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## RESPONSE OF TREE RING HOLOCELLULOSE $\delta^{13}\text{C}$ TO MOISTURE AVAILABILITY IN *POPULUS FREMONTII* AT PERENNIAL AND INTERMITTENT STREAM REACHES

Daniel L. Potts<sup>1,2</sup> and David G. Williams<sup>1,3</sup>

**ABSTRACT.**—We measured  $\delta^{13}\text{C}$  of tree ring holocellulose to assess intra- and interannual variation in integrated leaf gas exchange responses of Frémont cottonwood (*Populus fremontii*) to monsoonal moisture inputs in southeastern Arizona. We predicted that  $\delta^{13}\text{C}$  of trees growing along drought-susceptible intermittent reaches of this semiarid river system would be more responsive to monsoonal moisture inputs than trees found along perennial reaches, where groundwater is consistently available. We sampled stem xylem cores from 7 trees, each at an intermittent and perennial reach of the San Pedro River near Tombstone, Arizona. We identified and subdivided individual rings from 1990 to 2000.  $\delta^{13}\text{C}$  of holocellulose from these subdivisions was compared with precipitation amount, atmospheric vapor pressure deficit ( $D_a$ ), and 90% exceedence flows ( $Q_{90}$ ) calculated from seasonal flow duration data.  $\delta^{13}\text{C}$  values were higher at the intermittent reach than at the perennial reach. Furthermore, annual ring  $\delta^{13}\text{C}$  values at the perennial reach were not correlated with stream flow, precipitation, or  $D_a$ .  $\delta^{13}\text{C}$  values for trees at the intermittent reach were negatively correlated with monsoon season (1 July–15 September)  $Q_{90}$  ( $r^2 = 0.50$ ,  $P = 0.015$ ) and positively correlated with  $D_a$  ( $r^2 = 0.45$ ,  $P = 0.03$ ). Shifts in  $\delta^{13}\text{C}$  between the inner- and outer-third of the annual ring were used as a measure of intra-annual variation. These shifts were correlated with monsoon season  $D_a$  ( $r^2 = 0.57$ ,  $P = 0.01$ ) and  $Q_{90}$  ( $r^2 = 0.59$ ,  $P = 0.005$ ) for trees growing along the intermittent reach. Intra- and interannual variation in integrated photosynthetic response exists at the population-scale for these native, riparian forests. Changes in monsoonal precipitation and stream flow may differentially alter photosynthetic gas exchange of *P. fremontii* and function of these riparian ecosystems.

*Key words:* *Populus fremontii*, carbon isotopes, North American monsoon, riparian ecosystems.

Hydrologic processes operating at local, basin, and regional scales control the composition and function of riparian forests in arid and semiarid regions (Stromberg 1993, Lines 1999, Rood and Mahoney 2000, Shafroth et al. 2000). Native riparian ecosystems are threatened in the semiarid southwestern United States by groundwater pumping, land-use intensification, and surface water diversions (Stromberg 1993). Alterations to the hydrologic regime such as flood attenuation and water withdrawals induce structural and functional changes in native riparian forests (Stromberg et al. 1996) and facilitate replacement by exotic species such as *Tamarix* spp. (Stromberg 1998). Water availability to riparian trees in the southwestern U.S. is extremely variable due to seasonal and interannual drought and heterogeneous hydrogeomorphic conditions that characterize drainages in these basins. Obligate riparian tree species in these systems occur only where alluvial groundwater depths are <3 m (Stromberg

et al. 1996), and groundwater depths can fluctuate dramatically. Riparian ecosystems in arid and semiarid settings offer unparalleled opportunity to study linkages between climate, hydrology, and plant-water relations with important management implications.

Interpopulation variability in transpiration and water source use has been observed for native Frémont cottonwood (*Populus fremontii* Wats.) forests along southern Arizona's San Pedro River (Schaeffer et al. 2000, Snyder and Williams 2000). However, these studies focused only on a single growing season. Thus, the range of interannual variability in *P. fremontii* water relations and its linkage to climate dynamics in the upper San Pedro River basin have not been studied. Such variability has implications for catchment-scale hydrologic modeling and riparian forest management (Goodrich et al. 2000). Refining the role of riparian vegetation in catchment-scale hydrologic models will become increasingly important. Regional climate

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models predict changes in summer precipitation and temperature (Doherty and Mearns 1999, Mearns et al. 1999), and continued valley groundwater pumping in the coming decades will place increased demands on limited water resources in the arid and semiarid Southwest.

