

## Leaf gas exchange characteristics differ among Sonoran Desert riparian tree species

JONATHAN L. HORTON,<sup>1,2</sup> THOMAS E. KOLB<sup>1</sup> and STEPHEN C. HART<sup>1</sup>

<sup>1</sup> School of Forestry, College of Ecosystem Science and Management, Northern Arizona University, Flagstaff, AZ 86011-5018, USA

<sup>2</sup> Present address: Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24060-0406, USA

Received April 3, 2000

**Summary** We investigated leaf gas exchange responses to leaf temperature, leaf-to-air vapor pressure deficit (VPD), and predawn and midday shoot water potential ( $\Psi_{pd}$  and  $\Psi_{md}$ , respectively) of two native Sonoran Desert riparian tree species, Fremont cottonwood (*Populus fremontii* S. Wats.) and Goodding willow (*Salix gooddingii* Ball), and one exotic riparian tree species, saltcedar (*Tamarix chinensis* Lour. and related species). Measurements were made at two sites over 2 years that differed climatically. Because multiple linear regression models explained less than 29% of the variation in stomatal conductance ( $g_s$ ) and less than 48% of the variation in net photosynthetic rate ( $P_n$ ) of all species, we used boundary-line analysis to compare gas exchange responses among species. Gas exchange rates were high in all species. The hyperbolic relationship between  $P_n$  and  $g_s$  suggested that initial reductions in  $g_s$  at high  $g_s$  did not inhibit  $P_n$ . Reductions in  $g_s$  of cottonwood and willow occurred at  $\Psi_{md}$  values at or below previously reported xylem cavitation thresholds (–1.6 and –1.4 MPa, respectively), indicating tight stomatal regulation of water loss and a narrow cavitation safety margin. In contrast, reductions in  $g_s$  of saltcedar occurred at  $\Psi_{md}$  values well above the cavitation threshold (–7.0 MPa), but at much lower  $\Psi_{md}$  values than in cottonwood and willow, suggesting a wider cavitation safety margin and less tight regulation of water loss in saltcedar. High VPD had a smaller effect on leaf gas exchange in willow than in cottonwood. In contrast, willow had a less negative  $\Psi_{pd}$  threshold for stomatal closure than cottonwood. Compared with cottonwood and willow, leaf gas exchange of saltcedar was more tolerant of high VPD and low  $\Psi_{pd}$ . These physiological characteristics of saltcedar explain its widespread success as an invader of riparian ecosystems containing native Fremont cottonwood and Goodding willow in the Sonoran Desert.

**Keywords:** boundary-line analysis, Fremont cottonwood, Goodding willow, net photosynthetic rate, *Populus fremontii*, *Salix gooddingii*, saltcedar, stomatal conductance, *Tamarix chinensis*, water stress.

### Introduction

Most woody riparian species are phreatophytic, relying

heavily on shallow alluvial water tables (Bryan 1928, Turner 1974, Dawson and Ehleringer 1991, Busch and Smith 1995, Kolb et al. 1997, Mahoney and Rood 1998, Shafroth et al. 1998) to avoid drought stress (Foster and Smith 1991, Smith et al. 1991, 1998). Because of their phreatophytic nature, many riparian trees are thought to lack physiological and morphological adaptations to drought, and are assumed to be intolerant of water stress (Smith et al. 1991, 1998). However, in southwestern USA, riparian ecosystems occur over a wide range of hydrologic conditions from ephemeral washes to large perennial rivers. As a result of low annual precipitation, large intra- and interannual variations in precipitation and streamflow, and high atmospheric water demand caused by high temperature and low relative humidity, southwestern riparian trees may be exposed to greater water stress than riparian species from more mesic ecosystems (Smith et al. 1998). Consequently, southwestern riparian trees may have different responses to soil and atmospheric water stress than riparian trees from more mesic environments.

Human alteration of riparian hydrology by dams, diversions, and groundwater pumping has reduced alluvial water tables in many southwestern riparian ecosystems (Smith et al. 1991, Stromberg et al. 1991, 1996, Stromberg 1993, Busch and Smith 1995). These depressions in water tables are associated with increased stress in many riparian tree species (Smith et al. 1991, Stromberg et al. 1991, 1996, Stromberg 1993, Busch and Smith 1995, Scott et al. 1999, Horton et al. 2001). This stress is often associated with low xylem water potentials ( $\Psi$ ), which may lead to stomatal closure (Foster and Smith 1991, Smith et al. 1991), or xylem cavitation, which causes reductions in hydraulic conductivity and eventually leads to shoot mortality (Tyree et al. 1994). Riparian cottonwoods (*Populus* spp.) are very susceptible to xylem cavitation (Tyree et al. 1994, Pockman et al. 1995), and stress-induced xylem cavitation has been proposed as a mechanism underlying riparian cottonwood decline in response to altered hydrology (Tyree et al. 1994, Horton et al. 2001).

Tyree and Sperry (1988) hypothesized that, to maximize daily carbon gain, many plants regulate water loss to maintain xylem  $\Psi$  just above the cavitation threshold. Riparian cottonwoods appear to maintain xylem  $\Psi$  near this cavitation thresh-

old (Blake et al. 1996, Pockman and Sperry 2000). Species with narrow cavitation safety margins often have stomata that are very responsive to water stress (Blake et al. 1996). Further, riparian cottonwoods from different environments often differ in stomatal response to water stress, with trees from environments with greater evaporative demand showing greater control of water loss (Bassman and Zwier 1991, Sparks and Black 1999).

To manage threatened riparian ecosystems in the southwestern USA effectively, it is necessary to understand how both native and exotic species respond to variations in environmental factors that influence leaf gas exchange. We investigated leaf gas exchange responses to leaf temperature ( $T_{\text{leaf}}$ ), leaf-to-air vapor pressure deficit (VPD), and predawn and midday shoot water potentials ( $\Psi_{\text{pd}}$  and  $\Psi_{\text{md}}$ , respectively) of two important native Sonoran Desert riparian tree species, Fremont cottonwood (*Populus fremontii* S. Wats.) and Goodding Willow (*Salix gooddingii* Ball), and one invasive exotic tree species, saltcedar (*Tamarix chinensis* Lour. and related species). Gas exchange of trees growing in two riparian ecosystems in Arizona differing in mean annual temperature, precipitation, and streamflow was measured over two climatically different years. The first year, 1997, was warmer and drier than 1998, which was influenced by a strong El Niño event. Goodding willow is an obligate phreatophyte (Stromberg 1993) and was expected to be most sensitive to atmospheric and soil water stress. Fremont cottonwood is more deeply rooted than Goodding willow (Stromberg 1993, Stromberg et al. 1996) and is reported to be an obligate or facultative phreatophyte (Busch et al. 1992, Stromberg et al. 1996, Snyder et al. 1998). Thus, we expected cottonwood to be more tolerant of water stress than willow. Saltcedar is a facultative phreatophyte (Busch et al. 1992) that is more drought tolerant than both native species (Busch and Smith 1995, Cleverly et al. 1997, Smith et al. 1998), and we expected it to be the most tolerant of water stress. Based on the drought-tolerance of each species, we postulated that leaf gas exchange of willow would decline at lower VPD and less negative  $\Psi_{\text{pd}}$  and  $\Psi_{\text{md}}$  than cottonwood, and leaf gas exchange of saltcedar would be less sensitive to VPD,  $\Psi_{\text{pd}}$  and  $\Psi_{\text{md}}$  than gas exchange of the native species.

