VPD appeared to directly affect g_l in our species (Figs. 4B, 4C). In addition, seasonal osmotic adjustment in leaves, which we did not measure, could increase turgor pressure at a given ψ_l , decreasing the ψ_l necessary to induce stomatal closure (Abrams 1988). Such adjustment has been noted in alders and cottonwoods (Seiler 1985; Pezeshki and Hinckley 1988; Borghetti et al. 1989). Finally, root to shoot communication (presumably hormonal) when soils are drying can directly influence g_l independent of ψ_l (Schulze 1986; Küppers et al. 1988; Zhang and Davies 1989). This last effect seems unlikely in phreatophytes tapping water tables.

Increased g_1 at high elevations is in part due to lower atmospheric pressure increasing the diffusion coefficient of water vapor in air (cf. eq. 1; Smith and Geller 1979). This effect alone would produce 23% higher g_1 at 2305 m compared to sea level, insufficient to fully explain the 50–200% higher maximum g_{\max} of Wyoming phreatophytes compared to low-elevation phreatophytes. However, Küppers (1984) observed a positive correlation between g_{\max} and g_{s-1} in a variety of woody species.

A combination of large g_{s-1} , deep roots tapping water tables, and low atmospheric pressure may be necessary for attainment of the very high g_1 exhibited by Wyoming phreatophytes. Unless g_{s-1} is large most of the day and soil moisture is always readily available, as appears to be the case for the phreatophytes we studied, root water uptake will not keep pace with transpiration when both g_1 and VPD (and thus transpiration) are high, and ψ_1 will fall to levels that close the stomata. In desert phreatophytes, root access to water tables is not sufficient to avoid midday stomatal closure. These species can encounter VPD exceeding 5 kPa (Nilsen et al. 1981). In addition, because xylem hydraulic conductivity is proportional to pathway length (Heine 1971) and the water tables tapped by desert phreatophytes can be more than 15 m deep (Robinson 1958), the great length of these species' roots may result in small g_{s-1} .

What is the potential benefit of very high g_1 for high-elevation phreatophytes? These species have rapid growth rates compared to adjacent nonphreatophytes such as conifers. Such growth rates can only be sustained if maximum photosynthesis rates are also high. Because ambient CO_2 concentration declines substantially with increasing elevation, high g_1 may be necessary to minimize stomatal limitation (i.e., rate of CO_2 diffusion into leaves) of photosynthesis (Smith and Donahue 1991).

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