

## PHYSIOLOGICAL CONDITION AND WATER SOURCE USE OF SONORAN DESERT RIPARIAN TREES AT THE BILL WILLIAMS RIVER, ARIZONA, USA

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*(Received 30 May 2002; In final form 22 November 2002)*

We investigated the environmental water sources used in mid-summer by three Sonoran Desert phreatophytic riparian tree species, *Salix gooddingii*, *Populus fremontii*, and the exotic *Tamarix* spp., at sites that differed in water table depth. *Salix gooddingii* was most sensitive to water table decline, as evidenced by lower predawn water potentials. Although *P. fremontii* was less sensitive to water table decline than *S. gooddingii*, its leaf gas exchange was the most responsive to atmospheric water stress imposed by high leaf-to-air vapor pressure deficit. *Tamarix* spp. was least sensitive to water table decline and showed no reduction of predawn water potential over the measured range of depth to groundwater. Comparison between D/H of xylem and sampled environmental water sources suggest that *S. gooddingii* and *P. fremontii* used groundwater at most sites with no change in water source as depth to groundwater varied. In contrast, xylem D/H of *Tamarix* spp. was depleted in deuterium compared to groundwater at most sites, suggesting use of water from an unsampled source, or discrimination against deuterium during water uptake. This study highlights the difficulty in sampling all water sources in large-scale studies of riparian ecosystems with complex subsurface hydrogeology.

**Keywords:** Groundwater; Hydrogen 2; Leaf gas exchange; Natural variations; Riparian ecosystem; Sonoran Desert; Trees; Water stress

### INTRODUCTION

Riparian forests in the southwestern United States are important ecosystems that provide many services, such as wildlife habitat, high biodiversity, watershed protection, flood attenuation, improved water quality, and recreational opportunities [1–3]. In the past one hundred years, these valuable ecosystems have been in decline, primarily as a result of human-caused hydrologic changes, including the impoundment and diversion of surface water and the removal of groundwater [3–6]. This decline has included the conversion of native *Populus fremontii*–*Salix gooddingii* forests into thickets dominated by the exotic *Tamarix* spp. [7, 8] (*T. chinensis* and *T. ramosissima*, hereafter referred to as *Tamarix*).

Most woody vegetation of these low elevation southwestern riparian ecosystems is believed to be phreatophytic, relying heavily on alluvial groundwater and the associated capillary fringe

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[6, 9–12]. However, riparian trees can be classified as either obligate (plants that utilize only shallow alluvial groundwater) or facultative phreatophytes (plants that have the ability to utilize sources in addition to alluvial groundwater). *Salix gooddingii* has been listed as an obligate phreatophyte, and *P. fremontii* and *Tamarix* as facultative phreatophytes [13]. These phreatophytes have the ability to use water from the unsaturated soil, although this ability is somewhat less developed in *S. gooddingii* [15–17]. However, one study utilizing stable isotopes of water to determine environmental water sources used by riparian trees suggested that both *S. gooddingii* and *P. fremontii* were obligate phreatophytes that use only groundwater [14]. The exotic, *Tamarix*, utilizes only groundwater when this water source is shallow and relatively constant in depth, but is also able to extract water from unsaturated soil when groundwater is deeper and temporally more variable in depth [14].

Declining water tables and reduced water availability can reduce physiological condition and growth of riparian trees [12, 18–23]. Obligate phreatophytes would be expected to be more sensitive to changes in the alluvial water table than facultative phreatophytes that have the ability to utilize multiple water sources. We have found differences in growth and physiological responses of three important riparian species to declining water tables, with native *P. fremontii* and *S. gooddingii* being more sensitive to reduced water availability than the exotic, *Tamarix* [22–24]. In this study, we relate species' physiological performance to their use of environmental water sources along a groundwater depth gradient at a low elevation Sonoran Desert riparian ecosystem during the peak of the summer drought. Based on the work mentioned previously, we expected *S. gooddingii* to be least able to utilize water sources other than groundwater, and as such, *S. gooddingii* would experience the greatest reductions in water status and leaf gas exchange with increasing depth to groundwater. We anticipated *Tamarix* to be most plastic in water source use, with the ability to switch from groundwater to unsaturated soil water with little physiological consequence. *Populus fremontii* was predicted to have a response intermediate between *S. gooddingii* and *Tamarix*.

## MATERIALS AND METHODS

This study was conducted during the summer of 1997 at the Bill Williams National Wildlife Refuge (34°17'N, 114°13'W) in La Paz County, Arizona, USA (Fig. 1). The Bill Williams River (BWR) is a dam-regulated tributary of the Colorado River that drains into Lake Havasu above Parker Dam. Mean annual air temperature is 21.9 °C and mean annual precipitation is 12.3 cm (National Climatic Data Center, Station Parker 6NE; URL: <http://www.wrcc.dri.edu>), with over half of this occurring as winter precipitation. The BWR is a low elevation site (150–200 m) and occurs at the transition between the Sonoran and Mojave Desert ecosystems along the western edge of the summer monsoonal precipitation pattern (NOAA, Tucson, AZ). Summer growing seasons are very hot and dry.

