

Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin

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ABSTRACT

We investigated the physiological and growth responses of native (*Populus fremontii* S. Wats. and *Salix gooddingii* Ball) and exotic (*Tamarix chinensis* Lour.) riparian trees to ground water availability at the free-flowing Hassayampa River, Arizona, during dry (1997) and wet (1998) years. In the drier year, all species experienced considerable water stress, as evidenced by low shoot water potentials, low leaf gas exchange rates and large amounts of canopy dieback. These parameters were significantly related to depth of ground water (DGW) in the native species, but not in *T. chinensis*, in 1997. Canopy dieback was greater in the native species than in *T. chinensis* when ground water was deep in 1997, and dieback increased rapidly at DGW > 2.5–3.0 m for the native species. Analysis of combined data from wet and dry years for *T. chinensis* tentatively suggests a similar physiological sensitivity to water availability and a similar DGW threshold for canopy dieback. In 1998, shoot water potential and leaf gas exchange rates were higher and canopy dieback was lower for all species because of increased water availability. However, *T. chinensis* showed a much larger increase in leaf gas exchange rates in the wet year than the native species. High leaf gas exchange rates, growth when water is abundant, drought tolerance and the maintenance of a viable canopy under dry conditions are characteristics that help explain the ability of *T. chinensis* to thrive in riparian ecosystems in the south-western United States.

Key-words: *Populus fremontii*; *Salix gooddingii*; *Tamarix chinensis*; El Niño southern oscillation; leaf gas exchange; water stress.

Introduction

Riparian ecosystems in the south-western United States are important ecotones between upland and aquatic ecosystems. Riparian areas are highly productive and are valued for wildlife habitat, biodiversity, watershed protection, water quality and recreation (Carothers 1977; Knopf *et al.*

1988; Patten 1998). However, the decline of riparian ecosystems in the south-west in the past 100 years has been due, in part, to impoundments and diversions of surface water and the removal of ground water for human use (Stromberg 1993; Stromberg, Tiller & Richter 1996; Patten 1998). This decline has included the loss of native species and the spread of exotics, such as *Tamarix chinensis* Lour. and related species. (Robinson 1965; Cleverly *et al.* 1997).

In addition to human-caused hydrologic changes, south-western riparian ecosystems are also subject to large intra- and interannual fluctuations in precipitation and streamflow (Smith *et al.* 1998). The El Niño southern oscillation (ENSO) climate pattern is known to have a large influence on precipitation (Andrade & Sellers 1988) and streamflow (Molles & Dahm 1990) in the south-western United States, with increased moisture during El Niño years and drier conditions during La Niña years. Because alluvial ground water dynamics are closely linked to precipitation and high streamflows in some river systems (Rood *et al.* 1995), it is likely that depth of ground water would also be strongly affected by ENSO fluctuations, with shallow ground water occurring during El Niño years and deeper ground water occurring during drier La Niña years.

Riparian ecosystem dynamics are also linked to streamflow. Successful establishment of riparian trees requires high flows in the spring that scour competing vegetation and deposit fresh alluvium, creating safe germination sites (Stromberg, Patten & Richter 1991; Stromberg 1993). Seedling survival is often dependent on high flows and gradual recession of flows, allowing seedling roots to remain in contact with the alluvial water table and associated capillary fringe (Mahoney & Rood 1991, 1992; Horton & Clark 2000). Growth of mature riparian trees in the south-western United States is also influenced by streamflow, with greater growth in years with higher flows (Stromberg & Patten 1990, 1991; Willms *et al.* 1998). However, many riparian trees are phreatophytic, relying heavily on ground water (Bryan 1928; Turner 1974; Dawson & Ehleringer 1991; Busch & Smith 1995; Kolb, Hart & Amundson 1997; Mahoney & Rood 1998; Shafroth *et al.* 1998; Snyder, Williams & Gempko 1998), thus relationships between riparian tree growth and streamflow must also consider tree access to ground water (Stromberg & Patten 1990).

Understanding of the functioning of riparian ecosystems

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is limited by a lack of knowledge of the responses of native and exotic species to interannual variations in water availability, such as variations caused by ENSO. To that end, we investigated the physiological characteristics and growth of two native species, *Populus fremontii* S. Wats. and *Salix gooddingii* Ball, and one invasive exotic, *T. chinensis*, along a gradient of depth of ground water during two years that differed in precipitation. The winter, spring and early summer of 1997 were warmer and drier than average, while the autumn of 1997 and winter and spring of 1998 were much cooler and wetter than average due to the occurrence of a strong El Niño event (Wolter & Timlin 1998). Based on analyses of species composition in low elevation riparian ecosystems by Stromberg *et al.* (1996), we predicted leaf gas exchange rates, water relations and growth to be more sensitive to deeper ground water in dry years in *S. gooddingii* than in *P. fremontii*. *Tamarix chinensis* is known to be very drought-tolerant (Cleverly *et al.* 1997), and was predicted to be least sensitive to deep ground water in dry years. We predicted that the leaf gas exchange rates, water relations and growth of all species would respond favourably to the increased water availability in 1998, and we expected this response to be greatest in *P. fremontii* and *S. gooddingii*, as they are known to be very intolerant of drought (Stromberg 1993).

MATERIALS AND METHODS

Study site

We conducted our research at the Nature Conservancy's Hassayampa River preserve (HRP) near Wickenburg, Arizona. The Hassayampa River is an unregulated river draining approximately 2000 km² and flows intermittently through bedrock canyons and alluvial basins from its headwaters in the Bradshaw Mountains to its confluence with the Gila River. Perennial flow exists in portions of the HRP due to the presence of shallow bedrock. Base flows increase from 0.0 to 0.1 m³ s⁻¹ in the upper reach of the preserve and decrease to 0.0 m³ s⁻¹ in the lower reach (Jenkins 1989). There are populations of *P. fremontii* and *S. gooddingii* throughout the study site, while mature *T. chinensis* only occur at the lower reach, due to the active removal of mature *T. chinensis* in the upper part of the preserve by the Nature Conservancy. Mean annual air temperature at this site is 18.6 °C and mean annual precipitation is 288 mm, with about half of the precipitation occurring in winter and the other half occurring during the summer monsoon season between July and September (National Climatic Data Center, Station Wickenburg, AZ, USA, <http://www.wrcc.dri.edu/>). Typically, little precipitation occurs in May and June.

In February and March of 1997, seven transects were established at the preserve. The upper three transects were in the perennial reach where surface flow was always present, the middle transect was located where surface flow ended in August 1996, and the lower three transects were in the ephemeral reach where surface flow was absent in

the summer of 1996 (J. Horton personal observations). Populations of mature *P. fremontii* and *S. gooddingii* were present at all transects, whereas mature individuals of *T. chinensis* were only present at the lower four transects. In the winter of 1998, we established three additional transects in the ephemeral reach to increase the sample size of *T. chinensis*.

We installed one to three sand-point piezometers (Cook Screen Technologies Inc., Cincinnati, OH, USA) at each transect near populations of all species to monitor depth of ground water (DGW). Ground water was measured at each well once a month during the summer (May–August) of both years. Volumetric water content (θ_v) was measured monthly near each well at depths of 0–15, 15–30 and 30–60 cm using time domain reflectometry (Model 6050 × 1 Trase System; Soilmoisture Equipment Corp., Santa Barbara, CA, USA).

Physiological measurements

In April 1997, we chose trees with minimal canopy dieback (< 10%) from populations near each well to establish our sampling population for each species. The change in elevation between the base of each tree and the base of the closest well was surveyed with a laser surveying device (Criterion 400; Laser Technologies, Englewood, CO, USA) so that DGW could be estimated for individual trees. Physiological data were measured at the seven original transects (one transect per day for 7 d) in June, July and August 1997, and at the seven most downstream transects in June, July and August 1998. Monsoonal thunderstorms prevented sampling on two dates in July 1997 and several dates in August 1997 and August 1998.

