

## Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona

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### Abstract

Variation in the sources of water used by tree species has important ramifications for forest water balances. The fraction of tree transpiration water derived from the unsaturated soil zone and groundwater in a riparian forest was quantified for *Populus fremontii*, *Salix gooddingii*, and *Prosopis velutina* across a gradient of groundwater depth and streamflow regime on the San Pedro River in southeastern Arizona, US. The proportion of tree transpiration derived from different potential sources was determined using oxygen ( $\delta^{18}\text{O}$ ) and hydrogen ( $\delta\text{D}$ ) stable isotope analysis in conjunction with two- and three-compartment linear mixing models. Comparisons of  $\delta^{18}\text{O}$  and  $\delta\text{D}$  of tree xylem water with that of potential water sources indicated that *Salix gooddingii* did not take up water in the upper soil layers during the summer rainy period, but instead used only groundwater, even at an ephemeral stream site where depth to groundwater exceeded 4 m. *Populus fremontii*, a dominant 'phreatophyte' in these semi-arid riparian ecosystems, also used mainly groundwater, but at the ephemeral stream site during the summer rainy season this species derived between 26 and 33% of its transpiration water from upper soil layers. Similarly, at the ephemeral stream site during the summer rainy period, *Prosopis velutina* derived a greater fraction of its transpiration water from upper soil layers, than at a perennial stream site where groundwater depth was less than 2 m. Measurements of transpiration flux combined with stable isotope data revealed that *Populus fremontii* transpired a greater quantity of water from upper soil layers at the ephemeral stream site than at the perennial stream site. These results imply that transpiration from groundwater and unsaturated soil layers by riparian vegetation may depend on the interaction between site conditions and species assemblage. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:*  $\delta^{18}\text{O}$ ;  $\delta\text{D}$ ; Plant water sources; Cottonwood; Willow; Mesquite; *Salix gooddingii*; *Populus fremontii*; *Prosopis velutina*; Leaf water potential; Phreatophytes

### 1. Introduction

Riparian forests in the southwestern US are characterized by a mixed assemblage of obligate phreatophytes (plants that send their roots into or below the capillary fringe to use groundwater) and facultative phreatophytes (plants that can also survive in upland environments where groundwater is not available). However, extreme spatial and temporal dynamics of

water within riparian ecosystems in arid and semi-arid regions can place severe constraints on the ability of trees to meet transpiration requirements during key periods of the growing season. For example, groundwater pumping and surface water diversions have produced dramatic changes in stand structure and species composition of riparian areas in this region (Stromberg and Patten, 1990). Successful conservation of these forests will require knowledge on the dependence of riparian species on groundwater and conversely, on the feedback between riparian vegetation and stream and groundwater dynamics. Not all

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woody species in these forests use only groundwater for transpiration as the term ‘phreatophyte’ implies. Use of growing season precipitation can vary considerably among different woody species in the riparian environment (Smith et al., 1991; Busch et al., 1992; Thorburn and Walker, 1994; Kolb et al., 1997). However, many widely used hydrologic models assume that riparian trees derive water principally from the saturated zone (McDonald and Harbaugh, 1988), which is clearly an oversimplification. Characterization of the conditions that promote use of alternative water sources and identification of those species most likely to use these water sources in riparian forests is necessary to accurately assess water budgets at the catchment level in semi-arid and arid basins.

The long-term reliability of groundwater may encourage riparian trees to develop roots predominantly in the capillary fringe and saturated zone rather than throughout the soil profile, especially if precipitation during the growing season is unreliable (Ehleringer and Dawson, 1992). Conversely, plants that maintain roots in many soil layers, or that can rapidly deploy roots into moisture-rich patches in the soil, may respond opportunistically to precipitation. Research on riparian trees using stable isotope methodology has provided evidence for both modes of root system function. In Australia, *Eucalyptus* spp. used various combinations of groundwater, rainfall-derived shallow soil water, and stream water (Mensforth et al., 1994; Thorburn and Walker, 1994; Dawson and Pate, 1996; Jolly and Walker, 1996). Trees along a perennial, montane stream in California took up water from upper soil layers early in the growing season, then used primarily groundwater when soil dried (Smith et al., 1991). In western Arizona, *Populus fremontii* and *Salix gooddingii* used groundwater throughout the entire growing season at perennial and ephemeral streams, regardless of depth to groundwater (Busch et al., 1992). However, responses of these trees to precipitation events were not assessed in this Mojave Desert environment. Similarly, mature *Acer negundo* trees in northern Utah used only groundwater, and did not appear to use perennial stream water or shallow soil water (Dawson and Ehleringer, 1991). In contrast, this species did use soil water from precipitation at ephemeral and perennial stream reaches in Arizona (Kolb et al., 1997).

Although previous studies addressed various components of riparian ecosystems and tree water sources,

questions still remain about the integrated effects of groundwater depth and flow regime on the ability of riparian trees to take up precipitation during the growing season. Knowledge of species-specific responses to growing season precipitation and constraints on deep and shallow root function for water uptake will facilitate predictions of how habitat variation and declining groundwater affect patterns of transpiration in riparian ecosystems.

The upland species *Quercus gambelii*, *Juniperus osteosperma*, and *Pinus edulis* in the southwestern US derived greater proportions of their transpiration water from summer precipitation as the amount of these rains increased across a broad climatic gradient (Williams and Ehleringer, 2000). Intraspecific variation of this type implies that the distribution of functional roots in woody species varies significantly across resource supply gradients. However, the tradeoffs associated with this variation have not been addressed. For instance, it is not known if development of roots in one zone of the rhizosphere comes at the expense of root activity elsewhere. Additionally, plants with roots deployed in upper soil layers should experience a greater amplitude of soil water availability compared to plants that access a deep, stable water source. Plant predawn water potential ( $\Psi_{pd}$ ), therefore, should be correlated with plant water sources (Dawson and Ehleringer, 1998). A better understanding of the tradeoffs between plant water balance and active rooting depth will help resolve linkages between groundwater, soil water, and transpiration in riparian forests.

The riparian forest sites addressed in the current study receive a high proportion (approximately 60%) of annual precipitation from summer ‘monsoon’ storms. Thus, it was predicted that at least some of the dominant riparian trees would use summer precipitation. As in most riparian environments in semi-arid regions, the floodplains varied in depth to groundwater that may further differentiate shallow soil water use among the dominant riparian species. This study addressed seasonal patterns of water source use by dominant riparian tree species at sites with contrasting groundwater depths and streamflow conditions. This study was part of the Semi-Arid Land Surface Atmosphere (SALSA) program (USDA-ARS, Tucson, AZ) whose primary aim was to validate models for basin-wide water balances (Goodrich et al., 2000). The specific objectives of this study were to (1)

determine if riparian tree species along the San Pedro River in southeastern Arizona use growing season precipitation; (2) assess whether depth to groundwater influences the capacity for these trees to use precipitation and (3) characterize physiological consequences associated with specific rooting patterns.