Cottonwood water use has been explored at a variety of spatio-temporal scales (Leffler and Evans 1999, 2001, Sparks and Black 1999, Schaeffer et al. 2000, Snyder and Williams 2000). Using stable isotopes, Snyder and Williams (2000) found that uptake of summer precipitation by *P. fremontii* was at least in part a function of alluvial groundwater availability. During the summer rainy season in southern Arizona (July–September), cottonwood trees growing along an ephemeral tributary where groundwater depth exceeded 4 m derived a substantial portion of their transpiration water from upper, unsaturated soil layers. Uptake of seasonally available soil moisture was not observed in cottonwood trees growing along a perennial reach of the same stream, implying that precipitation use varies with depth to alluvial groundwater in this species.

Tree rings have long been used as a tool to study past climate in the western United States (Douglas 1920). Investigations of ring width in conifers have been used to reconstruct past drought events (Meko et al. 1995, Swetnam and Betancourt 1998), lake level fluctuations (Peterson et al. 1999), and snowpack (Peterson and Peterson 1994). Several authors have attempted to use cottonwood tree ring widths to reconstruct stream flow with mixed success (Johnson et al. 1976, Reily and Johnson 1982, Stromberg and Patten 1996, Dudek et al. 1998). For example, Stromberg and Patten (1996) measured tree ring width to relate radial growth of black cottonwood (*Populus trichocarpa*) to mean annual stream flow in the eastern Sierra Nevada.

To achieve intra-annual resolution in the tree ring record of southeastern Arizona, Meko and Baisan (2001) used conifer tree ring wood density and width of the latewood to reconstruct activity of the North American monsoon. Morphology distinguishes latewood bands in many ring porous species. Tree rings of the diffuse porous Frémont cottonwood lack such distinct features. Thus, we used carbon isotope ratios of holocellulose from subdivisions of the tree ring to quantify shifts in plant water status associated with monsoon intensity.

Carbon isotope ratios of tree ring holocellulose provide a record of plant photosynthetic responses to environmental variation (Francey and Farquhar 1982, McNulty and Swank 1995, Livingston and Spittlehouse 1996, Walcroft et al. 1997, Brooks et al. 1998, Leffler and Evans 1999, Waterhouse et al. 2000). Francey and Farquhar (1982) provide a widely accepted model of carbon isotope variation in photosynthetically fixed carbon. The ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  in photosynthate ( $\delta^{13}\text{C}_p$ ) is a function of the isotope ratio of the air surrounding the leaf ( $\delta^{13}\text{C}_a$ ), the ratio of leaf internal to ambient  $\text{CO}_2$  concentration ( $c_i/c_a$ ), the diffusive fractionation of  $^{13}\text{CO}_2$  in air ( $a = 4.4\text{‰}$ ), and the fractionation by Rubisco ( $b = 29\text{‰}$ ) in the form:

$$\delta^{13}\text{C}_p = \delta^{13}\text{C}_a - a - (b - a) c_i/c_a \quad (1)$$

Variation in observed isotopic ratios in tree ring holocellulose can be attributed to environmental, physiological and genetic factors that affect  $c_i/c_a$ . In the case of drought, stomata respond to limited water supply and high transpirational demand by closing and reducing the supply of  $\text{CO}_2$  in the leaf, thereby decreasing  $c_i/c_a$  and increasing  $\delta^{13}\text{C}_p$  (Farquhar et al. 1989). Photosynthate bearing the isotopic signature at the time of fixation is used to form holocellulose in tree rings. Fractionation during formation results in a systematic shift in  $\delta^{13}\text{C}$  between bulk photosynthate and holocellulose (Berninger et al. 2000).

Leffler and Evans (1999) extracted holocellulose from 15 annual rings (1981–1995) of 10 *Populus fremontii* trees growing along the Rio Grande near Socorro, New Mexico. Their study revealed a significant negative correlation between  $\delta^{13}\text{C}$  of holocellulose and stream flow. Below a threshold level of stream flow, precipitation became an important correlate with tree ring  $\delta^{13}\text{C}$ . Carbon isotope values of tree ring holocellulose were sensitive to stream flows early in the growing season. Response to spring flows was expected based on the results of *P. deltoides* branch-growth phenology in Alberta (Willms et al. 1998) and general patterns of vernal growth in riparian trees observed by Brown et al. (1977).

With its bimodal pattern of winter and summer precipitation, the San Pedro River of southeastern Arizona is ideal for studies on riparian plant-water interactions in a variety of

hydrologically, geomorphically, and lithologically distinct settings (Pool and Coes 1999). The objectives of this paper were (1) to explore the use of holocellulose  $\delta^{13}\text{C}$  from cottonwood tree ring subdivisions as a tool to examine interannual variation in  $c_i/c_a$  to moisture availability in the growing season, and (2) to address sensitivity in  $c_i/c_a$  to monsoonal moisture inputs in cottonwood populations growing under contrasting conditions of annual stream flow.

