Ecological Applications, 2(4), 1992, pp. 450–459
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WATER UPTAKE IN WOODY RIPARIAN PHREATOPHYTES OF THE SOUTHWESTERN UNITED STATES: A STABLE ISOTOPE STUDY[1]

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Abstract. Alluvial forest associations are often dominated by woody phreatophytes, plants that are tightly linked to aquifers for water uptake. Anthropogenic hydrological alterations (e.g., water impoundment or diversion) are of clear importance to riparian ecosystem function. Because decreased frequency of flooding and depression of water tables may, in effect, sever riparian plants from their natural water sources, research was undertaken to determine water uptake patterns for the dominant native and introduced woody taxa of riparian plant communities of the southwestern United States. At floodplain study sites along the Bill Williams and lower Colorado Rivers (Arizona, USA), naturally occurring D and ^{18}O were used to distinguish among potential water sources. Isotopic ratios from potential uptake locations were compared to water extracted from the dominant woody taxa of the study area (*Populus fremontii, Salix gooddingii,* and *Tamarix ramosissima*) to elucidate patterns of water absorption. Isotopic composition of water obtained from sapwood cores did not differ significantly from heartwood or branch water, suggesting that heartwood water exchange, stem capacitance, and phloem sap mixing may be inconsequential in actively transpiring *Salix* and *Populus*. There was evidence for close hydrologic linkage of river, ground, and soil water during the early part of the growing season. Surface soils exhibited D enrichment due to cumulative exposure to evaporation as the growing season progressed. Isotopic ratios of water extracted from *Populus* and *Salix* did not exhibit isotopic enrichment and were not significantly different from groundwater or saturated soil water sources, indicating a phreatophytic uptake pattern. Associations of isotopic ratios with water relations parameters indicated high levels of canopy evaporation and possible use of moisture from unsaturated alluvial soils in addition to groundwater in *Tamarix*.

Key words: deuterium; hydrogeology; oxygen-18; phreatophyte; Populus; *riparian;* Salix; *southwestern United States; stable isotopic ratios;* Tamarix; *water absorption.*

INTRODUCTION

Phreatophytes, by definition, are dependent on groundwater as a moisture source. However, the extent of this dependence is often unclear. Taxonomies using modifiers to this descriptor such as "facultative" and "obligate" (Reed 1988) have tended to blur the somewhat vague distinction between phreatophytic and mesophytic vegetation. An understanding of water sources for riparian plant associations is also complicated by naturally occurring hydrologic dynamics in alluvial ecosystems. Furthermore, impoundment and off-channel water diversion typically result in substantial alteration of the downstream physical environment (Williams and Wolman 1984). Such change clearly affects floodplain water tables, especially along losing reaches (i.e., effluent reaches where the hydrologic gradient causes the stream to lose water to the subsurface). Water regimes can strongly influence the vegetative composition of riparian forests (Stromberg and Patten 1990). However, little is known about how fluctuations in floodplain groundwater depth affect ecosystem function. Wetland inventories in western North America have been made problematic by hydrologic severance of riparian forests from former groundwater sources due to anthropogenic lowering of water tables (Tiner 1990). The linkage between hydrogeological factors and riparian plant community function is assuming increased importance as the economic value of water

[1] Manuscript received 30 September 1991; revised 3 February 1992; accepted 13 February.
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increases, and municipal, industrial, or agricultural uses for instream flows (e.g., Brown et al. 1990) are evaluated.

Low-elevation floodplain landscapes of the Southwest were historically dominated by gallery forests of *Populus fremontii* and *Salix gooddingii* (Grinnell 1914). Although these taxa are still present in relict distributions, the naturalized exotic *Tamarix ramosissima* now dominates many arid land alluvial communities. Where dominant, this species can alter whole ecosystem properties, including hydrologic processes (Vitousek 1990). *Salix* and *Populus* have long been recognized as indicators of shallow groundwater, just as changes in water table depth have long been cited for their potential to alter the structure of riparian forest assemblages (Meinzer 1927, Bryan 1928). Close functional associations between groundwater and riparian woody phreatophytes were demonstrated by diurnal water table fluctuations that were similar in periodicity to transpiration response curves (Robinson 1958). In studies involving seasonal soil moisture depletion, *Tamarix* and *Salix* showed little evidence for water acquisition from the unsaturated zone, while *Populus* used soil moisture even when groundwater was available (McQueen and Miller 1972). Consequently, there is some evidence for an "obligate–facultative" phreatophyte dichotomy. Similar indications come from the floodplain distributions of *Salix* and *Populus* in the lower Colorado River drainage. The former species is typically closely associated with active channels, while the latter is less tightly linked to perennial streams.

Ecophysiological reviews (Kozlowski 1984) have concentrated largely on the effects of flooding on riparian woody plants. Studies of rivers in Europe and western North America (e.g., Johnson et al. 1976, Pautou and Decamps 1985, Rood and Heinze-Milne 1989) consider the importance of geomorphology in structuring riparian communities. However, such efforts have tended to emphasize correlation with floodplain hydrogeologic factors rather than the mechanisms governing vegetation responses to physical variation in alluvial systems. Therefore, a more rigorous evaluation of water source dependence in alluvial forest and scrub communities of the southwestern United States was conducted. Our objectives were to: (1) investigate the importance of sampling location for the naturally occurring stable isotopes deuterium (D) and oxygen-18 (^{18}O) in plant water-relations research; (2) apply appropriate methods to distinguish among sources for water uptake in woody riparian phreatophytes; and (3) investigate potential correlations between stable isotopic ratios and certain water-relations parameters for dominant riparian forest taxa of the lower Colorado River basin.