### Materials and methods

The study site at Hassayampa River, a free-flowing tributary of the Gila River, is located on The Nature Conservancy's Hassayampa River Preserve (33°56' N, 112°43' W, elevation 550–600 m) in Maricopa County, Arizona. Mean annual air temperature is 18.6 °C and mean annual precipitation is 288 mm (National Climatic Data Center, Station Wickenburg, AZ, <http://www.wrcc.dri.edu>). The Bill Williams River is a dam-regulated tributary of the Colorado River that drains into Lake Havasu just above Parker Dam. The study site at Bill Williams River is located on the US Fish and Wildlife Service's Bill Williams River National Wildlife Refuge (34° 17' N, 114°13' W, elevation 150–200 m) in La Paz County, Arizona. Mean annual air temperature at this site is 21.9 °C

and mean annual precipitation is 123 mm (National Climatic Data Center, Station Parker 6NE, AZ, <http://www.wrcc.dri.edu>).

The Bill Williams study site is at a lower elevation than the Hassayampa River site and occurs at the transition between the Sonoran Desert and Mojave Desert ecosystems along the western edge of the summer monsoonal precipitation pattern (NOAA, Tucson, AZ, <http://www.wrh.noaa.gov/tucson/monsoon/monsoon.html>). Thus, the Bill Williams site is typically hotter and drier than the Hassayampa site. We selected a losing reach at each site where stream flows decreased from a base level of 1.1 m<sup>3</sup> s<sup>-1</sup> at the Bill Williams and 0.1 m<sup>3</sup> s<sup>-1</sup> at the Hassayampa to 0 m<sup>3</sup> s<sup>-1</sup> at both rivers (USGS stream gauge #90426620, <http://az.water.usgs.gov>, Jenkins 1989). Both sites support populations of Fremont cottonwood, Goodding willow and saltcedar along the gradient of surface flow.

In January and February 1997, seven transects were established along the losing reach at each river. The uppermost transect was located in the perennial reach, and the lowermost transect was located in the ephemeral reach, where surface flow was absent during the summer. These transects were installed to allow sampling of trees growing over a wide range of depth to groundwater. There were healthy populations of all species at each transect at the Bill Williams River. At the Hassayampa River, cottonwood and willow were found at all transects, whereas saltcedar occurred only at the four lowest transects. In March 1998, three additional transects were installed in the ephemeral reach of the Hassayampa River to increase the sample size of saltcedar.

Physiological data were collected monthly between June and August at all transects at both rivers in 1997, and at each transect at the Hassayampa River in 1998, although sampling was interrupted on several days in August of both years by monsoonal thunderstorms. At each sampling date, five mature individuals of each species were chosen randomly from the population at each transect for measurement. Shoot water potentials ( $\Psi$ ) of terminal twigs were measured before dawn and at mid-morning (0800–1000 h) and mid-afternoon (1300–1500 h) with a Scholander-type pressure chamber (Model 1000, PMS Instruments, Corvallis, OR). Leaf gas exchange was measured under full sun conditions at both mid-morning and mid-afternoon with an LI-6200 portable photosynthesis system (Li-Cor, Inc., Lincoln, NE). This system also measured leaf and air temperatures and relative humidity and calculated leaf-to-air vapor pressure deficit (VPD). The cuvette was kept shaded when not in use and between measurements to minimize heating. Leaf gas exchange measurements were made within 15 s to minimize changes in water vapor pressure and air temperature within the cuvette during measurement.

The timing of physiological measurements was based on diurnal measurements made in May 1997 (data not shown) showing that the measurement periods represent the time when environmental conditions are generally most favorable for gas exchange (mid-morning) and when environmental conditions may limit gas exchange (mid-afternoon). Gas exchange measurements were made on leaves from portions of

the lower canopy exposed to full sun. Measurements were made on leaves *in situ* where possible, and on twigs that were detached with pole pruners when leaves were inaccessible for *in situ* measurements. Leaves on detached twigs were measured within 30 s of detachment in a light environment similar to that in the canopy. Our preliminary studies showed that gas exchange measurements on recently detached twigs did not differ from those of leaves attached to the tree (data not shown). These methods have been used successfully in other studies (e.g., Gower et al. 1993, Meng and Arp 1993, Kolb et al. 1997). Gas exchange was measured at a photosynthetically active radiation (PAR) of  $> 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ , an irradiance known to be saturating for gas exchange of many *Populus* spp. (Pezeshki and Hinckley 1982, Bassman and Zwier 1991) and *Tamarix chinensis* (Anderson 1982).

After gas exchange had been measured, the leaf material inside the cuvette was excised and projected leaf area was measured with an image analysis system (Decagon Devices, Inc., Pullman, WA). Gas exchange was then calculated on the basis of projected leaf area. All leaf samples were oven-dried at 70 °C for 48 h and weighed, and specific leaf area ( $\text{m}^2 \text{kg}^{-1}$ ) determined for all samples.

#### Data analysis

Analysis of variance (ANOVA) was used to compare physiological parameters among species on data pooled from both rivers and both years. When differences were significant ( $P < 0.05$ ), means were compared among species with the Fisher's PLSD test. These analyses were performed with Statview (Abacus Concepts, Inc., Santa Barbara, CA).

We used two methods to assess the influence of environmental and physiological variables on gas exchange of each species. The first approach consisted of forward multiple linear regression between gas exchange parameters and environmental and physiological variables based on an entry probability value of 0.05. These multiple regressions were performed with the SAS software package (SAS Institute, Cary, NC). The second approach used scatter plots of gas exchange parameters and concurrently measured  $T_{\text{leaf}}$ , VPD,  $\Psi_{\text{md}}$  and  $\Psi_{\text{pd}}$ . Relationships between gas exchange parameters and these variables were assessed by boundary-line analysis where the upper limit of the scatter plots was used to delineate the responses of stomatal conductance ( $g_s$ ) and net photosynthetic rate ( $P_n$ ) to each independent variable (Jarvis 1976, Chambers et al. 1985). Response functions delineated from the upper

limit of the scatter plot probably measured the response with little confounding influence from other factors. Boundary lines and threshold values of the relationships between leaf gas exchange and environmental and physiological variables were visually estimated from the upper points of the scatter plots, a technique used in many other studies (e.g., Chambers et al. 1985, Foster and Smith 1991, Foster 1992, Kolb and Stone 2000).

