PHYSIOLOGICAL RESPONSE TO GROUNDWATER DEPTH VARIES AMONG SPECIES AND WITH RIVER FLOW REGULATION

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Abstract. We investigated the physiological response of two native riparian tree species (*Populus fremontii* and *Salix gooddingii*) and one exotic species (*Tamarix chinensis*) to groundwater availability along gradients of depth to groundwater at two rivers in Arizona. Depth to groundwater (DGW) at the dam-regulated Bill Williams River (BWR) was relatively constant and shallow (<4 m). *Populus fremontii* at BWR did not experience reduced water availability at deeper groundwater depths, as evidenced by high predawn water potential. However, leaf gas exchange of *P. fremontii* was sensitive to high vapor pressure deficit where surface flow was ephemeral at BWR. Lower predawn water potentials of *S. gooddingii* at BWR suggested reduced water availability at deeper groundwater depths, but these reductions did not adversely affect net photosynthetic rate. Along the range of depth to groundwater at BWR, all three species suffered little canopy dieback, and dieback was not related to depth to groundwater. Depth to groundwater at the free-flowing Hassayampa River (HRP) was much greater and declined more rapidly in the ephemeral reaches than at BWR. Both *P. fremontii* and *S. gooddingii* experienced reduced water availability at deeper groundwater depths at HRP, as evidenced by lower predawn water potential. Both species also experienced reduced leaf gas exchange at deeper groundwater depths. Canopy dieback of all species was higher at HRP than at BWR and increased with increasing DGW, especially when DGW fell below 3 m. There was evidence to support branch sacrifice in these three riparian tree species as a means of improving water status in the surviving shoot. However, branch sacrifice was insufficient to prevent mortality in some of the native trees where DGW fell below 3 m at HRP. In contrast to the native species, *T. chinensis* showed no change in water availability, leaf gas exchange, or canopy dieback with increasing DGW at either river. Leaf gas exchange was lower and dieback was greater for *T. chinensis* at HRP where depth to groundwater was greater than at BWR, but there was no mortality at either river. Our results show that deep groundwater is more detrimental to the physiological condition of *P. fremontii* and *S. gooddingii* than it is to *T. chinensis*. Also, the pronounced differences in DGW and tree physiological performance between BWR and HRP suggest that dam regulation can increase water availability to mature trees in some desert riparian ecosystems. Finally, our study also provides estimates of the range of DGW that can maintain healthy, mature *P. fremontii* and *S. gooddingii* trees.

Key words: groundwater; photosynthesis; Populus fremontii; *riparian;* Salix gooddingii; Tamarix chinensis; *water relations; water stress.*

Introduction

Riparian ecosystems in the American Southwest are important areas of biodiversity that support a majority of the region's animal species (Knopf et al. 1988), and they are also valued for recreation, watershed protection, and water quality (Carothers 1977, Patten 1998). However, in the past one hundred years, impoundments and diversions of surface water and removal of groundwater have contributed to a decline of southwestern riparian habitats (Rood and Mahoney 1990, Stromberg 1993, Busch and Smith 1995, Stromberg et al. 1996,

Patten 1998). Today <20% of the riparian habitat present in this region one hundred years ago remains (Swift 1984). At lower elevations (<1250 m), these habitats are dominated by *Populus fremontii–Salix gooddingii* forests, one of North America's rarest forest types (Brown 1982).

Most woody vegetation of low-elevation southwestern riparian ecosystems is believed to be phreatophytic, relying heavily on alluvial groundwater and the associated capillary fringe (Bryan 1928, Turner 1974, Busch and Smith 1995, Mahoney and Rood 1998, Shafroth et al. 1998). Decreases in water availability from these sources can cause decline in mature riparian trees (Reily and Johnson 1982, Groeneveld and Griepentrog 1985, Rood and Heinze-Milne 1989, Smith et al. 1991, Shafroth et al. 1998, Scott et al. 1999) which is often

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accompanied by invasion of facultative phreatophytic species (Smith et al. 1991, Freidman et al. 1995), including exotics like *Tamarix chinensis* Lour. and related species (Busch and Smith 1995). Invasion of *T. chinensis* into many Sonoran desert riparian ecosystems has followed alteration of river hydrology and decline of native species (Robinson 1965). *Tamarix chinensis* is known to be more tolerant of drought and salinity than native species, such as *Salix gooddingii* Ball and *Populus fremontii* S. Wats. (Cleverly et al. 1997, Smith et al. 1998; Horton et al., 2001), and appears to better adapted to these altered systems.

Whereas several studies have reported on community composition and regeneration of southwestern riparian communities at sites that differ in groundwater depth (Stromberg et al. 1991, 1996, Stromberg 1993), less is known about the ecophysiological mechanisms that cause these community changes (Rood and Heinze-Milne 1989, Smith et al. 1991, Busch et al. 1992, Busch and Smith 1995). Tyree et al. (1994) proposed drought-induced xylem dysfunction (cavitation) as a possible mechanism for the decline of riparian trees following a decrease in water availability. Native riparian species in the genera *Populus* and *Salix* are extremely prone to drought-induced xylem cavitation (Tyree et al. 1994, Pockman et al. 1995, Blake et al. 1996, Pockman and Sperry 2000). Xylem cavitation can reduce xylem hydraulic conductivity and can lead to tissue desiccation, loss of turgor, stomatal closure, reduced photosynthesis, and eventually to branch and crown mortality (Tyree et al. 1994, Rood et al. 2000). Better understanding of the influence of ground and stream water availability as a mechanism of riparian tree decline is needed for efforts to preserve and restore riparian ecosystems. For example, land managers would benefit from knowledge of streamflows and groundwater depths associated with decline of native riparian species (Smith et al. 1991, Scott et al. 1999).

We investigated the physiological condition of two native species, *P. fremontii* and *S. gooddingii,* and one invasive exotic, *T. chinensis,* along gradients of groundwater availability at a dam-regulated river and a free-flowing river in the Sonoran Desert in Arizona. Specifically, we addressed the following hypotheses:

1) An increase in groundwater depth will cause reductions in tree shoot water potential (ψ), leading to decreased stomatal conductance and net photosynthesis, and an increase in canopy dieback.

2a) The relationship between depth to groundwater and tree physiological condition will be nonlinear: tree physiological condition will decline rapidly after depth to groundwater exceeds a distinct threshold.

2b) An alternative to hypothesis 2a is that the relationship between depth to groundwater and tree physiological condition will be linear: any increase in depth to groundwater will cause a decline in tree physiological condition.

3) The relationship between depth to groundwater and tree physiological condition will differ among *P. fremontii, S. gooddingii,* and *T. chinensis*. Based on analyses of species composition in low-elevation riparian communities by Stromberg et al. (1996), we expected the physiological condition of *S. gooddingii* to be more sensitive to changes in depth to groundwater than *P. fremontii,* whereas *T. chinensis* is known to be very drought tolerant (Cleverly et al. 1997; Horton et al., 2001) and was expected to be least sensitive to changes in depth to groundwater.

4) The relationship between depth to groundwater and tree physiological condition will differ between an unregulated river (Hassayampa) and a dam-regulated river (Bill Williams). Specifically, we expected the trees at the Hassayampa River Preserve (HRP) to show less sensitivity to variation in groundwater depth than trees at the Bill Williams River (BWR). This prediction is based on groundwater availability being more constant at the Bill Williams River (BWR), as suggested by the higher base flows during the growing season at BWR than at the HRP, despite greater temperature and less precipitation at BWR. These higher flows result from the relatively constant flow releases from Alamo Dam (USGS stream gauge No. 09426620).[2] In contrast, surface flow at HRP peaks during the spring and diminishes during the growing season (Jenkins 1989). Alluvial groundwater at HRP is shallowest when surface flow peaks and declines during the growing season as surface flows diminish. Several investigators have found that a gradual decline (2–3 cm/d) in groundwater can promote root elongation of riparian trees (Fenner et al. 1985, Mahoney and Rood 1991, 1992, Horton and Clark 2001). Hence, we predicted that trees with a more constant supply of groundwater at BWR will have more shallow roots and thus greater physiological sensitivity to changes in groundwater depth than trees exposed to a more dynamic groundwater environment at HRP.