## 2. Methods

### 2.1. Study sites

Three sites were selected to represent a gradient in streamflow and groundwater availability. All sites were located within the San Pedro Riparian National Conservation area at elevations between 1150 and 1250 m (ca. 31°33'N; 110°07'W). The San Pedro River is a low-gradient alluvial drainage that flows from Sonora, Mexico north to the Gila River in southern Arizona. Mean precipitation at the three sites is 330 mm per year, with 60% of the rain falling in the summer and most of the remainder falling in winter months (NOAA, 1996). The hydrologic regime at the three sites was perennial (Lewis Springs), intermittent (Boquillas Ranch), and ephemeral (Escapule Wash). The riparian floodplain vegetation consisted of *P. fremontii* (Fremont cottonwood) and *S. gooddingii* (Goodding willow) as the dominant and sub-dominant overstory species. In this region these species, both classified as obligate phreatophytes, generally form a narrow gallery forest in active floodplains (Stromberg, 1993a). *Prosopis velutina* (Velvet mesquite) was present as a sub-dominant tree and as an understory shrub within the *Populus/Salix* gallery forests. *Prosopis velutina* is a facultative phreatophyte that also occurs in xeric upland sites where groundwater is unavailable. Hereafter, these taxa will be referred to as *Populus*, *Salix*, and *Prosopis*.

### 2.2. Sampling methods

Between five and eleven tree clusters with each of the three species present were randomly selected at each site. Clusters were not considered blocks in a statistical sense because species were analyzed separately. Trees were sampled in spring (19–24 April), summer (7–11 June, 9–11 July, 8–11 August) and fall

(20–27 September) in 1997. April sampling occurred after *Populus* experienced spring leaf-flush. June and July sampling periods coincided with the annual dry season for this region. Sampling in August was performed during the height of the growing season and after a large monsoon precipitation event which did not produce over-bank flooding. During this single precipitation event, 27 mm of rainfall was measured at the perennial stream site, which fell during a single hour; trees were sampled 7, 8, and 10 days after the rainfall event at the ephemeral, intermittent and perennial stream sites, respectively. September sampling followed a series of storms that produced over-bank flooding along the perennial reach at the end of the growing season.

Stable isotopes of oxygen in xylem water extracted from twigs were used as natural tracers for determining the fraction of water taken from groundwater and unsaturated soil layers (Ehleringer and Dawson, 1992; Brunel et al., 1995). Plant stems of approximately 0.5 cm in diameter were sampled at midday from sunlit branches and stored in airtight glass vials for subsequent analysis of hydrogen and oxygen isotope ratios ( $\delta D$  and  $\delta^{18}O$ ). Soils were collected at each site from 5, 10, 25, 50, and 100 cm depths for analysis of  $\delta D$  and  $\delta^{18}O$  of water and gravimetric water content ( $\theta_g$ ). Local floodplain groundwater was collected from wells at each sampling period and at all sites. At the perennial reach, regional groundwater was collected from a deep (11 m) well located approximately 300 m from the stream and outside the local floodplain. Precipitation was collected at all sites in standard rain gauges that contained a layer of mineral oil to minimize evaporation. These integrated precipitation samples were collected monthly throughout 1997. A Scholander-type pressure chamber (PMS, Corvallis, OR) was used to measure predawn leaf water potentials ( $\Psi_{pd}$ ) on every sampling date.

### 2.3. Stable isotope analysis

Water was extracted from plant stems and soils by cryogenic vacuum distillation (Ehleringer and Osmond, 1989). Water samples from plant, soil, precipitation stream, and groundwater were analyzed for oxygen isotope ratios ( $\delta^{18}O$ ) on a Finnigan Delta-S isotope ratio mass spectrometer using  $CO_2$  equilibration (University of Arizona Geosciences Stable

Isotope Facility). A subset of samples was also analyzed for hydrogen isotope ratios ( $\delta D$ ) using a chromium reduction furnace (HD-Device, Finnigan-Mat, Bremen, Germany) to convert liquid water to hydrogen gas.

#### 2.4. Data analysis

Plant  $\delta^{18}O$  values were compared with those of soil water from different depths and groundwater to determine sources of plant transpiration water. One-sided  $t$ -tests ( $\alpha = 0.05$ ) were used to determine if mean  $\delta^{18}O$  of a species at a given site was more positive (enriched) than  $\delta^{18}O$  of floodplain groundwater in June, July and August. Normality of  $\delta^{18}O$  data was determined with the Shapiro–Wilk test.  $\delta D$ – $\delta^{18}O$  relationships of isotopic values from 10, 25 and 100 cm soil depths, extracted plant water, precipitation and groundwater were used to determine further differences in plant water source use (Craig, 1961; Clark and Fritz, 1998). Source waters with similar  $\delta^{18}O$  or  $\delta D$  values may have different  $\delta D$ – $\delta^{18}O$  relationships due to evaporation conditions.

Although  $\delta^{18}O$  and  $\Psi_{pd}$  values are presented for all sampling periods, statistical analyses were restricted to June, July and August. This restriction was due to phenological differences among species (*Prosopis* and *Salix* were not fully leafed out in April), and because, large storms produced over-bank flooding at the perennial site in September. Over-bank flooding percolated through the soil creating similar  $\delta^{18}O$  values to a depth greater than 1 m. Therefore, it was not possible to distinguish use of monsoon precipitation from groundwater and floodwater use. Multivariate analysis of variance (MANOVA;  $\alpha = 0.05$ ) was used to analyze the effect of site and sampling date (June, July and August) on the difference between plant  $\delta^{18}O$  and groundwater  $\delta^{18}O$  for each species (Von Ende, 1993). This difference was used to standardize plant response across sites even when there were shifts in local groundwater  $\delta^{18}O$  values. ANOVA models ( $\alpha = 0.05$ ) were used to compare sites within sampling dates if MANOVA revealed a significant interactive effect. Since it was expected that sampling date would produce an effect on  $\delta^{18}O$ , differences within a site across dates were not analyzed. Contrasts ( $\alpha = 0.05$ ) were used to determine differences between sites. Plots of residuals indicated that cal-

culated  $\delta^{18}O$  differences were linear and normally distributed with homogenous error variances, thus meeting the assumptions of MANOVA.