The BWR drains approximately 13,800 km<sup>2</sup> and stream flow is regulated by the operation of Alamo Dam about 50 km upstream from the confluence with the Colorado River. Large flood events decreased after dam operations began in 1968, however, mean summer (May–September) discharge increased because of flow releases from the dam [25]. River flow on BWR varies between perennial and ephemeral reaches. Perennial flows occur where shallow bedrock raises the alluvial water table to the surface, whereas ephemeral flows occur where bedrock is deeper. Flow exists in the ephemeral reaches in the winter when evapotranspiration is reduced and sometimes in the summer after intense monsoonal thunderstorms. At the BWR National Wildlife Refuge, flows diminish along a losing reach from approximately 0.2 m<sup>3</sup>/s in the upper refuge to 0 m<sup>3</sup>/s in the lower refuge



**Bill Williams River National Wildlife Refuge, Arizona, USA**

FIGURE 1 The study site at the Bill Williams River National Wildlife Refuge in western Arizona, USA. Transects are located on the map and numbered 1 through 7, with transect 1 being in the downstream ephemeral reach and transect 7 in the upstream perennial reach.

above the confluence with the Colorado River at Lake Havasu (USGS stream gauge No. 09426620).

In the winter of 1997, we established seven transects that were perpendicular to the river along this gradient of surface flow along an 8.5 km stretch of the BWR (Fig. 1). The uppermost transect (transect 7) was located in the perennial portion of the reach, and the lowermost transect (transect 1) was located in the ephemeral reach where surface flow was absent during the summer. Six of these transects were placed where existing groundwater monitoring wells had been previously installed, while one additional transect was placed in the ephemeral reach. We installed three sand point piezometers (Cook Screen Technologies, Cincinnati, Ohio, USA) at this new transect and added additional piezometers to the other transects, where needed, for each transect to have two to four piezometers. Depth to groundwater was measured once a month at each piezometer at each transect. Soil volumetric water content was also measured monthly near (<1.5 m) each piezometer at three depths (0–15, 15–30, and 30–60 cm) using time domain reflectometry (TDR model 6050X1 Trase System, Soilmoisture Equipment Corp., Santa Barbara, California, USA). We chose healthy individuals with minimal dieback (<10% of canopy volume) at the beginning of our study from

populations near each well to establish a sampling population ( $n = 15$  to  $20$  at each transect) for each species. We chose healthy individuals initially, so that we could monitor the physiological response to water table declines during the growing season in which we conducted our study without confounding influences of stress from previous growing seasons. We then surveyed the change in elevation between the base of each tree and the base of the closest well using a laser surveying device (Criterion 400, Laser Technologies, Englewood, Colorado, USA) so that depth to groundwater could be estimated for individual trees.

For each sampling period, five individuals were chosen at random from the sampling population of each species at each transect (except for *P. fremontii* at transect 6 where there was only one individual). Physiological data were measured at all transects monthly between June and August 1997, during the same week that depth to groundwater (DGW) was measured. The sampling period spans a time of extreme summer drought (June and July) before the onset of the monsoon precipitation pattern in late July when plant water stress was expected to be greatest. We measured shoot water potential of each individual at predawn, mid-morning (0800–1000 h), and mid-afternoon (1300–1500 h) using a Scholander-type pressure chamber (Model 1000, PMS Instruments, Corvallis, Oregon, USA). Leaf gas exchange of water vapor and carbon dioxide and leaf internal  $[CO_2]$  were measured under full sun using a Li-Cor 6200 portable photosynthesis system (Li-Cor, Lincoln, Nebraska, USA). Leaf gas exchange measurements were conducted in the mid-morning when environmental conditions were generally most favorable for gas exchange and again in the mid-afternoon when environmental conditions may have been limiting to gas exchange, based on diurnal measurements made in late May 1997 (data not shown). Gas exchange measurements were 15 s in duration to minimize changes in water vapor pressure and air temperature in the cuvette during measurement. Data measured at excessively high ( $>400 \mu\text{mol/mol}$ )  $CO_2$  concentrations within the cuvette were removed before data analysis ( $<3\%$  of total measurements).

Gas exchange measurements were made on leaves from portions of the lower to mid-canopy exposed to full sun. Measurements were made *in situ* where possible, and on leaves attached to branches that were cut with pole pruners from portions of the canopy that were otherwise inaccessible. Leaves on detached branches were measured within 30 s after detachment in a light environment similar to that in the canopy. 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), a finding consistent with other studies [26–28]. Leaves used for gas exchange measurements were analyzed for nitrogen content by the Colorado Plateau Stable Isotope Laboratory (CPSIL) at Northern Arizona University, Flagstaff, AZ, USA.

Environmental and xylem water samples were collected in July for stable isotope analysis. July was chosen because it is a time of potentially severe water stress before the onset of the monsoon precipitation pattern and drought-induced cavitation was observed in some individuals during this sampling period. Suberized branch segments were collected from each sample tree prior to dawn and stored in glass vials sealed with parafilm. Groundwater was sampled from each well by first pumping three well volumes of water and filling a 20 ml scintillation vial that was then sealed with parafilm. Stream water, if present, was sampled from a well-mixed portion of the stream at each transect and stored in a similar manner. Soil was collected from a region near each well at three depths (0–15, 15–30, and 30–60 cm) and stored in 0.95 L glass canning jars. Xylem samples were frozen and soil samples were kept at  $4^\circ\text{C}$  until the water was extracted using cryogenic vacuum distillation [29]. Once extracted, water samples were stored at  $4^\circ\text{C}$  until prepped for stable hydrogen isotope analysis using the zinc reduction method with  $2 \mu\text{l}$  of water [30]. Hydrogen gas was then analyzed on a Finnegan Delta Plus isotope ratio mass spectrometer at CPSIL. The ratio of

deuterium to hydrogen in each sample was expressed relative to the Standard Mean Ocean Water (SMOW) standard as follows:

$$\delta D = \left( \frac{D/H_{\text{sample}}}{D/H_{\text{standard}}} \right) * 1000\text{‰} \quad (1)$$

