

Ecophysiology of riparian cottonwood and willow before, during, and after two years of soil water removal

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Abstract. Riparian cottonwood/willow forest assemblages are highly valued in the southwestern United States for their wildlife habitat, biodiversity, and watershed protection. Yet these forests are under considerable threat from climate change impacts on water resources and land-use activities to support human enterprise. Stream diversions, groundwater pumping, and extended drought have resulted in the decline of cottonwood/willow forests along many riparian corridors in the Southwest and, in many cases, the replacement of these forests with less desirable invasive shrubs and trees. Nevertheless, ecophysiological responses of cottonwood and willow, along with associated ecohydrological feedbacks of soil water depletion, are not well understood. Ecophysiological processes of mature Fremont cottonwood and coyote willow stands were examined over four consecutive growing seasons (2004–2007) near Salt Lake City, Utah, USA. The tree stands occurred near the inlet of a reservoir that was drained in the spring of 2005 and remained empty until mid-summer of 2006, effectively removing the primary water source for most of two growing seasons. Stem sap flux density (J_s) in cottonwood was highly correlated with volumetric soil moisture (θ) in the upper 60 cm and decreased sevenfold as soil moisture dropped from 12% to 7% after the reservoir was drained. Conversely, J_s in willow was marginally correlated with θ and decreased by only 25% during the same period. Opposite patterns emerged during the following growing season: willow had a lower whole-plant conductance (k_t) in June and higher leaf carbon isotope ratios ($\delta^{13}C$) than cottonwood in August, whereas k_t and $\delta^{13}C$ were otherwise similar between species. Water relations in both species recovered quickly from soil water depletion, with the exception that sapwood area to stem area ($A_s:A_{st}$) was significantly lower in both species after the 2007 growing season compared to 2004. Results suggest that cottonwood has a greater sensitivity to interannual reductions in water availability, while willow is more sensitive to longer periods of soil water depletion. These data shed light on the linkage between soil water deficits and ecophysiological processes of threatened riparian forests given potential land-use and long-term drought impacts on freshwater resources.

Key words: coyote willow; drought recovery; ecohydrology; Fremont cottonwood; leaf $\delta^{13}C$; *Populus fremontii*; Red Butte Canyon Research Natural Area, Utah, USA; riparian ecology; *Salix exigua*; stem sap flux; tree rings.

INTRODUCTION

Cottonwood (*Populus*) and willow (*Salix*) trees collectively make up the most widespread native riparian forest type in the southwestern United States. They are highly valued for their wildlife habitat, biodiversity, watershed protection, and recreation in otherwise unproductive arid regions of the Southwest (Patten 1998). However, global change impacts, including land-use change, climate change, and species invasions, threaten to alter the current composition of cottonwood/willow forests. In fact, cottonwood/willow forests along many major watersheds are considered among the most threatened forest types in the United States (Stromberg 1993, Webb et al. 2007).

Cottonwood and willow are drought-intolerant tree species that rely on shallow groundwater and/or high shallow soil water availability for establishment, growth, and reproduction (Smith et al. 1991, Busch et al. 1992, Stromberg 1993, Snyder and Williams 2000, Rood et al. 2003, Lite and Stromberg 2005). Therefore, they are typically restricted to local flood plains of rivers, streams, and dry washes that support shallow aquifers (Stromberg 1998, Schaeffer et al. 2000, Snyder and Williams 2000, Lite and Stromberg 2005). Water diversions, river damming, and groundwater pumping have brought substantial alterations to hydrologic systems in western riparian areas. Declines in cottonwood/willow populations, in response to changes in riparian ecosystem hydrology, have been well documented (Stromberg 1993, Rood et al. 2003, Lite and Stromberg 2005). Changes in stream regulation, groundwater pumping, and irrigation have also been cited as causes for conversion of native riparian woodlands to

Manuscript received 19 March 2009; accepted 5 June 2009.
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invasive shrublands, including the expansion of the invasive shrub, tamarisk (*Tamarix* spp.; Cleverly et al. 1997, Horton et al. 2001a). There is also evidence that, as climate has changed, annual snowpack and subsequent snowmelt that results in spring runoff and soil water recharge of many western U.S. watersheds is declining (McCabe and Clark 2005, Mote et al. 2005). The result is a potential decline in the water availability that supports native riparian vegetation. Combined with warmer and drier growing-season temperatures that are forecasted for the Southwest, climate change is expected to pose a considerable threat to the current composition of these forests.