## Results

#### Site characteristics

In 1997, mean annual air temperature was higher than the long-term mean, whereas total annual precipitation was close to the long-term mean at both sites (Table 1). As expected, the Bill Williams River site was hotter and received less precipitation than the Hassayampa River site in 1997. Because there was a strong El Niño event in the winter and spring of 1998, mean annual temperature was lower and total annual precipitation was higher than the long-term means at Hassayampa River in 1998 (Table 1).

#### Physiological parameters

Mean  $g_s$  values for cottonwood and willow were similar, but significantly higher than for saltcedar (Table 2). Mean  $P_n$  differed significantly among species and was lowest in cottonwood and highest in saltcedar (Table 2). Mean  $\Psi_{\text{pd}}$  was slightly, but significantly, lower in cottonwood than in willow. Predawn  $\Psi$  was much lower in saltcedar than in cottonwood

Table 1. Climate and hydrologic characteristics of study sites at Bill Williams River (BWR) in 1997 and Hassayampa River (HRP) in 1997 and 1998. Data for BWR are from the Western Regional Climate Center, Station Parker 6NE, AZ, and data for HRP are from the Western Regional Climate Center, Station Wickenburg, AZ.

	BWR	HRP	
	1997	1997	1998
Mean annual temperature (°C)	23.2	20.2	16.8
Mean annual temperature (90-year mean; °C)	21.9	18.6	18.6
Total annual precipitation (mm)	131	287	386
Mean annual precipitation (90-year mean; mm)	123	288	288

Table 2. Mean ( $\pm 1$  SE) values of various parameters for Fremont cottonwood, Goodding willow and saltcedar. Means were derived from all data combined from both rivers and years ( $n = 295\text{--}412$ ). Values with different letters are significantly different at  $P = 0.05$ .

Parameter	Cottonwood	Willow	Saltcedar
Stomatal conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$0.261 \pm 0.010$ a	$0.299 \pm 0.010$ a	$0.426 \pm 0.030$ b
Net photosynthetic rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$11.9 \pm 0.3$ a	$14.2 \pm 0.3$ b	$21.1 \pm 0.8$ c
Predawn $\Psi$ (MPa)	$-0.66 \pm 0.01$ b	$-0.58 \pm 0.01$ c	$-1.87 \pm 0.04$ a
Midday $\Psi$ (MPa)	$-1.70 \pm 0.01$ b	$-1.73 \pm 0.02$ b	$-3.05 \pm 0.04$ a
Specific leaf area ( $\text{m}^2 \text{kg}^{-1}$ )	$12.4 \pm 0.1$ b	$12.9 \pm 0.2$ c	$6.9 \pm 0.2$ a

and willow (Table 2). Mean  $\Psi_{md}$  values for cottonwood and willow were similar, and much higher than for saltcedar (Table 2). Among species, specific leaf area was highest for willow, slightly lower for cottonwood, and much lower for saltcedar (Table 2).

Photosynthetic capacity, i.e., maximum  $P_n$  when  $g_s$  is not limiting, was much higher in saltcedar than in cottonwood or willow, both on a projected leaf area basis (Figure 1) and on a leaf mass basis (approximately  $600 \text{ nmol g}^{-1} \text{ s}^{-1}$  for saltcedar versus 400 and  $300 \text{ nmol g}^{-1} \text{ s}^{-1}$  for willow and cottonwood, respectively). Net photosynthetic rate was highly correlated with  $g_s$  for all species (Figure 1). However, the response was nonlinear with a leveling trend in  $P_n$  at high  $g_s$ , suggesting that initial reductions in  $g_s$  at high  $g_s$  may not inhibit  $P_n$ . Because of this hyperbolic response, we examined the effects of environmental variables and xylem  $\Psi$  on  $g_s$  and  $P_n$  separately.

#### Multiple regression analysis

Vapor pressure deficit and  $\Psi_{pd}$  were both entered into the for-

ward multiple linear regression model for cottonwood, but they explained only a small portion of the overall variability in  $g_s$  and  $P_n$  (Table 3). For willow, among the variables examined, VPD explained the most variation in both  $g_s$  and  $P_n$ , and this relationship was stronger (higher  $r^2$ ) for  $P_n$  than for  $g_s$  (Table 3). Leaf temperature and  $\Psi_{pd}$  were also significantly related to  $g_s$  and  $P_n$ , and  $\Psi_{md}$  was significantly related to  $P_n$  of willow, but these variables explained little of the total variation (Table 3). For saltcedar, VPD explained the most variation in  $g_s$ , whereas  $\Psi_{md}$  explained the most variation in  $P_n$  (Table 3). Stomatal conductance of saltcedar was also related to  $\Psi_{md}$ , and to a lesser extent leaf temperature, whereas  $P_n$  was also related to VPD and, to a lesser extent,  $\Psi_{md}$  (Table 3). Overall, the multiple linear regression models explained no more than 48% of the variation in  $g_s$  and  $P_n$  of all species, and in most cases, the amount of variation explained by the models was less than 28% (Table 3).

#### Boundary line analysis

At the time of the gas exchange measurements, leaf temperatures were high, ranging up to  $50^\circ\text{C}$ , and air temperatures, measured at the study sites with a shaded thermocouple and data logger, ranged between  $45$  and  $48^\circ\text{C}$ . Gas exchange of all species showed the same response to leaf temperature;  $g_s$  and  $P_n$  increased up to some optimal temperature and then decreased (Figure 2). The optimum temperature for  $g_s$  and  $P_n$  of cottonwood and willow was between  $28$  and  $33^\circ\text{C}$ , whereas the corresponding temperature for saltcedar was higher, ranging between  $33$  and  $38^\circ\text{C}$  (Figure 2, Table 4).

Leaf gas exchange remained relatively constant at low VPD, but declined at VPDs above an apparent threshold for each species (Figure 3, Table 4). The threshold differed between  $g_s$  and  $P_n$  for all species. Stomatal conductance of cottonwood and willow decreased at VPDs above  $\approx 1.2$  kPa, whereas a reduction in  $P_n$  did not occur until VPD was greater than  $\approx 1.6$  kPa for cottonwood and  $\approx 2.8$  kPa for willow. Saltcedar was more tolerant of high VPDs than either cottonwood or willow, with reductions in  $g_s$  occurring at VPDs above  $\approx 2.5$  kPa and reductions in  $P_n$  occurring at VPDs above  $\approx 5.0$  kPa.