In August 1997, leaf samples were collected from a subset of individuals of all species at transects representing shallow, intermediate, and deep groundwater ( $n = 15$  per species). These samples were analyzed for carbon isotope ratios ( $\delta^{13}\text{C}$ ) at the Stable Isotope Ratio Facility for Ecological Research at the University of Utah, Salt Lake City, Utah, USA. Carbon isotope ratios were calculated relative to the Pee Dee Belemnite standard and were converted to carbon isotope discrimination ( $\Delta$ ) using the following Eq. (31):

$$\Delta = \frac{\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}}}{1 + \delta^{13}\text{C}_{\text{plant}}} \quad \text{assuming } \delta^{13}\text{C}_{\text{air}} = -8.0\text{‰} \quad (2)$$

Discrimination was then used to calculate integrated internal  $\text{CO}_2$  concentration ( $C_i$ ) for each species using the following Eq. (31):

$$C_i = (\Delta - a) * \frac{C_a}{b - a} \quad (3)$$

where  $C_i$  = internal [ $\text{CO}_2$ ]

$C_a$  = ambient [ $\text{CO}_2$ ] assumed to be  $365 \mu\text{mol/mol}$

$a = 4.4$  (discrimination due to diffusion through stomatal pore)

$b = 27$  (discrimination by RUBISCO)

Leaf and shoot physiological characteristics, water source use, and leaf carbon isotope discrimination were related to DGW using scatter plots, regression techniques, and analysis of variance. Statistical analyses were performed with SAS Version 8e (SAS Institute, Cary, NC, USA). Only three transects were sampled for leaf gas exchange in August 1997 due to the occurrence of monsoonal thunderstorms that prevented sampling on some days.

## RESULTS AND DISCUSSION

### Environmental Conditions

Annual precipitation in 1997 at the Bill Williams River (BWR) was near the long-term (1893 to 1998) average (13.1 and 12.3 cm, respectively), although precipitation during our study period (May–August) was lower than average (Tab. I). Mean annual temperature was higher than the long-term average (23.2 and 21.9 °C respectively), although mean temperature for June, July, and August was similar to the long-term average during our study (Tab. I). Discharge from Alamo Dam, as assessed by stream flow just below the dam, was relatively constant during our study. However, stream flow at our middle transect decreased to  $0.00 \text{ m}^3/\text{s}$ , with the largest decrease coming between June and July (Tab. I). Depth to groundwater in the ephemeral reach followed a similar pattern and decreased throughout the summer, with the greatest drop coming between June and July (Fig. 2). The lowest transect was

TABLE I Climatic and Hydrologic Data for the Bill Williams River, Arizona, USA.

Month	1997 Mean dam streamflow* (m <sup>3</sup> /s)	1997 Mean streamflow <sup>†</sup> (m <sup>3</sup> /s)	Mean monthly temp. <sup>‡</sup> (°C)		Monthly precipitation <sup>‡</sup> (cm)	
			1997	Long-term	1997	Long-term
May	0.49	0.14	29.2	25.3	0	0.18
June	0.52	0.10	29.5	30.1	0	0.08
July	0.50	0.03	32.3	33.8	0.38	0.84
August	0.49	0.00	34.1	33.1	0.64	1.57

\*Data from United States Geological Survey (USGS) gauging station No. 09426000 just below Alamo Dam.

<sup>†</sup>Data from USGS gauging station No. 09426620 at Transect 4 in the Bill Williams River National Wildlife Refuge.

<sup>‡</sup>Data from National Climatic Data Center, Station Parker 6NE; long-term represents 105 years of record.

likely influenced by the impoundment of Lake Havasu at the confluence of the Bill Williams and Colorado Rivers, thus it had shallower groundwater than the next transect, which was located ~0.5 km upstream.

### Water Relations and Leaf Gas Exchange

*Salix gooddingii* is generally known as an obligate phreatophyte that is relatively shallow rooted (0.1 to 3.2 m) [5, 13]. In June, there was no relationship between predawn water potential ( $\Psi_{pd}$ ) and depth to groundwater (DGW), suggesting that roots of *Salix* remained in contact with the alluvial water table over the range of DGW observed in this month (Fig. 3, Row A). However, the substantial drop in groundwater in the ephemeral reach between June and July reduced water availability to *S. gooddingii* trees at deeper water table depths in July and August, as evidenced by decreasing  $\Psi_{pd}$  with increasing DGW (Fig. 3). Mid-morning and mid-afternoon  $\Psi$  of *S. gooddingii* were unrelated to DGW, except for the morning in