At each sampling date (seven per month), five individuals of each species were chosen randomly from our sampling populations at one transect for the physiological measurements. Shoot water potential of terminal twigs (within 5 cm of the apex) was measured before dawn, at mid-morning (0800–1000 h) and at mid-afternoon (1300–1500 h) using a Scholander-type pressure chamber (Model 1000; PMS Instruments, Corvallis, OR, USA). Leaf exchange of water vapour and carbon dioxide was measured at both mid-morning and mid-afternoon using a portable photosynthesis system (Li-Cor 6200; Li-Cor, Lincoln, NE, USA). The timing of physiology measurements was based on diurnal measurements made in May 1997 (data not shown), which indicated that the mid-morning period represents a time when environmental conditions are generally most favourable to gas exchange and the mid-afternoon period represents a time when environmental conditions may limit gas exchange.

Leaf gas exchange was measured at photosynthetic photon flux density (PPFD) > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, an irradiance level known to be saturating for gas exchange in *Tamarix chinensis* (Anderson 1982) and many *Populus* spp. (Pezeshki & Hinckley 1982; Bassman & Zwier 1991). Gas exchange measurements were 15 s or less in duration to minimize changes in water vapour content and temperature

within the cuvette during the measurement. Data measured at excessively high ($> 400 \mu\text{mol mol}^{-1}$) CO_2 concentrations within the cuvette were removed before data analysis ($< 3\%$ of total measurements). Gas exchange measurements were made on leaves from the lower or mid-canopy that were exposed to full sun. Measurements were made on leaves *in situ* where possible, and on twigs detached with pole pruners where leaves were inaccessible. 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 also been used successfully in other studies (Gower, Reich & Son 1993; Meng & Arp 1993; Kolb *et al.* 1997). Foliar nitrogen concentration of leaves sampled for gas exchange was measured using a carbon–nitrogen analyser (Model NC 2100; CE Elantech Inc., Lakewood, NJ, USA).

In August of each year, leaves were collected from five randomly selected individuals of all three species at transects representing shallow, intermediate and deep ground water ($n = 15$ per species). These leaves were sent to the stable isotope ratio facility for ecological research at the University of Utah for carbon isotope analysis. Carbon isotope ratios ($\delta^{13}\text{C}$) were calculated relative to the Pee Dee Belemnite standard and were converted to carbon isotope discrimination (Δ) using the following equation:

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

(Farquhar, Ehleringer & Hubick 1989)

Canopy condition and tree growth

Recent canopy dieback, an integrative measure of plant physiological condition, was measured in late September or early October of each year before the onset of leaf senescence using a technique developed for forest health monitoring (Millers *et al.* 1991; Allen *et al.* 1992; Kolb & McCormick 1993). Two to three observers scored canopy dieback using a 12% class system. Recent canopy dieback was defined as the proportion of the entire crown volume that contained dead branches and twigs < 2.5 cm in diameter (Millers *et al.* 1991).

Annual radial growth in 1997 and 1998 was measured retrospectively for all species using increment cores collected in 1999. For *P. fremontii* and *S. gooddingii*, two increment cores were taken at right angles to each other at breast height (1.3 m). For *T. chinensis*, stem cross-sections were collected from the largest stem of each plant at ground level. All samples were progressively sanded with 100–400 grit sandpaper and annual increments were measured to 0.001 mm under a dissecting microscope. Average annual radial increment was calculated from the two cores per tree for *P. fremontii* and *S. gooddingii*, and from four measurements at right angles on the cross-sections from *T. chinensis*. Branch elongation for 1997 and 1998 was measured

in the winter of 1999 on *P. fremontii* and *S. gooddingii*; however, these measurements were not possible on *T. chinensis* due to the lack of discernible annual bud scars in this species. Branches of *P. fremontii* and *S. gooddingii* were sampled from well-lit portions of the middle to lower canopy, and from two to three different cardinal directions where possible. In 1998, branch elongation was measured from the apex of the twig to the first annual bud scar; in 1997, by measuring between the first and second bud scars (Busch & Smith 1995; Willms *et al.* 1998; Scott, Shafroth & Auble 1999). Mean annual branch increment was calculated for each tree.

Data analysis

Leaf stomatal conductance (g_s), net photosynthetic rate (P_n), leaf Δ , shoot water potential, canopy condition and annual radial and branch increments of each species were related to ground water availability using scatter plots and regression techniques. Similarly, relationships between gas exchange measurements and environmental and physiological variables were examined with scatter plots, non-linear and multiple linear regression techniques. Physiological response patterns were compared among species and between years by comparison of regression coefficients and fixed effects analysis of variance (ANOVA). All analyses were performed using SAS (SAS Institute, Cary, NC, USA) and Statview software (Abacus Concepts Inc., Berkeley, CA, USA). Physiological data are presented for July of both years, when plant stress was greater than in June for all species, as indicated by lower predawn water potentials and greater DGW. August data were not used because the occurrence of monsoonal thunderstorms prevented sampling at some transects in both years. Morning gas exchange measurements are presented because both stomatal conductance (g_s) and net photosynthetic rate (P_n) were higher and less variable in the morning than in the afternoon for all species in both years – the morning measurements are better estimates of maximum daily gas exchange rates. High variability among afternoon gas exchange measurements obscured relationships between leaf gas exchange and DGW. Also, afternoon sampling was curtailed on two dates in July 1997 due to monsoonal thunderstorms, resulting in a very low number of measurements on *T. chinensis*. Any analysis performed on the July 1997 afternoon data for *T. chinensis* would lack power and greatly limit inferences.

RESULTS AND DISCUSSION

Climate and ground water

Annual precipitation in 1997 was near the long-term average, but approximately 40% of this came in late September as a result of tropical storm Nora (Fig. 1). The spring and summer of 1997 were hotter and drier than average (Fig. 1), and the onset of monsoonal precipitation, which usually begins in the first week of July, did not begin until

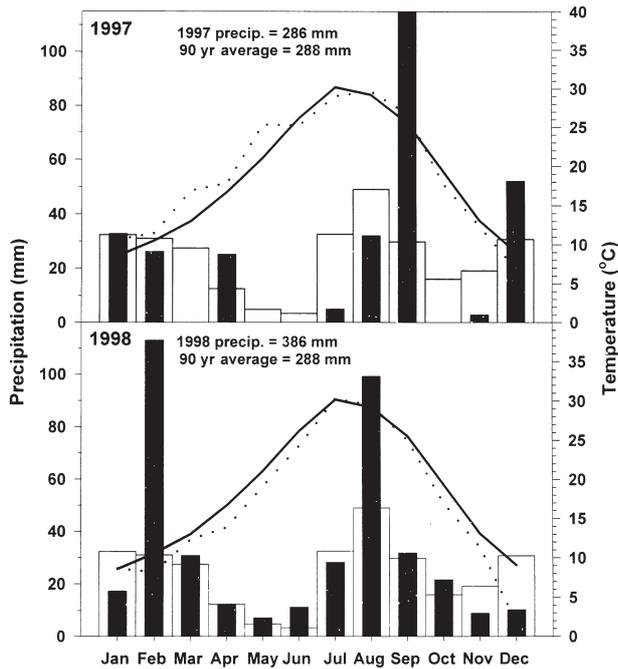


Figure 1. Mean monthly temperature and precipitation (both current year and 90 year mean values) at the Hassayampa River in 1997 and 1998. Open bars represent 90 years' mean monthly precipitation and filled bars represent current year (1997 or 1998) monthly precipitation. Solid lines represent 90 years' mean monthly air temperature and dotted lines represent current year mean monthly air temperature.

late July (National Oceanic and Atmospheric Administration [NOAA], Tucson, AZ, USA, <http://www.wrh.noaa.gov/tucson/monsoon/>). These factors caused extremely dry conditions during the summer of 1997. In contrast, 1998 was influenced by a strong El Niño event and was cooler than average, with above-average precipitation (Fig. 1).