Shoot  $\Psi_{md}$  had an effect on leaf gas exchange in all species (Figure 4, Table 4). Stomatal conductance of cottonwood was reduced when  $\Psi_{md}$  fell below  $\approx -1.6$  MPa; however, there was no apparent effect on  $P_n$  of cottonwood over the range of  $\Psi_{md}$  measured in this study. Willow showed reductions in  $g_s$  below a  $\Psi_{md}$  threshold of  $\approx -1.3$  MPa and reductions in  $P_n$  when  $\Psi_{md}$  declined below  $\approx -1.6$  MPa. The  $\Psi_{md}$  thresholds for leaf gas exchange were much lower for saltcedar than for the native species. Stomatal conductance of saltcedar was reduced when  $\Psi_{md}$  fell below  $\approx -2.5$  MPa and  $P_n$  was reduced when  $\Psi_{md}$  fell below  $\approx -2.8$  MPa. There were also apparent  $\Psi_{pd}$  thresholds affecting leaf gas exchange of all species (Figure 5, Table 4). Willow had the highest  $\Psi_{pd}$  threshold, with gas exchange decreasing when  $\Psi_{pd}$  was below  $\approx -0.5$  MPa. Cottonwood was more tolerant of low  $\Psi_{pd}$  than willow, with gas exchange reductions occurring at  $\Psi_{pd}$  values below  $\approx -0.8$  MPa. Among

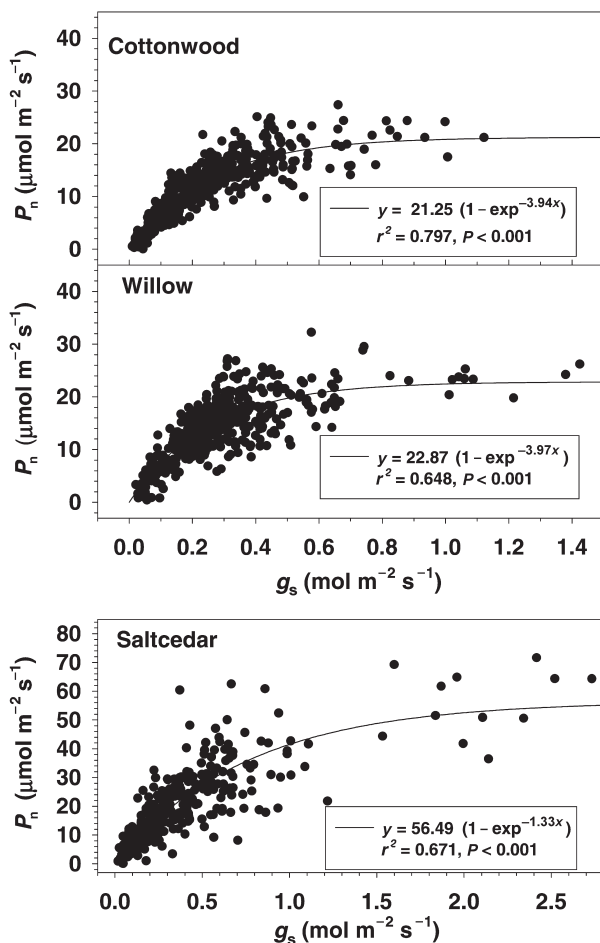


Figure 1. Relationship between net photosynthesis ( $P_n$ ) and stomatal conductance ( $g_s$ ) for Fremont cottonwood, Goodding willow, and saltcedar. The relationship was best described by the nonlinear function  $y = a(1 - \exp^{-bx})$ . Note the different  $x$  and  $y$  axes scales for cottonwood and willow compared with saltcedar.

Table 3. The amount of total variance ( $r^2$ ) in stomatal conductance ( $g_s$ ) and net photosynthetic rate ( $P_n$ ) of Fremont cottonwood, Goodding willow, and saltcedar explained by leaf temperature ( $T_{\text{leaf}}$ ), leaf-to-air vapor pressure deficit (VPD), shoot water potential at the time of gas exchange measurements ( $\Psi_{\text{md}}$ ), and predawn shoot water potential ( $\Psi_{\text{pd}}$ ) in forward multiple linear regressions. Abbreviations:  $n$  = number of measurements per species, and ns = variable was not entered into the regression at  $P = 0.05$ .

Variable	Cottonwood		Willow		Saltcedar	
	$g_s$	$P_n$	$g_s$	$P_n$	$g_s$	$P_n$
$n$	385	385	391	391	293	293
$T_{\text{leaf}}$	ns	ns	0.018	0.006	0.037	ns
VPD	0.023	0.059	0.251	0.407	0.126	0.093
$\Psi_{\text{md}}$	ns	ns	ns	0.007	0.087	0.171
$\Psi_{\text{pd}}$	0.010	0.018	0.018	0.058	ns	ns
Total $r^2$	0.033	0.077	0.287	0.478	0.250	0.274

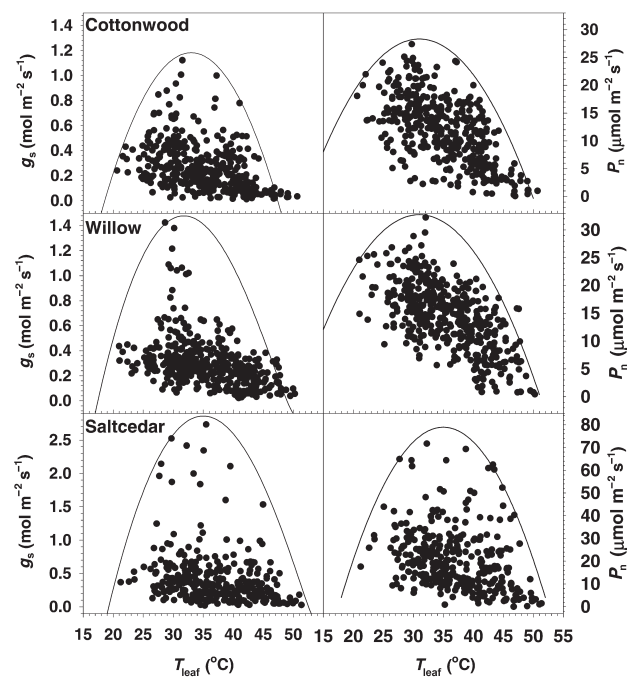


Figure 2. Boundary-line analysis of stomatal conductance ( $g_s$ ) and net photosynthesis ( $P_n$ ) as a function of leaf temperature ( $T_{\text{leaf}}$ ) for Fremont cottonwood, Goodding willow and saltcedar. The boundary line curves were fitted by the method described by Jarvis (1976). Note the different y-axis scale for cottonwood and willow compared with saltcedar.

species, gas exchange of saltcedar was most tolerant of low  $\Psi_{\text{pd}}$ , with a  $\Psi_{\text{pd}}$  threshold of  $\approx -1.2$  to  $-1.5$  MPa.

