2.11 WATER SOURCE DETERMINATION IN COTTONWOOD/WILLOW AND MESQUITE FORESTS ON THE SAN PEDRO RIVER IN ARIZONA

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1. **ABSTRACT**

This research investigated physiological and environmental controls on plant water-use and transpiration loss at the species-level. We identified water sources (precipitation, stream, soil moisture and/or groundwater) utilized by cottonwood (*Populus fremontii*), willow (*Salix goodingii*) and mesquite (*Prosopis velutina*) in relation to patterns of seasonal moisture stress, and consequences of plant water sources for stomatal regulation of transpiration. Results indicate that cottonwood, along perennial and intermittent stream reaches in Arizona did not utilize soil moisture derived from monsoon precipitation and were primarily dependent on groundwater, however, at an ephemeral site cottonwood utilized monsoon derived soil moisture. Mesquite shifted between groundwater and soil moisture in response to changing climatic and hydrologic conditions. Mesquite likewise had a greater ability to withstand increasingly negative midday water potentials. In contrast, cottonwood and willow appeared to regulate midday water potentials to -1.5 MPa, indicating that reliance on deep groundwater may be indicative of highly regulated stomatal control on transpiration.

2. **INTRODUCTION**

Of great concern is how human alterations of hydrology and climate influence terrestrial vegetation. One such example is the alteration of riparian ecosystems by groundwater pumping and surface water diversions. In semiarid and arid regions of the world, these impacts have produced dramatic structural and species composition changes in riparian systems (Stromberg and Patten 1990). Obligate riparian species, such as cottonwood and willow, will regulate water-use in a markedly different manner than the more drought resistant mesquite, which affects water-use efficiency and carbon acquisition, ultimately influencing competitive advantage and plant distribution. This research attempts to elucidate how different tree species found within riparian systems and adjacent uplands utilize available water and how these patterns of water-use affect species distribution and productivity.

Recent studies in arid environments have shown that plants may not be using water from all potential sources (Dawson and Ehleringer 1991, Lin *et al.* 1996). Depth of water extraction has been found to vary among species (Ehleringer and Dawson 1992, Flanagan *et al.* 1992) as well as within a species (Donovan and Ehleringer 1994, Williams and Ehleringer *in review*). We investigated seasonal patterns of water source utilization of semi-arid riparian tree species because it is likely that species-specific ability to utilize water from one or more hydrologic compartments has implications for plant and stand-level transpiration (Schaeffer and Williams, *this volume*) and plant hydraulic architecture.

Hydraulic architecture of dominant plants may have an important role in determining the structure and sustainability of plant communities and ecosystem processes. Xylem cavitation, the vaporization of water under negative pressure during drought, interrupts plant water transport. Cavitation occurs when xylem sap, which is under tension (Pockman *et al.* 1995), reaches critically low pressures and air bubbles are pulled into xylem conduits (Tyree and Sperry 1988). Xylem pressure is a result of transpiration, which is regulated by stomata, and soil water potential. Cavitation is injurious to plants, so stomata may operate to control transpiration at a level below the critical xylem pressures that induce cavitation (Tyree and Sperry 1988). Previous research demonstrates that cavitation occurs in cottonwood and willow shoots at less negative xylem pressures (Pockman *et al.* 1995) than in mesquite (Pockman 1996). Plants adapted to using soil moisture will necessarily experience low soil water potentials favoring cavitation. Consequently, vulnerability to cavitation may correlate with water source acquisition strategies and stomatal behavior for these species.

In this research, we related patterns of water source utilization with patterns of stomatal regulation, both of which may be operating to avoid cavitation. To examine these patterns we contrasted the obligate phreatophytes cottonwood (*Populus fremontii*) and willow (*Salix goodingii*), with mesquite (*Prosopis velutina*) which is able to exist in both riparian and upland environments. Three principal research questions were posed. First, we asked if variations in groundwater or stream water availability influence the amount of rainfall derived soil moisture used by these species. We hypothesized that species with access to a stable water source, in this case groundwater or

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perennial streamwater, would be less likely to expend carbon to grow lateral surface roots to acquire sporadic precipitation. To examine this hypothesis, we studied stomatal and water acquisition behavior at sites characterized by different streamflow and groundwater characteristics. Although other studies have found that obligate phreatophytes did not utilize soil moisture (Busch *et al.* 1992), we speculated that, as conditions become less favorable for species existence and cavitation becomes more excessive, a species will utilize other water sources.