STUDY SITES

The Bill Williams River (BWR) is a dam-regulated tributary of the Colorado River that drains into Lake Havasu above Parker Dam. Our study sites at BWR are located on the U.S. 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 is 21.9°C and mean annual precipitation is 12.3 cm (National Climatic Data Center, station Parker 6NE),[3] with over half occurring as winter precipitation (November–March; Table 1). Flows on the BWR have been regulated by the operation of Alamo Dam since its completion in 1968.

The BWR study site is at low elevation and occurs at the transition between the Sonoran and Mojave des-

TABLE 1. Long-term mean climatic (BWR, 1893–1998; HRP, 1908–1998) and hydrologic data at the Bill Williams River (BWR) and Hassayampa River (HRP) study sites.

Site	Drainage area (km²)†	Discharge (m³/s)†	Annual air temp. (°C)‡	Annual precip. (cm)‡	Precip. in winter (%)‡	Precip. in summer monsoons (%)‡
BWR	13 823	1.1	21.9 (23.2)	12.3 (13.1)	58 (39)	30 (35)
HRP	2 062	0.1	18.6 (20.2)	28.8 (28.7)	49 (22)	39 (52)

Note: Mean temperature and precipitation for the year of our study, 1997, are in parentheses. Temperature = temp., percipitation = percip., winter = Nov–Mar, summer monsoons = Jul–Sep.

† Data from USGS gauging station No. 09426620 for BWR (1988–1998) and Jenkins (1989) for HRP.

‡ Data from National Climatic Data Center stations Parker 6NE for BWR and Wickenburg, Arizona for HRP.

ert ecosystems along the western edge of the summer monsoonal precipitation pattern (NOAA, Tucson, Arizona).[4] As such, this site is typically hotter and drier than the higher elevation HRP study site, and has a greater proportion of annual precipitation occurring in the winter season (Table 1).

The Hassayampa River (HRP) is a free-flowing tributary of the Gila River. Our study sites at HRP are located at 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 in this area is 18.6°C and mean annual precipitation is 28.8 cm (National Climatic Data Center, station Wickenburg, Arizona),[4] with about half occurring as winter precipitation and most of the remainder occurring during the monsoon season (July–September; Table 1).

The BWR drains a much larger basin than the HRP and flows on this river are regulated by Alamo Dam. Mean flows on the BWR are much higher than on the HRP (Table 1), because of constant flow releases from Alamo Dam during the summer. River flows at both sites vary between perennial and ephemeral reaches. Perennial flow occurs in areas where shallow bedrock raises the alluvial water table to the surface. Where bedrock is deeper, water flows only through the underlying alluvium, except during floods caused by large spring snow melts in the surrounding uplands or intense summer thunderstorms. Base flows at our study sites decrease along a losing reach from 1.1 m³/s at BWR and 0.1 m³/s at HRP to 0 m³/s at both sites (USGS stream gauge No. 09426620,[5] Jenkins 1989). There are populations of *P. fremontii, S. gooddingii,* and *T. chinensis* along the gradient of surface flow at both rivers.

MATERIALS AND METHODS

In the winter of 1997, seven transects were established along a losing reach at each river. The uppermost

[4] URL: ⟨http://www.nimbo.wrh.noaa.gov/Tucson/monsoon/⟩
[5] URL: ⟨http://az.water.usgs.gov⟩

transect was located in the perennial portion of the reach, and the lowermost transect was located in the ephemeral reach where surface flow was absent during the summer. Depth to groundwater (DGW) was measured once a month at one to four wells per transect (total number of wells = 18 at BWR and 15 at HRP) located near sampling populations of all three species. At both rivers, we used a combination of sand-point piezometers (Cook Screen Technologies, Cincinnati, Ohio, USA) that we installed (n = 6 at BWR and 14 at HRP) and older wells that were installed prior to our study. We chose trees that had minimal canopy dieback (<10%) from the populations surrounding each well to establish a sampling population for each species. The change in elevation between the base of each tree and the base of the closest well was surveyed using a laser surveying device (Criterion 400, Laser Technologies, Englewood, Colorado, USA) so that depth to groundwater could be estimated for individual trees.

Physiological data were measured at all transects monthly between June and August 1997, during the same week that depth to groundwater (DGW) was measured. At each sampling time, five mature individuals of each species were chosen randomly from the sampling population at each transect for measurement, except at transect 6 at BWR where only one mature *P. fremontii* was available to measure. Shoot water potential (ψ) of terminal twigs was measured before dawn, at mid-morning (0800–1000), and at mid-afternoon (1300–1500) using a Scholander-type pressure chamber (Model 1000, PMS Instruments, Corvallis, Oregon, USA). Leaf gas exchange of water vapor and carbon dioxide was measured under full sun conditions in both mid-morning and mid-afternoon using a Li-Cor 6200 Portable Photosynthesis System (Li-Cor, Lincoln, Nebraska, USA). Gas exchange measurements were 15 s in duration to minimize changes in water vapor pressure and air temperature in the cuvette during the measurement. Data measured at excessively high (>400 μmol/mol) CO_2 concentrations within the cuvette were

removed before data analysis (<3% of total measurements).

The timing of physiological measurements during the day was based on diurnal measurements made in May 1997 (data not shown), which showed that environmental conditions are generally most favorable for gas exchange in the mid-morning and may be limiting to gas exchange in the mid-afternoon. Gas exchange measurements were made on leaves from portions of the lower to mid-canopy that were exposed to full sun. Measurements were made on leaves in situ where possible, and on leaves attached to twigs that were cut with pole pruners from portions of the canopy that were otherwise inaccessible. Leaves on detached twigs were measured within 30 s after 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), a finding that is consistent with other studies (Gower et al. 1993, Meng and Arp 1993, Kolb et al. 1997).

Recent crown dieback, an integrative measure of canopy condition, was measured on all trees in the sampling population in late September and early October 1997 before the onset of leaf senescence using a technique developed for forest health monitoring (Millers et al. 1991, Allen et al. 1992, Kolb and McCormick 1993). Two or three observers scored canopy dieback using a 12 percentage class system. Recent crown dieback was defined as the proportion of the entire crown volume that contained recently dead branches and twigs (Millers et al. 1991).

Leaf physiological characteristics and canopy condition of each species were related to DGW using scatter plots and regression techniques. Statistical analyses were performed using the SAS Version 7 (SAS 2000) and StatView Version 4.5 (Abacus Concepts Inc., Berkeley, California, USA) software packages. Physiological data are presented for July, when plant water stress was greater than in June for all species as indicated by lower predawn water potential (ψ_{pd}) and greater DGW. August data were not used because the occurrence of intense thunderstorms prevented sampling at some transects. Only morning gas exchange measurements are presented for several reasons. Both stomatal conductance (g_s) and net photosynthesis (P_n) were higher in the morning than in the afternoon for all species, and thus the morning data are better estimates of maximal daily gas exchange rates. Further, leaf gas exchange was lower, but more variable, in the afternoon than in the morning for all species at all transects, which resulted in weaker relationships between leaf gas exchange and DGW in the afternoon than in the morning. Also, afternoon sampling was curtailed on two dates in July due to intense thunderstorms, resulting in a very low number of afternoon measurements on *T. chinensis* at HRP. Thus, analyses performed on the afternoon leaf gas exchange data for *T. chinensis* at HRP lacked power and limited our inferences about potential groundwater effects. Mid-afternoon shoot water potential was measured despite afternoon thunderstorms and was included in the analysis.

RESULTS AND DISCUSSION

Climate and groundwater

Annual precipitation in 1997 was close to the long-term average at both sites, but the mean annual temperature in 1997 was higher than average (Table 1). The spring and summer at both sites were hotter and drier in 1997 than average (Fig. 1), and the onset of the monsoonal precipitation pattern, which usually occurs in the first week of July, did not occur until the third week of July (NOAA Tucson, Arizona[4]). These factors caused extremely dry conditions in the summer of 1997 at both sites.