In cases where plant  $\delta^{18}O$  differed significantly from that of local groundwater, the fraction ( $f$ ) of total plant xylem water derived from shallow soil layers (0–50 cm) was calculated using a two-compartment linear mixing equation of the form

$$\delta^{18}O_t = f(\delta^{18}O_s) + (1 - f)(\delta^{18}O_{gw}) \quad (1)$$

where  $\delta^{18}O_t$  was the measured  $\delta^{18}O$  of tree xylem sap,  $\delta^{18}O_s$  was a weighted average of the measured  $\delta^{18}O$  values of soils sampled at 5, 10, 25 and 50 cm depths. Soil  $\delta^{18}O$  values were weighted by gravimetric water content ( $\theta_g$ ) at each depth by dividing mean  $\theta_g$  at each depth by the sum of  $\theta_g$  at all depths.  $\delta^{18}O_{gw}$  was the measured  $\delta^{18}O$  value of groundwater. The equation was solved for  $f$ , with  $f$  being the fraction of total plant water obtained from water in shallow soil layers. Differences between sites were determined for each species using  $t$ -tests.

At the intermittent stream site, the use of a two-compartment model was inappropriate because of the existence of a third source of plant water. Therefore, a three-compartment linear mixing model was used. This was done using plant and source  $\delta^{18}O$  and  $\delta D$  to produce two equations for tree water source. These two equations, in combination with a third equation (for constraining the sum of the source fractions to one) produced a system of three equations and three unknown variables of the form

$$\delta^{18}O_t = a(\delta^{18}O_{S1}) + b(\delta^{18}O_{S2}) + c(\delta^{18}O_{S3}) \quad (2)$$

$$\delta D_t = a(\delta D_{S1}) + b(\delta D_{S2}) + c(\delta D_{S3}) \quad (3)$$

$$1 = a + b + c \quad (4)$$

where  $\delta^{18}O_t$  and  $\delta D_t$  are the oxygen and deuterium values of extracted plant water. The subscripts S1, S2, S3 are sources 1, 2, and 3, respectively.  $a, b, c$  are the fractions of total plant xylem water derived from sources 1, 2, and 3. Equations were solved simultaneously using algebraic substitution. Results were checked using MatLab (MathWorks, Inc., Natwick, MA).

To analyze effects of site and date (June, July, August) on  $\Psi_{pd}$ , MANOVA, ANOVA and contrasts were used as described above. Data were transformed

as necessary to meet the assumptions of MANOVA based on inspection of residual plots. Non-transformed values are presented in the figures and text. For each species within a site, linear regression analysis was used to quantify the relationship between  $\Psi_{pd}$  and  $\delta^{18}\text{O}$  measured throughout the growing season.

### 3. Results

Mean depth to groundwater was 1.80, 2.61 and 4.26 m at the perennial, intermittent, and ephemeral stream sites, respectively (Table 1). Median streamflow along the perennial reach of the San Pedro River measured downstream of our study site at the Charleston gauge for the period January–October 1997 was  $0.2\text{ m}^3\text{ s}^{-1}$ . (Tayadon et al., 1998). Streamflow was observed along the intermittent reach for 11 months of 1997, but there was no flow in July. Flow occurred only briefly during storm events at the ephemeral stream site. Streamflow was observed twice in August at this site, but may have occurred during other storms as well.

Monsoon rains had  $\delta^{18}\text{O}$  values ranging from 2.0‰ to  $-3.5\text{‰}$  (Fig. 1), while winter precipitation had more negative  $\delta^{18}\text{O}$  values ranging from  $-4.4\text{‰}$  to  $-8.7\text{‰}$  (data not shown).  $\delta^{18}\text{O}$  values of groundwater sampled from the local floodplain did not vary much over the growing season at the perennial and ephemeral reach, averaging  $-8.3 \pm 0.2\text{‰}$  ( $\pm 1$  S.E.) and  $-8.4 \pm 0.2\text{‰}$ , respectively (Fig. 1). In late September, after a

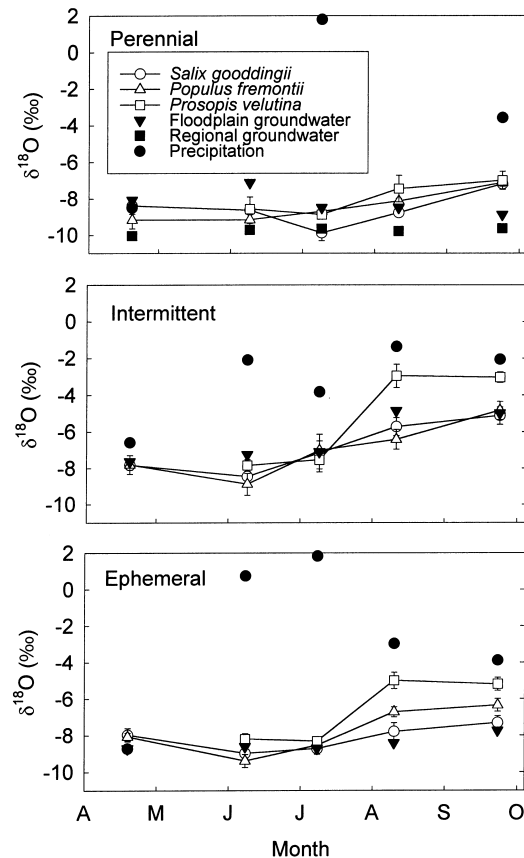


Fig. 1. Mean  $\delta^{18}\text{O}$  values of *Salix gooddingii*, *Populus fremontii*, and *Prosopis velutina*, regional groundwater, floodplain groundwater, and precipitation during the 1997 growing season along perennial, intermittent and ephemeral reaches of the San Pedro River in southeastern Arizona. Vertical bars represent  $\pm 1$  S.E. of the mean.