Stable Isotopes of Water

Lack of attention to the functional responses of riparian plants to subsurface moisture availability can be attributed to the difficulties inherent in studies of root zone water absorption. The finding that water taken up by trees and shrubs may be characterized as to source by stable isotopic analysis of tree sap (White et al. 1985, Ehleringer and Osmond 1989) demonstrated the possibilities for distinguishing between unsaturated zone and groundwater absorption sources. Physical processes, notably evaporation and condensation, govern the extent to which isotopic enrichment occurs in water. The most abundant water molecule, $^{1}H_2{}^{16}O$, has a higher vapor pressure than molecules with the heavier isotopes D or ^{18}O. Evaporation causes the fractionation of these isotopes, with the heavier isotopes tending to concentrate in the liquid phase. Results are reported as "δ values," variations from Standard Mean Ocean Water (SMOW), a worldwide standard, by:

$$\delta X = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 10^3, \qquad (1)$$

where X represents either D or ^{18}O, R is the absolute isotopic ratio of either the sample or standard, and δ is stated in parts per thousand. Deuterium and ^{18}O δ-values of precipitation generally show the linear relationship described by the equation for the meteoric water line (MWL; Craig 1961):

$$\delta D = 8\delta^{18}O + 10. \qquad (2)$$

Water subjected to evaporation generally falls along lines with slopes lower than 8 in δD–$\delta^{18}O$ space. Thus, interpretations as to the source of water may be made by examining isotopic compositions as well as deviations from the MWL. Isotopic enrichment in leaf water has also been investigated using δD–$\delta^{18}O$ evaporation line slopes (Allison et al. 1985, Cooper and DeNiro 1989), although it appears that the analytical value in evaluating plant water use is currently rather limited (Flanagan and Ehleringer 1991).

Due to evaporative losses to the atmosphere, water in the soil unsaturated zone tends toward isotopic enrichment relative to groundwater. Soil water shows decreasing evaporative enrichment in D and ^{18}O from the surface to the zone where liquid transport is dominant (Allison and Hughes 1983, Allison et al. 1983). Differences in the δ values of groundwater and soil water are the basis for determining plant uptake sources using isotopic ratios of free water extracted from plant tissues. The isotopic composition of groundwater is less affected by precipitation in arid landscapes because direct recharge is infrequent in low-precipitation, high-evaporation environments. Conversely, alluvial influences are likely to dominate the isotopic characteristics of groundwater because of the prevalence of losing stream reaches in desert landscapes (Fetter 1988). Flooding and water table fluctuations are thus the principal sources of moisture replenishment in floodplain soils.

Implicit in the cohesion theory of the ascent of sap is the premise that water in transpiring plants forms a

continuous system, from the leaf surfaces through the xylem to the absorbing surfaces of the roots (Kramer 1983). Water extracted from the plant xylem prior to transpiration is isotopically equivalent to water that is absorbed by the roots (Sternberg 1989). Diffuse porous wood in the Salicaceae is characterized by indistinct sap-movement patterns within a number of peripheral xylem annual increments (Kramer and Kozlowski 1979). Active conduction of water in *Populus* and *Salix* is therefore thought to occur over radially broad areas of sapwood, so that water extracted from sapwood cores would offer the clearest depiction of root zone absorption. Mixing of water between heartwood and sapwood may play an important role in determining sap δD at certain sites during dry periods (White et al. 1985). Stem capacitance (Tyree 1988) may affect water residence time within wood tissue. Xylem–phloem water exchange (Ziegler 1989) or stem cuticular transpiration (Dawson and Ehleringer 1991) could cause isotopic enrichment in branch water. This brings into question the suitability of using various wood tissues for isotopic studies of water uptake.

Previous research efforts have used radioactive or stable isotopes to examine water absorption in forest communities. Uptake of tritiated water demonstrated the importance of groundwater during dry periods for trees on semiarid and mesic sites (Rickard and Price 1989, Stringer et al. 1989). Riparian *Quercus* and *Acer* xylem water δD analysis showed a water absorption shift from surface to deeper water sources as trees mature (Dawson and Ehleringer 1991). Hydrogen isotope ratios showed that riparian trees of the Sierra Nevada may shift dependence on uptake sources—from soil moisture, to surface runoff, to groundwater—as soils dry and flows diminish (Smith et al. 1991). Using stable isotopes, White et al. (1985) were able to distinguish the use of soil water associated with individual precipitation events from groundwater use in eastern forests; trees on progressively more hydric sites were less dependent on soil moisture and more dependent on groundwater. Although Wershaw et al. (1970) reported δD values for *P. sargentii* sap that were higher than nearby surface water sources and consistent with water extracted from soils, they failed to consider groundwater as a potential source for absorption. Such information gaps and contradictions hinder our understanding of the nature of the dependence on various water sources in riparian forest communities.