Cottonwood and willow species may have different sensitivities to changes in stream regulation, climate, and groundwater depth. Riparian willow species are obligate phreatophytes (Snyder and Williams 2000); their root systems extract nearly all of their water for transpiration from the water table. Riparian willows, therefore are typically restricted to immediate stream margins or where groundwater is shallow and temporally reliable. Cottonwood species, on the other hand, are more facultative, and extract some water from shallower unsaturated zones within the soil profile in locations where groundwater is less dependent (Snyder and Williams 2000, Butler et al. 2007). This allows cottonwood trees to occupy areas where groundwater is spatially and temporally less reliable.

The rate in which plants extract and transpire water from the soil has direct consequences on plant performance and productivity. Not only is the amount of water used by plants directly proportional to carbon uptake (Enquist 2002), transpiration varies considerably depending on plant responses to disturbance, land-use change, and climate change. Mature cottonwood/willow trees require high rates of transpiration to support their large canopies and the fast growth necessary to compete in highly productive environments (Schaeffer et al. 2000, Hultine et al. 2007a, Nagler et al. 2007). Measurements of transpiration fluxes have previously been used to gauge the sensitivity of cottonwood/willow stands to changes in streamflow and groundwater depth (Schaeffer et al. 2000, Horton et al. 2001a, Baird et al. 2005, Gazal et al. 2006). Relative to other co-occurring tree species, including tamarisk, transpiration rates of both cottonwood and willow have been shown to decline spatially with soil water availability (Horton et al. 2001a), and intra-annually from wet years to dry years (Horton et al. 2001a). Moreover, large amounts of canopy dieback in riparian cottonwood and willow have been correlated with steep declines in leaf-level transpiration during a single dry year (Scott et al. 1999, Horton et al. 2001a, Cooper et al. 2003). Nevertheless, there is still a considerable lack of information on how water use and productivity of mature cottonwood and willow stands respond to rapid declines and recovery of soil water availability over multiple years.

In this paper, we report results from a four-year study (2004–2007) conducted on mature co-occurring Fremont cottonwood (*Populus fremontii*) and coyote willow (*Salix exigua*) trees occurring near Salt Lake City, Utah, USA. The trees were located on a delta on the inlet of a dammed reservoir in the Red Butte Canyon Research Natural Area along the front range of the Wasatch Mountains. During the spring of 2005, the reservoir was drained to reconstruct the dam that supports the reservoir and remained empty until mid-summer of 2006. The reconstruction of the dam effectively removed the primary water source for the trees for nearly all of one growing season (2005) and most of the following growing season (2006). Although community- and population-level responses of cottonwood/willow forests to water diversions and drought have been well documented, few studies have comprehensively investigated the associated physiological response of these forests to soil water depletion. Our goal was to take advantage of the dam reconstruction and subsequent draining of the reservoir to (1) investigate the physiological response of Fremont cottonwood and coyote willow to severe declines in available soil moisture over two consecutive growing seasons and to (2) investigate the physiological recovery of both cottonwood and willow during a full growing season (2007) after the refilling of the reservoir. We measured stem sap flux, leaf carbon isotope ratios and chemistry, leaf water potentials, and tree ring widths to gauge species responses to long-term soil water loss and drought recovery potential.

MATERIALS AND METHODS

Study area

Research was conducted from July 2004 through September 2007 in the Red Butte Canyon Research Natural Area (RBC) east of Salt Lake City, Utah, USA. The research area was near the inlet of an artificial reservoir constructed near the mouth of Red Butte Canyon (40°46'45.01" N, 111°48'29.73" W, elevation 1640 m). Extensive flooding from spring runoff during the 1983 and 1984 El Niño years caused upstream erosion that resulted in the development of a large delta composed of sandy loam soils at the inlet of the reservoir where stands of Fremont cottonwood (*Populus fremontii* Wats.) and coyote willow (*Salix exigua* Nutt.) quickly established. The reservoir is fed by a perennial stream that flows ~30 m south of the cottonwood/willow stand. The reservoir was temporarily drained in the spring of 2005 by the Central Utah Water Conservation District. Draining commenced in mid-April before cottonwood/willow leaf flush and was completed in late June. Construction of the dam was completed the following summer and the reservoir was completely refilled to previous levels by mid-August 2006.

Ten mature Fremont cottonwood and coyote willow trees were selected for study. Each tree was dominant or codominant within the stand and had little or no visible

signs of canopy dieback. Diameters at breast height (dbh) at the beginning of the study ranged from 14.2 to 25.4 cm (mean = 18.6 cm) for cottonwood trees and 9.0 to 16.6 cm (mean = 12.3 cm) for willow trees.