Table 1

Depth to groundwater (m) from the ground surface at the three study sites along the San Pedro River, Arizona in 1997<sup>a</sup>

Month	Perennial	Intermittent	Ephemeral
February	–	2.28	3.86
March	0.95	2.27	3.90
April	1.98	–	4.21
June	1.42	2.61	4.43
July	2.43	3.32	4.69
August	2.08	2.67	4.48
September	1.91	2.53	4.31
Average	1.8	2.61	4.26

<sup>a</sup> Data were obtained from a single well that penetrated the local floodplain groundwater at the perennial and intermittent site. Data at the ephemeral study site are an average of two wells. All wells were located within 10 m of the stream channel.

particularly large series of storms, groundwater at the ephemeral reach was enriched (more positive) ( $\delta^{18}\text{O} = -7.8\text{‰}$ ) relative to previous sampling periods.  $\delta^{18}\text{O}$  of local floodplain groundwater at the intermittent stream site varied substantially (Fig. 1). During April, June, and July, the local floodplain groundwater ( $\delta^{18}\text{O} = -7.8\text{‰}$ ) isotopically resembled  $\delta^{18}\text{O}$  of winter precipitation ( $-6.1 \pm 0.35\text{‰}$ ) at the intermittent stream site. However, during the summer rainy season in response to storm and flow events,  $\delta^{18}\text{O}$  of local floodplain groundwater at this site was substantially enriched ( $-4.9 \pm 0.07\text{‰}$ ) and reflected  $\delta^{18}\text{O}$  of monsoon precipitation and recent streamflow. Isotopic composition of regional groundwater was

stable throughout the growing season, with mean  $\delta^{18}\text{O}$  of  $-9.7 \pm 0.07\%$ . Stream water was tightly linked with groundwater in these reaches, and  $\delta^{18}\text{O}$  values of stream water (data not shown) were generally related to those of floodplain groundwater; therefore, stream water was not treated as a separate source.

### 3.1. $\delta^{18}\text{O}$ of tree xylem water

#### 3.1.1. *Salix gooddingii*

*Salix* (willow) exhibited little variation in water-source use over the growing season among the three sites and relied predominantly on groundwater (Fig. 1).  $\delta^{18}\text{O}$  values of this species were not significantly enriched above those of groundwater at any site or any sampling period ( $p > 0.13$ ).  $\delta^{18}\text{O}$  values of *Salix* were not different among sites or sampling periods ( $p > 0.07$ ), and this species did not appear to use significant amounts of precipitation at any site, even in August after a significant precipitation event. Although  $\delta^{18}\text{O}$  values of *Salix* increased at the intermittent and ephemeral stream sites in August, these shifts mirrored changes in groundwater  $\delta^{18}\text{O}$  within the floodplain.

#### 3.1.2. *Populus fremontii*

$\delta^{18}\text{O}$  values of xylem water in *Populus* (cottonwood) varied seasonally and apparently responded to monsoon precipitation events (Fig. 1). *Populus* relied on groundwater during the rainless period in June and July, but showed evidence of water use from shallow soil during the rainy season. The  $\delta^{18}\text{O}$  values of *Populus* did not differ from that of floodplain groundwater in June and July at any of the three sites ( $p > 0.19$ ). However, use of water from shallow soil layers during the summer rainy period (August) developed differently among the three riparian habitats studied. These habitat-related differences in  $\delta^{18}\text{O}$  of *Populus* were reflected statistically in a significant interaction between sampling date and site ( $p = 0.05$ ). Specifically, the difference between  $\delta^{18}\text{O}$  of *Populus* and that of floodplain groundwater varied between all sites in August ( $p < 0.0025$ ).  $\delta^{18}\text{O}$  values of *Populus* were 0.4‰ more positive than that of floodplain groundwater at the perennial stream site ( $p = 0.01$ ), and showed the greatest difference (+2.1‰) above floodplain groundwater at the ephemeral stream site ( $p < 0.0001$ ). However,  $\delta^{18}\text{O}$  of *Populus* was more negative

than that of floodplain groundwater at the intermittent site (two-sided  $t$ -tests;  $p < 0.03$ ).

#### 3.1.3. *Prosopis velutina*

Similar to *Populus*, water sources of *Prosopis* (mesquite) varied seasonally in response to monsoon rain events (Fig. 1).  $\delta^{18}\text{O}$  values of *Prosopis* were affected by the interaction between site and sampling date ( $p = 0.04$ ). During the dry season (June and July), mean  $\delta^{18}\text{O}$  of *Prosopis* was similar to floodplain groundwater ( $p > 0.12$ ) except at the ephemeral stream site in July ( $p = 0.04$ ). *Prosopis*  $\delta^{18}\text{O}$  values were enriched relative to floodplain groundwater in August at the intermittent and ephemeral site ( $p < 0.02$ ) indicating use of monsoon-derived shallow soil water. *Prosopis*  $\delta^{18}\text{O}$  did not differ from floodplain groundwater at the perennial stream site in August ( $p = 0.11$ ). However, there was considerable variation among  $\delta^{18}\text{O}$  values of individual trees at the perennial stream site that indicated some trees used groundwater while others used a combination of shallow soil water and groundwater. This was reflected in the difference between plant  $\delta^{18}\text{O}$  and groundwater  $\delta^{18}\text{O}$ . These data indicated that  $\delta^{18}\text{O}$  values of *Prosopis* were similarly enriched relative to floodplain groundwater in June and August at the intermittent and perennial stream sites ( $p > 0.11$ ). However, trees at the ephemeral site were more enriched relative to groundwater than at the other two sites ( $p < 0.01$ ).

### 3.2. $\delta\text{D}$ – $\delta^{18}\text{O}$ plots

Isotope values of *Populus*, *Salix*, and *Prosopis* water in  $\delta\text{D}$ – $\delta^{18}\text{O}$  space plotted near groundwater and soil water from 100 cm depth at the perennial stream site (Fig. 2). At the intermittent stream site, values for *Populus* and *Salix* were between local floodplain groundwater (sampled in July and August) and water from the 100 cm depth, but *Prosopis* plotted between soil water from the 10, 25 and 100 cm depths. *Salix* values were similar to those of groundwater at the ephemeral stream site and *Populus* values were between those of groundwater and 100 cm soil demonstrating potential use of shallow soil water. *Prosopis* plotted with soil water from the 25 and 100 cm at the ephemeral stream site.

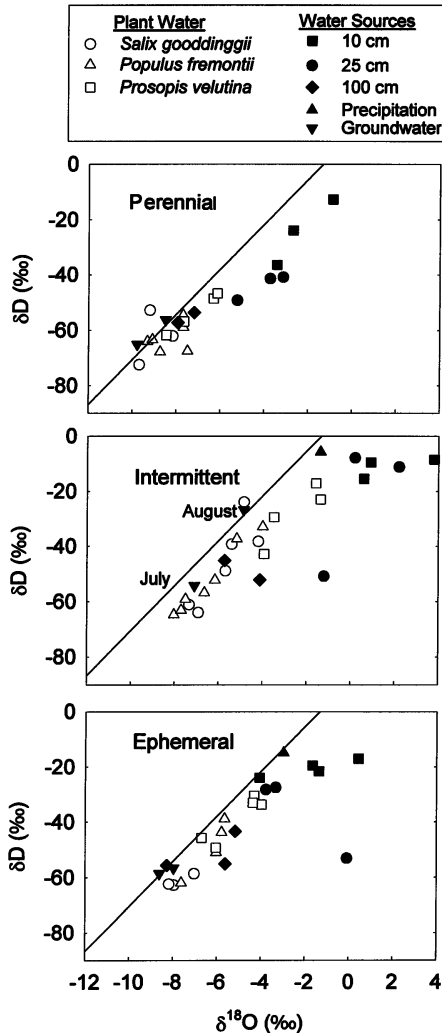


Fig. 2.  $\delta D$ - $\delta^{18}O$  values from trees, soil, groundwater, and rainfall in August 1997 along perennial and intermittent reaches and an ephemeral tributary of the San Pedro River in southeastern Arizona. Fitted line is the global meteoric water line (GMWL) ( $\delta D = 8.31\delta^{18}O + 10.8$ ) (Clark and Fritz, 1998). Soil water was extracted from 10, 25, and 100 cm depths.