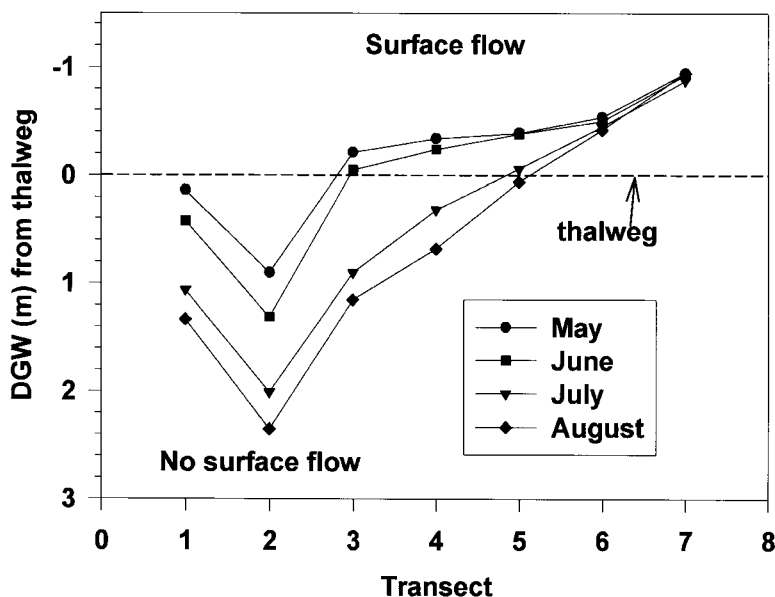


FIGURE 2 Depth to groundwater (DGW) in 1997 relative to the stream thalweg at each transect from the well closest to the stream. Points above the thalweg denote areas with surface flow.

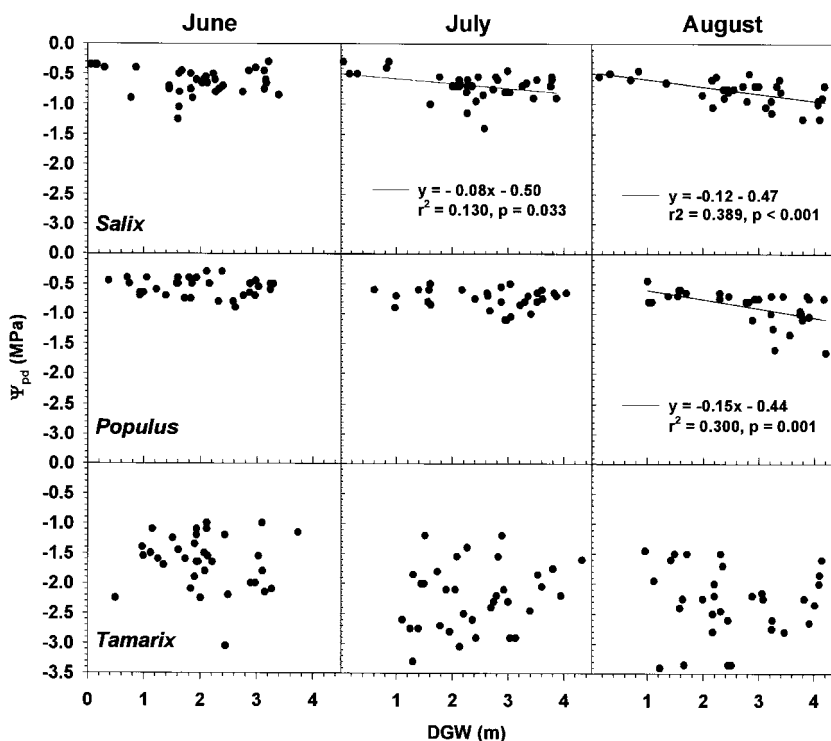


FIGURE 3 Predawn water potential ( $\Psi_{pd}$ ) as a function of depth to groundwater (DGW) for *Salix gooddingii*, *Populus fremontii*, and *Tamarix* spp. for June, July, and August 1997. Equations describe the least squares linear regression model relating  $\Psi_{pd}$  to DGW. All others were not significant ( $p < 0.05$ ).

July ( $y = -0.13x - 1.32$ ,  $r^2 = 0.302$ ,  $p = 0.001$ ). Regression analysis showed no relationship between stomatal conductance ( $g_s$ ) or net photosynthesis ( $P_n$ ) and DGW in June, although morning  $C_i$  decreased with increasing DGW ( $y = -11.7x + 312.6$ ,  $r^2 = 0.115$ ,  $p = 0.046$ ). In July, morning  $g_s$  and  $C_i$  both decreased with increasing DGW, but there was no corresponding reduction in  $P_n$  ( $g_s$ :  $y = -0.8x + 0.51$ ,  $r^2 = 0.368$ ,  $p < 0.001$ ,  $C_i$ :  $y = -9.2x + 281.7$ ,  $r^2 = 0.129$ ,  $p = 0.034$ ). It is likely that the initial reductions in  $g_s$  did not limit  $P_n$  because the photosynthetic apparatus was saturated at the high  $g_s$  rates measured in this study [22, 24]. The lack of relationship between integrated  $C_i$  estimated from leaf carbon isotope discrimination and DGW (Fig. 4) also suggests a lack of stomatal limitation on photosynthesis with increasing DGW. There were no significant relationships between any gas exchange parameter and DGW in August, however, care should be taken interpreting these results, as monsoonal thunderstorms prevented sampling on many dates and sample size was much lower in August than in previous months ( $n = 15$  in August versus 35 in other months).