Meteorological and volumetric soil moisture measurements

Climate within RBC is characterized by hot, dry summers and long, cold winters. Most precipitation falls during the winter and spring with some precipitation falling during the summer monsoon season (July–September). Mean annual precipitation at the mouth of the canyon is ~500 mm (Ehleringer et al. 1992). Mean monthly air temperature at the mouth of the canyon ranges from about -2°C in January to ~25°C in July (Ehleringer et al. 1992). Relative humidity, air temperature, and photosynthetic active radiation were measured continuously at the reservoir over the duration of the investigation. Relative humidity and air temperature were measured with a Vaisala HMP 45 AC humidity and temperature probe (Vaisala, Woburn, Massachusetts, USA) placed ~2 m above the ground surface. Photosynthetic active radiation (Q) was measured with a LI-COR LI-190SZ quantum sensor (LI-COR, Lincoln, Nebraska, USA). Micrometeorological data were measured every 30 s and stored as 10-min means with a Campbell CR10X-2M data logger (Campbell Scientific, Logan, Utah, USA). Measurements of relative humidity and air temperature were used to calculate atmospheric vapor pressure deficit (vpd).

A frequency domain capacitance probe (Paltineanu and Starr 1997) was used to monitor volumetric soil moisture (θ) at four depths concurrently from June 2005 through September 2006. The probes contained four annular capacitance sensors (Sentek PTY, Adelaide, Australia) mounted on a single plastic manifold, and were placed in a weatherproof PVC access tube installed in the center of the cottonwood/willow stand. The sensors were mounted at depths of 10, 20, 40, and 60 cm within the soil profile. Measurements were recorded every 30 s and stored as 30-min means with a Campbell CR10X-2M data logger. Each sensor was calibrated in the laboratory to locate the air and water frequency reading endpoints for determination of the normalized frequency. At the conclusion of the study, the sensors were calibrated at multiple volumetric soil moistures using soil from the field site.

Sap flux density and sapwood area measurements

Granier-type sensors (Granier 1987, Hultine et al. 2007b) were constructed in the laboratory to measure sap flux density, J_s (grams of water per square meter of sapwood per second). Each sensor consisted of a pair of 20 mm long, 2 mm diameter stainless steel probes inserted ~15 cm apart along the axis of the hydroactive xylem (i.e., sapwood). A single sensor was inserted in each tree at ~1.5 m above the ground. Azimuth direction of each sensor was randomly selected to

eliminate potential biases due to nonuniformity in sap flux around the stem. The upper probe (i.e., toward the canopy) was supplied with constant power of 200 mW, and the temperature difference between the heated (powered) probe and the lower, unheated reference probe was converted to sap flux density according to Granier (1987):

$$J_s = 0.0119 \left(\frac{\Delta T_0}{\Delta T} - 1 \right)^{1.23} \quad (1)$$

where ΔT is the temperature difference between the heated and unheated probes and ΔT_0 is the temperature difference obtained under 0 flow conditions. We assumed that 0 flow only occurred at night when vpd was at or near 0. At the conclusion of each growing season, the sensors were removed and new sensors were installed the following spring at different locations on the stem. Sap flux was measured in 2004 from 18 July (DOY 199) through 1 September (DOY 244), and in 2005, 2006, and 2007 from late May through 1 September. (Cottonwood and willow trees in RBC both show signs of senescence in early September.)

Discrete measurement periods were used to compare patterns of sap flux before and after the reservoir was drained. Sap flux measured in May and June of 2005 was compared with measurements conducted in May and June of 2007 to gauge the recovery of tree water use during the early growing season. Sap flux measured in August 2004 was compared to measurements conducted in August of 2007 to gauge the recovery of tree water use during later periods of the growing season (sap flux in August 2005 and 2006 was likely affected by reservoir draining). Mean daytime sap flux density was calculated in order to correlate with mean daytime vpd, Q , and θ . Daytime hours were defined by the period when Q was $\geq 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Sapwood area was measured for each tree in 2004 and in 2007 by determining the relationship between stem diameter (D) at 1.5 m above the ground and sapwood area. Sapwood area (A_s) was obtained from two cores per tree by first determining the inside bark diameter, then determining the depth of hydroactive xylem by measuring the length of translucence of each core (Pataki et al. 2000, Hultine et al. 2007b), then subtracting the sapwood area from the total stem cross-sectional area. Sapwood area to stem diameter relationships were determined using a power function:

$$A_s = b_1 \times D^{b_2} \quad (2)$$

where b_1 and b_2 are fitting parameters.