Methods

Study area

Data were collected at two sites on the Bill Williams River in west-central Arizona (34°15′ N, 114°0′ W, elevation 150 m). These sites were selected to represent an alluvial forest association characteristic of the region's floodplains during presettlement times. Vegetation of these study sites corresponds to the *Populus–Salix* forest community type of Szaro (1989). Common understory shrubs include *Tamarix, Tessaria sericea,* and *Baccharis glutinosa.* Although floodplain vegetation is subject to frequent natural disturbance from flooding, perturbation from flood control, fire, and agriculture has altered this association. Frequent establishment of *Tamarix* in forest canopy gaps has been facilitated by these forms of perturbation. Despite this, germination and establishment of native tree taxa still occur on these sites.

Sites adjacent to the lower Colorado River provided a setting where the same forms of perturbation affecting the Bill Williams River are more pronounced and have been active over a longer time. Additional sampling was thus conducted near Needles, California (34°50′ N, 114°35′ W, elevation 150 m), and near Blythe, California (33°25′ N, 114°45′ W, elevation 125 m), where a *Tamarix* community (Szaro 1989) is dominant. Germination of native tree taxa is infrequent on these sites, as *Tamarix* appears to competitively exclude *Populus* and *Salix* from throughout much of the lower Colorado River Valley. At the Needles site a tall-thicket association codominated by *Tamarix* and *Salix* is present. The latter species occurs in a relict distribution along a previous river channel. *Prosopis pubescens* and *Tessaria* are subdominant shrubs at this site. The Blythe site is a riparian habitat reestablishment area (Anderson et al. 1984). Cuttings of various native riparian tree and shrub taxa were planted here in 1979. Due to poor survival of *Salix,* only *Populus* was sampled at this site. Although apparently stressed, sampled trees had grown to heights >10 m in the 10 yr since planting.

Field sampling

Data were collected seasonally at the two sites on the Bill Williams River and in late summer at the two sites on the lower Colorado River. River water samples were taken from well-mixed, accessible points on each river near each study site. At each site, piezometers were installed to sample groundwater in the unconfined aquifer. All wells consisted of slotted polyvinyl chloride (PVC) pipe which was placed in holes drilled to >6 m. After determining the depth to the water table, water samples were obtained by hand pump and sealed in 100-mL glass vials. Three well volumes were pumped prior to collecting water samples to assure that standing water with recent atmospheric exposure was not sampled.

From each piezometer, or central point between piezometer pairs, variable-length transects ($n = 4$, in each season) were selected along randomly derived azimuths. Where transects intercepted canopies of the taxa selected for study (*Populus, Salix,* and *Tamarix*), soil and plant samples were collected. For the former two tree taxa, single individuals >25 cm in diameter at breast height (dbh) were sampled by coring with a 1.2 cm diameter increment borer. Bark tissue was discarded, then cores were separated into sapwood and

heartwood segments for later analysis. These two wood sources were not subsequently considered independent samples. Branch segments and leaves from sunlit portions at the midcanopy level were also collected from these individuals. Because of its shrub morphology we were unable to core *Tamarix,* so only the latter two types of tissue were sampled. Sampling was conducted near midday (≈1100 to 1400) to maximize the probability of gathering data from actively transpiring trees and shrubs. All samples were rapidly sealed in 40-mL glass vials. Although evaporation and condensation occurred in the vials, upon sealing they constituted a closed system, so that stable isotope ratios were constant within them.

Near individuals of each taxon selected for tissue water sampling, composite soil samples at 50 and 100 cm depths were collected by augering. For each depth, samples to be used for subsequent soil water isotopic analysis were bulked in the field by collecting equal amounts at each of three points along each study transect. There was, therefore, one sample for each soil depth per transect. All soil water samples were sealed rapidly in 950-mL glass jars. Data on volumetric soil moisture content (Θ) were gathered seasonally using time-domain reflectometry (TDR; Topp and Davis 1985). TDR probes were inserted in the soil at nine randomly selected locations at the Bill Williams River sites. Probe orientation was vertical, and probe lengths were 30 and 90 cm. We were thus able to compare soil water isotopic ratio data at the 50 and 100 cm depths with Θ at 30 and 90 cm, and to an integrated value of Θ from the upper 90 cm of the soil profile.

Total water potential (ψ) was measured on plants selected for tissue water isotope analysis or on adjacent individuals within the same stand. Measurements were made in the field using the pressure chamber technique (Turner 1988) on 10–20 cm terminal branch segments taken from the midcanopy level before dawn, at the time of assumed maximum diel ψ (ψ_{max}), and at the presumed midday ψ minimum (ψ_{min}).

Laboratory procedures

Azeotropic toluene distillation methodology followed the guidelines first described by Dewar and McDonald (1961). This has been shown to be a satisfactory method for extracting free water from soil and plant tissues for isotopic analysis (Allison and Hughes 1983, Allison et al. 1985, Revesz and Woods 1990, Yakir et al. 1990). Water derived from all sources was exposed to the same water extraction regime to minimize potential experimental bias. Samples together with sample bottles were placed in the toluene distillation apparatus to assure that all condensate was collected during the distillation process.

Hydrogen gas was produced by converting 5-μL aliquots of sample water using uranium as a reducing agent (Bigeleisen et al. 1952). Isotopic ratios were determined by introducing hydogen gas into a Nuclide 3-60 double collector mass spectrometer (Nuclide, State College, Pennsylvania, USA). Leaf, branch, soil, and groundwater samples were selected for oxygen isotope analysis. For this process, 10-μL aliquots of the water samples were reacted with guanidine hydrochloride to produce CO_2 (Dugan et al. 1985). The resultant CO_2 gas was introduced directly into a Finnigan-Mat delta E mass spectrometer (Finnigan, Bremen, Germany). The reproducibility of δD values derived using this method is ± 1‰ while that of the δ^{18}O values is ± 0.2‰.