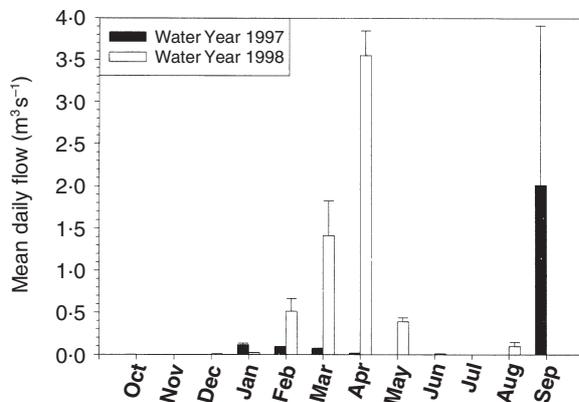


Figure 2. Mean daily streamflow (mean \pm 1 SE) at the lower end of the Hassayampa River preserve (USGS stream gauge #09516500 near Morristown, AZ) during water years 1997 and 1998 (1 October–30 September). Missing bars denote the absence of surface flow.

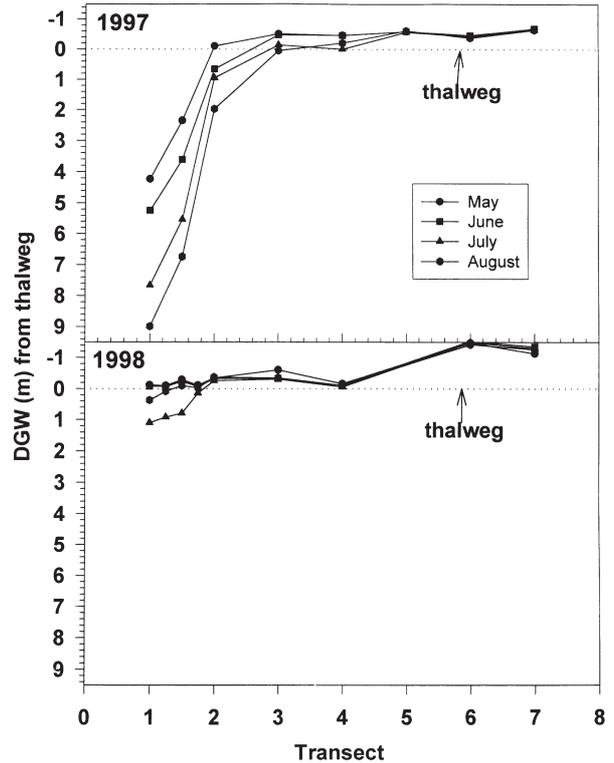


Figure 3. Depth of ground water (DGW) relative to the stream thalweg (the lowest point of the stream channel) at each transect from the well closest to the stream channel between May and August 1997 and 1998 at the Hassayampa River. Points above the thalweg denote areas with surface flow.

Streamflow also differed between years, with lower streamflow in 1997 than in 1998 (Fig. 2). Surface flow was absent from the lower end of the preserve between May and August of 1997, while in 1998, streamflow was present and persisted into June in the ephemeral reach. Streamflow was again present in August 1998 after the onset of monsoonal rains (Fig. 2). Depth of ground water was much greater and more variable in the ephemeral reach during summer 1997 compared to summer 1998 (Fig. 3).

Water relations and gas exchange

Populus fremontii

Populus fremontii is a facultative phreatophyte that typically occurs in areas with a depth of ground water (DGW) of less than 5 m (Busch *et al.* 1992; Busch & Smith 1995; Stromberg *et al.* 1996). Predawn water potential (Ψ_{pd}) of *P. fremontii* decreased significantly with increasing DGW in 1997 when DGW reached \approx 9 m, but not in 1998 when DGW reached \approx 4 m (Fig. 4). Reductions in Ψ_{pd} for *P. fremontii* in 1997 suggest reduced water availability at deeper DGW, assuming equilibrium between Ψ_{pd} and soil Ψ at rooting depth. There were significant reductions in both g_s (Fig. 5) and P_n (Fig. 6) with increasing DGW for *P. fremontii* in

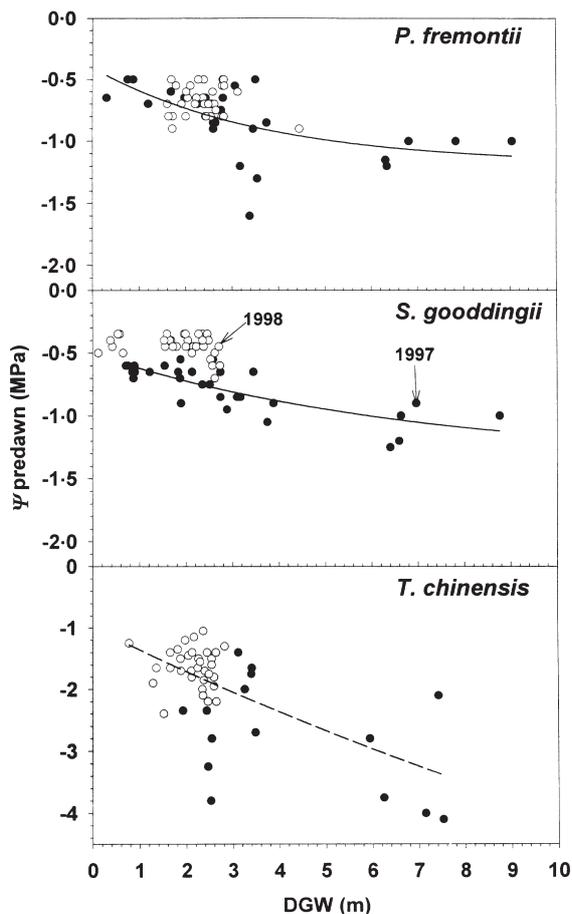


Figure 4. Predawn water potential (Ψ_{predawn}) as a function of depth of ground water (DGW) for *Populus fremontii* (1997 $n = 30$; 1998 $n = 33$), *Salix gooddingii* (1997 $n = 30$; 1998 $n = 32$) and *Tamarix chinensis* (1997 $n = 15$; 1998 $n = 33$) at the Hassayampa River (1997 data: ●; 1998 data: ○). Solid lines represent an exponential decay function of Ψ_{predawn} in relation to DGW for yearly data (*P. fremontii* 1997: $y = -1.21 + 0.74 \exp^{-0.24x}$, $r^2 = 0.315$, $P = 0.006$; *S. gooddingii* 1997: $y = -1.35 + 0.85 \exp^{-0.15x}$, $r^2 = 0.631$, $P < 0.001$). The dashed line for *T. chinensis* represents an exponential decay function of Ψ_{predawn} in relation to DGW for combined 1997 and 1998 data ($y = -8.83 + 7.85 \exp^{-0.05x}$, $r^2 = 0.397$, $P < 0.001$). All other yearly relationships were not significant at $P < 0.05$. Note the different y-axis scale used for *T. chinensis*.

1997, but not in 1998, suggesting that reduced water availability at deeper DGW in 1997 may have led to stomatal closure and reduced carbon gain.

Leaf carbon isotope discrimination (Δ) decreased with increasing DGW for *P. fremontii* in 1997, suggesting stomatal closure and greater water use efficiency (WUE) at deeper ground water depths (Fig. 7). Mean leaf Δ of *P. fremontii* was similar in 1997 (20.75 ± 0.51 ‰) and 1998 (21.33 ± 0.24 ‰) ($P = 0.33$). However, there was no relationship between Δ and DGW in 1998 (Fig. 7).

Net photosynthetic rate of *P. fremontii* was positively correlated with g_s in both years (Fig. 8), but this relationship

was not as strong in 1998. In 1998, high g_s in the morning probably ensured ample CO_2 supply to the leaf mesophyll, thus P_n was likely to be limited more by RuBP regeneration than by internal CO_2 concentration (Farquhar & Sharkey 1982). Multiple regression analysis showed that g_s of *P. fremontii* in both years was negatively correlated with leaf-to-air vapour pressure deficit (VPD) (Fig. 9). This relationship could be a result of stomatal closure to maintain shoot Ψ above xylem cavitation thresholds, which would result in greater VPD as a consequence of higher leaf temperature, or it could be due to stomatal closure in response to high VPD in the ephemeral reach as a consequence of lower relative humidity.