Second, we hypothesized that the water acquisition strategy and vulnerability to cavitation of a species would translate into definable patterns of stomatal regulation of transpiration. If this is the case, trees primarily dependent on groundwater should be relatively insensitive to seasonal soil moisture drought. Third, it is hypothesized that differences in these integrated patterns of water-use will explain differences in the species distribution of cottonwood, willow and mesquite.

3. METHODS

A pilot study was conducted in 1996 along an intermittent reach of Rincon Creek. In 1997 a more extensive study was conducted along the San Pedro River in southeastern Arizona. Three San Pedro sites were selected to represent a gradient in surface water availability and depth to groundwater. The hydrologic regime varied from perennial to intermittent to ephemeral at Lewis Springs (LS), Boquillas Ranch (BQ) and Escapule Wash (EW), respectively. Sites along the San Pedro were selected in close proximity to encompass varying hydrologic regimes and with the target species (cottonwood, willow and mesquite) present. The ephemeral site appears to be the extreme hydrologic boundary of willow and cottonwood. At EW the stand of cottonwood and willow was sparse and graded into a mesquite community upstream.

At each site 7-10 individuals of each species were randomly selected as study plants. Each individual was repeatedly sampled at key times (spring, summer drought and monsoon season) throughout the growing season to determine seasonal patterns of water source use. Stable isotopes of oxygen in xylem sap extracted from twig samples were used as a natural tracer for measuring plant fractional uptake from groundwater, soil moisture, streamwater and precipitation (Ehleringer and Dawson 1992, Brunel *et al.* 1995). During each sample period, soils for isotopic analysis were collected at each site from 5, 10, 25, 50 and 100-cm depths. At each sampling period and at all sites, streamwater was collected and groundwater was sampled from wells with a peristaltic pump. Precipitation was collected at all sites in standard rain gages containing a layer of mineral oil to minimize evaporation. Precipitation was collected monthly throughout 1997 and more frequently during the monsoon season (July – September). Using a pressure chamber, water stress was quantified with measurements of predawn leaf water potential (Ψ_{pd}) and midday leaf water potential (Ψ_{md}).

4. RESULTS AND DISCUSSION

Monsoon rains had $\delta^{18}O$ values ranging from 0.8 to 2.0 (‰), and groundwater had stable values throughout the year, averaging –8.6 (‰). We found little variation in the $\delta^{18}O$ values of cottonwood xylem sap sampled at LS during the June drought and in August after a significant input of monsoon precipitation (26.7 mm). This indicates that cottonwood did not utilize surface soil moisture at the perennial site (LS), and relied primarily on groundwater (Fig. 1), even after significant

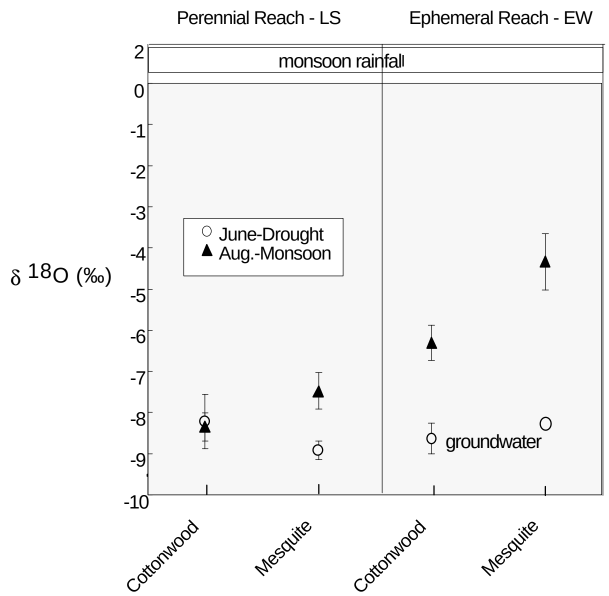

Figure 1. Variations in the mean $\delta^{18}O$ value of xylem sap in cottonwood and mesquite during drought conditions in June and following a monsoon rain in August.