## METHODS

### Study Sites

Our research was conducted on the San Pedro River within the San Pedro National Riparian Conservation Area in southeastern Arizona. We identified 2 Frémont cottonwood populations separated by less than 15 km and approximately 50 m in elevation. Populations occur on coarse, alluvial soils and possess similar understory vegetation. We selected a population along a gaining, perennial reach immediately downstream of the USGS Charleston stream gauge (#09741000,  $31^\circ 37' 33''\text{N}$ ,  $110^\circ 10' 26''\text{W}$ , elevation 1205 m). The 2nd population, 15 km downstream from the 1st, is on a broad floodplain where stream flow is lost to the underlying alluvium and flow is intermittent ( $31^\circ 45' 03''\text{N}$ ,  $110^\circ 12' 02''\text{W}$ , elevation 1152 m).

### Field Sampling and Preparation of Tree Cores

To minimize canopy boundary layer influences on carbon isotope content of tree ring holocellulose, we chose trees growing in similar, open stands at the populations. We selected 7 trees at each site and extracted cores at breast height from opposite sides of the trunk with a 5.15-mm-increment borer. Based on experience with unusable, rotten cores, we avoided trees exhibiting "wet wood" symptoms (Hofstra et al. 1999). We took care to sample trees with full crowns, growing in similar position relative to the active channel. Ages of the trees sampled at the 2 sites varied from 15 to 50 years and ranged in diameter at breast height from 28 cm to 120 cm. Trees suitable for sampling at the intermittent reach had wider variation in stem diameter, which resulted in an intermittent reach sample population with a mean diameter larger than at

the perennial reach. However, differences in diameter at breast height of the sample populations were not statistically significant (Student's  $t$  test,  $t = -1.93$ ,  $df = 12$ ,  $P = 0.07$ ). We sampled 2 cores from each tree to account for potential radial variation in isotope composition. Cottonwood stems typically possess an elliptical morphology in cross section (Mike Merigliano personal communication). For consistency, tree cores were extracted  $180^\circ$  from each other on the minor axis of the elliptically shaped stem. We noted tree location by GPS, elevation, and distance from main channel; we also recorded crown condition for each tree.

Tree cores were prepared according to Fritts (1976) with minor modification. To avoid ring-to-ring holocellulose transfer, we prepared cores with razor blades rather than sandpaper. Core preparation with razor blades had the added benefit of preserving subtle variation in xylem morphology, greatly facilitating ring identification. Cores were visually cross-dated and rings were assigned a year of growth according to the methods of Yamaguchi (1991). Cores were measured for width to the nearest 0.1 mm using a semiautomated measuring system.

### Holocellulose Extraction and $\delta^{13}\text{C}$ Analysis

We focused on the response of  $\delta^{13}\text{C}$  to late growing season moisture availability similar to the ring growth responses in latewood of high-elevation conifers of the basin (Meko and Baisan 2001). Halving individual tree rings could potentially obscure a late growing season signal with material added earlier in the growing season. Dividing rings into thirds was a compromise between the potential fidelity of a late growing season signal and sample mass requirements for cellulose extraction. From each tree core we excised individual tree rings using a scalpel. Individual rings were subdivided into thirds corresponding to inner, middle, and outer portions of growth. Corresponding tree ring portions from the same tree were combined and ground in a mill (Model #3383-L10, Thomas Scientific, Swedesboro, NJ) to pass a 40-gauge screen.

We extracted holocellulose from inner- and outer-growth portions of rings corresponding to the growing seasons in 1990–2000. Raw wood contains a myriad of compounds, each with its own pathway of synthesis and set of isotope fractionations. Holocellulose, a major

component of raw wood, is a favored compound for analysis as it is immobile once formed in the tree ring of a given year and is relatively easy to extract. We followed the procedures described by Leavitt and Danzer (1993), using a refined pouching technique suggested by Wright and Leavitt (personal communication) to extract holocellulose from the raw wood of *P. fremontii* tree rings. Briefly, the process involved several steps over 5 days to process ~45 samples of raw wood contained in heat-sealed polyethylene pouches (Ankom Technologies, Fairport, NY). Pouching eliminates sample loss due to transfer and reduces the risk of sample contamination (Leavitt and Danzer 1993). Organically soluble compounds were dissolved from the raw wood by boiling in a 2:1 solution of toluene and ethanol followed by bleaching the samples in an acetic acid/sodium chlorite solution. Samples were rinsed in distilled water and dried. The remaining holocellulose was analyzed for  $\delta^{13}\text{C}$  on a continuous flow stable isotope mass spectrometer (Delta Plus, Finnigan MAT, Inc., San Jose, CA) at the University of Arizona Department of Geosciences. Error variation associated with holocellulose extraction and analysis was evaluated by including a raw wood lab standard that yielded holocellulose with a mean carbon isotope value of  $-25.67\text{‰}$  ( $s = 0.26$ ,  $n = 30$ ). Additionally, to evaluate the precision of the mass spectrometer, an acetanilide standard was measured along with the holocellulose samples ( $-29.59\text{‰}$ ,  $s = 0.18$ ). Data are reported relative to the PDB carbonate standard using delta ( $\delta$ ) notation in parts per thousand ( $\text{‰}$ ; Craig 1957).