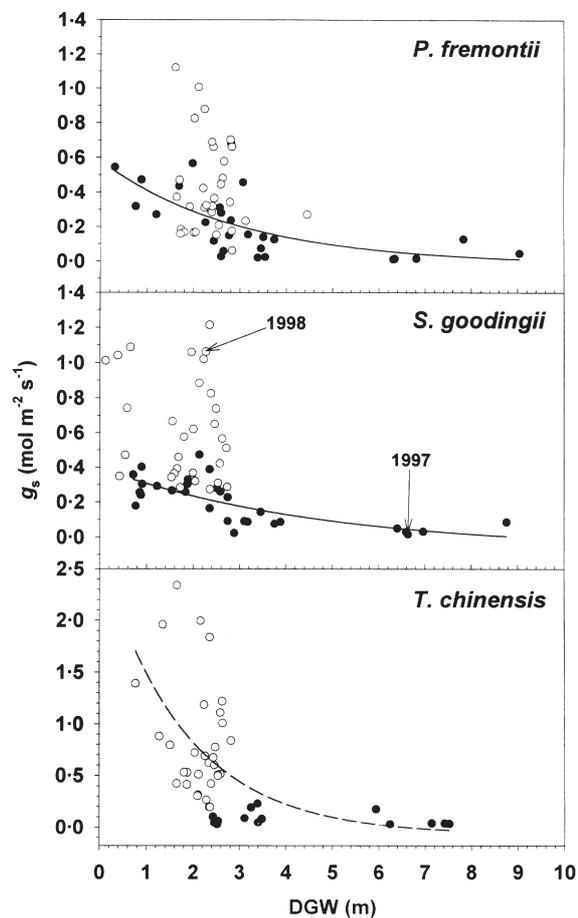


Figure 5. Stomatal conductance (g_s) as a function of depth of ground water (DGW) for *Populus fremontii* (1997 $n = 28$; 1998 $n = 33$), *Salix gooddingii* (1997 $n = 30$; 1998 $n = 32$) and *Tamarix chinensis* (1997 $n = 15$; 1998 $n = 33$) at the Hassayampa River (1997 data: ●; 1998 data: ○). Solid lines represent an exponential decay function of g_s in relation to DGW for yearly data (*P. fremontii* 1997: $y = -0.02 + 0.60 \exp^{-0.34x}$, $r^2 = 0.420$, $P = 0.001$; *S. gooddingii* 1997: $y = -0.07 + 0.46 \exp^{-0.02x}$, $r^2 = 0.536$, $P < 0.001$). The dashed line for *T. chinensis* represents an exponential decay function of g_s in relation to DGW for combined 1997 and 1998 data ($y = -0.07 + 2.73 \exp^{-0.56x}$, $r^2 = 0.273$, $P = 0.001$). All other yearly relationships were not significant at $P < 0.05$. Note the different y-axis scale used for *T. chinensis*.

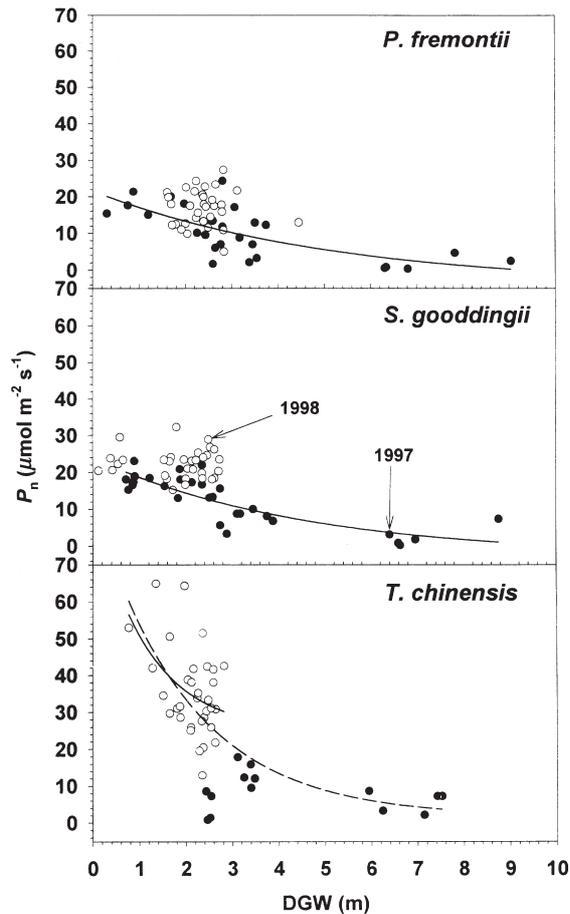


Figure 6. Net photosynthetic rate (P_n) as a function of depth of ground water (DGW) for *Populus fremontii* (1997 $n = 28$; 1998 $n = 33$), *Salix gooddingii* (1997 $n = 30$; 1998 $n = 32$) and *Tamarix chinensis* (1997 $n = 15$; 1998 $n = 33$) at the Hassayampa River (1997 data: ●; 1998 data: ○). Solid lines represent an exponential decay function of P_n in relation to DGW for yearly data (*P. fremontii* 1997: $y = -4.27 + 25.81 \exp^{-0.19x}$, $r^2 = 0.497$, $P < 0.001$; *S. gooddingii* 1997: $y = -2.70 + 26.65 \exp^{-0.22x}$, $r^2 = 0.687$, $P < 0.001$; *T. chinensis* 1998: $y = 24.97 + 62.20 \exp^{-0.88x}$, $r^2 = 0.201$, $P = 0.034$). The dashed line for *T. chinensis* represents an exponential decay function of P_n in relation to DGW for combined 1997 and 1998 data ($y = 1.63 + 85.96 \exp^{-0.50x}$, $r^2 = 0.476$, $P < 0.001$). All other yearly relationships were not significant at $P < 0.05$. Note the different y-axis used for *T. chinensis*.

Salix gooddingii

Salix gooddingii is an obligate phreatophyte that grows at sites with shallower ground water than *P. fremontii*, suggesting more shallow rooting depths (Stromberg *et al.* 1991; Busch *et al.* 1992; Stromberg 1993; Stromberg *et al.* 1996). As with *P. fremontii*, Ψ_{pd} of *S. gooddingii* decreased with increasing DGW in 1997, suggesting reduced water availability at deeper DGW for this species (Fig. 4). There was no significant relationship between Ψ_{pd} and DGW for *S. gooddingii* in 1998 (Fig. 4). Both g_s (Fig. 5) and P_n (Fig. 6)

of *S. gooddingii* were significantly reduced at deep DGW in 1997, but not in 1998 (similar to the responses of *P. fremontii*). Leaf Δ of *S. gooddingii* decreased with increasing DGW in 1997, suggesting stomatal closure and greater WUE at deeper ground water depths (Fig. 7). Mean leaf Δ was similar in 1997 ($20.13 \pm 0.39 \text{ ‰}$) and 1998 ($20.56 \pm 0.20 \text{ ‰}$) ($P = 0.36$). However, as with *P. fremontii*, there was no significant relationship between Δ and DGW in 1998 (Fig. 7).