monsoon rain. However, at the ephemeral site $\delta^{18}O$ of cottonwood showed enrichment in August relative to xylem sap sampled in June, indicating a fraction of xylem sap was derived not from groundwater, but from soil moisture. This contrasts with previous research (Busch et al. 1992) which found cottonwood to utilize only deep groundwater at the Colorado River and the Bill Williams River in Arizona. Cottonwood trees at EW experienced greater water stress with mean Ψ_{md} declining to -2.5 MPa during the summer drought, while cottonwoods at LS maintained mean Ψ_{md} of –1.5 MPa. Whether cottonwood switches to water uptake by lateral surface roots is not known as the isotopic profile of the soil water still remains to be determined. If the large rain event, just prior to sampling, percolated to deep depths, then the shift in isotopic value may not represent a shift in the activity of roots used to take up water. However, the $\delta^{18}O$ value of the groundwater remained a consistent –8.7 (‰) throughout the summer, suggesting that roots higher in the soil profile were being used to uptake water. Regardless of the functional rooting depth for water uptake, these results indicate that summer rainfall is an important contribution to cottonwood water supply at a site marginal for the existence of this species.

Mesquite xylem water, sampled in August, showed $\delta^{18}O$ enrichment at both sites compared to xylem water sampled in June, indicating that mesquite utilized monsoon moisture at both the ephemeral and perennial sites (Fig. 1). August mesquite xylem water was enriched relative to June xylem water by 3.9‰ at the ephemeral site and by 1.4‰ at the perennial site. Mesquite appeared to respond more dramatically to rainfall events at the ephemeral site compared to mesquite populations at the perennial site. Two processes may be responsible for the apparent difference in the magnitude of response of mesquite: 1) sites with less groundwater and surface water promote greater utilization of soil moisture, or 2) the magnitude of response is actually the same at both sites, but the clayey soil texture at LS has a dampening effect on the isotopic value of rainfall by mixing with older soil water. Construction of the isotopic profile of the soil will elucidate which explanation is more plausible.

Results at Rincon Creek indicate that willow experienced a response intermediate to that of cottonwood and mesquite, in its ability to utilize monsoon moisture ($\delta^{18}O$=-6.8) (Fig. 2). Willow samples were collected after a rainfall event in July of 1996. This is in contrast to previous research (Busch *et al*. 1992) that found willow to utilize only deep groundwater. Further analysis of samples will need to be completed before specific conclusions can be reached about willow growing along the San Pedro.

Stomatal regulation patterns differed between the obligate phreatophytes and mesquite. The relationship between Ψ_{pd} and Ψ_{md} at LS (Fig. 3) indicates that regardless of Ψ_{pd}, Ψ_{md} are maintained at -1.5 MPa for both willow and cottonwood. In contrast, mesquite exhibited considerable variation in Ψ_{md}. Ψ_{pd} are a measure of soil moisture conditions with more negative values reflecting decreased soil moisture availability. The negligible slope of the relationship for cottonwood and willow indicates that these species maintain a critical level of Ψ_{md} as water availability declines. Maintenance of stable Ψ_{md} under conditions of decreased water availability may be accomplished either by 1) dynamic regulation of transpirational water loss by stomatal regulation 2) increased soil-to-leaf hydraulic conductance, or 3) decreased leaf area. In contrast, mesquite tolerates a wide range of Ψ_{md}, indicating greater tolerance to low water potentials, and less stomatal regulation of transpiration.