#### Environmental Data and Analysis

The growing season was divided into an early (1 April–30 June) and late (1 July–15 September) period. April 1 approximates the beginning of the growing season for *P. fremontii* on the San Pedro River following leaf-out in late March. The North American monsoon commences in early July in southeastern Arizona and lasts through the middle of September.

The ratio of leaf internal to ambient  $\text{CO}_2$  concentration ( $c_i/c_a$ ) is a function of photosynthetic demand and stomatal conductance of the leaf. Assuming that photosynthetic  $\text{CO}_2$  demand over time is constant, changes in stomatal

conductance in response to changing leaf water conditions would induce changes in  $c_i/c_a$  and  $\delta^{13}\text{C}$  (Eq. 1) via 2 processes: (1) water availability to roots and its impact on hydraulic limitations from soil to leaf and (2) atmospheric demand for transpiration at the leaf. Therefore we limited our analysis to 3 environmental variables: (1) summer precipitation, (2) stream flow, and (3) atmospheric vapor pressure deficit.

Historic precipitation data for Tombstone, Arizona, 14 km from our field sites ( $31^\circ 43' \text{N}$ ,  $110^\circ 04' \text{W}$ , elevation 1384 m), were provided by the Western Regional Climate Center (Reno, NV). Based on the precipitation record at Tombstone, Arizona, we determined that August was the peak month of monsoon precipitation (87.58 mm,  $s = 32.48$ ,  $n = 11$ ). Temperature and relative humidity from Walnut Gulch Experimental Watershed at Tombstone, Arizona for the period of climate record, 1991–2000, was obtained from the USDA–ARS in Tucson, Arizona (~14 km from our sites, elevation 1380 m). Using temperature data, we calculated saturation water vapor pressure ( $e_s$ ) according to Dille (1968):

$$e_s = 0.61078 \exp [17.269T / (T + 237.8)] \quad (2)$$

Combined with the concurrent relative humidity data, we calculated seasonal mean atmospheric vapor pressure deficit ( $D_a$ ) for the early and late portions of the growing season defined above for 1991–2000, according to the equations provided by Landsberg (1986):

$$\text{Relative humidity} = e_a/e_s \quad (3)$$

$$D_a = e_s - e_a \quad (4)$$

Growing season precipitation typically comes in the form of intense, highly localized convective storms during the monsoon season. Runoff from these storms produces episodic stream flow several orders of magnitude greater than base flow. Given these conditions, stream flow statistics such as seasonal mean discharge are misleading and mask important stream flow variation within and between years. We obtained mean daily discharge data for the San Pedro River's Charleston stream gauge (#09741000) from the U.S. Geological Survey Water Resources Division. From these data we calculated flow-duration curves according to Searcy (1959) to summarize stream flow

during the early (April–June) and late (July–15 September) periods of the growing season. Briefly, mean daily discharge data for a period of interest in a given year was assigned a rank in order of descending discharge magnitude. An exceedence frequency ( $F$ ) was calculated for each ranked discharge value ( $r$ ) according to the formula:

$$F = [r / (n + 1)] * 100 \quad (5)$$

where  $n$  is the number of ranked discharge values for the period of interest. For example, the largest mean daily discharge value ( $r = 1$ ) for a 99-day period ( $n = 99$ ) would have an exceedence frequency ( $F$ ) equal to 1. Likewise, the median discharge value ( $r = 50$ ) for the same period would have an exceedence frequency ( $F$ ) equal to 50. By this method the 50% exceedence value ( $Q_{50}$ ) expresses the median stream flow for any given period of time.

Flow-duration analysis provides a convenient and repeatable standard for comparing seasonal patterns of stream flow across years at the same site. By ranking and assigning a frequency to discharge values, flow-duration analysis incorporates episodic, high-flow events and sustained groundwater discharge into a single calculation (Vogel and Fennessey 1995). Using these calculated flow-duration data from the Charleston stream gauge, we estimated early and late growing season 90% exceedence stream flow values ( $Q_{90}$ ) for each year to characterize the availability of alluvial groundwater at both sites. Estimated from flow-duration analysis,  $Q_{90}$  is a common, low-flow index in water resource planning and hydropower design (Gordon et al. 1992). In effect, we generated a mean daily stream flow discharge value for each period that is equivalent to the discharge value exceeded 9 days out of 10 during that period.