Constant flow releases from Alamo Dam at BWR caused pronounced differences in surface flow and groundwater dynamics between sites. At BWR, the uppermost perennial transect had constant surface flow and DGW relative to the channel thalweg, with DGW remaining near −0.95 m throughout the summer (BWR Transect 7, Fig. 2). The negative value for DGW relative to the thalweg (Fig. 2) indicates the presence of surface flow. The lowest transect at BWR (BWR Transect 1, Fig. 2) was likely influenced by the impoundment of Lake Havasu at the confluence of the Bill Williams and Colorado Rivers, and thus had shallower groundwater than the next transect, which was located ~0.5 km upstream (Fig. 2). Transect 2 at BWR had the deepest and most variable DGW ranging from 0.90 m in May to 2.35 m in August (BWR Transect 2, Fig. 2). At HRP, the uppermost perennial transect also had relatively constant surface flow and DGW relative to the channel thalweg, with DGW remaining near −0.70 m throughout the summer (HRP Transect 7, Fig. 2). In contrast, surface flow was absent at the lowermost ephemeral transect at HRP, and DGW increased dramatically throughout the summer from 4.23 m in May to 8.99 m in August (HRP Transect 1, Fig. 2).

Populus fremontii *response to groundwater depth*

Populus fremontii is known to be a facultative phreatophyte that typically occurs in areas with DGW <5 m (Busch et al. 1992, Busch and Smith 1995, Stromberg et al. 1996). Predawn shoot water potential (ψ_{pd}) of *P. fremontii* did not change significantly with increasing DGW at BWR (Fig. 3), suggesting that roots of *P. fremontii* remained in contact with the alluvial water table over the range of DGW observed at BWR (0.5–4.0 m). At HRP, where the alluvial water table was deeper and more variable than at BWR, ψ_{pd} of *P. fremontii* decreased with increasing DGW (Fig. 3).

We were also interested in how DGW influenced leaf gas exchange characteristics given that stomatal ap-
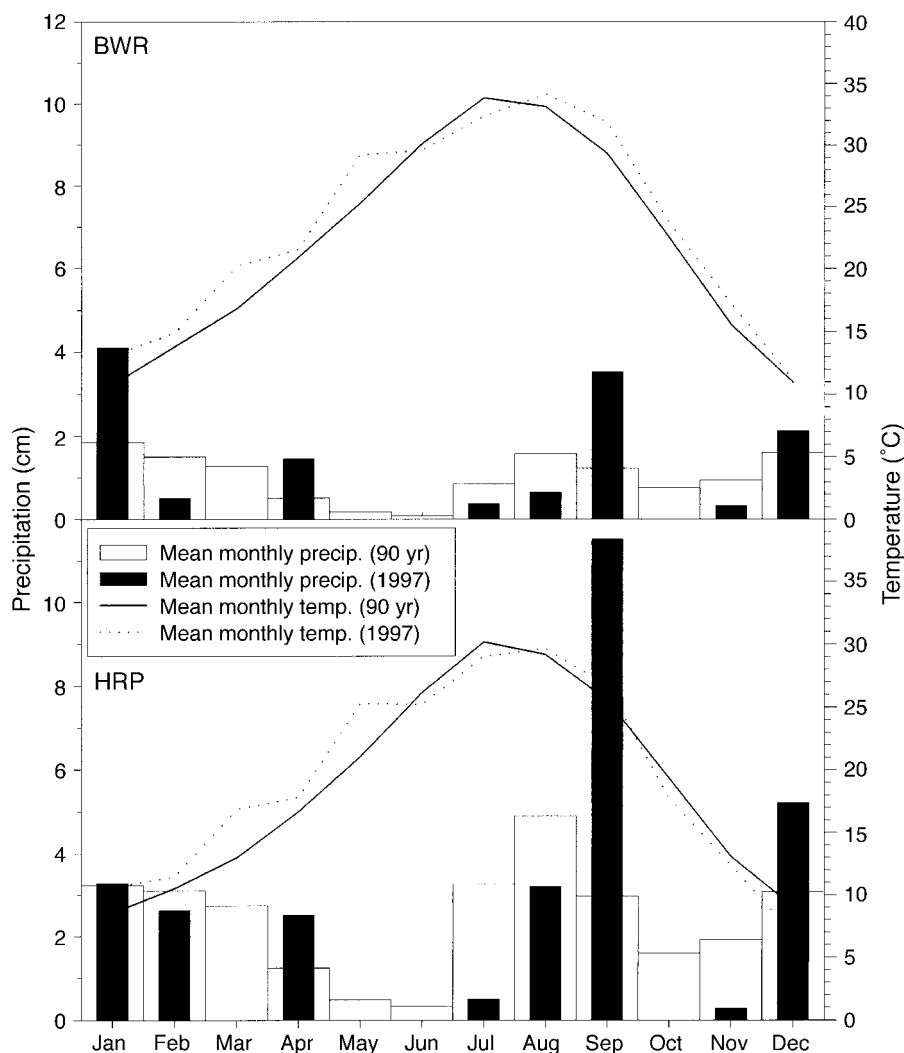
FIG. 1. Mean monthly temperature and precipitation, both 1997 and long-term (BWR, 1893–1998; HRP, 1908–1998) values, at the Bill Williams (BWR) and Hassayampa (HRP) rivers.

erture and photosynthesis are highly sensitive to soil water availability in *Populus* species (e.g., Blake et al. 1996). Stomatal conductance (g_s) of *P. fremontii* decreased with increasing DGW at both rivers (Fig. 4), and these reductions in g_s also corresponded with a decrease in P_n (Fig. 5). Low ψ_{pd} caused by deep groundwater at least partly explains why g_s and P_n decreased for *P. fremontii* with increasing DGW at HRP, as g_s and P_n of this species decline at ψ_{pd} lower than -0.8 MPa at our study sites (Horton et al. 2001). However, this explanation cannot be applied to BWR, where g_s and P_n declined with increasing DGW in the absence of a change in ψ_{pd}. A likely explanation for this response at BWR is that g_s of *P. fremontii* was limited by high leaf-to-air vapor pressure deficit (VPD) at the ephemeral stream sites. Consistent with this explanation, VPD at BWR increased with increasing DGW ($r^2 = 0.350$, $P = 0.001$) because of lower relative humid-