3.3.  $\delta^{18}O$  and gravimetric content of soil water

The large rainfall event in August caused gravimetric water content ( $\theta_g$ ) in the shallow soil layers to increase at all sites (Fig. 3).  $\theta_g$  increased from 5% in June to 18% in August in the upper 10 cm at the perennial reach, whereas  $\theta_g$  at this depth increased from 2 to 6% and from 2 to 8% at the ephemeral and

intermittent stream sites, respectively. Changes in  $\theta_g$  at the 25, 50, and 100 cm depths between June and August were minimal along the perennial and intermittent reaches.  $\theta_g$  increased slightly over the same period at the 25 and 50 cm depths along the ephemeral reach. Soil water  $\delta^{18}O$  values were more positive in upper than in lower layers (Fig. 3), and became more negative with depth.  $\delta^{18}O$  values at 100 cm ( $-8.0\text{‰}$ ) were similar to those of groundwater at the perennial site, however,  $\delta^{18}O$  values at the same depth were approximately  $-6.0\text{‰}$  at the ephemeral and intermittent reaches.  $\delta^{18}O$  values of soil water in the upper 25 cm of soil resembled  $\delta^{18}O$  of summer monsoon rainfall (Fig. 1).

3.4. Fraction of transpiration water derived from shallow soil

$\delta^{18}O$  of *Salix* did not differ from groundwater at any period and therefore the fraction of water derived from shallow unsaturated soil layers was assumed to be zero. When  $\delta^{18}O$  of *Prosopis* and *Populus* differed from groundwater at the perennial and ephemeral stream sites, the percentage of shallow (0–50 cm) soil water use was calculated from the two-compartment mixing model (Eq. (1) and Table 2). Initially, the percentage of transpiration water derived from shallow soil was calculated using  $\delta^{18}O$  of floodplain ground-

Table 2  
Percentage of xylem water ( $\pm 1$  S.E.) derived from shallow soil layers in August after a monsoon rain event<sup>a</sup>

Species	Perennial stream site			Ephemeral stream site		
	June	July	August	June	July	August
<i>Salix gooddingii</i>	0	0	0	0	0	0
<i>Populus fremontii</i>	0	0	$8 \pm 8$ a	0	0	$26 \pm 7$ b
<i>Prosopis velutina</i>	0	0	$16 \pm 2$ a <sup>b</sup>	0	0	$33 \pm 7$ b <sup>b</sup>
						$52 \pm 5$
						$57 \pm 7$ b <sup>b</sup>

<sup>a</sup> Percent shallow soil water was calculated with a two-compartment mixing model (Eq. (1)). Normal type indicates the percent of water derived from shallow soil layers with local floodplain groundwater as an end member of the model. Different letters indicate significant differences between the ephemeral tributary and the perennial reach of the San Pedro River, Arizona.

<sup>b</sup> Indicates an estimate based on an average of regional groundwater and local floodplain water.

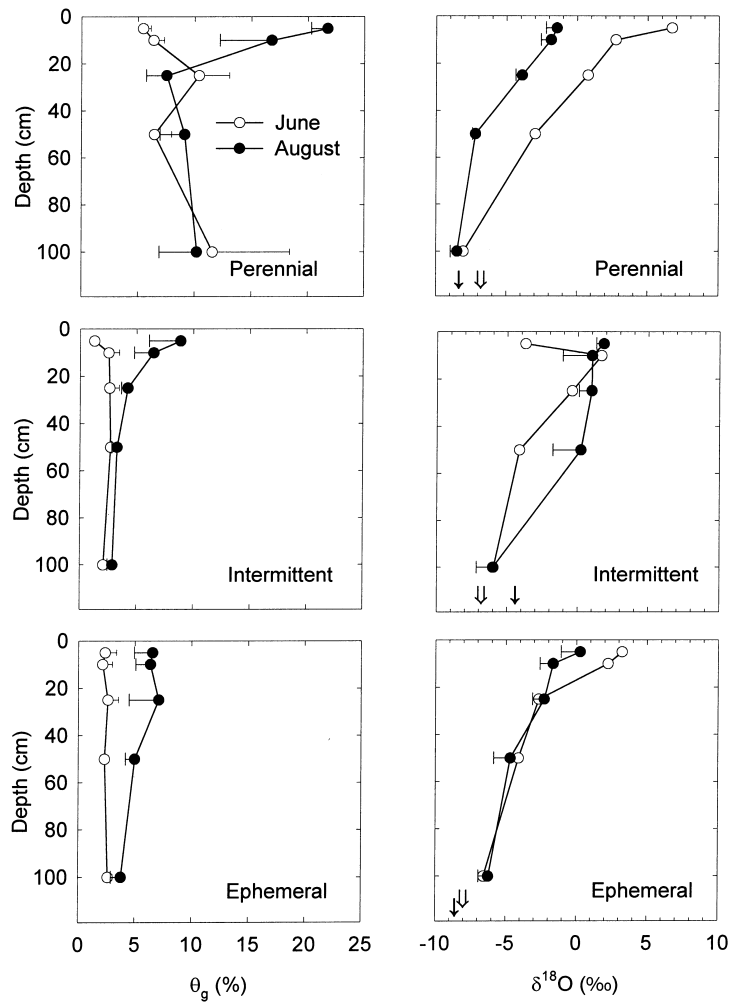


Fig. 3. Gravimetric soil water content ( $\theta_g$ ) and soil water  $\delta^{18}\text{O}$  at 5, 10, 25, 50, and 100 cm depths in June prior to the onset of the summer 'monsoon' rainy season, and August after a large precipitation event. The arrows on  $\delta^{18}\text{O}$  plots indicate the  $\delta^{18}\text{O}$  values of local floodplain groundwater in June (open arrow) and August (closed arrow). Soils were sampled in 1997 along a perennial and intermittent reach and an ephemeral tributary of the San Pedro River in southeastern, Arizona. Horizontal bars represent  $\pm 1$  S.E. of the mean and are presented when possible with the exception of soil  $\delta^{18}\text{O}$  values sampled in June.

water. However, trees at all sites appeared to have access to a source of water that was more negative in  $\delta^{18}\text{O}$  than local floodplain groundwater, such as regional groundwater. This produced negative values for soil water use for three trees, which were set to zero. Therefore, the average of local floodplain groundwater and regional groundwater  $\delta^{18}\text{O}$  was used for comparison, which may overstate the percentage of soil water used by *Populus* and *Prosopis*. The average difference between the two models was 7%.