Isotope data were checked for normality and analyzed with JMP IN Statistical Discovery software version 4 (SAS Institute, Inc., Cary, NC). We used linear regression analysis to examine dependence of tree ring holocellulose  $\delta^{13}\text{C}$  values on late growing season  $D_a$ ,  $Q_{90}$ , total monsoon, and August precipitation.

## RESULTS

We averaged early and late season  $\delta^{13}\text{C}$  values to generate a growing season average at

TABLE 1. Correlations ( $r$ ) among environmental variables collected during the late growing season for 1990–2000. Relationships significant at the  $P < 0.05$  level are noted with an asterisk (\*).

	Total ppt.	August ppt.	$Q_{90}$
$D_a$	0.57	0.53	0.72*
$Q_{90}$	0.52	0.56	
August ppt.	0.76*		

each site for each year. The years were then averaged to create a grand mean for each site from 1990 to 2000. The mean  $\delta^{13}\text{C}$  value for the population growing at the gaining, perennial reach site ( $-26.33\text{‰}$ ,  $s_{\bar{x}} = 0.08$ ,  $n = 11$ ) was significantly lower (Student's  $t$  test,  $t = 3.87$ ,  $df = 19$ ,  $P = 0.001$ ) than that for the population growing at the losing, intermittent reach ( $-25.68\text{‰}$ ,  $s_{\bar{x}} = 0.08$ ,  $n = 11$ ). The more positive  $\delta^{13}\text{C}$  value for the population at the losing, intermittent reach is consistent with decreased  $c_i/c_a$ , indicative of stomatal response to comparatively elevated atmospheric demand or limited water supply during the growing season.

To better understand the relationship between tree ring width and carbon isotope content, we compared mean ring-width measurements with the associated mean  $\delta^{13}\text{C}$  for each year for both populations in 1990–2000. There was no relationship between mean ring width and mean annual  $\delta^{13}\text{C}$  among cottonwood trees growing at either the losing, intermittent or gaining, perennial reach ( $r^2 = 0.10$ ,  $P = 0.33$ , and  $r^2 = 0.09$ ,  $P = 0.37$ , respectively).

Environmental parameters recorded during the late growing season were significantly intercorrelated (Table 1). Flow duration at the 90% exceedence value ( $Q_{90}$ ) correlated with  $D_a$  during this period. Stream discharge integrates highly localized, summer convective storms in the watershed. The frequency and extent of these storms is in part a function of atmospheric moisture content. Total late growing season precipitation and August precipitation were less correlated with  $Q_{90}$  than was  $D_a$ .

Within the intermittent and perennial reach growing populations, there was no significant relationship between outer-third holocellulose  $\delta^{13}\text{C}$  variation and annual tree ring width for 1990–2000 ( $r^2 = 0.08$ ,  $P = 0.39$ , and  $r^2 = 0.04$ ,  $P = 0.55$ , respectively). Interannual  $\delta^{13}\text{C}$  values in outer-third holocellulose from trees