ity, and VPD at the ephemeral sites exceeded threshold values (1.2–1.6 kPa) associated with stomatal closure and reduced P_n of *P. fremontii* at our study sites (Horton et al., 2001). It is also possible that reductions in g_s and P_n for *P. fremontii* at both rivers with increasing DGW occurred in response to the development of low daytime values of shoot ψ at the ephemeral stream sites. However, there is little evidence for this explanation as the lowest values of daytime shoot ψ measured for *P. fremontii* were not obviously associated with reduced P_n at our study sites (Horton et al. 2001), and daytime ψ did not decrease for this species with decreasing ψ_{pd} at either river (Fig. 6). Collectively, these factors suggest that reductions in g_s and P_n with increasing DGW occurred primarily because of high VPD at BWR, and because of a combination of high VPD (VPD vs. DGW $r^2 = 0.612$, $P < 0.001$) and low shoot ψ_{pd} at HRP.
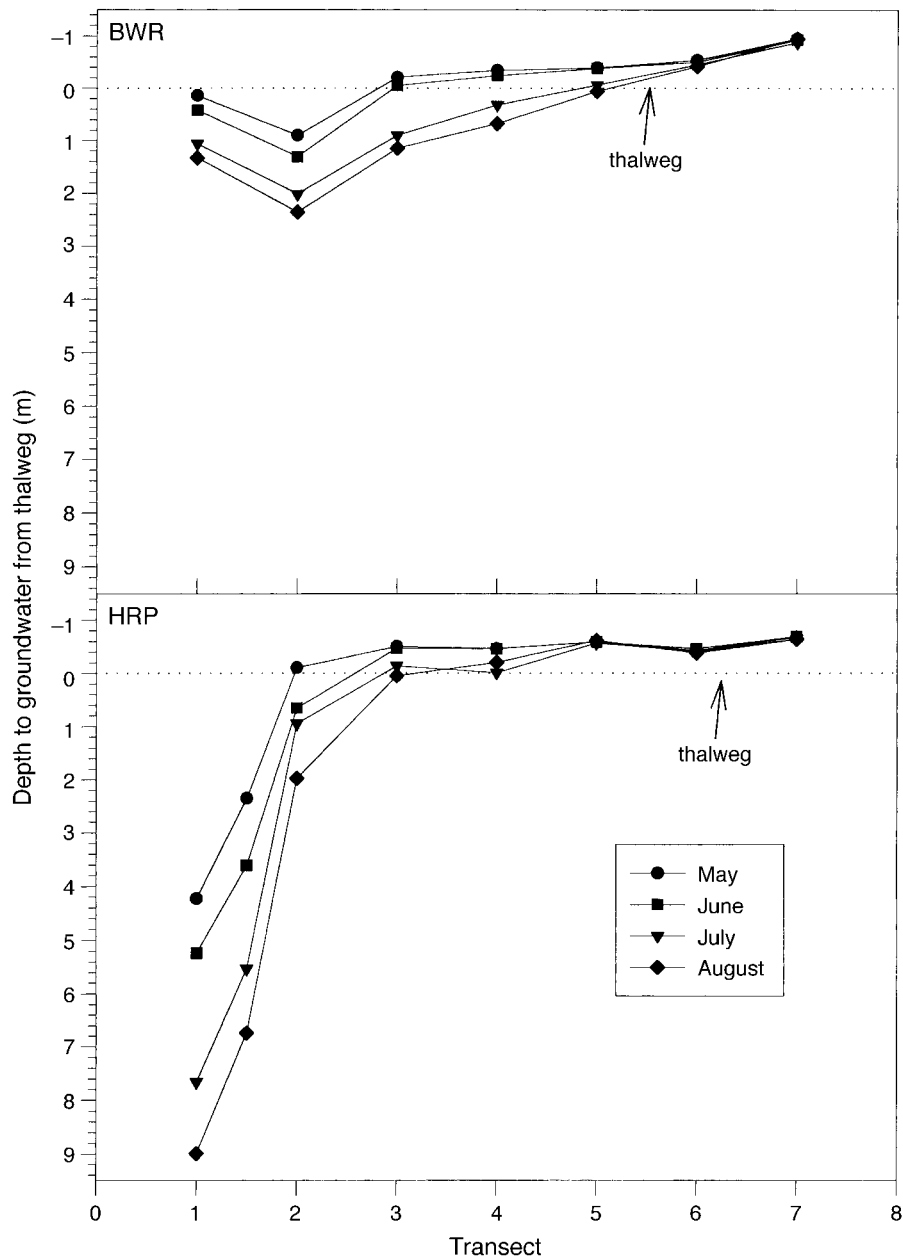
FIG. 2. Depth to groundwater relative to the stream thalweg at each transect from the well closest to the stream during May–August 1997 at the Bill Williams (BWR) and Hassayampa (HRP) rivers. Points above the thalweg denote areas with surface flow.

If the disparity between water supply to and water loss from a tree is great, stomatal closure may be insufficient to prevent xylem cavitation caused by low shoot ψ (Tyree and Ewers 1991, Cochard et al. 1992, Rood et al. 2000). Recent canopy dieback occurred in *P. fremontii* at both rivers, and the pattern of dieback, rapid branch mortality starting in the outer crown during extremely hot, dry weather in late summer, and our measurements of shoot ψ below cavitation thresholds in some individuals (Table 2), strongly suggest that this canopy dieback was caused by xylem cavitation. However, canopy dieback of *P. fremontii* at BWR was generally <40%, except for a few individuals that were affected by a fungal pathogen, and dieback was not significantly related to DGW (Fig. 7).

Branch sacrifice associated with canopy dieback following xylem cavitation has been interpreted as an adaptive response to extreme drought in semiarid riparian *Populus* species because water supply to remaining branches may increase (Rood et al. 2000). We
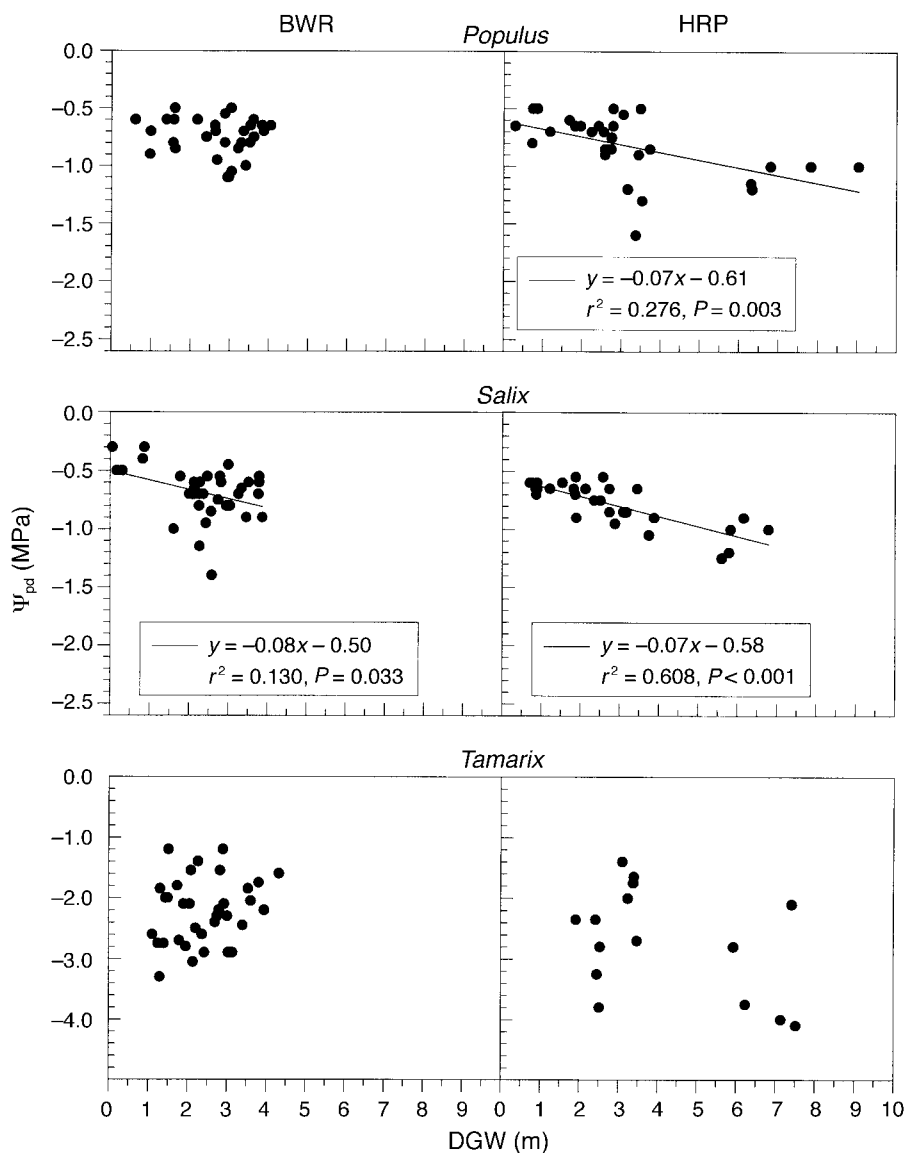
FIG. 3.   Predawn water potential (ψ_{pd}) as a function of depth to groundwater (DGW) for *Populus fremontii* (BWR, $n =$ 31; HRP, $n = 30$), *Salix gooddingii* (BWR, $n = 35$; HRP, $n = 30$), and *Tamarix chinensis* (BWR, $n = 35$; HRP, $n = 15$) at the Bill Williams (BWR) and Hassayampa (HRP) rivers. Equations describe the least squares linear regression model relating ψ_{pd} to DGW. Other relationships were not significant at $P < 0.05$. Note the different y-axis scale used for *Tamarix*.