Xylem water potential measurements

Xylem water potential measurements were performed on trees that were instrumented with sap flux sensors. Leaf water potential (Ψ) was measured using a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon, USA) in mid June, July, and August of 2005, 2006, and 2007. A single shoot tip from each of

the six trees was cut with a sharp razor blade and measured at predawn (Ψ_{pd}) between 02:00 and 04:00 hours and at midday (Ψ_{md}) between 11:00 and 13:00 hours.

Hydraulic conductance from the soil to the leaves (k_t) was calculated by dividing J_s by the water potential difference between Ψ_{pd} and Ψ_{md} . Here we assume that Ψ_{pd} is equal to soil water potential, although disequilibrium may occur between both variables (Donovan et al. 1999). In this case, k_t would be overestimated.

Leaf $\delta^{13}C$, and leaf nitrogen

Leaf carbon isotope ratios ($\delta^{13}C$, ‰) were measured to assess the relative balance between the supply of CO_2 via leaf conductance and the demand for CO_2 by photosynthetic enzymes. Specifically, decreases in stomatal conductance and/or increases in photosynthetic capacity (from increased leaf N content) will result in reduced fractionation against ^{13}C and less negative values of leaf $\delta^{13}C$ (Ehleringer 1991). Leaf carbon isotope ratios of bulk leaf tissue ($\delta^{13}C$, ‰), and leaf nitrogen content per unit leaf mass (N_{mass} , mg/g) were measured in leaves collected from each tree in August of 2004, and June, July and August of 2005, 2006, and 2007. The most recent fully expanded sun leaves were collected from the south side of the canopy from 4 m heights with a pole pruner. Leaves were then oven dried for 72 hours at 70°C, ground to a fine powder, and analyzed for nitrogen content and carbon isotope ratios using an elemental analyzer (Carlo Erba, Model 1108, Milano, Italy) coupled with a Finnigan MAT delta S isotope ratio mass spectrometer (San Jose, California, USA) at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) Lab, at the University of Utah (Salt Lake City, Utah, USA). Carbon isotope ratios were calculated using δ notation:

$$\delta = \left(\frac{R_{samp}}{R_{std}} - 1 \right) \times 1000 \quad (3)$$

where R is the ratio of the heavy isotope (^{13}C) to the lighter isotope (^{12}C), and the standard was Vienna Pee Dee belemnite (V-PDB). The instrument error (twice the standard deviation) associated with each observation was $\pm 0.1\%$.

Tree ring width measurements

Tree ring widths were measured to assess radial growth variations in response to mean growing season (May–September) vapor pressure deficit and groundwater removal from draining of the reservoir. A single core was extracted from the south side of each tree at breast height using a 12 mm diameter increment borer. The cores were placed in a coin envelop and dried for 72 hours at 70°C. The cores were sawed in half with a band saw then sanded with sand paper. The half cores were scanned on a flatbed scanner (Epson Perfection 2400 Photo, Epson America, Long Beach, California, USA). Scanned images were imported into NIH Image J v1.35l

(available online) for measurement of individual widths.² Cores were cross-dated to account for any false rings, and whole ring widths (early wood plus latewood) were measured to the nearest 0.1 mm.

Statistics

Regression analysis was performed to relate J_s of each species to vpd, Q , and θ . Intra-annual variance in J_s response to vpd, Q , and θ were analyzed using analysis of covariance (ANCOVA), where vpd, Q and θ , and vpd \times Q were used as independent variables in the regression equation for each species. Interannual variance of J_s response to vpd was analyzed using ANCOVA, where year, vpd, and year \times vpd were used as independent variables in the regression equations for each species. Interannual differences between A_s and D were tested for each species using ANCOVA, where year, D , and year \times D were used as independent variables. Interannual differences in leaf water potential, k_t , $\delta^{13}C$, and N_{mass} were analyzed for each sampling period and for each species using least square differences (LSD) tests. Species differences in J_s response to changes in mean θ was tested using ANCOVA, where species, θ , and species \times θ were used as independent variables. Species differences in k_t , $\delta^{13}C$, N_{mass} , and tree ring widths were assessed by repeated-measures analysis of variance (MANOVA) where multiple measurements on a given plant constituted the repeated variables (Potvin et al. 1990). In each analysis the main effect of species was tested as a between-subjects effect. Species differences in k_t , $\delta^{13}C$, and N_{mass} , and ring widths during individual sampling periods were tested using Student's t tests. JMP 7.0 (SAS institute, Cary, North Carolina, USA) was used for all statistical analysis, with $P \leq 0.05$ as the significance level.