Net photosynthetic rate of *S. gooddingii* was positively correlated with g_s in 1997, but this relationship was not significant in 1998 (Fig. 8). Again, this is likely to be due to

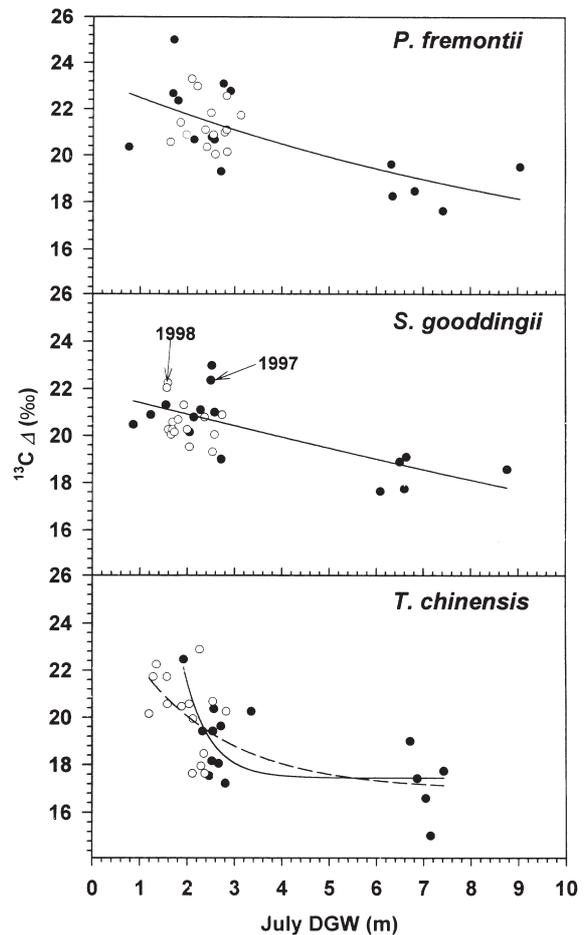


Figure 7. Leaf carbon isotope discrimination (Δ) as a function of depth of ground water (DGW) for *Populus fremontii*, *Salix gooddingii* and *Tamarix chinensis* at the Hassayampa River ($n = 15$ for all; 1997 data: ●; 1998 data: ○). Solid lines represent an exponential decay function of leaf Δ in relation to DGW in 1997 (*P. fremontii* $y = 14.18 + 9.10 \exp^{-0.09x}$, $r^2 = 0.470$, $P = 0.022$; *S. gooddingii*: $y = -2.76 + 24.78 \exp^{-0.02x}$, $r^2 = 0.540$, $P = 0.010$; *T. chinensis*: $y = 17.46 + 167.97 \exp^{-1.86x}$, $r^2 = 0.474$, $P = 0.021$). The dashed line for *T. chinensis* represents an exponential decay function of leaf Δ in relation to DGW for combined 1997 and 1998 data ($y = 16.96 + 8.77 \exp^{-0.52x}$, $r^2 = 0.437$, $P < 0.001$). Relationships between leaf Δ and DGW in 1998 were not significant at $P < 0.05$.

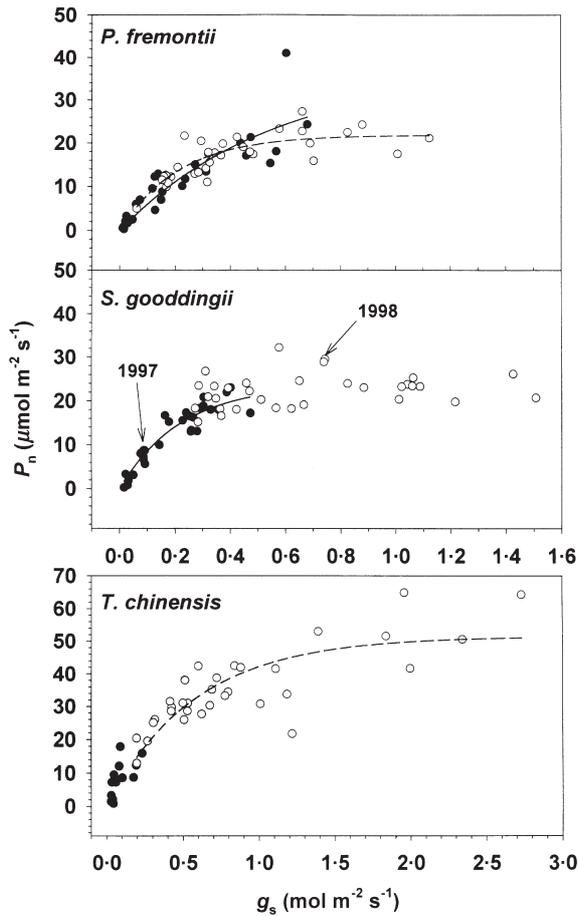


Figure 8. Net photosynthetic rate (P_n) as a function of stomatal conductance (g_s) for *Populus fremontii* (1997 $n = 28$; 1998 $n = 33$), *Salix gooddingii* (1997 $n = 30$; 1998 $n = 32$) and *Tamarix chinensis* (1997 $n = 15$; 1998 $n = 33$) at the Hassayampa River (1997 data: ● and solid lines; 1998 data: ○ and dashed lines). Lines represent the non-linear regression model that best related P_n to g_s (*P. fremontii* 1997: $y = 37.4(1 - \exp^{-1.7x})$, $r^2 = 0.781$, $P < 0.001$, 1998: $y = 21.9(1 - \exp^{-4.7x})$, $r^2 = 0.665$, $P < 0.001$; *S. gooddingii* 1997: $y = 23.7(1 - \exp^{-4.5x})$, $r^2 = 0.898$, $P < 0.001$; *T. chinensis* 1998: $y = 51.5(1 - \exp^{-1.7x})$, $r^2 = 0.602$, $P < 0.001$). All other yearly relationships were not significant at $P < 0.05$. Note the different x- and y-axis scales used for *T. chinensis*.

high g_s in 1998, resulting from greater water availability, which ensured an adequate supply of CO_2 to the mesophyll. Regression analysis showed that in 1997, g_s of *S. gooddingii* was negatively correlated with VPD (Fig. 9), and to a much lesser extent with mid-morning Ψ (Ψ_{mm}) ($r^2 = 0.044$, $P = 0.028$) and θ , 15–30 cm ($r^2 = 0.041$, $P = 0.02$). The negative relationship between g_s and Ψ_{mm} for *S. gooddingii* in 1997 could be due to stomatal closure in response to low Ψ_{mm} . Alternatively, high g_s and transpiration rates might have reduced Ψ_{mm} if water supply to leaves from xylem was less than g_s . Stomatal conductance of some riparian angiosperm trees is sensitive to soil water availability, with g_s increasing when more water is available (Bond & Kavanagh 1999). Therefore, it is likely that the weak nega-

tive relationship between g_s and θ , 15–30 cm is not biologically significant. Stomatal conductance of *S. gooddingii* was also negatively correlated with VPD in 1998 (Fig. 9).

Tamarix chinensis

Tamarix chinensis had lower Ψ_{pd} than either *P. fremontii* or *S. gooddingii* (Table 1). Predawn Ψ of *T. chinensis* was generally lower and more variable in 1997 than in 1998, but unlike the native species, there was no relationship between Ψ_{pd} and DGW in either year for *T. chinensis* (Fig. 4). One explanation for this lack of a relationship in 1997 could be the absence of *T. chinensis* trees at shallow ground water in