*Populus fremontii* is known to be more deeply rooted (0.1 to 5.1 m) than *S. gooddingii* [5, 13]. There was no relationship between  $\Psi_{pd}$  and DGW for *P. fremontii* until August (Fig. 3), suggesting that *P. fremontii* trees maintained root contact with the alluvial water table and capillary fringe except for those at the deepest groundwater sites in August. Neither morning nor afternoon  $\Psi$  were correlated with DGW for any month (data not shown). Morning  $g_s$ ,  $P_n$ , and  $C_i$  of *P. fremontii* decreased with increasing DGW in June ( $g_s$ :  $y = -0.11x + 0.59$ ,  $r^2 = 0.282$ ,  $p = 0.002$ ,  $P_n$ :  $y = -2.1x + 19.8$ ,  $r^2 = 0.146$ ,  $p = -0.031$ ,  $C_i$ :  $y = -29.8x + 350.1$ ,  $r^2 = 0.167$ ,  $p = 0.021$ ), while there were no relationships

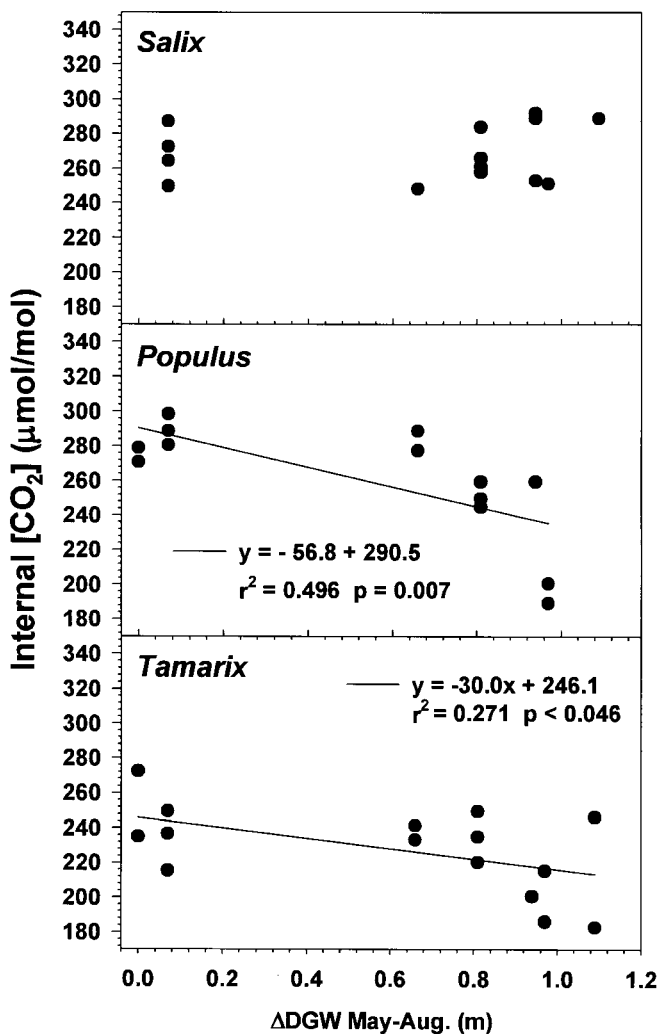


FIGURE 4 Integrated internal leaf  $[CO_2]$  as determined from leaf carbon isotope analysis [Eq. (3)] related to the change in depth to groundwater ( $\Delta DGW$ ) between May and August for *Salix gooddingii* (mean =  $269.1 \pm 4.1 \mu\text{mol/mol}$ ), *Populus fremontii* (mean =  $260.5 \pm 9.2 \mu\text{mol/mol}$ ), and *Tamarix* spp. (mean =  $228.1 \pm 6.4 \mu\text{mol/mol}$ ). Least squares linear regression equations relating internal  $[CO_2]$  to  $\Delta DGW$  are shown where they are statistically significant ( $P < 0.05$ ).

in the afternoon. The lack of an apparent decrease in water availability, as determined by  $\Psi_{pd}$ , suggest that gas exchange of *P. fremontii* responded to some other stress. For instance, atmospheric water stress caused by very high leaf-to-air vapor pressure deficit (VPD) at the ephemeral sites (data not shown) in the morning were above the threshold reported to induce partial stomatal closure in this species [24]. By afternoon, rising temperatures had increased VPD at all transects above this threshold (data not shown), thus there was no relationship between gas exchange and DGW in the afternoon. In July, both  $g_s$  and  $P_n$  decreased with increasing DGW in the morning and afternoon ( $g_s$  morning:  $y = -0.12x + 0.54$ ,  $r^2 = 0.440$ ,  $p < 0.001$ ,  $g_s$  afternoon:  $y = -0.06x + 0.28$ ,  $r^2 = 0.234$ ,  $p = 0.007$ ,  $P_n$  morning:  $y = -3.9x + 22.0$ ,  $r^2 = 0.347$ ,  $p = 0.001$ ,  $P_n$  afternoon:  $y = -2.3x + 11.4$ ,  $r^2 = 0.279$ ,  $p = 0.003$ ), although the slopes of these relationships were lower in the afternoon. Again,

there was no apparent reduction in water availability with increasing DGW in July, suggesting that reductions in leaf gas exchange were likely due to atmospheric water stress caused by high VPD. The large drop in the alluvial water table in the ephemeral reach may have contributed to lower relative humidity and higher VPD, causing an even greater reduction in leaf gas exchange rates at the ephemeral transects than at the perennial sites [20]. In August, both  $g_s$  and  $P_n$  decreased with increasing DGW in the morning but not in the afternoon ( $g_s$ :  $y = -0.13x + 0.64$ ,  $r^2 = 0.350$ ,  $p = 0.026$ ,  $P_n$ :  $y = -4.4x + 23.2$ ,  $r^2 = 0.503$ ,  $p = 0.003$ ), which was likely the result of both atmospheric water stress and reduced soil water availability (Fig. 2). Again, caution should be used interpreting August results because of the smaller sample size. Integrated  $C_i$  (estimated from leaf carbon isotope analysis) decreased with increasing DGW, reflecting the stomatal limitations placed on photosynthesis in the ephemeral reach (Fig. 4).