Data analysis

Paired *t* tests were used to compare heartwood and sapwood δD means. For comparisons of >2 samples, analysis of variance (ANOVA) was used to test for differences among mean δD values. Data from each species were considered as "sources" in separate ANOVAs, with the plant tissues sampled considered "locations" within these sources. Another set of locations consisted of soil, ground, and river water within a substrate source. Confounding of sources, and significant ($F = 4.944$, $P < .001$) season × location interactions when the three taxa were considered jointly in nested and complex two-way models, necessitated the use of simpler two-way and one-way ANOVAs. Substrate locations were thus used repeatedly in the separate ANOVAs for each species in each season. The two sites sampled at the Bill Williams River were treated as blocks in these analyses. Evidence for water location homogeneity came from means that were not significantly different. Therefore, estimated statistical powers ($1 - \beta$, given $\alpha = .05$) of ANOVAs are presented as recommended by Peterman (1990). The Fisher's protected least significant difference test, a liberal procedure for multiple comparison testing (Petersen 1985), was used to assure that all possible differences in δD means were identified.

Stable isotope ratios of sampled waters were plotted in δD–δ^{18}O space using least-squares linear regression models. Slopes of the resultant evaporation lines were compared using analysis of covariance and the Newman-Keuls multiple-range test (Zar 1983). Correlation analysis was used to examine the functional relationship between physical and physiological factors and δ values. Following all regression analyses and ANOVAs, residual and normal probability plots were constructed to evaluate the assumptions of normality and independence. Departures from these assumptions were minor.

Results

U.S. Geological Survey gauging station stream-discharge data indicate that the hydrographs of the two rivers differ substantially (Fig. 1). During our study the lower Bill Williams River was characterized by low flows, which declined to zero by the end of April. Daily variation of flow was beneath gauge detection limits in the Bill Williams River. In addition to being several

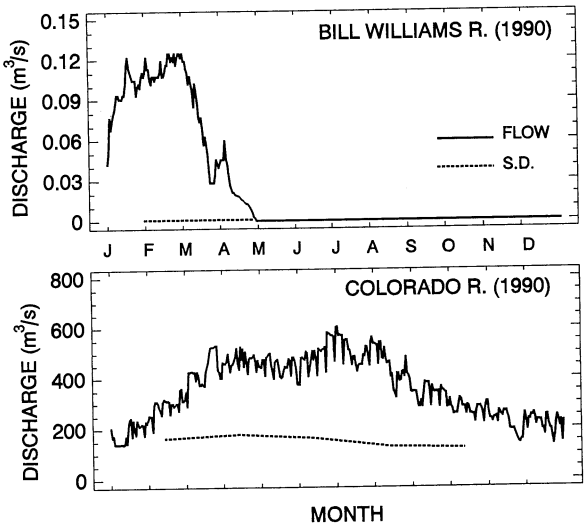

FIG. 1. Hydrographic data from U.S. Geological Survey gauging stations on the Bill Williams and lower Colorado Rivers (Arizona). Discharges presented are daily means over the study period. Standard deviations (SD) of discharge daily means were calculated from hourly instantaneous flow rates as an indication of within-day variation. Note contrasting ordinate scales for the two rivers.

orders of magnitude greater, Colorado River discharge was more variable on both an absolute annual and a diel basis. Groundwater in the alluvial aquifers of the two river systems exhibited depth variation that was similar to surface water hydrographs. Growing season mean (±1 SD) water table depth from a representative piezometer near the Bill Williams study sites (1.24 ± 0.32 m, n = 6 dates) was shallower and more stable over an annual scale than that from a piezometer in the lower Colorado River valley (3.53 ± 0.47 m, n = 6 dates). Midsummer mean groundwater depths in the vicinity of the Bill Williams sites (1.08 ± 0.01 m, n = 5 times) were also shallower and less variable on a diel basis than those from the Colorado River floodplain piezometer (2.91 ± 0.13 m, n = 7 times). When midsummer water table depths from multiple wells near each study area are compared, there is also evidence for shallower groundwater and less spatial variability in Bill Williams River valley piezometers (2.62 ± 0.81 m, n = 4) than in the Colorado River valley (3.89 ± 1.89 m, n = 4).

Floodplain soil moisture differences were consistent with the variation in aquifer characteristics between river systems. Over the course of the study, volumetric soil moisture content (Θ; n = 12) at the Bill Williams River study sites averaged 7.7 ± 5.7% (mean ± 1 SD) at the 30 cm depth and 18.4 ± 11.0% at the 90 cm depth. Colorado River valley site soils tended to have lower Θ, averaging 4.9 ± 0.5% at the 30 cm depth and 4.2 ± 0.5% at 90 cm.