In August after a summer rainfall event, *Populus* derived 8–16% of its transpiration from shallow soil layers at the perennial stream site and between 26 and 33% from soil water at the ephemeral stream site (Table 2). The proportion of *Populus* transpiration water from shallow soil layers at the perennial site was significantly less than that at the ephemeral stream site ( $p < 0.03$ ). After the August rain event, shallow soil water comprised 53–57% of transpiration water of *Prosopis* at the ephemeral stream site. (Table 2).



*Prosopis* was not different from groundwater ( $p = 0.11$ ) at the perennial site therefore mixing was assumed to be zero. In July at the ephemeral stream site,  $\delta^{18}\text{O}$  of *Prosopis* was significantly enriched relative to floodplain groundwater, but since shallow soil water content was low (<2%) at this time, this source was unlikely to have contributed to plant transpiration.

The fraction of transpiration water derived from shallow soil layers was calculated with the three-compartment mixing model (Eqs. (2)–(4)) at the intermittent site. Groundwater  $\delta^{18}\text{O}$  at this site changed substantially in August from prior periods (Fig. 1), yet many trees in August had  $\delta^{18}\text{O}$  values comparable to floodplain groundwater sampled in June and July. It appears that the August runoff moving through the stream channel flowed laterally through the gravelly substrate at this site, creating a saturated zone of water that was above the floodplain groundwater and had more positive  $\delta^{18}\text{O}$  values than the underlying aquifer. Therefore,  $\delta^{18}\text{O}$  values from three sources were used in the model: shallow soil water in August; shallow groundwater sampled in August; and deeper floodplain groundwater sampled in July. If  $\delta^{18}\text{O}$  of a species differed significantly from  $\delta^{18}\text{O}$  of shallow groundwater sampled in August then the three-compartment mixing model was applied.  $\delta^{18}\text{O}$  of *Prosopis* was enriched relative to August groundwater ( $p = 0.02$ ). However,  $\delta^{18}\text{O}$  of *Populus* was more negative than August groundwater ( $p = 0.03$ ).  $\delta^{18}\text{O}$  of *Salix* did not differ from August groundwater, and therefore shallow soil water use was assumed to be zero. *Prosopis* used 67% of the shallow August groundwater, 30% shallow soil water, and 2% of the deeper floodplain groundwater sampled in July (Table 3). *Populus* used –5% of the shallow August groundwater, 9% shallow soil water, and 97% of the deeper floodplain groundwater (Table 3). Negative percentages are an artifact produced by inherent matrix sensitivity. The three-compartment mixing model had high matrix sensitivity, which produced large standard errors (Table 3). This was likely due to the limited variation in the isotopic composition of water sources. To synthesize two- and three-compartment model results and provide a conceptual interpretation of root function in this system, the fraction of transpiration water derived from shallow soil water was plotted in relation to groundwater depth (Fig. 4).

Table 3

Percentage of xylem water ( $\pm 1$  S.E.) derived from shallow soil layers in August after a monsoon rain event for trees along an intermittent reach of the San Pedro River, Arizona<sup>a</sup>

Species	Intermittent stream reach		
	Shallow soil water (%)	Deep groundwater (%)	Shallow groundwater (%)
<i>Populus fremontii</i>	9 $\pm$ 4	97 $\pm$ 16	–5 $\pm$ 13
<i>Prosopis velutina</i>	30 $\pm$ 14	3 $\pm$ 27	67 $\pm$ 40

<sup>a</sup> Percent soil water was calculated with a three-compartment linear mixing model (Eq. (3)) for species whose mean  $\delta^{18}\text{O}$  values were significantly different than that of groundwater ( $p < 0.05$ ).

### 3.5. Predawn water potential

Predawn water potentials ( $\Psi_{\text{pd}}$ ) in *Salix* and *Populus* were high (between –0.75 and –0.25 MPa) and changed little over the growing season (Fig. 5). These two species apparently had access to groundwater even at the ephemeral stream site, where groundwater depth averaged 4 m. In June, when stream flow was still present and groundwater tables were less than 3 m deep at the intermittent site (Table 1), the effect of site ( $p < 0.045$ ) on  $\Psi_{\text{pd}}$  was consistent across all species. During June,  $\Psi_{\text{pd}}$  values did not differ between the perennial and intermittent reaches ( $p > 0.12$ ) and trees at these sites exhibited higher water potentials

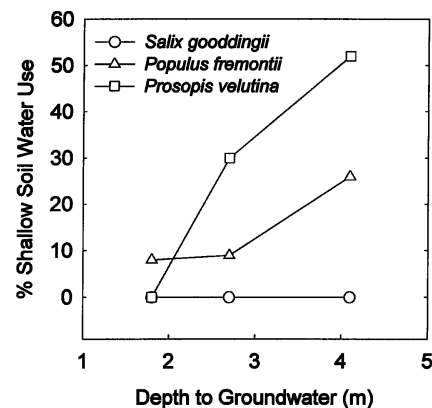


Fig. 4. The relationship between depth to groundwater and the percentage of plant transpiration water derived from shallow soil water in August after a monsoon rain event for *Salix gooddingii*, *Populus fremontii*, and *Prosopis velutina* sampled along the San Pedro River in Arizona.