found evidence for such an adaptive role of branch sacrifice for *P. fremontii* at HRP where canopy dieback increased significantly with increasing DGW (Fig. 7). At HRP, canopy dieback of *P. fremontii* was greatest at deep groundwater sites (Fig. 7) where ψ_{pd} was lowest (Fig. 2), and ψ_{midday} increased as ψ_{pd} decreased (Fig. 6). Thus, canopy dieback caused by xylem cavitation appears to have increased water supply to noncavitated branches as shown by the increase in ψ_{midday} at deep groundwater sites at HRP as ψ_{pd} decreased. Water supply to these branches also may have increased because of stomatal closure at deep groundwater sites at HRP (Fig. 4), a response that also is consistent with the

increase in ψ_{midday} as ψ_{pd} declined (Fig. 6). Despite the apparent adaptive role of canopy dieback in *P. fremontii* at deep groundwater sites at HRP, canopy loss was >50% for six trees in our sample population (Fig. 7) and three of these trees died by the next year. Thus, branch sacrifice, while apparently effective for increasing water supply to noncavitated branches, did not prevent mortality of some *P. fremontii* trees under the extremely hot, dry conditions at HRP.

Salix gooddingii *response to groundwater depth*

Salix gooddingii is generally known as an obligate phreatophyte that is more shallowly rooted than *P. fre-*
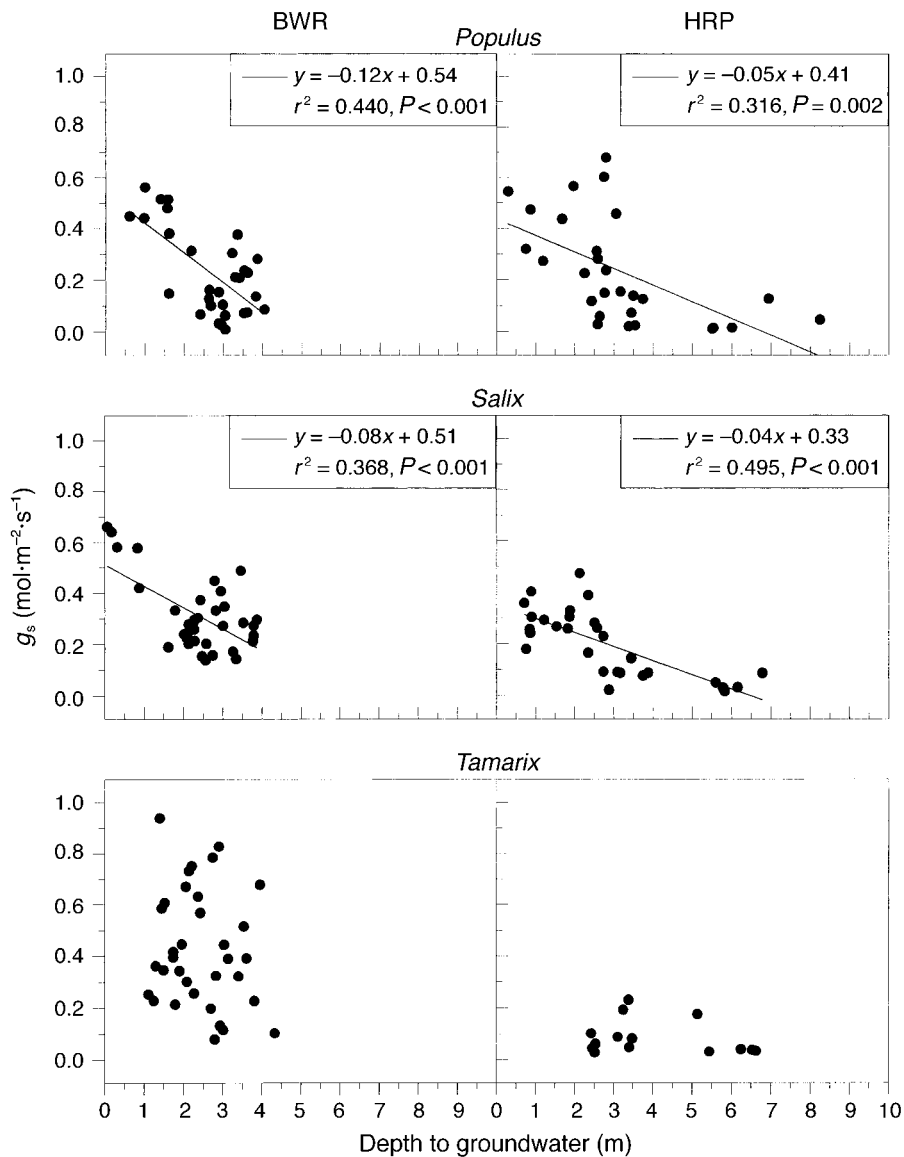
FIG. 4. Mid-morning stomatal conductance (g_s) as a function of depth to groundwater (DGW) for *Populus fremontii* (BWR, $n = 31$; HRP, $n = 28$), *Salix gooddingii* (BWR, $n = 35$; HRP, $n = 30$), and *Tamarix chinensis* (BWR, $n = 35$; HRP, $n = 15$) at both the Bill Williams (BWR) and Hassayampa (HRP) rivers. Equations describe the least squares linear regression model relating g_s to DGW. Other relationships were not significant at $P < 0.05$.

montii (Stromberg et al. 1991, 1996, Stromberg 1993). Predawn ψ of *S. gooddingii* decreased similarly with increasing DGW at both rivers (Fig. 3), although the relationship was stronger (higher r^2) at HRP than at BWR. This decrease in ψ_{pd} with increasing DGW suggests reduced water availability in the ephemeral reaches at both rivers, especially at HRP where maximum DGW was 7 m.

We expected leaf gas exchange of *S. gooddingii* to be more sensitive to increasing DGW than that of *P. fremontii* due to the shallower rooting depth of *S. gooddingii*. Stomatal conductance of *S. gooddingii* decreased with increasing DGW at both rivers (Fig. 4),