## Discussion

Values of  $g_s$  and  $P_n$  measured in our study were considerably higher than those previously reported for these species, especially for saltcedar (Anderson 1982, Busch and Smith 1995, Cleverly et al. 1997, Smith et al. 1998). This difference might be associated with our use of projected leaf area to calculate  $g_s$  and  $P_n$ . Because saltcedar has needle- or scale-like leaves that are not flat, the use of projected leaf area produces higher estimates of area-based leaf gas exchange measurements for this species than other area measurements. However, our specific leaf area values were similar to those reported by Busch and Smith (1995) for cottonwood and willow, but higher than those reported by Sala et al. (1996) for saltcedar, both of whom used projected leaf area to calculate leaf gas exchange. We note that mean leaf nitrogen concentration was also higher for saltcedar in our study ( $26.4 \text{ g kg}^{-1}$ ) than that reported for saltcedar in other studies ( $20.4 \text{ g kg}^{-1}$ , Busch and Smith 1995;  $< 15.0 \text{ g kg}^{-1}$ , Cleverly et al. 1997), suggesting a higher capacity for photosynthesis in our saltcedar trees. Furthermore,  $\Psi_{\text{pd}}$  was higher for all three species in our study than values previously reported for these species growing along the Bill Williams and Colorado Rivers (Busch and Smith 1995), suggesting greater water availability during our study. Be-

Table 4. Optimum leaf temperature ( $T_{\text{leaf}}$ ) ranges and threshold values of leaf-to-air vapor pressure deficit (VPD), xylem water potential at the time of gas exchange measurements ( $\Psi_{\text{md}}$ ), and predawn water potentials ( $\Psi_{\text{pd}}$ ) derived from boundary-line analysis of stomatal conductance ( $g_s$ ) and net photosynthetic rate ( $P_n$ ) of Fremont cottonwood, Goodding willow and saltcedar. There was no apparent  $\Psi_{\text{md}}$  threshold for  $P_n$  of cottonwood.

Variable	Cottonwood		Willow		Saltcedar	
	$g_s$	$P_n$	$g_s$	$P_n$	$g_s$	$P_n$
Optimum $T_{\text{leaf}}$	28–33 °C	28–33 °C	28–33 °C	28–33 °C	33–38 °C	33–38 °C
Threshold VPD (kPa)	$\approx 1.2$	$\approx 1.6$	$\approx 1.2$	$\approx 2.8$	$\approx 2.5$	$\approx 5.0$
Threshold $\Psi_{\text{md}}$ (MPa)	$\approx -1.6$	–	$\approx -1.3$	$\approx -1.6$	$\approx -2.5$	$\approx -2.8$
Threshold $\Psi_{\text{pd}}$ (MPa)	$\approx -0.8$	$\approx -0.8$	$\approx -0.5$	$\approx -0.5$	$\approx -1.2$	$\approx -1.5$

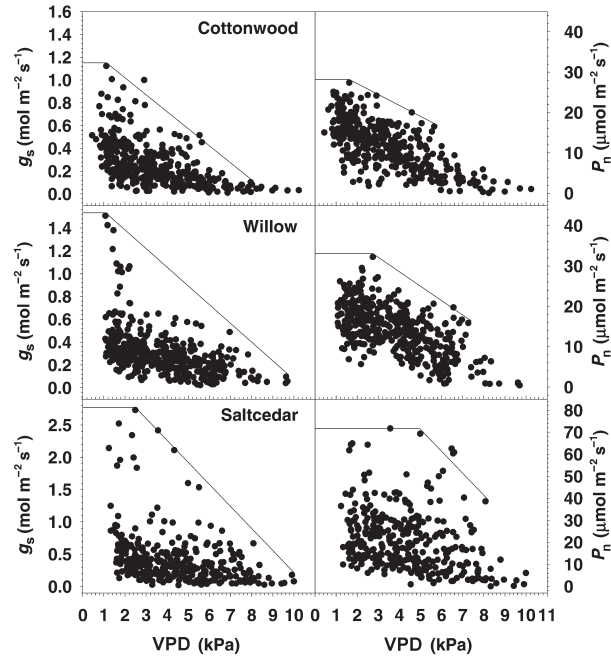


Figure 3. Boundary-line analysis of stomatal conductance ( $g_s$ ) and net photosynthesis ( $P_n$ ) as a function of leaf-to-air vapor pressure deficit (VPD) for Fremont cottonwood, Goodding willow and saltcedar. Note the different y-axis scale for cottonwood and willow compared with saltcedar.

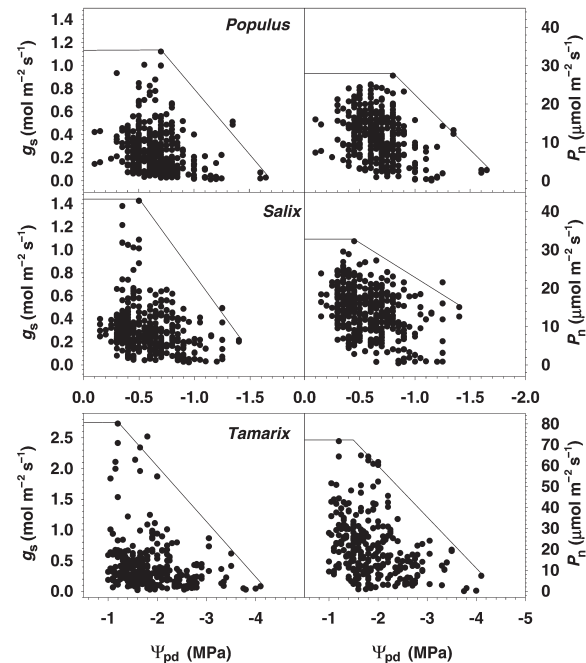


Figure 5. Boundary-line analysis of stomatal conductance ( $g_s$ ) and net photosynthesis ( $P_n$ ) as a function of predawn water potential ( $\Psi_{pd}$ ) for Fremont cottonwood, Goodding willow and saltcedar. Note the different x- and y-axis scales for cottonwood and willow compared with saltcedar.