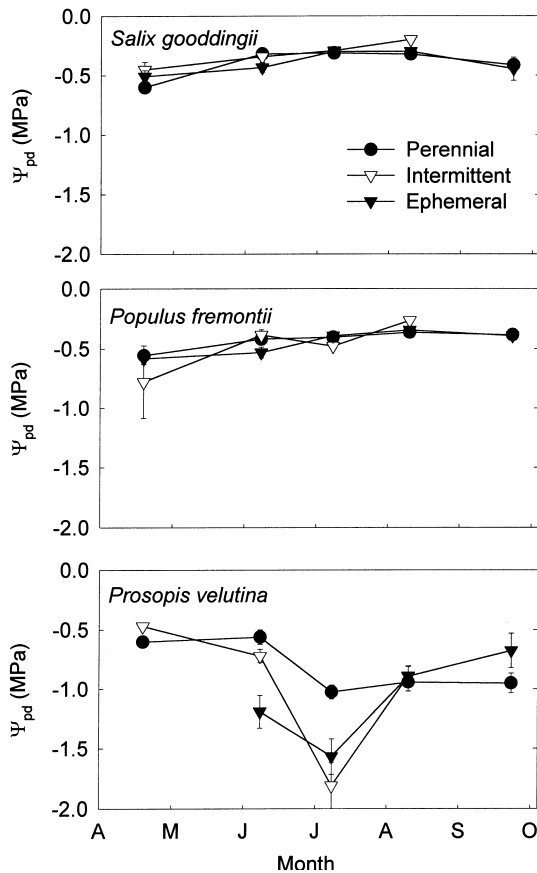


Fig. 5. Mean predawn leaf water potential ( $\Psi_{pd}$ ) of *Salix gooddingii*, *Populus fremontii*, and *Prosopis velutina* along perennial and intermittent reaches, and an ephemeral tributary of the San Pedro River in southeastern Arizona in 1997. Horizontal bars represent  $\pm 1$  S.E. of the mean.

relative to those at the ephemeral stream site ( $p < 0.02$ ).  $\Psi_{pd}$  of *Salix* and *Populus* did not vary between sites in July ( $p > 0.10$ ). In August, *Salix* and *Populus*  $\Psi_{pd}$  values were similar at the ephemeral and perennial reaches ( $p > 0.73$ ), but both species exhibited slightly higher water potentials along the intermittent reach compared to those measured at the other two sites ( $p < 0.05$ ).  $\Psi_{pd}$  of *Prosopis* showed considerable seasonal variation (Fig. 5). The lowest  $\Psi_{pd}$  values (between  $-1.0$  and  $-1.75$  MPa) were observed in July just before the onset of the summer rainy period. The lowest  $\Psi_{pd}$  values in *Prosopis* during the dry season were observed at the intermittent stream site, but did not differ significantly from those at the ephemeral

site ( $p = 0.27$ ). In July, *Prosopis* along these reaches had lower water potentials than at the perennial reach ( $p = 0.0005$ ).

The relationship between  $\Psi_{pd}$  and  $\delta^{18}\text{O}$  of xylem water during the growing season was evaluated for trees at the perennial and ephemeral stream sites. Mean values at each sampling period are shown (Fig. 6), however, regression analyses were based on all observations. There were no significant relationships between these variables at either of the two sites in *Salix* ( $p > 0.09$ ).  $\Psi_{pd}$  and  $\delta^{18}\text{O}$  likewise were not correlated in *Populus* and *Prosopis* at the perennial stream site. However, at the ephemeral stream site, seasonal changes in water source availability that produced enriched  $\delta^{18}\text{O}$  values of plant were accompanied by less negative  $\Psi_{pd}$  values for both *Populus* ( $p = 0.0091$ ;  $\Psi_{pd} = -0.14 + 0.04\delta^{18}\text{O}$ ,  $r^2 = 0.15$ ) and *Prosopis* ( $p = 0.0007$ ;  $\Psi_{pd} = 0.02 + 0.17\delta^{18}\text{O}$ ,  $r^2 = 0.43$ ).

#### 4. Discussion

Reed (1988) classified these dominant species of low-elevation riparian ecosystems in southern Arizona as obligate wetland (*Salix gooddingii*), facultative wetland (*Populus fremontii*) and facultative upland (*Prosopis velutina*) based on their probability of occurrence within the heterogeneous floodplain environment. This study provides new insight into belowground responses of these species across sites with very different patterns of groundwater availability and within a climatic region that receives a substantial input of precipitation late in the growing season from the regional monsoon. Within this setting, substantial variation among species and populations was found for fractional use of soil water derived from these late summer storms. Sites where groundwater was deep and streamflow duration was intermittent or ephemeral promoted greater fractional use of soil water by *Populus* and *Prosopis*, but not *Salix*. This study, as well as others (Dawson and Ehleringer, 1991; Smith et al., 1991; Busch et al., 1992; Mensforth et al., 1994; Thorburn and Walker, 1994; Dawson and Pate, 1996; Jolly and Walker, 1996; Kolb et al., 1997), confirms that 'phreatophytes' encompass a wide spectrum of functional types that respond uniquely to spatial and temporal variation in the distribution of available water in the rhizosphere.

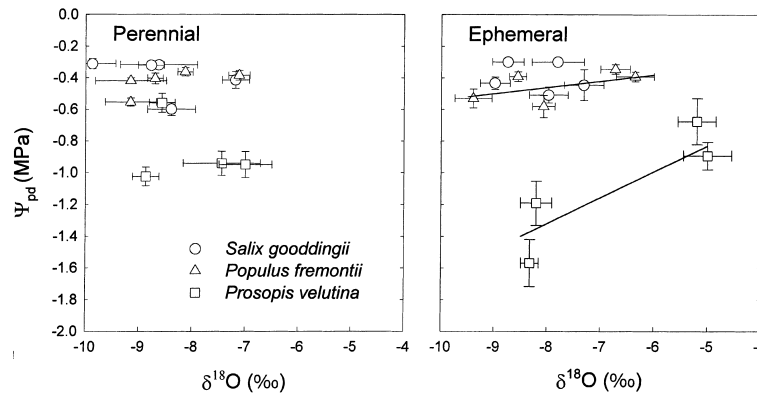


Fig. 6. Relationship between mean  $\delta^{18}\text{O}$  and mean predawn leaf water potential ( $\Psi_{\text{pd}}$ ) at each sampling period over the 1997 growing season for *Salix gooddingii*, *Populus fremontii*, and *Prosopis velutina* at a perennial reach and an ephemeral tributary of the San Pedro River in southeastern Arizona. Horizontal and vertical bars represent  $\pm 1$  S.E. of the mean. Fitted lines are the statistically significant regression relationships for a given species ( $\alpha = 0.05$ ).

*Salix* appeared to be most critically tied to groundwater among the three species examined at our sites within the San Pedro River drainage system. Predawn leaf water potentials in this species were high and did not change in response to seasonal inputs of precipitation, and isotopic composition of xylem water mirrored that of groundwater in the local floodplain aquifer. *Salix* apparently used water only from the saturated zone or capillary fringe above the water table (Figs. 1 and 2), and therefore did not respond to precipitation, even at the ephemeral stream site where groundwater depth was greater than 4 m. *Salix* apparently develops roots for water uptake only in the capillary fringe or saturated zone in these alluvial soils.