Previous research found that cottonwood and willow stems may reach complete cavitation by xylem

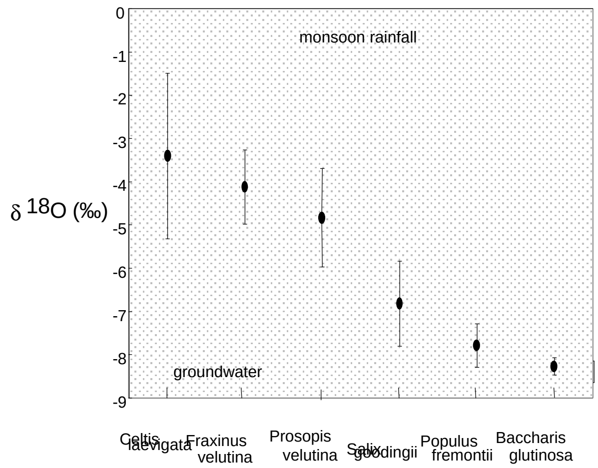

Figure 2. Variations in the mean $\delta^{18}O$ signature of xylem sap for dominant woody plant at Rincon Creek an intermittent stream in southeastern Arizona. Plant species are netleaf hackberry (*Celtis laevigata*), velvet ash (*Fraxinus velutina*), mesquite (*Prosopis velutina*), Goodding willow (*Salix goodingii*), Fremont cottonwood (*Populus fremontii*), and seep willow (*Baccharis glutinosa*).

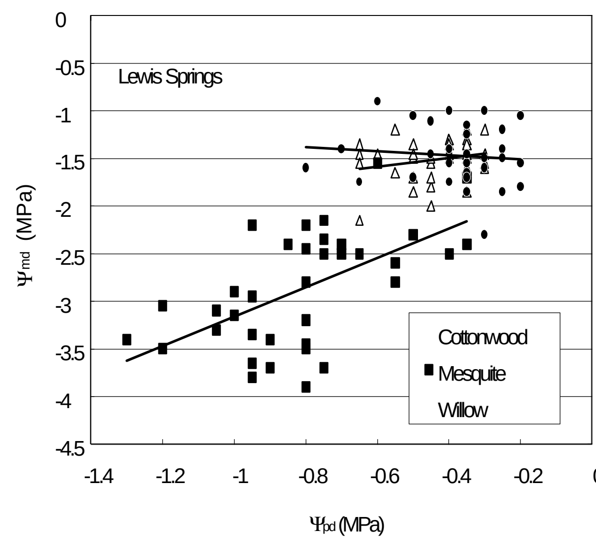

Figure 3. Relationship between predawn (Ψ_{pd}) vs. midday water potential (Ψ_{md}), throughout the entire growing season, of cottonwood, willow and mesquite sampled at a perennial reach (Lewis Springs) of the San Pedro River.

pressure of –2 to –3 MPa (Pockman *et al.* 1995). This indicates that cottonwood and willow at LS may be regulating Ψ_{md} to avoid cavitation. At the ephemeral site cottonwood utilized precipitation derived soil moisture, perhaps as a result of the decrease in Ψ_{md} to –2.5 MPa, a level which is likely causing significant cavitation.

5. CONCLUSIONS

Site hydrology has an influence on the functional architecture of riparian tree root systems; not all sources of available water are used equally. Water usage depends on the species present and the hydrologic conditions. Stable isotopic analysis identifies plant water uptake from various hydrologic compartments. The complex and highly plastic behavior of mesquite must be considered in relation to water availability. Similarly, even obligate phreatophytes may exhibit flexibility in water sources at ecotones where the conditions for their survival are marginal. Our data indicate that obligate phreatophytes regulate critical water potentials in a different manner than the more drought tolerant mesquite. Patterns of stomatal regulation coupled with water source investigations could prove to be useful for determining plant functional types (Wiliams *et al.*, this issue). Reliance on a single water source, while other sources of water are available may be indicative of plants that are extremely vulnerable to cavitation and exhibit more stomatal regulation of transpiration. If these water-use relationships are determined for a variety of functional types then it may be possible to scale up functional type relationships to characterize processes controlling transpiration at ecosystem or basin scales. One critical parameter may be the regulation of stomata to near critical cavitation levels.

Cottonwood and willow appear to rely on groundwater until irreversible cavitation levels are reached. Their tolerance of low water potentials is substantially less than that of mesquite, and they must maintain a high degree of transpiration regulation. These data provide further evidence that declining water tables will have a disproportionate effect on the sustainability of obligate riparian trees, such as cottonwood and willow, which are critically tied to groundwater levels.

6. ACKNOWLEDGMENTS

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