Bill Williams River valley water δD was compared among locations likely to be linked to changing river discharge. This comparison involved waters from river, aquifer, and hyporheic (i.e., saturated soil at the 100 cm depth) locations. Although there was little probability of two-factor, location × season interaction or location effect among river, ground, or 100-cm soil water, there were significant seasonal differences in δD values from these locations (Table 1). Multiple-comparisons testing showed that summer δD from substrate locations (−61.4 ± 0.4‰; mean ± 1 SE) was significantly (P < .05) more enriched than autumn levels (−63.8 ± 0.7‰). Exposure to evaporative forces is likely to be responsible for slightly enriched summer δD from all substrate locations and for the tendency for river (i.e., surface) water to be enriched in all seasons (Fig. 2). These results depict a seasonal tracking of δD among river, aquifer, and hyporheic waters. Although δD of soil water taken from 50 cm beneath the ground surface was similar to that of soil water from 100 cm and groundwater in March, a tendency toward D enrichment occurred in June and became significant by September (Table 2). Soil water δD at 50 cm exhibited a linear relationship with depth to groundwater (r^2 = 0.57, P < .005) and season (r^2 = 0.51, P < .009), but not Θ (r^2 = 0.26, P > .08). Although δD of water from Bill Williams floodplain soils at both levels was weakly correlated with Θ (r^2 = 0.20, P < .03), a similar relationship was not present in the comparison of water table depth to δD of water from soil at both depths (Fig. 3).

The Colorado River sites demonstrated a trend toward δD enrichment at both the 50 and 100 cm depths, but this tendency was not statistically significant (Table 2). Regression analysis demonstrated that δD of water from Colorado River floodplain soils from both depths was correlated with water table depth (Fig. 3). The Bill Williams water table depth increase occurred over the growing season (i.e., the scale was temporal) whereas the groundwater depth variation reported for the Colorado River occurs over a spatial scale within a single season.

Table 2 provides evidence for continuity between zones of active water uptake and groundwater in all three taxa. There were no significant differences in δD between potential rhizosphere water sources and water taken up by Bill Williams River valley *Tamarix, Salix,*

TABLE 1. ANOVA summary for δD of waters extracted from Bill Williams River (Arizona) substrate source locations.

Source*	df	F	P	$1 - \beta$
Location	2	1.67	0.22	0.24
Season	2	5.61	0.01	0.70
Location × season	4	0.20	0.94	...
Area	1	0.663	...	...
Residual	18	...	...	...

* Locations were river, ground, and 100 cm depth (i.e., hyporheic) soil waters. Season represented March, June, and September data collection periods. Area was treated as a blocking factor.

TABLE 2. Values of δD (‰) from plant and potential water uptake source locations. Data for water from substrate and plant locations are means ± 1 SE. Bracketed values are estimated P and $1 - \beta$ for ANOVAs of plant and substrate water source locations.†

Water sources	Bill Williams River			Colorado River	
	March (4)	June (4)	September (4)	September (3)	August (2)
Groundwater	−62.6 ± 0.5	−62.0 ± 0.4	−64.0 ± 0.6	−107.0 ± 1.2	−99.0 (1)
Soil (100 cm)	−63.1 ± 0.1	−61.3 ± 0.6	−64.0 ± 1.5	−84.3 ± 18.4	−78.0 ± 16.0
Soil (50 cm)	−60.8 ± 1.3	−50.0 ± 6.5	−33.5 ± 8.5*	−62.7 ± 18.7	−50.0 ± 16.0
Tamarix	[0.272, 0.25]	[0.051, 0.48]	[0.003, 0.93]	[0.127, 0.28]	...
Branch	−62.0 ± 1.1	−63.3 ± 0.9	−65.6 ± 1.2	−102.7 ± 3.8	...
Salix	[0.268, 0.25]	[0.058, 0.42]	[0.001, 0.96]	[0.061, 0.46]	...
Sapwood	−63.0 ± 1.0	−60.5 ± 0.9	−62.5 ± 0.5	−108.0 ± 1.0	...
Branch	−62.3 ± 1.1	−62.0 ± 0.7	−63.5 ± 2.0	−108.0 ± 0.0	...
Populus	[0.085, 0.44]	[0.068, 0.41]	[0.001, 0.97]	...	[0.159, 0.35]
Sapwood	−61.5 ± 0.5	−61.0 ± 0.6 (3)	−61.1 ± 1.2	...	−99.3 ± 2.0 (3)
Branch	−62.8 ± 0.3	−62.0 ± 0.6	−62.5 ± 0.6	...	−98.0 (1)

* Indicates a significant ($P < .05$) difference from the other means in the column.

† Months are followed by sample sizes for all means in each column, with exceptions noted by values in parentheses following means.

or *Populus* in March. This was also true in June despite the nonsignificant trend toward D enrichment of soil water from the 50 cm depth. In September, δD was significantly lower in soil water from this depth than it was in recently absorbed water in study-site trees and shrubs. This occurred despite substantial root development within the upper 50 cm of the soil profile in all three taxa (D. Busch, *personal observation*). Although sampling limitations restricted our ability to make inferences for the Colorado River valley, data from these sites appear to confirm the linkage of roots of these taxa and groundwater. Only in *Tamarix* from the Colorado River floodplain is a trend toward possible partial use of unsaturated soil moisture evidenced by δD values intermediate between those of groundwater and those of water extracted from surface soils.