*Populus* and *Prosopis* exhibited greater flexibility for use of precipitation than did *Salix* along the San Pedro River. Use of monsoon precipitation may have reduced water stress as evidenced by the relationship between  $\Psi_{\text{pd}}$  and  $\delta^{18}\text{O}$  in these species at the ephemeral stream site (Fig. 6). Greater depth to groundwater was associated with greater fractional use of soil water during the monsoon season for these species (Fig. 4). Thus, groundwater depth may be a good predictor of fractional water source use in this ecosystem. *Prosopis* exhibited a linear response in the proportion of soil water used for transpiration along a gradient of greater depth to groundwater. The response of *Populus* indicated that this species used shallow soil water at all sites, but used a greater proportion of soil water at the ephemeral stream reach

when depth to groundwater exceeded 4 m. *Populus* potentially exhibits a threshold response in contrast to the linear response observed in *Prosopis*. In contrast, Busch et al., (1992) observed no shallow soil water use by *Populus* on the Lower Colorado and Bill Williams Rivers in western Arizona. Our sites in southeastern Arizona receive summer precipitation inputs substantially greater than in the arid Mojave Desert, where Busch et al., conducted their study. Leffler and Evans (1999) found that adult *Populus* along the Rio Grande River floodplain in central New Mexico responded photosynthetically to growing season precipitation in years when streamflow along the river was low, but not when streamflow was high. Temporal variation for precipitation use in *Populus* observed in the Rio Grande study apparently was similar to the spatial variation that was observed along the San Pedro River.

*Prosopis* exhibited substantial use of soil water during the summer rainy period at the intermittent and ephemeral stream sites (Fig. 4).  $\delta\text{D}-\delta^{18}\text{O}$  plots (Fig. 2) from ephemeral and intermittent stream reaches indicated that soil water from the 10, 25 and 100 cm depths were important sources of transpiration water for this species. Along the perennial reach the amount of shallow soil water use was assumed to be zero because  $\delta^{18}\text{O}$  was not different than that of floodplain groundwater (Fig. 4). This was likely due to the high variability in  $\delta^{18}\text{O}$  values of *Prosopis* at this site, which indicated that some individual trees were using shallow soil water (up to 54%), while several trees relied

solely on groundwater. *Prosopis* apparently is highly flexible in its use of various water sources. *Prosopis* predawn water potentials (Fig. 5) declined abruptly in July when water table levels dropped and stream flow ceased at the intermittent site (see also Stromberg et al., 1993). However, monsoon rains quickly ameliorated water stress in this species at all sites. These data suggest that *Prosopis* may not develop extensive roots into saturated zones within the soil profile and likely uses water from the capillary fringe.

The amount of summer rainfall in southeastern Arizona is enough to promote soil water use in *Populus*. While the proportion of soil water use was higher at sites with greater depth to groundwater, isotopic data do not indicate whether the amount of soil water extracted by these trees differed between sites. This is an important distinction because the amount of water gained from a soil compartment by root systems illustrates the potential constraints and allocation tradeoffs that may explain root system dynamics in these heterogeneous environments. The amount of water moving through *Populus* trees from shallow soil layers was calculated by multiplying the fraction of xylem water from this source and maximum sap flux in August at the perennial and ephemeral stream sites. Sap flux data were obtained from Schaeffer et al. (2000) using the same trees that were sampled for water sources. Three trees of similar size (0.5–0.8 m stem diameter) were selected at each site to minimize tree size effects. The total amount of transpiration flux derived from soil water based on this calculation was 2.8 and 10.5 g cm<sup>-2</sup> sapwood area h<sup>-1</sup> at the perennial and ephemeral stream sites, respectively. Based on this simple calculation, nearly four times as much water moving through the sapwood of *Populus* trees was coming from shallow soil at the ephemeral stream site compared to that at the perennial stream site. However, maximum sap flux was approximately the same at the perennial and ephemeral stream reaches (35.0 and 40.7 g cm<sup>-2</sup> sapwood area per day, respectively). Total daily transpiration was compared by selecting days with similar solar radiation and vapor pressure deficit. Total transpiration flux was 415.9 and 458.9 g cm<sup>-2</sup> sapwood area per day at the perennial at ephemeral stream sites, respectively. Hence, 382.7 and 338.9 g cm<sup>-2</sup> sapwood area per day was derived from groundwater, and 33.2 and 119.1 g cm<sup>-2</sup> sapwood area per day were derived from shallow soil water at

the perennial and ephemeral reach, respectively. Total water use was similar, but the amount of water from shallow soil layers was greater, while the amount from groundwater was less at the ephemeral reach relative to the perennial reach. Root excavation studies of *Populus* trees along the Mojave River in southern California (Lines, 1999) revealed a greater percentage (between 10 and 50%) of roots in the upper meter of soil at sites where groundwater levels were more than 3 m in depth, compared to sites where groundwater was only 1.5 m deep. Taken together, these data suggest that there may be allocation tradeoffs associated with deploying roots in a particular soil layer. Exploitation of groundwater may come at the expense of water use from other sources, or, alternatively, when groundwater becomes deep or unreliable, trees may develop more shallow roots to exploit other water sources.

Declining groundwater in the San Pedro River system will have a strong negative impact on the survival of *Salix*, because water sources appear to be limited to groundwater. If mature *Populus* is able to continue deep root growth during groundwater recession by augmenting transpiration needs with precipitation taken up by shallow lateral roots, this species may be able to tolerate some recession of groundwater depth. However, it appears that *Populus* must keep roots in the saturated zone to maintain high predawn water potentials. Therefore, persistent long-term declines in groundwater levels will likely limit this species as well (see also Stromberg et al., 1996). *Prosopis* is highly flexible in its use of water sources and is likely to become more dominant in the riparian landscape if declining groundwater levels persist. However, *Prosopis* tree growth may be limited in stature relative to historic riparian mesquite woodlands if groundwater is limited (Stromberg et al., 1993; Stromberg, 1993b).

In conclusion, some riparian trees, even those commonly associated with shallow groundwater, can use substantial amounts of precipitation to meet transpiration requirements. One of the main goals of the SALSA program is to estimate and model transfer of groundwater via riparian evapotranspiration on a basin-wide scale (see Goodrich et al., 2000). These data suggest that species composition in riparian forests (abundances of *Salix*, *Populus*, and *Prosopis*) together with habitat conditions (depth to groundwater) will interactively determine the fraction of

transpiration derived from groundwater at the stand level. Integrated over a large area, the contribution of soil water to transpiration in these forests can be substantial, yet easily misrepresented in scaling algorithms. Results of this study indicate that water balance calculations in riparian forests from semi-arid regions should take into consideration species-environment responses within the heterogeneous floodplain ecosystem.

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