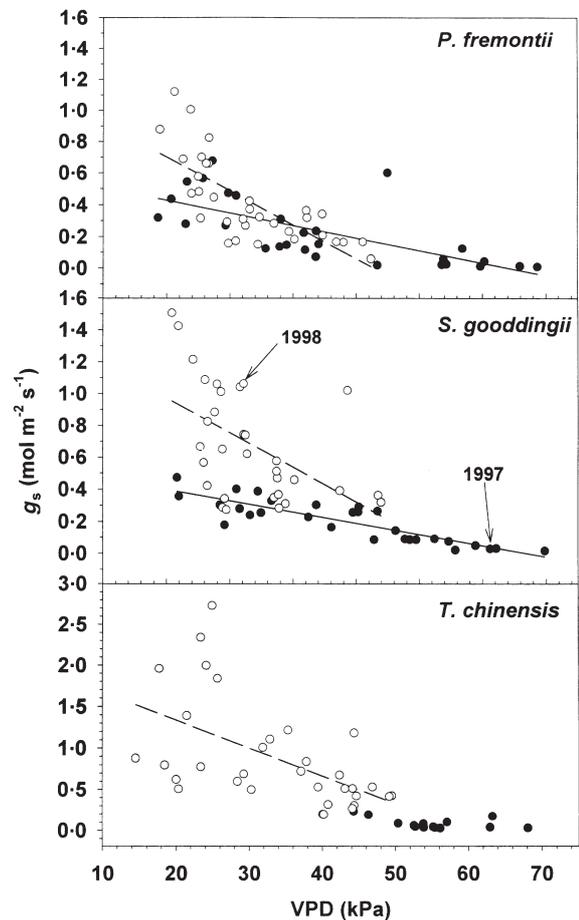


Figure 9. Stomatal conductance (g_s) as a function of leaf-to-air vapour pressure deficit (VPD) for *Populus fremontii* (1997 $n = 28$; 1998 $n = 33$), *Salix gooddingii* (1997 $n = 30$; 1998 $n = 32$) and *Tamarix chinensis* (1997 $n = 15$; 1998 $n = 33$) at the Hassayampa River (1997 data: ● and solid lines; 1998 data: ○ and dashed lines). Lines represent the least squares linear regression model relating P_n to g_s (*P. fremontii* 1997: $y = -0.008x + 0.507$, $r^2 = 0.490$, $P < 0.001$, 1998: $y = -0.021x + 0.916$, $r^2 = 0.545$, $P < 0.001$; *S. gooddingii* 1997: $y = -0.007x + 0.471$, $r^2 = 0.760$, $P < 0.001$, 1998: $y = -0.022x + 1.190$, $r^2 = 0.002$; *T. chinensis* 1998: $y = -0.934x + 2.010$, $r^2 = 0.299$, $P = 0.001$). All other yearly relationships were not significant at $P < 0.05$. Note the different y-axis scale used for *T. chinensis*.

Table 1. Upper: mean (± 1 SE) predawn water potential (Ψ_{pd}), mid-morning water potential (Ψ_{mm}), stomatal conductance (g_s), net photosynthetic rate (P_n) and leaf carbon isotope discrimination (Δ) of three species at the lower end of the Hassayampa River preserve in 1997 and 1998. Lower: analysis of variance results comparing physiological characteristics between years and among species

	Populus fremontii		Salix gooddingii		Tamarix chinensis	
Characteristic	1997	1998	1997	1998	1997	1998
Ψ_{pd} (MPa)	-1.03 ± 0.07	-0.68 ± 0.02	-0.91 ± 0.18	-0.44 ± 0.02	-2.72 ± 0.23	-1.64 ± 0.06
Ψ_{mm} (MPa)	-1.31 ± 0.04	-1.43 ± 0.04	-1.19 ± 0.48	-1.18 ± 0.04	-3.77 ± 0.15	-2.78 ± 0.08
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	0.07 ± 0.02	0.42 ± 0.05	0.11 ± 0.03	0.68 ± 0.06	0.09 ± 0.02	0.88 ± 0.11
P_n ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	4.73 ± 1.01	16.78 ± 0.87	7.11 ± 1.52	22.34 ± 0.68	8.15 ± 1.39	35.37 ± 2.06
Characteristic	Species		Year		Species-year interaction	
Ψ_{pd} (MPa)	$F = 231.1$	$P < 0.0001$	$F = 101.6$	$P < 0.0001$	$F = 13.3$	$P < 0.0001$
Ψ_{md} (MPa)	$F = 478.9$	$P < 0.0001$	$F = 22.7$	$P < 0.0001$	$F = 32.7$	$P < 0.0001$
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	$F = 3.9$	$P = 0.0219$	$F = 66.4$	$P < 0.0001$	$F = 3.3$	$P = 0.0388$
P_n ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	$F = 24.4$	$P < 0.0001$	$F = 194.0$	$P < 0.0001$	$F = 12.6$	$P < 0.0001$

1997. The Nature Conservancy actively removes *T. chinensis* from the upper, perennial portion of the preserve, where all public use areas are located. Thus, there are no mature *T. chinensis* in the perennial reach and DGW experienced by *T. chinensis* at the lower end of the preserve in 1997 was generally > 2.5 m. In 1998, DGW was much shallower at the lower end of the preserve and most individuals of *T. chinensis* experienced DGW < 2.5 m.

Stromberg *et al.* (1996) reported that at the San Pedro River in Arizona, *T. chinensis* occurred over a range of DGW of 0.4–2.5 m, suggesting a potential DGW threshold of 2.5 m. At DGW > 2.5 m, reduced water availability may limit the presence of *T. chinensis*. To examine the response of *T. chinensis* to a larger range of DGW (like that experienced by *P. fremontii* and *S. gooddingii* in 1997), we combined data from 1997 (deep ground water) and 1998 (shallow ground water) using the same sampling population. This combined analysis assumes that differences in response between years are due solely to differences in DGW and not to other factors, such as temperature and relative humidity. When data from both years were combined, *T. chinensis* showed a relationship between Ψ_{pd} and DGW similar to those observed in the native species, although the decrease in Ψ_{pd} with increasing DGW was steeper in *T. chinensis* than in the native species (Fig. 4).

Stomatal conductance (Fig. 5) and P_n (Fig. 6) of *T. chinensis* were much lower in 1997 than in 1998, but there was no relationship between either g_s or P_n and DGW in 1997. In contrast to the native species, there was a significant negative relationship between P_n and DGW in 1998 (Fig. 6). When data from both years were combined, both g_s and P_n of *T. chinensis* decreased with increasing DGW (Figs 5 and 6). The decline in g_s with increasing DGW was also steeper for *T. chinensis* than for *P. fremontii* or *S. gooddingii*. The steep response of g_s in *T. chinensis* to DGW was likely to be due to the much higher rates of g_s in *T. chinensis* relative to the native species when DGW was low. Combining the P_n data from both years strengthened the response (higher r^2) between P_n and DGW (Fig. 6). The P_n

at low DGW for *T. chinensis* was much higher than for *P. fremontii* or *S. gooddingii*; however, P_n declined rapidly in *T. chinensis* as DGW approached 3 m (Fig. 6).

Leaf Δ of *T. chinensis* decreased with increasing DGW in 1997, suggesting stomatal closure and greater WUE at deeper ground water depths, as was observed in the native species (Fig. 7). Mean leaf Δ of *T. chinensis* was significantly lower in 1997 (18.56 ± 0.45 ‰) than in 1998 (20.20 ± 0.41 ‰) ($P = 0.015$), suggesting reduced g_s and greater WUE in 1997 when water availability was reduced. As observed in the native species, there was no significant relationship between Δ of *T. chinensis* and DGW in 1998 (Fig. 7). Leaf Δ of *T. chinensis*, when combined over both years, decreased significantly with increasing DGW (Fig. 7).

Net photosynthesis of *T. chinensis* was positively correlated with g_s in 1998 (Fig. 8). Regression analysis showed that g_s of *T. chinensis* was positively correlated with Ψ_{mm} in 1997 ($r^2 = 0.513$, $P = 0.004$), with reductions in g_s at lower Ψ_{mm} . *Tamarix chinensis* is known to regulate g_s to maintain Ψ_{mm} within a wide safety margin above a xylem cavitation threshold, and loses hydraulic conductivity gradually as Ψ_{mm} decreases (Pockman & Sperry 2000). In contrast, the native species have a very narrow safety margin and very tight stomatal control and lose hydraulic conductivity rapidly as xylem Ψ approaches cavitation thresholds (Pockman, Sperry & O'Leary 1995). Perhaps under the dry conditions in 1997, xylem Ψ was low enough to cause stomatal closure in some individuals of *T. chinensis*. In 1998, g_s of *T. chinensis* was negatively correlated with VPD (Fig. 9).