and this reduction corresponded with a decrease in P_n at HRP, but not at BWR (Fig. 5). At BWR, low ψ_{pd} caused by deep groundwater could be responsible for decreased g_s in *S. gooddingii*, as g_s of this species declined at ψ_{pd} below -0.5 MPa at our study sites (Horton et al. 2001). Reductions in g_s of *S. gooddingii* with increasing DGW could also be due to high VPD in the ephemeral reaches, which exceeded the threshold (1.2 kPa) associated with stomatal closure in this species (Horton et al. 2001). However, the threshold VPD associated with reduced P_n of *S. gooddingii* (2.8 kPa) is higher than the VPD threshold associated with reduced g_s (1.2 kPa), likely because P_n is saturated with CO_2 at
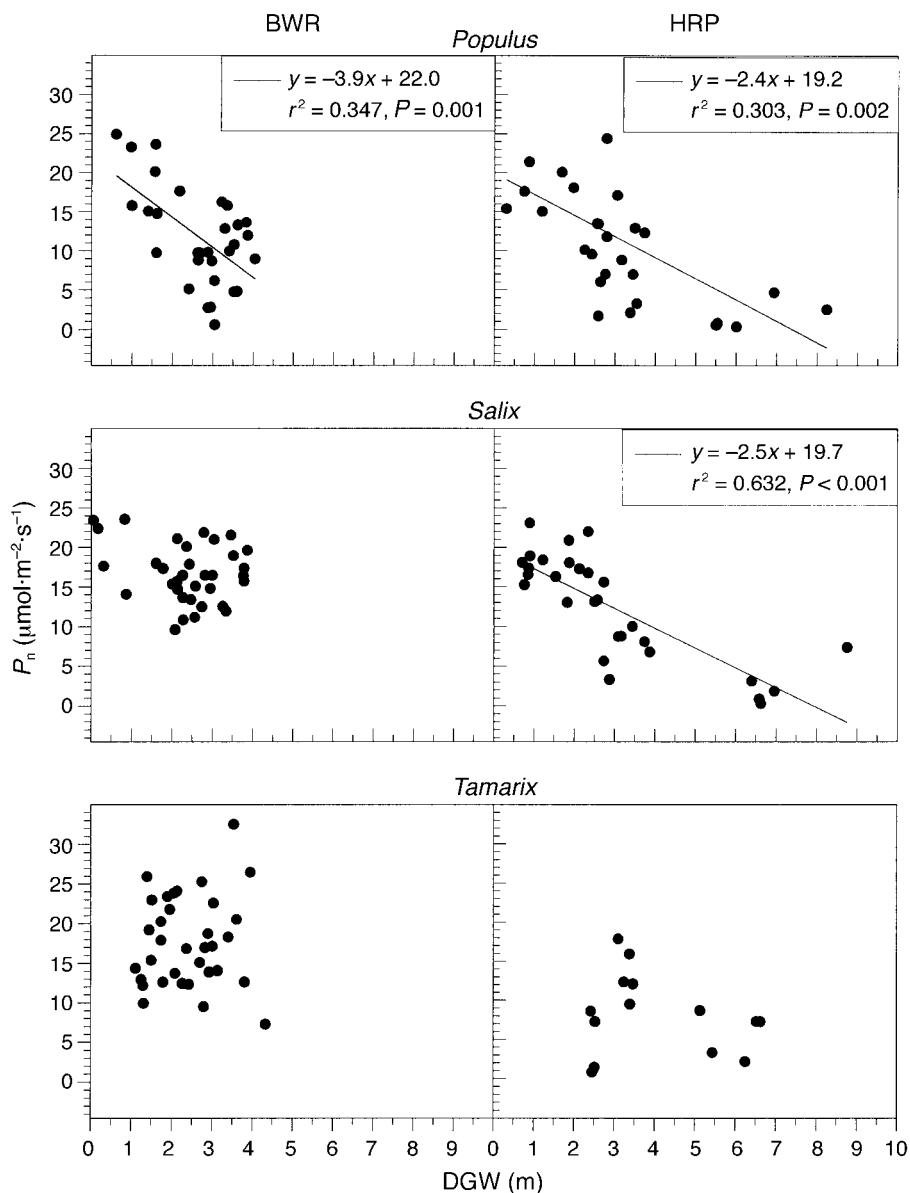
FIG. 5. Mid-morning net photosynthetic rate (P_n) as a function of depth to groundwater (DGW) for *Populus fremontii* (BWR, $n = 31$; HRP, $n = 28$), *Salix gooddingii* (BWR, $n = 35$; HRP, $n = 30$), and *Tamarix chinensis* (BWR, $n = 35$; HRP, $n = 15$) at both the Bill Williams (BWR) and Hassayampa (HRP) rivers. Equations describe the least squares linear regression model relating P_n to DGW. Other relationships were not significant at $P < 0.05$.

high g_s and initial reductions in g_s do not limit P_n (Horton et al. 2001). At HRP, reductions in g_s and P_n of *S. gooddingii* are likely the result of both low ψ_{pd} caused by deep groundwater and high VPD in the ephemeral reach. The development of low daytime shoot ψ might also contribute to these reductions in g_s and P_n. However, at BWR, morning ψ (Table 2) was generally above the thresholds (-1.3 MPa for g_s and -1.6 MPa for P_n) associated with reductions in leaf gas exchange of this species (Horton et al. 2001), whereas at HRP, daytime shoot ψ (Table 2) was well below these thresholds. Thus, low daytime shoot ψ likely contributed to re-

duced leaf gas exchange of *S. gooddingii* at HRP, but not at BWR.

Drought-induced canopy dieback occurred in *S. gooddingii* at both rivers. At BWR, canopy dieback was low (<30% in most individuals) and was unrelated to DGW (Fig. 7). At HRP, canopy dieback increased significantly when DGW exceeded 2.5–3.0 m compared to sites with DGW <2.5 m (Fig. 7). Although branch sacrifice in response to drought has not been reported for this species as a mechanism to improve water supply in the surviving portions of the tree, *S. gooddingii* is closely related to *P. fremontii* (i.e., same family) and
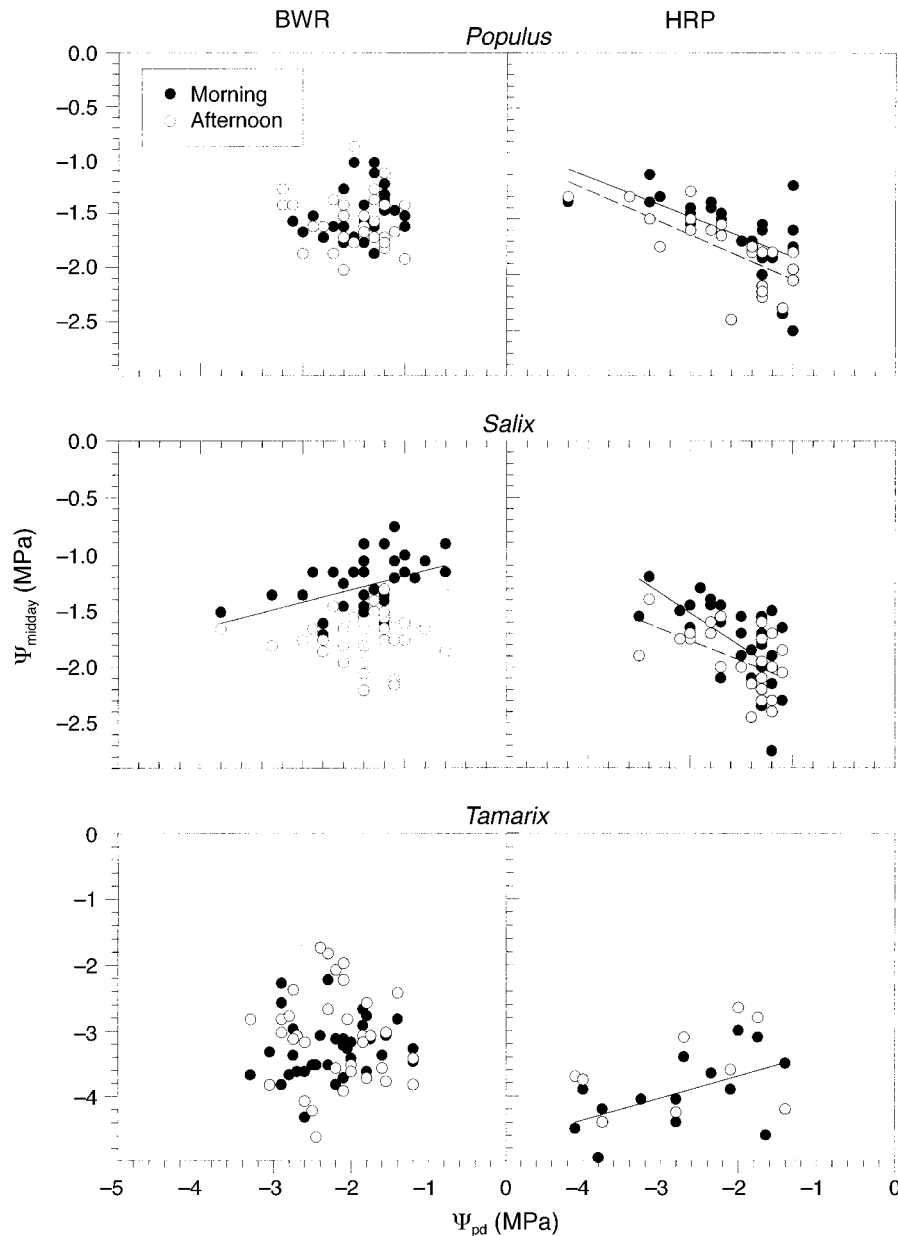
FIG. 6. Mid-morning (AM, closed circles) and mid-afternoon (PM, open circles) shoot water potential (ψ_{midday}) as a function of predawn water potential (ψ_{pd}) for *Populus fremontii* (BWR, $n = 31$ for both AM and PM; HRP, $n = 28$ AM, $n = 30$ PM), *Salix gooddingii* (BWR, $n = 35$ for both AM and PM; HRP, $n = 30$ for both AM and PM), and *Tamarix chinensis* (BWR, $n = 35$ for both AM and PM; HRP, $n = 14$ AM, $n = 9$ PM) at both the Bill Williams (BWR) and Hassayampa (HRP) rivers. Equations describe the least squares linear regression model relating ψ_{midday} to ψ_{pd} (*Populus*: HRP AM, $y = -0.7x - 2.2$, $r^2 = 0.392$, $P < 0.001$; HRP PM, $y = -0.8x - 2.7$, $r^2 = 0.547$, $P < 0.001$. *Salix*: BWR AM, $y = 0.5x - 1.0$, $r^2 = 0.191$, $P = 0.009$; HRP AM, $y = -1.2x - 2.7$, $r^2 = 0.388$, $P < 0.001$; HRP PM, $y = -0.7x - 2.5$, $r^2 = 0.271$, $P = 0.008$. *Tamarix*: HRP AM, $y = 0.3x - 3.0$, $r^2 = 0.295$, $P = 0.045$). Other relationships were not significant at $P < 0.05$. Please note the different *x*- and *y*-axes used for *Tamarix*.