Hydrogen isotope ratios from different plant tissue sources were compared to test the hypothesis that sapwood provides the most accurate depiction of water recently absorbed by the roots (Table 2). There was a tendency for water extracted from *Populus* branch samples taken in the Bill Williams River valley to be more depleted in D than water extracted from sapwood taken by coring the boles of this species. However, this tendency was reversed for our limited Colorado River valley sampling, and was not significant statistically in any season. Differences between sapwood and branch water in *Salix* from both sites are even less distinct and, with one exception, are within the ±1‰ laboratory precision. Paired comparisons of sapwood and heartwood from all sites also showed indistinct variation. For *Salix*, heartwood water δD (−71.2 ± 4.8‰) was not significantly different ($P > .99$, $1 - \beta > .99$) from sapwood water values (−71.2 ± 4.9‰). Similarly, no difference ($P > .16$, $1 - \beta > .99$) could be detected between heartwood (−69.7 ± 3.6‰) and sapwood (−69.4 ± 4.4‰) water in *Populus*.

Correlation of plant water δD and ψ_{max} was statistically significant only for *Tamarix* leaf tissue from Bill Williams River sites (Table 3). Midday water potential and δD of water from *Tamarix* leaves and branches and *Salix* branches were also significantly correlated. Correlations of tissue water δD and ψ were low for *Salix* leaves and for *Populus* branches and leaves.

Evaporation lines for each species and for substrate locations were plotted using ratios for both stable isotopes. Plots in δD–δ^{18}O space (Fig. 4) were derived using least-squares linear regression equations for plant leaf and stem tissue water δ values, and for substrate locations using δ values for groundwater and soil water from the 50 and 100 cm depths. All trajectories deviated substantially from the meteoric water line (MWL) (see Eq. 2, above). Water extracted from branches of all three taxa generally fell near the cluster of points

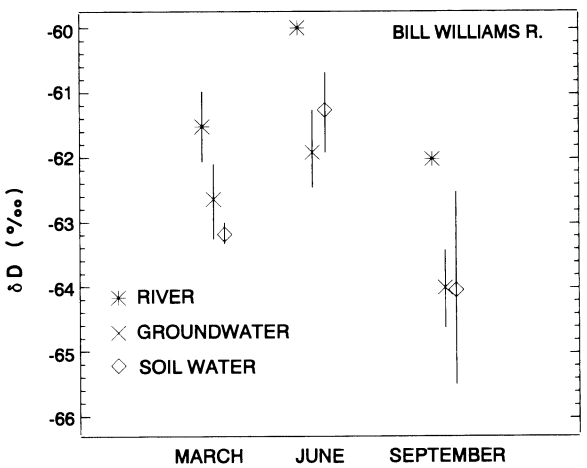

FIG. 2. Hydrogen isotope composition (δD) of water from substrate sources at Bill Williams River (Arizona) study sites. (δ values are parts per thousand (‰) variations from Standard Mean Ocean Water.) Soil water represents water extracted from soil samples from the 100 cm (i.e., hyporheic) depth. Vertical lines are ±1 SE around the means. June and September river water values are each from a single sample.

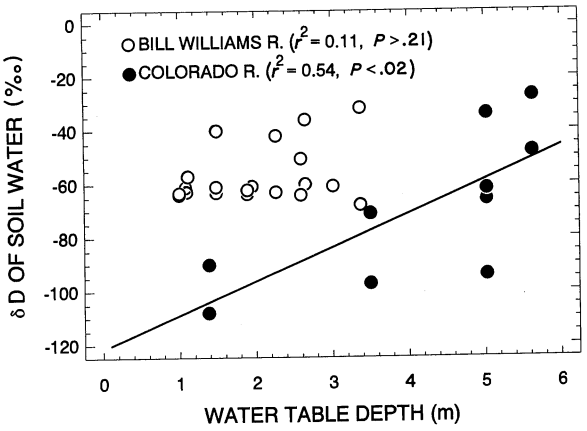

FIG. 3. Relationship of soil water δD (i.e., water extracted from unsaturated soils above the water table; see Fig. 1 for definition of δ) and depth to groundwater for study sites in the Bill Williams and Colorado River valleys (Arizona). Reported water table depths varied temporally over the growing season at study sites in the Bill Williams River floodplain. Between-site variation in groundwater depth is reported for the Colorado River Valley. The plotted line represents the least-squares regression model for the Colorado River Valley sites.

representing groundwater and hyporheic soil water. Analysis of covariance indicated that the slopes of the evaporation lines were not equivalent ($F = 3.329$, $P <$ .03). With the exception of the *Populus–Salix* comparison, slopes of all pairs of regression models were significantly different (Table 4). Evaporation line slopes for all plant sources were more negative than that for the substrate source. The slope for *Tamarix* was significantly lower than those for the other two taxa.

DISCUSSION

Isotopic analysis of water extracted from *Salix* and *Populus* indicated that there is little difference in δD among locations of free water in sapwood, heartwood, and branch tissue in these taxa (Table 2). From a procedural standpoint, sampling branch tissue water is potentially less injurious to trees and is easier than coring trees with an increment borer. However, comparisons of sapwood and branch water δ values should be made before embarking on extensive sampling of free water in branches in other taxa or in other ecosystems. Our comparison of water from wood sources produced no evidence that stem capacitance altered δD in *Salix* or *Populus* boles. Likewise, water mixing between heartwood and sapwood was not observed in these taxa as it was in moisture-stressed *Pinus strobus* (White et al. 1985). Phreatophytes are presumably not as likely to utilize stem water storage as are trees growing on mesic sites that may be subjected to cycles of drought. Branch water δD was not affected by phloem sap isotopic enrichment, as had been detected by Ziegler (1989). Mixing of isotopically enriched phloem water with xylem water either is minor or is overridden in actively transpiring *Populus* and *Salix*.