Little information is available on the rooting depth of *Tamarix*. Stromberg *et al.* [13] found that mature *Tamarix* occurred at sites with DGW <2.5 m at the San Pedro River in Arizona, although others have found *Tamarix* at sites with much deeper groundwater [6, 22, 23], and *Tamarix* is known to be more drought tolerant than the native species [8, 22–24]. There was no significant relationship between  $\Psi_{pd}$  and DGW for any month (Fig. 3), suggesting no reduction in water availability to *Tamarix* over the range of groundwater measured in this study. June afternoon  $\Psi$  increased with increasing DGW ( $y = 0.3x - 3.5$ ,  $r^2 = 0.155$ ,  $p = 0.026$ ), but there was no relationship between  $\Psi$  and DGW at any other sampling period (data not shown). Leaf gas exchange was unrelated to DGW in any month, except for the June afternoon sampling period where  $g_s$  and  $P_n$  increased and  $C_i$  decreased with increasing DGW ( $g_s$ :  $y = 0.11x + 0.03$ ,  $r^2 = 0.217$ ,  $p = 0.005$ ,  $P_n$ :  $y = 10.6x - 5.8$ ,  $r^2 = 0.281$ ,  $p = 0.001$ ,  $C_i$ :  $y = -28.1x + 307.7$ ,  $r^2 = 0.136$ ,  $p = 0.032$ ). *Tamarix* integrated  $C_i$  was significantly lower than the natives ( $p < 0.01$ ; Fig. 4), suggesting higher water-use efficiency, higher photosynthetic capacity, or both for the exotic. *Tamarix* leaf N concentration was significantly higher than the natives (*S. gooddingii* =  $0.216 \pm 0.052$  mg/g, *P. fremontii* =  $0.184 \pm 0.038$  mg/g, *Tamarix* =  $0.242 \pm 0.060$  mg/g,  $F = 29.8$ ,  $p < 0.0001$ ) hence higher photosynthetic capacity could account for lower integrated  $C_i$  of *Tamarix*. Integrated  $C_i$  of *Tamarix* decreased with increasing DGW, suggesting stomatal limitation to photosynthesis at deeper groundwater depths; however, stomatal limitation was not apparent in the instantaneous gas exchange measurements. The increase in June afternoon photosynthetic rates with increasing DGW could cause internal  $C_i$  to decrease and could be indicative of higher photosynthetic capacity in individuals at deeper groundwater depth; however, leaf N concentration was unrelated to DGW ( $p > 0.05$ ).

### Environmental Water Source Use

Groundwater  $\delta D$  values were consistent with our suspicion that our lowest transect (transect 1) was impacted by the impoundment of Lake Havasu at the confluence of the Bill Williams and Colorado Rivers. The  $\delta D$  value at transect 1 was lower than those at the other transects (Fig. 5) and likely represents a mixing of water from the BWR and the Colorado River, which is typically more depleted ( $\delta D = -107.0 \pm 1.2\text{‰}$ ) [14]. Mean  $\delta D$  values of water from the unsaturated soil were highly variable both spatially and temporally, but were not statistically significant from groundwater (Tab. II) and were not correlated with volumetric water content at any depth (data not shown).

Mean xylem water  $\delta D$  of all species averaged over all transects was more depleted than  $\delta D$  of sampled environmental water sources (Tab. II). There was no relationship between xylem  $\delta D$  and DGW for any species (data not shown), suggesting that there was no shift in water source as water availability decreased. When analyzed by transect, xylem  $\delta D$  of native