its xylem cavitates at a similar shoot ψ as *P. fremontii* (Pockman et al. 1995). Thus, it is likely that these species share branch sacrifice as a mechanism for surviving periods of extreme water stress. Similar to *P. fremontii*, *S. gooddingii* showed and increase in ψ_{midday} as ψ_{pd} decreased at HRP (Fig. 6) where canopy dieback

increased with increasing DGW (Fig. 7). This increase in ψ_{midday} as ψ_{pd} decreased (Fig. 7) suggests an improvement in water supply to the noncavitated branches at sites with low soil water availability at HRP as a result of stomatal closure and/or branch sacrifice. Canopy dieback at deep groundwater sites at HRP was >50% for

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TABLE 2. Mean, minimum, and maximum July water potential of midmorning (AM) and midafternoon (PM) measurements for *Populus fremontii* (BWR, $n = 31$ for both; HRP, $n = 28$ AM, $n = 30$ PM), *Salix gooddingii* (BWR, $n = 35$ for both; HRP, $n = 30$ for both), and *Tamarix chinensis* (BWR, $n = 35$ for both; HRP, $n = 15$ AM, $n = 9$ PM) at the Bill Williams (BWR) and Hassayampa (HRP) rivers.

Site and species	Measurement time	July water potential (MPa)			Cavitation threshold (MPa)
		Mean $\pm$ 1 SE	Minimum	Maximum	
Bill Williams River					
Populus fremontii	AM	-1.50 ± 0.04	-1.85	-1.00	-1.60†
	PM	-1.58 ± 0.04	-2.05	-0.90	
Salix gooddingii	AM	-1.30 ± 0.04	-1.70	-0.75	-1.40†
	PM	-1.75 ± 0.04	-2.20	-1.30	
Tamarix chinensis	AM	-3.25 ± 0.07	-4.35	-2.25	-7.00‡
	PM	-3.10 ± 0.12	-4.65	-1.75	
Hassayampa River					
Populus fremontii	AM	-1.60 ± 0.06	-2.50	-1.10	-1.60†
	PM	-1.80 ± 0.07	-2.40	-1.25	
Salix gooddingii	AM	-1.80 ± 0.05	-2.75	-1.20	-1.40†
	PM	-1.95 ± 0.06	-2.45	-1.40	
Tamarix chinensis	AM	-3.95 ± 0.15	-4.95	-3.00	-7.00‡
	PM	-3.60 ± 0.21	-4.40	-2.65	

† From Pockman et al. (1995).
‡ From Pockman and Sperry (2000).

eighteen trees in our sampling population (Fig. 7), nine of which died by the following year. Thus, like *P. fremontii*, branch sacrifice in *S. gooddingii* apparently increased water supply to noncavitated branches at deep groundwater sites at HRP, but this apparent adjustment in shoot-to-root ratio was not sufficient to prevent mortality in some trees.

Tamarix chinensis *response to groundwater depth*

Tamarix chinensis is known to be a facultative phreatophyte (Busch et al. 1992, Busch and Smith 1995) that is more drought tolerant than native riparian tree species (Cleverly et al. 1997; Horton et al. 2001). Predawn ψ of *T. chinensis* was lower than that of the native species, but ψ_{pd} of *T. chinensis* was highly variable and was unrelated to DGW at both rivers (Fig. 3). The low ψ_{pd} observed in *T. chinensis* could be an indication of low soil water availability, however, *T. chinensis* is known to have low tissue ψ as a result of salt accumulation (Busch and Smith 1995), which may help it to extract water from the unsaturated soil.

Leaf gas exchange of *T. chinensis* is known to be less sensitive to soil and atmospheric water deficits than that of the native species (Horton et al. 2001). Consistent with this report, there were no significant relationships between g_s and P_n of *T. chinensis* and DGW at either river (Figs. 4 and 5). However, both g_s and P_n were lower at HRP, where *T. chinensis* occurred at greater DGW than at BWR. The lower leaf gas exchange rates measured at HRP could be due to stomatal closure in response to low daytime shoot ψ. Mean daytime shoot ψ at both rivers (Table 2) was below thresholds (-2.5 MPa for g_s and -2.8 MPa for P_n) associated with reduced leaf gas exchange (Horton et al. 2001). Reductions in leaf gas exchange because of low daytime shoot ψ were likely more pronounced at HRP than at BWR because of lower shoot ψ at HRP (Table 2).

Tamarix chinensis differs from the native species in both vulnerability to xylem cavitation and in stomatal regulation of water loss. The native species are extremely vulnerable to xylem cavitation, yet maintain high rates of xylem hydraulic conductivity and g_s until shoot ψ approaches cavitation thresholds (Pockman et al. 1995; Horton et al. 2001). In contrast, *T. chinensis* is much less vulnerable to xylem cavitation and experiences a more gradual loss in xylem hydraulic conductivity as shoot ψ decreases (Pockman and Sperry 2000), suggesting a different pattern of stomatal regulation of water loss for it compared to the native species. At both rivers, shoot ψ of *T. chinensis* was higher in the mid-afternoon when evaporative demand was higher than in the mid-morning (Table 2), suggesting stomatal closure in the afternoon and subsequent recovery of shoot ψ. In contrast, shoot ψ of both native species was lower in the mid-afternoon than in the mid-morning (Table 2), suggesting less stomatal closure and less recovery of shoot ψ.