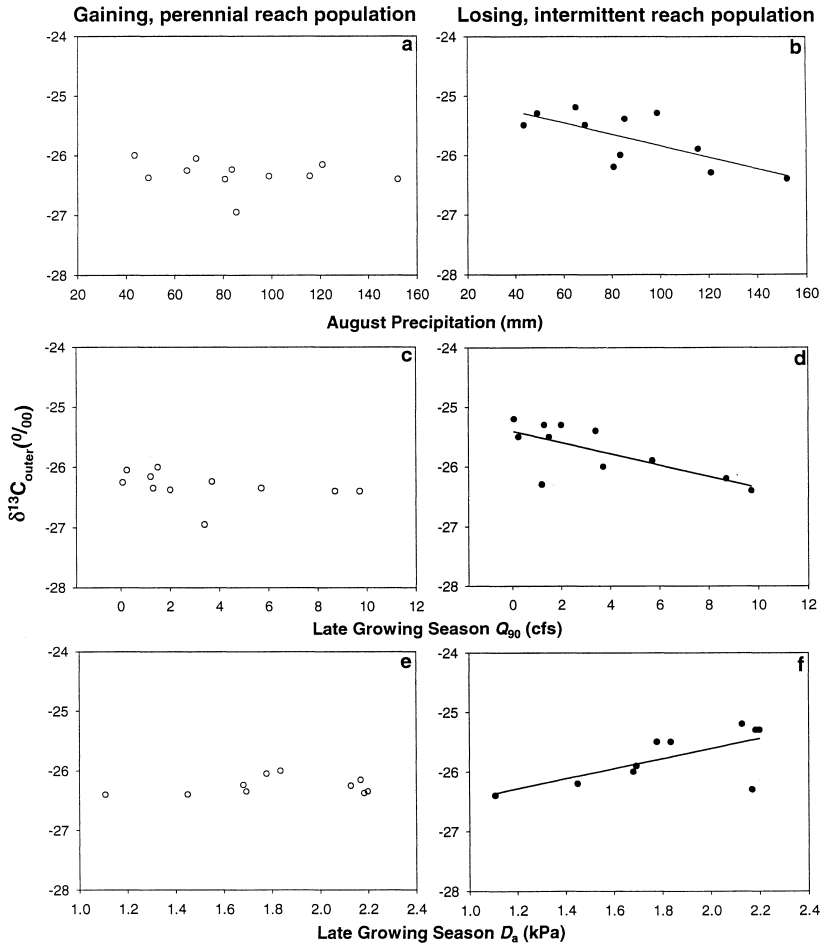


Fig. 1. Relationships between outer-third tree-ring holocellulose  $\delta^{13}\text{C}$  in *Populus fremontii* and (a,b) August precipitation amount, (c,d) late growing season 90% exceedence flows ( $Q_{90}$ ), and (e,f) atmospheric vapor pressure deficit ( $D_a$ ) at perennial and intermittent reaches on the San Pedro River in southeastern Arizona.

at the losing, intermittent reach were negatively correlated with August precipitation (Fig. 1b;  $r^2 = 0.50$ ,  $P = 0.015$ ) and late season  $Q_{90}$  (Fig. 1d;  $r^2 = 0.50$ ,  $P = 0.015$ ).  $\delta^{13}\text{C}$  values were highest during years when August precipitation and late season stream flows were low. Outer-third  $\delta^{13}\text{C}$  values were positively correlated with late season  $D_a$  at this site (Fig. 1f;  $r^2 = 0.45$ ,  $P = 0.03$ ). There was no significant correlation between tree ring  $\delta^{13}\text{C}$  values and total monsoon rainfall at the intermittent reach site.  $\delta^{13}\text{C}$  values from outer-third tree ring subdivisions at the gaining, perennial reach were not significantly correlated with any of the environmental variables examined (Figs. 1a, 1c, 1e).

We calculated the shift in  $\delta^{13}\text{C}$  values from the inner- to outer-third tree-ring subdivisions for each year. No systematic intra-annual shift was found in  $\delta^{13}\text{C}$  in response to late growing season moisture conditions at the gaining, perennial reach site (Figs. 2a, 2c, 2e). However, there were correlations between the magnitude of the intra-annual shift in  $\delta^{13}\text{C}$  and late season moisture conditions at the losing, intermittent reach site. August precipitation (Fig. 2b;  $r^2 = 0.37$ ,  $P = 0.05$ ),  $Q_{90}$  (Fig. 2d,  $r^2 = 0.59$ ,  $P = 0.005$ ), and late growing season  $D_a$  (Fig. 2f;  $r^2 = 0.57$ ,  $P = 0.01$ ) were correlated with intra-annual shifts in carbon isotope values for trees along the losing, intermittent reach. There was no intra-annual shift in  $\delta^{13}\text{C}$