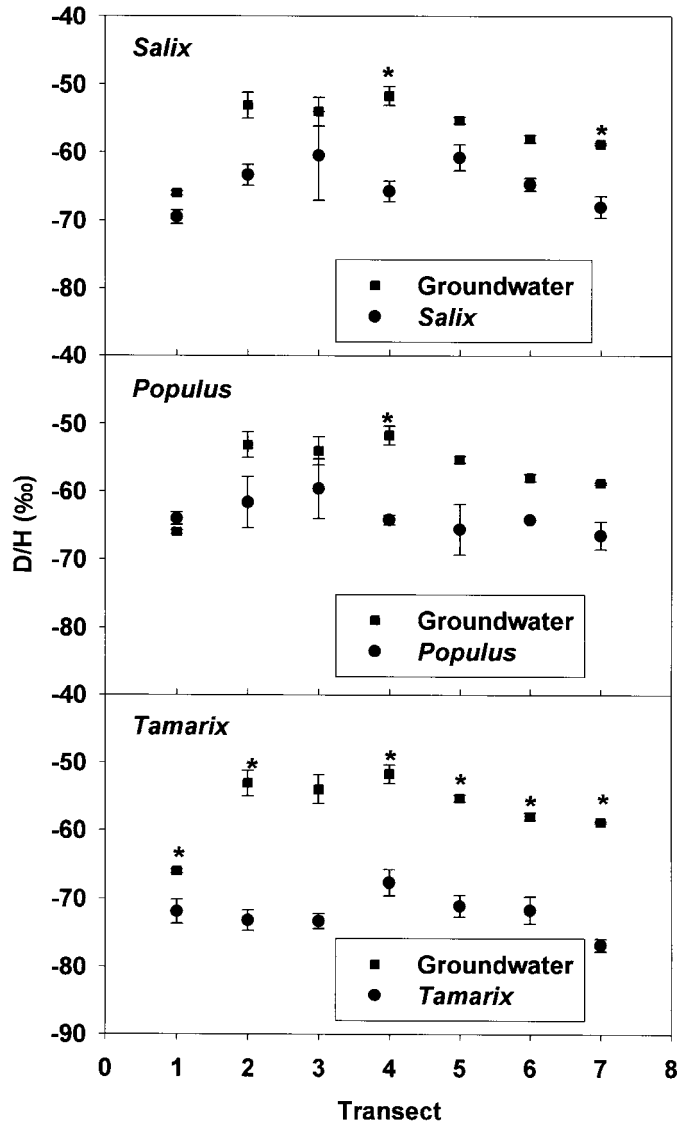


FIGURE 5 *Salix gooddingii*, *Populus fremontii*, and *Tamarix* spp. xylem water (circles) and groundwater (diamonds)  $\delta D$  values. Xylem and groundwater  $\delta D$  values were compared with ANOVA and Tukey's multiple comparison test of means. An asterisk (\*) denotes a significant difference ( $p < 0.05$ ) between xylem water and groundwater.

species generally did not differ significantly from groundwater  $\delta D$  except at transects 4 and 7 for *S. gooddingii* and transect 4 for *P. fremontii* where xylem  $\delta D$  was more depleted than groundwater (Fig. 5). In contrast, *Tamarix* xylem  $\delta D$  was more depleted than groundwater  $\delta D$  at six of the seven transects (Fig. 5).

What can explain the discrepancy between tree xylem and potential source  $\delta D$  values? First, there could have been methodological problems with sampling of groundwater. Water sampled from piezometers may have become evaporatively enriched, causing our samples to be unrepresentative of the alluvial groundwater isotopic signature. Our sampling protocol was designed to avoid this, by pumping three well volumes of water from the well

TABLE II Mean ( $\pm$ st. err.)  $\delta$ D Values for Xylem of Tree Species and Environmental Water Sources over all Transects for July 1997.

<i>Tree species</i>	$\delta$ D( $\lambda$ )	<i>n</i>
<i>Populus</i>	$-63.6 \pm 6.4^a$	30
<i>Salix</i>	$-64.7 \pm 6.6^a$	35
<i>Tamarix</i>	$-72.3 \pm 4.1^b$	34
<i>Environmental sources</i>		
Soil 0–15 cm	$-57.9 \pm 15.9^c$	17
Soil 15–30 cm	$-49.5 \pm 15.7^c$	18
Soil 30–60 cm	$-53.3 \pm 16.1^c$	16
Groundwater	$-57.4 \pm 5.5^c$	18
Stream water	$-56.4 \pm 4.2^c$	3

Note: Different superscript symbols denote significantly different  $\delta$ D values based on analysis of variance and Tukey's multiple comparison test.

before sampling the groundwater. This protocol would likely remove any artificially enriched water and sampled only unenriched alluvial water and, the similarity between groundwater and stream water  $\delta$ D suggests that we successfully sampled alluvial groundwater that was not enriched by extraneous evaporation. If sampled well water was enriched by extraneous evaporation, then we would expect groundwater  $\delta$ D values to be higher than stream water, which they were not. Hence, we do not believe that this potential methodological problem explains the discrepancy between tree xylem and potential source  $\delta$ D values.

Another methodological problem that could explain the results is incomplete cryogenic extractions of xylem water. During cryogenic vacuum distillation, lighter water evaporates and is extracted first. If all water was not completely extracted from the sample, the resulting extracted water would have a lower  $\delta$ D relative to the water originally present in the sample. However, we performed extraction trials to determine the minimum time needed for complete extraction of water from xylem and soil samples, and we exceeded this minimum time for all samples. In addition, if there were problems with the extraction technique, then we would expect water samples from the unsaturated soil to demonstrate the same pattern. Water from unsaturated soil samples was extracted with the same technique and was not depleted in deuterium relative to groundwater. Therefore, the discrepancy between xylem and groundwater is not likely due to extraction problems.

Another explanation for the discrepancy between xylem and groundwater  $\delta$ D values is the hydrogeological complexity of the study site. Many studies using stable isotopes in water to trace environmental water sources used by trees have been on a much smaller spatial scale than our study and have included a few trees growing around a single groundwater source. Our study is more complex, with seven transects along 8.5 km of a river. Each transect ran perpendicular to the river channel and had two to four piezometers arranged along transects up to a half a kilometer long. Although, we established sampling populations near each piezometer, some of the trees were located over 100 m from the nearest piezometer. Furthermore, there was considerable spatial variability in the  $\delta$ D of sampled groundwater, which ranged from  $-49.3$  to  $-66.7\%$ . This variability may have resulted from complex mixing of groundwater from side channels or from water in different alluvial strata, such as clay lenses. Other studies in southwestern riparian ecosystems have shown xylem water more depleted than the measured environmental sources. Snyder and Williams [17] presented data in which  $\delta^{18}\text{O}$  of xylem waters in three riparian tree species, *P. fremontii*, *S. gooddingii*, and *Prosopis velutina*, from the San Pedro River, Arizona were 1.5 to 2% more depleted than groundwater in one of their sampling periods. This difference corresponds to a 9 to 13%

difference in  $\delta D$ , similar to the range of differences observed in our study. Cooper *et al.* [15] also found that 20 year old *P. fremontii* trees at the Yampa River in Colorado had  $\delta D$  values of xylem water 10 to 15‰ lower than groundwater, although this difference was not statistically significant.