Canopy condition and tree growth

There was more recent canopy dieback for all species in 1997 than there was in 1998 (Fig. 10). Canopy dieback increased with increasing DGW for *P. fremontii* in 1997, but this relationship varied greatly among individuals. A three-parameter sigmoidal function best described the relationship between 1997 canopy dieback and DGW for *P. fremontii* and suggested a threshold DGW of ≈ 3 m, beyond

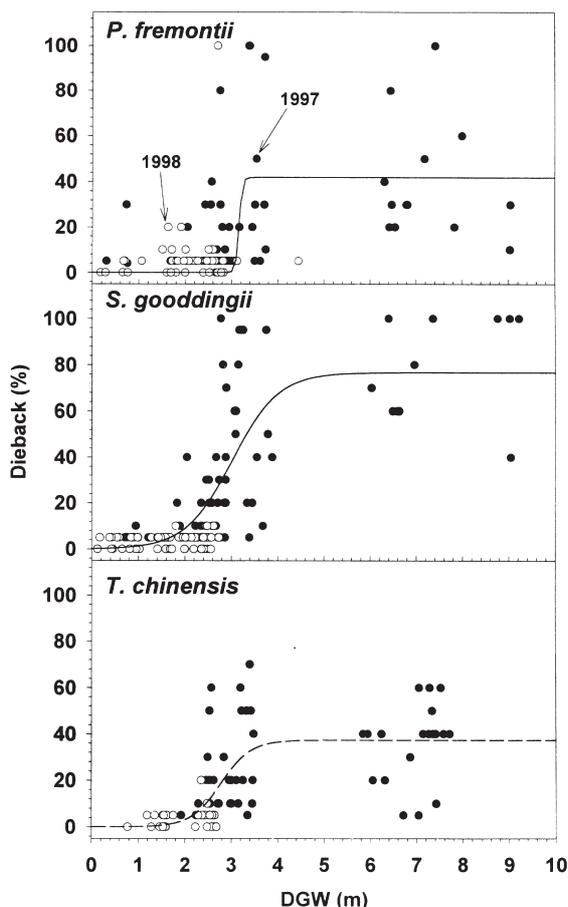


Figure 10. Recent canopy dieback as a function of July depth of ground water (DGW) for *Populus fremontii* (1997 $n = 69$; 1998 $n = 70$), *Salix gooddingii* (1997 $n = 81$; 1998 $n = 74$) and *Tamarix chinensis* (1997 $n = 52$; 1998 $n = 66$) at the Hassayampa River in 1997 and 1998 (1997 data: ●; 1998 data: ○). Solid lines describe a three-parameter sigmoidal function of canopy dieback in relation to DGW for yearly data (*P. fremontii* 1997: $y = 41.89/(1 + \exp^{-(x-3.16)/0.04})$, $r^2 = 0.450$, $P < 0.001$; *S. gooddingii* 1997: $y = 76.69/(1 + \exp^{-(x-3.01)/0.50})$, $r^2 = 0.544$, $P < 0.001$). The dashed line for *T. chinensis* represents a three-parameter sigmoidal function of canopy dieback in relation to DGW for combined 1997 and 1998 data ($y = 37.29/(1 + \exp^{-(x-2.78)/0.32})$, $r^2 = 0.463$, $P < 0.001$). All other yearly relationships were not significant at $P < 0.05$.

which dieback increased (Fig. 10). In 1998, *P. fremontii* experienced little dieback, and the dieback that did occur was unrelated to DGW (Fig. 10). For *S. gooddingii*, 1997 canopy dieback increased with increasing DGW, and this response was similar to that observed in *P. fremontii*, although there was generally more dieback above the DGW threshold of ≈ 2.5 m for this species (Fig. 10). In 1998, there was little dieback in *S. gooddingii* and the dieback that did occur was unrelated to DGW (Fig. 10). There was substantial dieback (up to 70%) in some individuals of *T. chinensis* in 1997, when DGW was generally > 2 m. In contrast to the native species, the 1997 dieback of *T. chinensis*

was unrelated to DGW (Fig. 10), perhaps because of the lack of individuals at shallow DGW in that year. In 1998, there was much less canopy dieback in *T. chinensis*, and dieback was again unrelated to DGW (Fig. 10), perhaps due to the lack of individuals at deep DGW in 1998. However, when canopy dieback of *T. chinensis* from both years was combined to obtain a wider range of DGW, dieback increased significantly with increasing DGW, and the response suggested a DGW threshold of 2–3 m for the onset of dieback. Interestingly, the dieback response of *T. chinensis* for data combined over years was similar to that observed for the native species in 1997 – dieback started when DGW was > 2.5 m. However, *T. chinensis* showed less dieback (35%) than *P. fremontii* (40%) or *S. gooddingii* (70%), and no individuals died (Fig. 10).

Annual branch increment (ABI) in riparian trees is known to be sensitive to variations in streamflow (Willms *et al.* 1998) and ground water availability (Scott *et al.* 1999). In 1997, there was no significant relationship between ABI and DGW for *P. fremontii* ($P = 0.47$). Annual branch increment of *S. gooddingii* was larger than that of *P. fremontii* in both years (Fig. 11). Surprisingly, ABI of *S. gooddingii* increased significantly with increasing DGW in 1997 ($r^2 = 0.236$, $P = 0.009$). In 1997, ABI of *S. gooddingii* was also positively correlated with canopy dieback ($r^2 = 0.260$, $P = 0.004$), suggesting a high capacity for recovery from drought-induced canopy dieback in this species. Many trees that suffered extensive dieback in the summer of 1997 resprouted in October 1997, presumably in response to a large storm that recharged the alluvial aquifer and increased water availability (Figs 1 and 2); substantial branch elongation occurred before the end of the growing season in early December 1997 (J. Horton personal observation). Annual branch increment was significantly larger for both native species in 1998 than in 1997, suggesting increased ABI in response to increased water availability

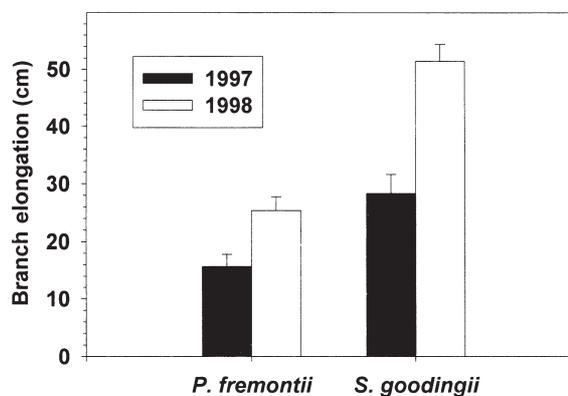


Figure 11. Annual branch increment of *Populus fremontii* ($n = 44$) and *Salix gooddingii* ($n = 41$) at the Hassayampa River in 1997 and 1998. Bars represent mean ± 1 SE (ANOVA: species $F = 50.2$, $P < 0.001$; year $F = 36.0$, $P < 0.001$; species-year interaction $F = 6.0$, $P = 0.015$).

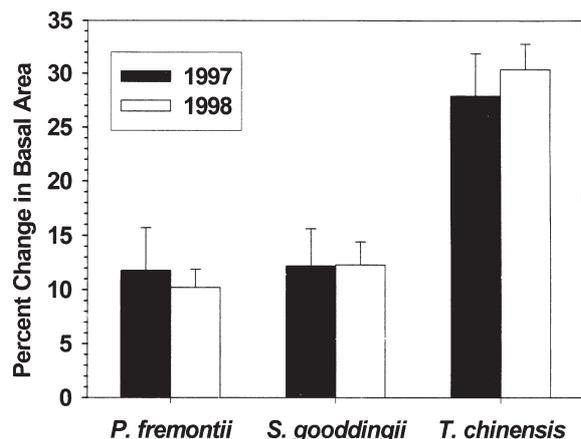


Figure 12. Annual per cent change in basal area of *Populus fremontii* ($n = 36$), *Salix gooddingii* ($n = 40$) and *Tamarix chinensis* ($n = 35$) at the Hassayampa River in 1997 and 1998. Bars represent mean ± 1 SE (ANOVA: species $F = 21.6$, $P < 0.0001$; year $F = 0.0$, $P = 0.90$, species-year interaction $F = 0.2$, $P = 0.80$).

(this increase was greater in *S. gooddingii*; Fig. 11). As in 1997, there was no relationship between ABI and DGW for *P. fremontii* in 1998, but 1998 ABI decreased with increasing DGW in *S. gooddingii* ($r^2 = 0.210$, $P = 0.003$).