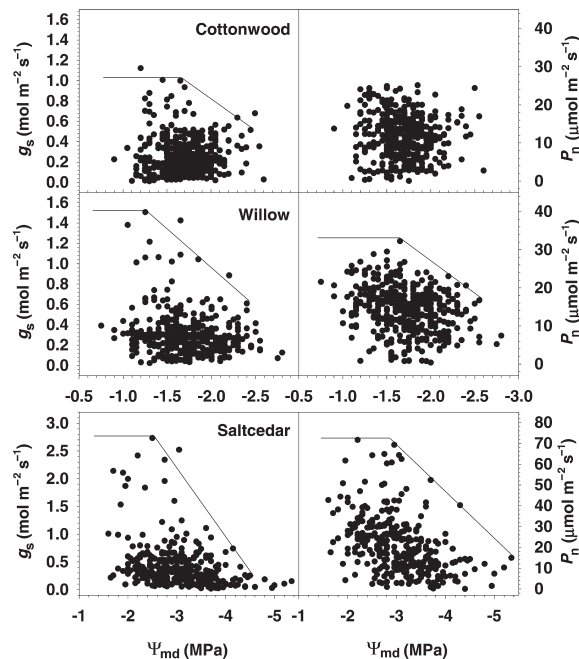


Figure 4. Boundary-line analysis of stomatal conductance ( $g_s$ ) and net photosynthesis ( $P_n$ ) as a function of shoot water potential at the time of  $g_s$  exchange measurements ( $\Psi_{md}$ ) for Fremont cottonwood, Goodding willow and saltcedar. Note that no boundary line could be drawn for  $P_n$  of cottonwood because no boundary was apparent over the range of  $\Psi$  measured. Note the different x- and y-axis scales for cottonwood and willow compared with saltcedar.

cause stomatal behavior of riparian tree species is responsive to soil water deficits (Bond and Kavanagh 1999), it is likely that  $g_s$  would be greater when water is more available. Based on these findings, we conclude that differences in leaf gas exchange rates between our study and others (Anderson 1982, Busch and Smith 1995, Cleverly et al. 1997, Smith et al. 1998) are associated with differences in water or nitrogen availability rather than with the technique used to calculate leaf area.

Gas exchange in the initial linear portion of the hyperbolic response of  $P_n$  to  $g_s$  is RuBP saturated (Farquhar and Sharkey 1982); therefore, increases in  $\text{CO}_2$  concentration in leaf mesophyll with increasing  $g_s$  caused a linear increase in  $P_n$ . However, beyond this linear range,  $P_n$  probably became RuBP-limited and further increases in  $g_s$  had smaller effects on  $P_n$ . Thus, it is likely that initial stomatal closure at high values of  $g_s$  would reduce water loss without affecting  $P_n$ , thereby increasing water-use efficiency. Therefore, we examined the responses of both  $g_s$  and  $P_n$  to environmental variables and shoot  $\Psi$ .

The multiple linear regression model explained less than 10% of the variation in  $g_s$  and  $P_n$  of cottonwood. This suggests either a nonlinear response of leaf gas exchange to some of the independent variables used in the regression, a weak relationship to these variables, or the exclusion of important driving variables from our analysis. Variation in  $g_s$  and  $P_n$  explained by multiple regression was higher for saltcedar (25–27%) and willow (29–48%) than for cottonwood (3–8%). For willow, among the variables examined, VPD explained the most variation in gas exchange, and the effect was stronger for  $P_n$  than

for  $g_s$ . The two variables explaining the most variation in gas exchange of saltcedar were VPD and  $\Psi_{md}$ . However, for both willow and saltcedar, the multiple linear regression models usually explained much less than 50% of the variation in leaf gas exchange. Foster and Smith (1991) also found that multiple linear regression of leaf gas exchange on environmental and plant variables yielded models that explained less than 40% of the variation in their measurements. Techniques for constructing predictive models of leaf gas exchange response to environmental variables include empirical relationships based on nonlinear regression (Jarvis 1976), transformation of the data to create linear responses (Chambers et al. 1985), and theoretical models relating gas exchange and water availability in the soil, leaf and atmosphere (Bond and Kavanagh 1999). We found boundary-line analysis to be a useful technique for comparing leaf gas exchange responses among co-occurring species.

The response of leaf gas exchange to leaf temperature followed the pattern predicted by Jarvis (1976), and was similar for both  $g_s$  and  $P_n$  in all species. The optimum leaf temperature for gas exchange was higher in our study than has been previously reported for saltcedar (23–28 °C, Anderson 1982) and other cottonwood species ( $\approx$  25 °C, Bassman and Zwier 1991). However, trees in these other studies were growing at higher elevations or latitudes, or both, and were probably not exposed to the extreme temperatures that occur at our low-elevation desert sites. Trees growing in areas where temperatures are extremely high throughout the growing season may be more tolerant of high temperatures than trees growing in more moderate climates because of genetic adaptation or physiological acclimation.

Threshold responses of  $g_s$  and  $P_n$  to increasing VPD and decreasing  $\Psi$  have been shown in many tree species (Pezeshki and Hinckley 1982, 1988, Chambers et al. 1985, Foster and Smith 1991, Kolb and Stone 2000), although this response is not always observed in riparian tree species (Foster 1992). We observed apparent threshold responses to increasing VPD and decreasing  $\Psi$  in all three species. Further, the VPD thresholds were lower for  $g_s$  than for  $P_n$  for all species. Stomatal conductances of cottonwood and willow responded similarly to VPD, and the threshold values were similar to those observed in other riparian tree species (Pezeshki and Hinckley 1982, 1988, Foster and Smith 1991). However, reductions in  $P_n$  occurred at a lower VPD in cottonwood than in willow. Busch and Smith (1995) reported that willow had tissue water relations that imparted greater drought tolerance than cottonwood. Saltcedar, which is known to be more drought tolerant than cottonwood and willow (Busch and Smith 1995, Cleverly et al. 1997), had much higher VPD thresholds for  $g_s$  and  $P_n$  than either of the native species. The ability to maintain high leaf gas exchange rates at higher VPDs than native species may impart a competitive advantage to saltcedar over the native species, especially in ephemeral reaches where VPD is generally high (Smith et al. 1991, Horton et al. 2001).

All species showed distinct  $\Psi_{md}$  thresholds below which  $g_s$  was reduced. Willow and saltcedar also showed  $\Psi_{md}$  thresh-

olds below which  $P_n$  was reduced. Stomatal conductance of cottonwood was reduced when  $\Psi_{md}$  fell below  $-1.6$  MPa, which is lower than the  $-1.0$  MPa threshold for stomatal closure reported for plains cottonwood (*Populus deltoides* Bartr. ex Marsh) (Bassman and Zwier 1991), but similar to the thresholds of  $-1.5$  MPa reported for black cottonwood (*Populus trichocarpa* Torr. & Gray) (Sparks and Black 1999) and  $-1.7$  MPa reported for narrow-leaf cottonwood (*Populus angustifolia* James) (Foster and Smith 1991). The  $\Psi_{md}$  threshold for  $g_s$  of willow in our study ( $-1.3$  MPa) was higher than that reported for two montane *Salix* species ( $-1.7$  MPa) (Foster and Smith 1991).