Our transect 4 was one of the sites used by Busch *et al.* [14] in a study of riparian plant water sources. Busch *et al.* [14] found no differences among xylem  $\delta D$  of *P. fremontii*, *S. gooddingii*, and *Tamarix*, and xylem  $\delta D$  did not differ from groundwater. In our study, xylem  $\delta D$  was similar among species at this transect and was similar in range to results reported by Busch *et al.* [14]. However,  $\delta D$  values of xylem water of all species was significantly lower than groundwater in our study. Both wells used by Busch *et al.* [14] were on the south side of the river, while we installed an additional well on the north side of the river that may have possibly added more variability to our samples. The similarity between our xylem  $\delta D$  data and that of Busch *et al.* [14] at the same site in different years further reinforces our argument that our extractions were not flawed.

Another possible reason for the discrepancy between xylem and groundwater  $\delta D$  could be that fractionation occurred during water uptake by these species. It has long been assumed that there is no fractionation of hydrogen isotopes during water uptake in plants [32, 33]; however, Lin and Sternberg [34] reported fractionation during water uptake in some coastal halophytes resulting in xylem water being depleted in deuterium (about 10‰) relative to source water. The degree of deuterium depletion in coastal halophytes increased with transpiration and growth rates [34]. The authors hypothesized that deuterium depletion in halophytes occurs because root membranes are less porous than those of terrestrial glycophytes because of functions associated with salt exclusion. This decreased porosity requires dissociation of large aggregates of water molecules before crossing the membrane, especially under high transpiration rates. The hydrogen bonds holding these aggregates together must be broken prior to water uptake and the stronger hydrogen bonds of deuterium-laden water molecules results in deuterium depletion in the xylem water relative to source water. However, the authors found no discrimination against  $^{18}O$  in water during plant uptake by these species.

While this mechanism of deuterium depletion is unlikely in the native *P. fremontii* and *S. gooddingii*, because both are known to be salt sensitive glycophytes, it may explain the lower xylem  $\delta D$  values of the exotic, *Tamarix*, also known as “saltcedar” compared with all measured sources. *Tamarix* is known to tolerate saline soils by active removal of salt from its tissues [35, 36], and it is also known to sustain high transpiration rates at the whole plant level due to the maintenance of high leaf area to sapwood ratio [37]. It is possible that *Tamarix* exhibits similar fractionation against deuterium under high transpiration as that reported for coastal halophytes. This phenomenon should be further explored and, if it occurs, should be taken into account when trying to utilize stable isotopes to identify water sources used by this species. If deuterium depletion occurs in this species during water uptake, then future studies in water source use of desert halophytes should utilize stable isotopes of oxygen instead of hydrogen.

## CONCLUSIONS

The obligate phreatophyte, *S. gooddingii*, experienced decreases in water availability as the water table dropped in the ephemeral reach throughout the summer. Although this decrease in water availability resulted in decreases in stomatal conductance, there appeared to be no stomatal limitation on plant carbon gain. The facultative phreatophyte, *P. fremontii*, was

less sensitive to water table declines than *S. gooddingii*, and experienced decreased water availability only in August. However, leaf gas exchange of *P. fremontii* appears to be more sensitive to atmospheric water stress imposed by high leaf-to-air vapor pressure deficits than *S. gooddingii*. This stress resulted in decreased stomatal conductance and net photosynthesis where groundwater was deep. The exotic *Tamarix* was least sensitive to water table decline and showed no apparent reduction in water availability over the range of DGW in any month of this study. *Tamarix* also had the highest photosynthetic capacity, which contributed to high water-use-efficiency as indicated by leaf  $\delta^{13}\text{C}$ .

There was little evidence of water use from the unsaturated soil by any species during any month of the study. However, there were discrepancies between xylem and groundwater  $\delta\text{D}$  for all species. These discrepancies were rare for *S. gooddingii* and *P. fremontii*, but were more common for *Tamarix*. They likely result from the complexity of subsurface hydrogeology and mixing of multiple groundwater sources that was not adequately sampled by our experimental design. Also, isotopic fractionation during water uptake may explain differences in xylem  $\delta\text{D}$  between the salt-tolerant *Tamarix* and the native species, although this phenomenon needs to be investigated further. Our study highlights the difficulty in sampling all water sources in large-scale studies of riparian ecosystems with complex subsurface hydrogeology.

### Acknowledgements

The authors would like to thank K. Alstad, D. Bauman, N. Carter, J. Clark, R. Cobb, A. DiSalvo, D. Huffman, J. Kaye, J. Roberts, J. Stone, and S. Wood for their invaluable help in the field. We would also like to thank G. Gamble and V. Little of the Nature Conservancy and N. Gilbertson, B. Raulston, and K. Blair of the U.S. Fish and Wildlife Service for their help and access to field sites. Also, C. Cook and M. Wheeler for their help in constructing the vacuum lines needed for preparation of water samples for isotopic analysis. The authors would like to thank two anonymous reviewers and J. Shannon whose comments on an earlier version helped strengthen this manuscript. This research was supported by a Mission Research grant from Northern Arizona University (NAU), an Organized Research grant from NAU, a Forrest Shreve Desert Research Award from the Ecological Society of America, and a Doctoral Dissertation Improvement Grant from the National Science Foundation. Support for J.L. Horton was provided by the US Environmental Protection Agency's STAR Fellowship Program.

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