Branch sacrifice has not been reported to be an adaptation for surviving extreme water stress in *T. chinensis*. Canopy dieback occurred in *T. chinensis* at both rivers, but it was unrelated to DGW (Fig. 7). Dieback was 30% or less for most trees at BWR, whereas dieback ranged up to 70% at HRP. In contrast to the native species, daytime shoot ψ of *T. chinensis* declined as ψ_{pd} declined at both rivers (Fig. 6), suggesting less improvement in shoot water availability from branch sacrifice in *T. chinensis* than in the native species. However, the fact that there was no mortality of *T. chinensis* in our sampling populations at either river suggests that *T. chinensis* uses other mechanisms, such as low tissue osmotic potential that allows extraction of water from the unsaturated soil (Busch and Smith 1995), and stomatal regulation of water loss to maintain favorable shoot ψ (Devitt et al. 1997) to survive periods of ex-
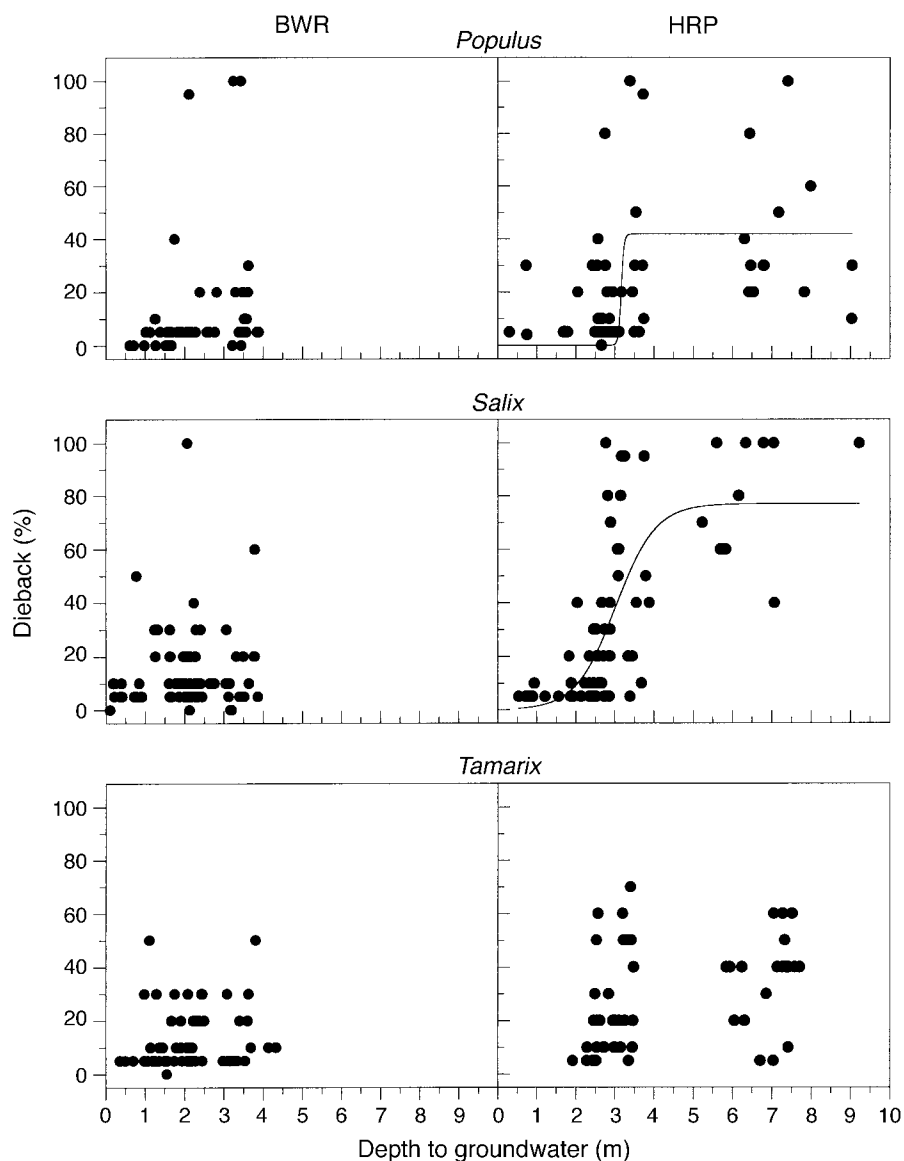
FIG. 7. Recent canopy dieback as a function of July depth to groundwater (DGW) for *Populus fremontii* (BWR, $n = 69$; HRP, $n = 63$), *Salix gooddingii* (BWR, $n = 86$; HRP, $n = 84$), and *Tamarix chinensis* (BWR, $n = 56$; HRP, $n = 64$) at both the Bill Williams (BWR) and Hassayampa (HRP) rivers. The *P. fremontii* trees at BWR that experienced 100% dieback appeared to be victims of a fungal pathogen (J. L. Horton, *personal observation*). Solid lines describe a three-parameter sigmoidal function of canopy dieback in relation to DGW (*P. fremontii*, HRP, $y = 41.89/(1 + \exp[-(x - 3.16) / 0.04])$, $r^2 = 0.450$, $P < 0.001$; *S. gooddingii*, HRP, $y = 76.69/(1 + \exp[-(x - 3.00) / 0.51])$, $r^2 = 0.544$, $P < 0.001$). Other relationships were not significant at $P < 0.05$.

treme water stress that kill some individuals of *P. fremontii* and *S. gooddingii*.

Conclusions

Our results support Hypothesis 1 for the native species by demonstrating that increases in DGW caused reduction in shoot ψ that led to decreased g_s and P_n and increased canopy dieback and mortality in both *P. fremontii* and *S. gooddingii*. Both *P. fremontii* and *S. gooddingii* experienced increased canopy dieback and mortality when DGW increased above an apparent

threshold of 2.5–3.0 m (Fig. 7) supporting Hypothesis 2a. Although there was evidence of increased water stress in *T. chinensis* at HRP where DGW was greater than at BWR, no mortality occurred for *T. chinensis* over the range of DGW measured in this study. Consistent with Hypothesis 3, *T. chinensis* was more tolerant of extreme water stress imposed by deep groundwater than either *P. fremontii* or *S. gooddingii*, whereas *P. fremontii* was more tolerant of deeper groundwater than *S. gooddingii*.

In Hypothesis 4, we predicted differences in the

physiological response of riparian trees to DGW between the two rivers, with the trees at BWR expected to be more sensitive changes in DGW. However, we were unable to evaluate this hypothesis because groundwater at BWR was consistently shallow, and did not appear to seriously limit the physiological condition of *P. fremontii, S. gooddingii,* or *T. chinensis* over the range of DGW observed in our study. In contrast, DGW varied greatly over time and space at HRP, and all three species experienced water stress at sites with deeper DGW along this river.

Management implications

Human impacts on alluvial water tables have been proposed to 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). This decline has often been coupled with the invasion of *T. chinensis* (Robinson 1965). Dams and diversions often alter the hydrological regime of riparian ecosystems by shifting peak flows from their usual spring occurrence to late summer (Fenner et al. 1985). These regulated peak flows are then out of phase with the spring seed drop of native riparian trees (Reilly and Johnson 1982), but encourage the establishment of *T. chinensis,* which produces seed from April to October (Warren and Turner 1974, Shafroth et al. 1998). Often flow regulation causes channel narrowing that allows establishment of trees in the former floodplain channel (Friedman et al. 1995). If flow regimes have been altered, this establishment would likely be by *T. chinensis* rather than native tree species. Once established, *T. chinensis* has many traits that allow it to persist and outcompete native vegetation in areas where water availability may be reduced (Cleverly et al. 1997, Smith et al. 1998).

However, it is not the dams themselves, but the pattern of stream flow management that leads to downstream forest decline (Mahoney and Rood 1998). There has been much interest in "naturalizing" flow regimes on managed rivers in order to restore degraded riparian ecosystems (Briggs 1996, Poff et al. 1997, Stromberg 1997, Mahoney and Rood 1998, Shafroth et al. 1998). Our study demonstrates that regulated flows may be beneficial to mature riparian trees. At BWR, flow releases from Alamo Dam maintained DGW within 3.5 to 4.0 m of the surface during our study. In this range of DGW, riparian trees were in better physiological condition than those that occurred at deeper groundwater sites at the free flowing HRP. When DGW fell below ~3 m, the physiological condition of both native species declined, resulting in mortality in some individuals, and this response was more pronounced in *S. gooddingii* than in *P. fremontii.* There was evidence of increased water stress in *T. chinensis* at deep groundwater sites, yet no trees died, demonstrating that *T. chinensis* is better able to tolerate water stress caused

by deep groundwater than the native species. Thus, in order to effectively manage river systems to conserve or restore native riparian forests, it will be necessary to reduce human activities that lower groundwater beyond the rooting depth of desired native riparian tree species, because deep groundwater has greater negative physiological impacts on native *P. fremontii* and *S. gooddingii* than on the exotic, *T. chinensis.*

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