Shoot  $\Psi_{md}$  measured in our study may overestimate xylem tension (Ritchie and Hinckley 1971). However, we note that the shoot  $\Psi_{md}$  thresholds for stomatal closure of both cottonwood ( $-1.6$  MPa) and willow ( $-1.4$  MPa) were near the xylem cavitation thresholds reported for these species growing in similar southwestern desert environments (Pockman et al. 1995). Both cottonwood and willow maintain narrow safety margins above distinct cavitation thresholds. For example, Fremont cottonwood exhibited no loss of xylem hydraulic conductivity due to xylem cavitation at a  $\Psi$  of  $-1.5$  MPa, but was completely cavitated at a  $\Psi$  at or below  $-1.6$  MPa (Pockman et al. 1995). In contrast, saltcedar had a much lower and less distinct xylem cavitation threshold. Pockman and Sperry (2000) reported that xylem of saltcedar became 50% cavitated at a  $\Psi$  of  $-4.5$  MPa and was completely cavitated at a  $\Psi$  at or below  $-7.0$  MPa.

Stomatal responses to water stress may be related to the margin of safety from cavitation, with more responsive stomata occurring in species with narrow safety margins (Blake et al. 1996). Both native species demonstrated stomatal sensitivity and closure when  $\Psi_{md}$  approached or exceeded reported xylem cavitation thresholds. The lower cavitation threshold and the wider margin of safety above the cavitation threshold in saltcedar suggests lower stomatal sensitivity to VPD and  $\Psi_{md}$  compared to cottonwood and willow, a pattern confirmed by our results.

Predawn  $\Psi$  of trees provides an indication of water status in the rooting zone of soil. Goodding willow is relatively shallow rooted ( $< 3.2$  m, Stromberg et al. 1996) and is considered to be an obligate phreatophyte that relies solely on groundwater (Busch et al. 1992). Therefore, we expected willow to be the most sensitive of the three species to changes in soil water availability. Predawn  $\Psi$  of willow decreases with increasing depth to groundwater, suggesting reduced water uptake at deeper groundwater depths (Horton et al. 2001). In this study, we found that gas exchange of willow was reduced when  $\Psi_{pd}$  was  $-0.5$  MPa or below, suggesting that reduced water availability limits leaf gas exchange of this species. Fremont cottonwood is often more deeply rooted than willow ( $< 5.0$  m, Stromberg et al. 1996) and can use both groundwater (Busch et al. 1992) and water from unsaturated soil (Snyder et al. 1998). The lower  $\Psi_{pd}$  threshold ( $-0.8$  MPa) observed for cottonwood suggests lower stomatal sensitivity to soil water deficits in this species relative to willow. Saltcedar is known as a

facultative phreatophyte with the ability to utilize both groundwater and water from unsaturated soil (Busch et al. 1992). Busch and Smith (1995) observed lower osmotic potential in saltcedar relative to native riparian woody species, a characteristic that may enable saltcedar to extract water from unsaturated soil that is unavailable to the native species. The lower  $\Psi_{pd}$  threshold for saltcedar supports this claim and suggests that it has greater tolerance of soil water deficits than the native species.

## Conclusions

Leaf gas exchange was high in all species and the relationship between  $P_n$  and  $g_s$  was hyperbolic, suggesting that initial reductions in  $g_s$  at high  $g_s$  may not inhibit  $P_n$ . Leaf gas exchange rates of willow were higher than those of cottonwood, probably because it tends to grow in areas with shallower groundwater. Willow was somewhat more tolerant of high VPDs than cottonwood, but was less tolerant of low soil water availability. Stomata of cottonwood and willow were very responsive to water stress, showing declines when shoot  $\Psi$  approached the cavitation thresholds reported for these species. Saltcedar had much higher leaf gas exchange rates than the native species and was much more tolerant of both atmospheric and soil water stress than the native species.

Human impacts on alluvial water tables may cause riparian forest decline (Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Mahoney and Rood 1991, 1992, Stromberg 1993, Busch and Smith 1995, Stromberg et al. 1996, Patten 1998). Such alterations often result in seasonal hydrographs being out of phase with spring seed dispersal of native trees, thus inhibiting native tree regeneration while promoting the establishment of saltcedar, which produces seed continuously between April and October (Everitt 1980, Shafroth et al. 1998). As a result, saltcedar has invaded many riparian ecosystems in the southwestern USA, replacing the native forests (Brock 1994). Saltcedar combines many characteristics that make it a successful invader including prolific seed production, rapid growth, greater root allocation, vigorous vegetative reproduction, high transpiration rates and water stress tolerance (Smith et al. 1998). Native cottonwood and willow species are known to be more sensitive to drought-induced water stress than saltcedar (Busch and Smith 1995, Cleverly et al. 1997, Smith et al. 1998).

Our study provides further understanding of the physiological mechanisms that underlie the greater ability of saltcedar to maintain high leaf gas exchange rates under extremely hot, dry conditions relative to Fremont cottonwood and Goodding willow. Specifically, saltcedar leaf gas exchange is less sensitive to high VPD, high temperature and low soil water availability than the native species. These physiological characteristics help explain the widespread success of saltcedar as an invader of riparian ecosystems containing native Fremont cottonwood and Goodding willow in the Sonoran Desert.

## Acknowledgments

The authors thank K. Alstad, D. Bauman, N. Carter, J. Clark, R. Cobb, D. Huffman, J. Kaye, J. Stone and S. Wood for invaluable help in the field. We also thank G. Gamble and V. Little of the Nature Conservancy and N. Gilbertson, B. Raulston and K. Blair of the US Fish and Wildlife Service for help and access to field sites. This research was supported by a Mission Research grant from Northern Arizona University (NAU), an Organized Research grant from NAU and a Forrest Shreve Desert Research Award from the Ecological Society of America. Support for J.L. Horton was provided by the US Environmental Protection Agency STAR Fellowship Program.