Several mechanisms could be responsible for the seasonal progression of δD in surface, ground, and soil waters from the Bill Williams River valley (Table 1, Fig. 2). Higher evaporation rates during summer are the likely cause of the slight enrichment in June substrate water D. Variations in reservoir releases or altered agricultural groundwater withdrawals upstream of our study sites may have affected evaporative processes occurring in potential source waters as well. The apparent seasonal tracking of δD among surface, ground, and hyporheic water locations provides evidence that hydrologic processes in the floodplain of this losing stream reach are dominated by Bill Williams River flows. Although this implies an inability to distinguish among these locations in plant water uptake analyses, plant moisture availability below the 100-cm substrate depth was evidently governed by alluvial dynamics in this system.

Variation in water isotopic ratios between substrate locations provided a basis for distinguishing among potential plant absorption sources (Table 2). The seasonal decoupling of δD in soil water taken at 50 cm from that in water taken at other possible uptake source locations is evidence for decreasing groundwater effect and increasing atmospheric evaporative influence in the shallow Bill Williams River floodplain soils. Cor-

TABLE 3. Pearson product–moment correlation coefficients (r) for δD of water extracted from the plant tissues of three Bill Williams River (Arizona) floodplain taxa with predawn (ψ_{max}) and midday (ψ_{min}) water potential. Sample size (n) = 12 in all cases.

Species Location	ψ_{max}	ψ_{min}
Tamarix		
Branch	0.46	0.60*
Leaf	−0.75**	−0.62*
Salix		
Branch	0.42	0.61*
Leaf	−0.44	−0.28
Populus		
Branch	−0.10	−0.02
Leaf	−0.05	0.20

* = $P < .05$; ** = $P < .005$.

TABLE 4. Comparison of δD-δ^{18}O least-squares regression models for water extracted from plant and substrate sources.*

Source	b_0	b_1	r^2	P
Substrate	−38.18	3.14[a]	0.92	<.00001
Populus	−43.26	2.67[b]	0.97	<.00001
Salix	−42.88	2.62[b]	0.95	<.00001
Tamarix	−44.48	2.34[c]	0.95	<.00001

* Regression coefficients are intercept (b_0) and slope (b_1). The latter is followed by different superscript letters for slopes that are significantly different following the Newman-Keuls multiple-range test. Coefficients of determination (r^2) and P values associated with tests of the hypothesis that slope is not significantly different from zero are also reported.

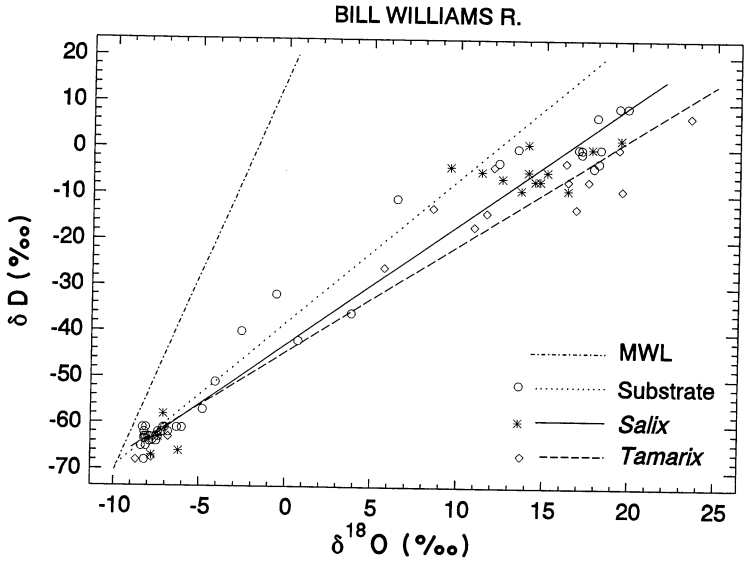

FIG. 4. Evaporation lines in δD–δ^{18}O space (see Fig. 1 for definition of δ) for water extracted from plant and substrate sources in the Bill Williams River Valley (Arizona). Table 4 contains information regarding the significance and comparisons of the regressions shown here. Because slopes for *Populus* and *Salix* were nearly identical, only the data for the latter are plotted here, for clarity. The meteoric water line (Craig 1961) is denoted as MWL (–·–·–).

relation of seasonally declining water table levels and δD at the 50 cm depth is further evidence of progressive diminishing of the aquifer's influence on unsaturated floodplain soil moisture. In spite of this, the monotonic δD response to groundwater depth for all soil levels (Fig. 3) shows the influence of the alluvial aquifer as the dominant soil moisture source in this system. This occurred despite the attenuation of surface water flows at the Bill Williams River floodplain sites (Fig. 1). It is unclear why correlations of δD with Θ were not stronger for either shallow or total soil profiles, although highly variable Θ values may be partially responsible.