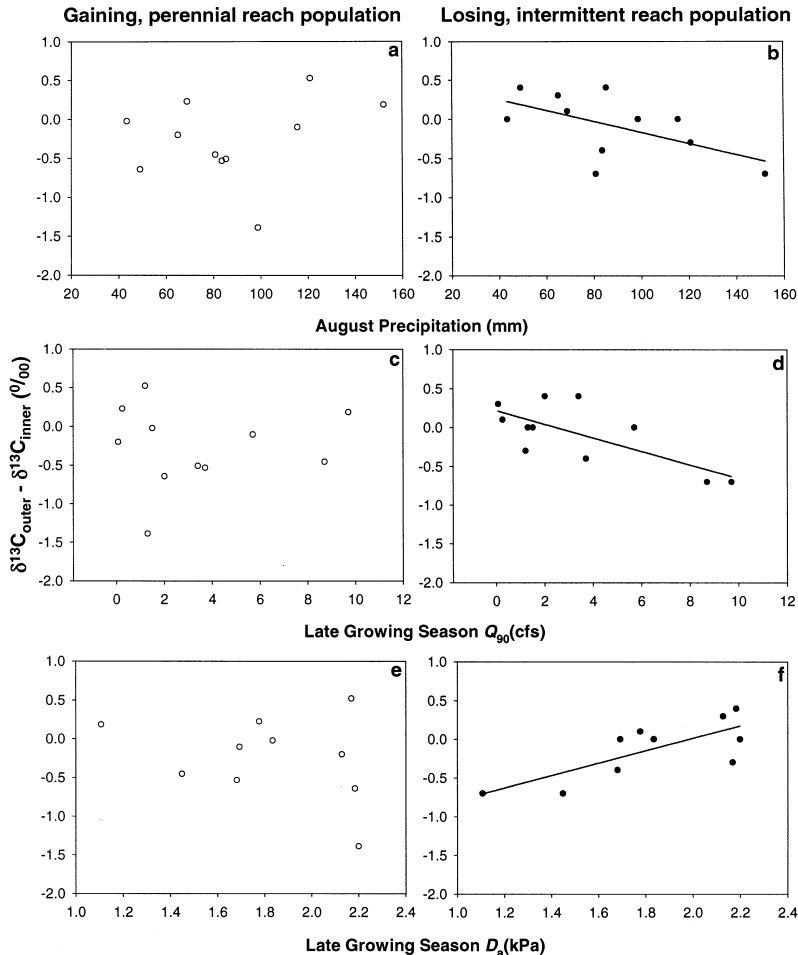


Fig. 2. Differences between  $\delta^{13}\text{C}$  of tree ring holocellulose inner- and outer-third portions in relation to August precipitation for 1990–2000 (a,b); late growing season  $Q_{90}$  for 1990–2000 (c,d); late growing season atmospheric vapor pressure deficit ( $D_a$ ) for 1991–2000 (e,f) for *Populus fremontii* growing at perennial and intermittent reaches on the San Pedro River in southeastern Arizona.

values associated with total monsoon rainfall at either site.

#### DISCUSSION

This study provides a decade-long record of physiological response of a dominant riparian tree species to hydrologic and climatic variation. Our data demonstrate the utility of carbon isotope analysis of tree rings to document leaf physiological response to intra- and interannual environmental variability in semi-arid riparian ecosystems. Equal subdivision of tree rings for carbon isotope analysis allowed us to achieve intra-annual resolution in tree

response to climate in populations of *Populus fremontii*—a species that lacks visible late-wood bands. Because we compared only 2 populations, each growing at different reaches of the San Pedro River, our statistical scope of inference is limited to these sites. Leaf gas exchange in *P. fremontii* responded significantly to variation in moisture conditions during the late growing season at the intermittent reach site, but not at the perennial reach site. Ring  $\delta^{13}\text{C}$  remained fairly constant at the perennial reach site despite widely fluctuating stream flow and atmospheric moisture conditions.



We found no evidence for a physiological response to threshold values of late growing season flow for 1990–2000 among the populations of *P. fremontii* that were sampled on the San Pedro River. Leffler and Evans (1999) reported that during years of abundant flow in the middle Rio Grande, whole-ring holocellulose  $\delta^{13}\text{C}$  of Frémont cottonwood trees did not correlate with variation in stream flow. However, in years when flow was below a threshold value,  $\delta^{13}\text{C}$  values were negatively correlated with stream flow. Other studies have documented nonlinear responses of riparian vegetation to environmental conditions at the individual and community level (Stromberg et al. 1996, Friedman and Auble 1999, Scott et al. 1999). Stream flow and associated alluvial soil water potential at the perennial reach site may have never reached the point beyond which stomatal conductance was impacted. Conversely, alluvial soil water potentials at the intermittent reach site may have been at or below the threshold value over the entire period covered by our isotope sampling. Despite the close proximity of the 2 populations to one another, a genetic difference in drought sensitivity between populations is another possible explanation of these results.

Positive growth responses in *Populus* to spring and early summer stream flow have been inferred from whole-ring  $\delta^{13}\text{C}$  (Leffler and Evans 1999) and branch elongation (Willms et al. 1998). We found no such relationships between tree ring inner-third  $\delta^{13}\text{C}$  values and flow. It is possible that stored photosynthate from prior years contributes to early season tree ring formation (Hill et al. 1995, Robertson et al. 1997). Products of photosynthesis in the early growing season may be allocated to the growth of new leaves (Terwilliger 1997) and fine roots (Burton et al. 2000), blurring the early growth isotopic signature of tree ring holocellulose. We reject a 3rd alternative hypothesis: moisture stored in the upper-soil profile carried over from winter rains ameliorates leaf-water status, and thereby masks the environmental signal in  $\delta^{13}\text{C}$  of the rings. We tested the hypothesis that in years of abundant winter moisture, as measured by precipitation totals from October through March, inner-third portions of tree ring holocellulose  $\delta^{13}\text{C}$  would tend toward greater discrimination, indicative of greater stomatal conductance and more favorable leaf-water status. There was no evidence

for such a relationship with winter moisture at either site (data not shown).