## References

- Anderson, J.E. 1982. Factors controlling transpiration and photosynthesis in *Tamarix chinensis* Lour. *Ecology* 63:48–56.
- Bassman, J.H. and J.C. Zwier. 1991. Gas exchange characteristics of *Populus trichocarpa*, *Populus deltoides* and *Populus trichocarpa* × *P. deltoides* clones. *Tree Physiol.* 8:145–159.
- Blake, T.J., J.S. Sperry, T.J. Tschaplinski and S.S. Wang. 1996. Water relations. In *Biology of Populus and its Implications for Management and Conservation*. Eds. R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman and T.M. Hinckley. NRC Research Press, Ottawa, pp 401–422.
- Bond, B.J. and K.L. Kavanagh. 1999. Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. *Tree Physiol.* 19:503–510.
- Brock, J.H. 1994. *Tamarix* spp. (saltcedar), an invasive exotic woody plant in arid and semi-arid riparian habitats in the western USA. In *Ecology and Management of Invasive Riverside Plants*. Eds. L.C. de Waal, L.E. Child, P.M. Wade and J.H. Brock. John Wiley and Sons Ltd., New York, pp 27–44.
- Bryan, K. 1928. Change in plant associations by change in ground water level. *Ecology* 9:474–478.
- Busch, D.E., N.L. Ingraham and S.D. Smith. 1992. Water uptake in woody riparian phreatophytes of the Southwestern United States: a stable isotope study. *Ecol. Appl.* 2:450–459.
- Busch, D.E. and S.D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the Southwestern U.S. *Ecol. Monogr.* 65:347–370.
- Chambers, J.L., T.M. Hinckley, G.S. Cox, C.L. Metcalf and R.G. Aslin. 1985. Boundary-line analysis and models of leaf conductance for four oak–hickory forest species. *For. Sci.* 31:437–450.
- Cleverly, J.R., S.D. Smith, A. Sala and D.A. Devitt. 1997. Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: the role of drought. *Oecologia* 111:12–18.
- Dawson, T.E. and J.R. Ehleringer. 1991. Streamside trees that do not use stream water. *Nature* 350:335–337.
- Everitt, B.L. 1980. Ecology of saltcedar—a plea for research. *Environ. Geol.* 3:77–84.
- Farquhar, G.D. and T.D. Sharkey. 1982. Stomatal conductance and photosynthesis. *Annu. Rev. Plant Physiol.* 33:317–345.
- Foster, J.R. 1992. Photosynthesis and water relations of the floodplain tree, Box elder (*Acer negundo*). *Tree Physiol.* 11:133–149.
- Foster, J.R. and W.K. Smith. 1991. Stomatal conductance patterns and environment in high elevation phreatophytes of Wyoming. *Can. J. Bot.* 69:647–655.
- Gower, S.T., P.B. Reich and Y. Son. 1993. Canopy dynamics and aboveground production of five tree species with different leaf longevities. *Tree Physiol.* 12:327–345.

- Horton, J.L., T.E. Kolb and S.C. Hart. 2001. Tree physiological response to ground water depth: influence of species and river flow regulation. *Ecol. Appl.* In press.
- Jarvis, P.G. 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Phil. Trans. Royal Soc. London B.* 273:593–610.
- Jenkins, M.E. 1989. Surface and groundwater assessments supporting instream flow protection at the Hassayampa River Preserve, Wickenburg, Arizona. *In Proc. Symp. Headwaters Hydrology.* Eds. W. W. Woessner and D.P. Pots. American Water Resources Assoc., Bethesda, MD, pp 307–316.
- Kolb, T.E., S.C. Hart and R. Amundson. 1997. Box elder water sources and physiology at perennial and ephemeral stream sites in Arizona. *Tree Physiol.* 17:151–160.
- Kolb, T.E. and J.E. Stone. 2000. Differences in leaf gas exchange and water relations among species and tree sizes in an Arizona pine–oak forest. *Tree Physiol.* 20:1–12.
- Mahoney, J.M. and S.B. Rood. 1991. A device for studying the influence of declining water table on poplar growth and survival. *Tree Physiol.* 8:305–314.
- Mahoney, J.M. and S.B. Rood. 1992. Response of a hybrid poplar to water table decline in different substrates. *For. Ecol. Manage.* 54:141–156.
- Mahoney, J.M. and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. *Wetlands* 18:634–645.
- Meng, F.R. and P.A. Arp. 1993. Net photosynthesis and stomatal conductance of red spruce twigs before and after detachment. *Can. J. For. Res.* 23:716–721.
- Patten, D.T. 1998. Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* 18:498–512.
- Pezeshki, S.R. and T.M. Hinckley. 1982. The stomatal response of red alder and black cottonwood to changing water status. *Can. J. For. Res.* 12:761–771.
- Pezeshki, S.R. and T.M. Hinckley. 1988. Water relations characteristics of *Alnus rubra* and *Populus trichocarpa*: responses to field drought. *Can. J. For. Res.* 18:1159–1166.
- Pockman, W.T. and J.S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *Am. J. Bot.* 87:1287–1299.
- Pockman, W.T., Sperry J.S. and J.W. O’Leary. 1995. Sustained and significant negative water pressure in xylem. *Nature* 378:715–716.
- Ritchie, G.A. and T.M. Hinckley. 1971. Evidence for error in pressure bomb estimates of stem xylem potentials. *Ecology* 52:534–536.
- Rood, S.B. and S. Heinze-Milne. 1989. Abrupt downstream forest decline following river damming in southern Alberta, Canada. *Can. J. Bot.* 67:1744–1749.
- Rood, S.B. and J.M. Mahoney. 1990. The collapse of riparian poplar forests downstream from dams on the western prairies: probable causes and prospects for mitigation. *Environ. Manage.* 14: 451–464.
- Sala, A., S.D. Smith and D.A. Devitt. 1996. Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave Desert floodplain. *Ecol. Applic.* 6:888–898.
- Scott, M.L., P.B. Shafroth and G.T. Auble. 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environ. Manage.* 23:347–358.
- Shafroth, P.B., G.T. Auble, J.C. Stromberg and D.T. Patten. 1998. Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands* 18:577–590.
- Smith, S.D., A.B. Wellington, J.L. Nachlinger and C.A. Fox. 1991. Functional responses of riparian vegetation to streamflow diversion in the eastern Sierra Nevada. *Ecol. Applic.* 1:89–97.
- Smith, S.D., D.A. Devitt, A. Sala, J.R. Cleverly and D.E. Busch. 1998. Water relations of riparian plants from warm desert regions. *Wetlands* 18:687–696.
- Snyder, K.A., D.G. Williams and V.L. Gempko. 1998. Water source determination in cottonwood/willow and mesquite forests on the San Pedro River in Arizona. *In Proc. Special Symp. Hydrology.* Eds. E.F. Wood, A.G. Chebouni, D.C. Goodrich, D.J. Seo and J.R. Zimmerman. American Meteorological Society, Boston, MA, pp 185–188.
- Sparks, J.P. and R.A. Black. 1999. Regulation of water loss in populations of *Populus trichocarpa*: the role of stomatal control in preventing xylem cavitation. 1999. *Tree Physiol.* 19:453–459.
- Stromberg, J.C. 1993. Fremont cottonwood–Goodding willow riparian forests: a review of their ecology, threats, and recovery potential. *J. Ariz. Nev. Acad. Sci.* 26:97–110.
- Stromberg, J.C., D.T. Patten and B. Richter. 1991. Flood flows and dynamics of Sonoran riparian forests. *Rivers* 2:221–235.
- Stromberg, J.C., R. Tiller and B. Richter. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. *Ecol. Applic.* 6:113–131.
- Turner, R.M. 1974. Quantitative and historical evidence of vegetation changes along the upper Gila River, Arizona. USGS Professional Paper 655-H, pp 1–20.
- Tyree, M.T. and J.S. Sperry. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiol.* 88:574–580.
- Tyree, M.T., K.J. Kolb, S.B. Rood and S. Patino. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? *Tree Physiol.* 14: 455–466.