In order to compare stem radial growth among different-sized individuals of the three species, radial growth increments were converted into a per cent change in basal area for each year. In 1997, the per cent change in basal area of all species was unrelated ($P > 0.05$) to DGW in any summer month (May–August). In 1998, the per cent change in basal area of *P. fremontii* and *T. chinensis* was unrelated ($P > 0.05$) to DGW in any summer month, while that of *S. gooddingii* was negatively correlated with July DGW ($r^2 = 0.194$, $P = 0.004$), suggesting that deep ground water in July limited radial growth. *Tamarix chinensis* had a much higher per cent increase in basal area in both years than either *P. fremontii* or *S. gooddingii* (Fig. 12), but there was no difference in this increase between the two years for any species. This finding only applies to trees living at the end of 1998 as trees that died in 1997 or 1998 ($n = 3$ for *P. fremontii* and $n = 6$ for *S. gooddingii*) were excluded from the analysis.

One explanation for the similarity in basal area growth between years could be that most radial growth in these species occurs in the spring, when water is readily available. Pockman & Sperry (2000) proposed the production of new xylem vessels as a possible mechanism explaining a decrease in the per cent of xylem embolism between April and July in *Tamarix ramosissima*. Stromberg & Patten (1990) found radial growth in *Populus trichocarpa* in the eastern Sierra Nevada to be positively correlated with stream flow. These findings suggest that radial growth of all species at the Hassayampa River occurred in the early spring, when surface flow was high and ground water was shallow.

Species responses to increased water availability

We conducted analyses on trees of all species found at the lower (ephemeral) reach of the preserve in 1997 and 1998. Because there were no co-occurring *T. chinensis* in the upper perennial reach, data from *P. fremontii* and *S. gooddingii* in this portion of the preserve were not used in these analyses in order to minimize bias in our comparison of species responses between years. There was more water stress for all species in 1997 than in 1998, as evidenced by lower Ψ_{pd} , Ψ_{mm} , g_s and P_n (Table 1) and greater canopy dieback in 1997 (Fig. 10). Increased water stress in 1997 was probably due to deeper ground water in the ephemeral reach in 1997 compared to 1998. Predawn Ψ was significantly higher in all species in 1998 than in 1997 (Table 1). However, the magnitude of the increase in Ψ_{pd} differed among species, as evidenced by a significant interaction in the ANOVA (Table 1). The increase in Ψ_{pd} between 1997 and 1998 was largest in *T. chinensis* (1.08 MPa), intermediate in *S. gooddingii* (0.47 MPa) and smallest in *P. fremontii* (0.35 MPa). While Ψ_{pd} of *T. chinensis* was always lower than that of the native species, this relationship is most likely to be due to a lack of equilibration between soil and plant Ψ overnight due to the high solute concentrations in *T. chinensis* tissues (Busch & Smith 1995). Thus, the larger increase in Ψ_{pd} observed in *T. chinensis* suggests that it experienced a larger increase in water availability in 1998 than the native species. *Tamarix chinensis* is known to be a facultative phreatophyte (Busch *et al.* 1992) that is capable of utilizing water from both the alluvial aquifer and the unsaturated soil. Perhaps in 1998, when the alluvial water table and soil water content were higher, *T. chinensis* had greater access to water than either *P. fremontii* or *S. gooddingii*.

The difference in Ψ_{mm} between the years also varied among species (Table 1). There was little change in the mean Ψ_{mm} of both *P. fremontii* (-0.12 MPa) and *S. gooddingii* ($+0.01$ MPa) between years, and Ψ_{mm} was above the xylem cavitation thresholds reported by Pockman *et al.* (1995) for these species (-1.6 MPa for *P. fremontii* and -1.4 MPa for *S. gooddingii*). However, xylem Ψ in the mid-afternoon exceeded the xylem cavitation threshold in some individuals of each species in 1997 (data not shown). *Tamarix chinensis* showed the largest change ($+0.99$ MPa) in Ψ_{mm} between years (Table 1), and in both years, Ψ_{mm} was well above the 100% cavitation threshold of -7.0 MPa reported for this species by Pockman & Sperry (2000). Moreover, *T. chinensis* has a much wider Ψ safety margin than the native species, with a more gradual reduction in hydraulic conductivity as Ψ decreases than the native species (Pockman & Sperry 2000).

In 1997, both mean g_s and mean P_n of all species in the ephemeral reach were very low, while there were substantial increases in the leaf gas exchange rates of all species in 1998 (Table 1). However, the change in leaf gas exchange rates between 1997 and 1998 differed significantly among species (Table 1). The increase in g_s was largest in *T.*

chinensis ($0.79 \text{ mol m}^{-2} \text{ s}^{-1}$), intermediate in *S. gooddingii* ($0.57 \text{ mol m}^{-2} \text{ s}^{-1}$) and smallest in *P. fremontii* ($0.35 \text{ mol m}^{-2} \text{ s}^{-1}$). The increase in P_n between years was largest in *T. chinensis* ($27.22 \mu\text{mol m}^{-2} \text{ s}^{-1}$), intermediate in *S. gooddingii* ($15.23 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and smallest in *P. fremontii* ($12.05 \mu\text{mol m}^{-2} \text{ s}^{-1}$).

These interannual comparisons of physiological and growth characteristics suggest that *T. chinensis* is more responsive to increased water availability than either *P. fremontii* or *S. gooddingii* and that *S. gooddingii* may be more responsive to increased water availability than *P. fremontii*. When ground water was shallow, *T. chinensis* had much higher gas exchange rates than either *P. fremontii* or *S. gooddingii* (Figs 4 and 5, Table 1). The more favourable response of *S. gooddingii* to increased water availability in 1998 relative to *P. fremontii* could be due to its location in the river basin. *Salix gooddingii* typically establishes closer to the stream channel than *P. fremontii* (Stromberg 1993), which would increase water availability and support higher leaf gas exchange rates.

Summary and conclusions

In the drier year (1997), *P. fremontii*, *S. gooddingii* and *T. chinensis* all experienced water stress, as evidenced by low Ψ_{pd} , g_s and P_n and higher canopy dieback compared to 1998. For *P. fremontii* and *S. gooddingii*, these parameters were significantly related to DGW in 1997. As expected, the physiological condition of all species was improved in 1998 relative to 1997, as evidenced by greater Ψ_{pd} , g_s , P_n , and less dieback. The increase between years in these parameters was marginally greater in *S. gooddingii* than in *P. fremontii*, probably because of its location in the river basin relative to *P. fremontii*. *Salix gooddingii* typically establishes closer to the active stream channel than *P. fremontii* and is more shallowly rooted (Stromberg 1993; Stromberg *et al.* 1996). Hence, *S. gooddingii* appears to be more sensitive than *P. fremontii* to declines in water availability such as those observed in the ephemeral reach in 1997, and is more responsive to increased water availability, as occurred in 1998.

Contrary to our expectations, the response patterns of Ψ_{pd} , g_s , P_n and canopy dieback shown for *T. chinensis* by the combined data over both years suggests that it is quite sensitive to changes in water availability. Furthermore, *T. chinensis* may have a DGW threshold for the onset of canopy dieback of 2–3 m. However, this relationship needs to be examined further with concurrent measurements of physiological parameters and dieback on individuals occurring over a wide range of DGW. The response pattern observed for *T. chinensis* in the combined data set is generally similar to that observed for the native species in 1997 over a comparable range of DGW. However, despite this similarity, *T. chinensis* had a much higher leaf gas exchange rate than the native species when ground water was shallow. Moreover, canopy dieback and tree mortality at deep ground water sites were less for *T. chinensis* than for the native species. The combination of high leaf gas exchange rates, growth

when water is abundant, drought tolerance and, especially, the maintenance of a viable canopy under dry conditions are characteristics that help explain the ability of *Tamarix* spp. to thrive in riparian ecosystems of the south-western United States that are subject to large interannual fluctuations in water availability.

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