Differences in  $\delta^{13}\text{C}$  of tree ring holocellulose could be explained without invoking stomatal conductance changes in response to leaf water conditions. High photosynthetic capacity can reduce  $c_i/c_a$ , independent of changes in stomatal conductance.  $\text{CO}_2$  demand by chloroplasts is related to soil nitrogen availability, temperature, and other factors that impact photosynthetic enzyme activity or concentrations in the leaf. However, given similarities in elevation, vegetation community, management history, and soils at the 2 sites, it seems unlikely that these factors are important for explaining differences.

Intra- and interannual variation in the carbon isotope content of atmospheric  $\text{CO}_2$  could also account for variation in  $\delta^{13}\text{C}$  of tree ring holocellulose. We used atmospheric  $\text{CO}_2$   $\delta^{13}\text{C}$  data for 1990–2000 from Mauna Loa Observatory, Hawaii (NOAA CMDL, <http://www.cmdl.noaa.gov/ccgg/flask/index.html>), to calculate the isotopic discrimination of cellulose formation ( $\Delta_{\text{holocellulose}}$ ) from Farquhar et al. (1989):

$$\Delta_{\text{holocellulose}} = (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{holocellulose}}) / (1 + \delta^{13}\text{C}_{\text{holocellulose}}) \quad (6)$$

We compared early and late growing season  $\Delta_{\text{holocellulose}}$  to the corresponding  $\delta^{13}\text{C}$  value using regression analysis. We found high correlations between  $\delta^{13}\text{C}_{\text{holocellulose}}$  and  $\Delta_{\text{holocellulose}}$  during the early and late growing seasons at both sites (Table 2). We conclude that variation in carbon isotope composition of holocellulose, whether calculated as  $\delta^{13}\text{C}_{\text{holocellulose}}$  or  $\Delta_{\text{holocellulose}}$ , does not change the interpretation of the influence of intra- and interannual variability in water availability on  $c_i/c_a$ .

There is no satisfying physiological explanation for why tree ring  $\delta^{13}\text{C}$  values would reflect August and not monsoon total rainfall during a growing season. These findings highlight the difficulty of assessing the ecophysiological impact of monsoonal precipitation at the catchment scale. Because of the narrow spatial extent of summer convective storm activity, storms recorded at the Tombstone rain gauge might miss the cottonwood populations growing 14 km away. Ideally, a long-term weather station would be situated at both sites

TABLE 2. Correlations ( $r$ ) between holocellulose  $\delta^{13}\text{C}$  and  $\Delta_{\text{holocellulose}}$  for 1990–2000. Relationships significant at the  $P < 0.0001$  level noted with ##. Relationships significant at the  $P < 0.0005$  noted with #.

	Early growing season	Late growing season	Growing season shift
Intermittent reach	0.94##	0.98##	0.98##
Perennial reach	0.98##	0.89#	0.99##

to provide a spatially explicit record of summer convective storm precipitation for the period of tree ring record.

Frequency-duration analysis provided useful stream flow information by incorporating both sustained low flows and occasional extreme events into a single calculation comparable across years. To validate the utility of flow duration analysis in semiarid riparian ecology, we examined the correlation between mean late growing season stream flow and  $\delta^{13}\text{C}$  of outer-third tree ring subdivisions at the losing, intermittent reach for 1990–2000. Sensitive to extreme high-flow events, mean late growing season stream flow failed to significantly correlate with  $\delta^{13}\text{C}$  of outer-third tree ring portions ( $r^2 = 0.28$ ,  $P = 0.09$ ). We recommend that future plant-water relations studies in semiarid and arid riparian zones carefully consider the importance of stream flow variability in plant response. Flow-duration analysis is a tool that accounts for biases with integrated seasonal variables as a result of extreme events.

The ratio of leaf internal to ambient  $\text{CO}_2$  concentration and thus  $\delta^{13}\text{C}$  is regulated to a large degree by stomatal conductance (Farquhar et al. 1982). Stomatal conductance together with aerodynamic conductance regulates transpiration rate at the ecosystem scale (Jarvis and McNaughton 1986). Understanding intra- and interannual variation of  $\delta^{13}\text{C}$  in native, riparian forests has implications for the scaling of water relations in this ecosystem. Catchment-scale models should take into account the dynamic role of hydrologic setting and riparian forest water use in response to summer moisture conditions. Multiscale modeling efforts such as those used by Goodrich et al. (2000) might benefit from refinement of the evapotranspiration component by spatially integrating seasonal patterns of vegetation response with changing seasonal moisture conditions.

From a management perspective, this study adds to a growing body of evidence that hydrologic setting plays a key role in how riparian plant populations respond to regional drought.

Demonstrable population-level variability in  $\delta^{13}\text{C}$  associated with stream flow and hydrogeomorphic setting provides a starting point for additional investigations on tree-water relations and carbon exchange in this ecosystem. Future isotope dendrochronological studies on riparian species should carefully consider the influence of hydrologic conditions on  $\delta^{13}\text{C}$  values.

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