Colorado River flows were substantially greater and more variable than those of the Bill Williams River on both a diel and an annual basis, while Colorado River valley water table depths and fluctuations were also greater over both temporal and spatial scales. These factors contributed to D enrichment at both the 50 and 100 cm depths in floodplain soils (Table 2), and reduced aquifer influence on soil moisture in the Colorado River valley. The correlation of soil water δD with groundwater depth (Fig. 3) implies decreasing evaporative exposure with soil depth, increasing frequency of groundwater moisture replenishment with depth, or both. Anthropogenic lowering of riparian water tables appears to have diminished this source of shallow soil moisture supply. This may be a causative factor in the increasing impoverishment of lower Colorado River floodplain vegetation with respect to its formerly dominant native trees.

Despite seasonal and spatial variation exhibited in root zone δD within and between river systems, there was little evidence for absorption of water from substrate locations not closely linked to groundwater (Table 2). One plausible deviation from this rule was *Tamarix* branch water from the lower Colorado River floodplain, where δD values intermediate between groundwater and soil water from 100 cm were found. However, more extensive sampling in the Bill Williams River valley failed to produce similar isotopic enrichment relative to groundwater in water extracted from this species. Based on δD comparisons among potential water source locations and free water extracted from woody plant tissues, uptake in *Populus* and *Salix* may be characterized as consistently phreatophytic within our study area. This applies even in lower Colorado River floodplain areas where groundwater depths averaged ≈3.5 m. These findings differ somewhat from the soil vs. groundwater use characteristics determined for these taxa by McQueen and Miller (1972) and from the seasonally shifting water absorption patterns shown for riparian trees of the eastern Sierra Nevada (Smith et al. 1991). Although surface–subsurface hydrologic linkage was closer here than it was in the ecosystem described by Dawson and Ehleringer (1991), both studies document phreatophytic uptake in mature riparian trees.

Evaporation in surface soils accounted for a substrate δD–δ^{18}O regression with substantially lower slope than that for the meteoric water line (MWL) (Fig. 4). Significantly lower evaporation line slopes for the three woody taxa can be attributed to higher evaporative flux from saturated leaf surfaces relative to that from the unsaturated soil surface. Evaporation line slope differences have been attributed to leaf water residence time and exposure to repeated isotopic enrichment by evapotranspiration (Cooper and DeNiro 1989). However, for riparian trees with presumably high transpi-

ration ratios, the pool of water affected by multiple enrichment via transpiration is likely to be insignificant. A more negative evaporation line slope in *Tamarix* compared to either *Salix* or *Populus* may indicate higher unit transpiration, analogous to the proposal of Allison et al. (1985). However, this could also occur due to a less extensive boundary layer in *Tamarix* and consequent dissimilar exposure to vapor pressure gradients or air moisture isotopic equilibration. Positive deviations from modeled δD–$\delta^{18}O$ slopes have been reported for leaf water from dehydration-stressed *Cornus stolonifera* (Flanagan and Ehleringer 1991). Evidence for water stress in the native riparian taxa relative to *Tamarix* would be consistent with the interspecific evaporation line slope differences reported here. Similarly, if *Tamarix* does absorb isotopically enriched water from unsaturated alluvial soils, lower δD–$\delta^{18}O$ slopes would be likely in this species.

Tamarix leaves became more enriched in D as ψ_{min} and ψ_{max} declined (Table 3). This may be another manifestation of seasonally increasing diurnal transpiration demand, which is vapor pressure gradient driven. Correlation in *Tamarix* but not in the broad-leaved native taxa may also be a reflection of augmented boundary-layer effects in the latter group. Correlations of ψ_{min} with δD in water extracted from *Tamarix* and *Salix* branches suggest an increasingly close linkage with a groundwater uptake source. Stringer et al. (1989) found that higher ψ correlated with ^3H activity in transpirational water was an indicator of the adaptation of *Quercus–Carya* forest trees to utilize deep water sources to ameliorate the effects of drying soils. For *Tamarix* and *Salix,* correlation of ψ_{min} and δD implies that water stress increased despite groundwater uptake. Evidence for facultative groundwater use in *Tamarix* where water tables were depressed (i.e., the lower Colorado River) and indications that this species maintains high transpiration through periods of stress appear to be adaptations that *Populus* and *Salix* do not possess. If the native woody taxa are obligate phreatophytes while *Tamarix* can extract soil moisture from less saturated soils in areas with depressed water tables, the putative competitive exclusion of *Salix* and *Populus* in southwestern riparian forests would be partially explained.

Research into plant water absorption that includes analyses of the stable isotopes of water allows a degree of refinement not attainable in correlative ecological or hydrological approaches. Plant dependence on groundwater vs. moisture from unsaturated soils, which may have its source in periodic floods or precipitation events, is key to a phreatophytic classification. With the possible exception of *Tamarix,* it appears that the dominant woody taxa of the study area are obligate phreatophytes. Current efforts to classify and inventory wetland vegetation, and to establish instream flow maintenance requirements for alluvial forest vegetation, should be aided by this type of information. Similarly, the relative degree of dependence of riparian vegetation upon various potential uptake waters is pertinent in determinations dealing with multiple hydrologic sources, including artificially maintained wetlands.

Acknowledgments

Efforts of C. Shadel in the laboratory and J. Kahl and D. Smereck in the field helped make this work possible. We appreciate their assistance as well as funding provided by the U.S. Bureau of Reclamation and cooperation of U.S. Fish and Wildlife Service personnel in providing study locations on the Havasu National Wildlife Refuge. Review comments of P. Schulte, L. Pitelka, and anonymous reviewers also improved the quality of this paper.

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