RESULTS

Volumetric soil moisture and leaf water potentials

Measurements of volumetric soil moisture commenced on 14 June 2005 (DOY 165). By this time, volumetric soil moisture (θ) was rapidly declining in response to the draining of the reservoir (Fig. 1a). Mean θ from all depths decreased from a high of 15.8% on June 14 to 7.7% on 1 September (DOY 244), about the time leaves of both cottonwood and willow trees began to senesce. Mean volumetric soil moisture (θ) recovered in the following spring (2006) from snowmelt before reaching a low of 8.7% on July 30 (Fig. 1b). The reservoir was refilled in late July and θ at 20, 40, and 60 cm depths subsequently recovered to pre-drained levels by mid-August (Fig. 1b).

Leaf water potential at predawn (Ψ_{pd}) of both species were higher (less negative) in June 2005 than at any other time during the investigation: -0.18 ± 0.04 and -0.20 ± 0.03 MPa (mean \pm SE) for cottonwood and

² (<http://rsb.info.nih.gov/ij/>)

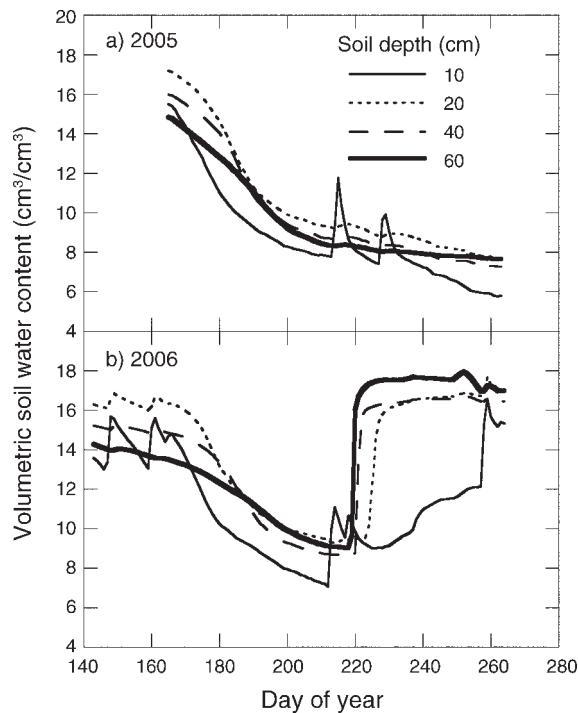


FIG. 1. Volumetric soil water content (θ) measured during the 2005 and 2006 growing seasons near the inlet of the Red Butte Canyon reservoir, near Salt Lake City, Utah, USA. Day 1 of the year is 1 January. A frequency domain capacitance probe containing four annular capacitance sensors (Sentek PTY, Adelaide, Australia) was used to measure θ at 10, 20, 40, and 60 cm depths. Soil moisture progressively declined during the 2005 growing season in response to the reservoir draining. Soil moisture recovered in 2006 after the reservoir was refilled to previous levels on about day 220.

willow, respectively. At this time, mean θ in the upper 60 cm of the soil profile was 14.6%. Mean Ψ_{pd} of cottonwood dropped to -0.55 ± 0.04 MPa in July and -1.00 ± 0.08 MPa (mean \pm SE) in August 2005 (Fig. 2).

Mean Ψ_{pd} in July 2005 was significantly lower than Ψ_{pd} in July 2007 ($P = 0.0037$; Table 1), while August 2005 values were much lower than either 2006 ($P < 0.0001$) or 2007 ($P < 0.0001$), periods after the reservoir was refilled. In contrast to cottonwood, willow did not show a steep decline in mean Ψ_{pd} in response to reservoir draining (Fig. 2), although Ψ_{pd} in July 2005 and 2006 were lower than in 2007 ($P = 0.0046$ for 2005–2007 and $P = 0.0011$ for 2006–2007; Table 1). There were no differences detected among the three years in August (Fig. 2, Table 1). Mean Ψ_{pd} in 2005 was significantly lower in cottonwood than willow in July ($P = 0.0056$) and August ($P < 0.0001$). Mean water potential at midday (Ψ_{md}) remained static in both species throughout the investigation, with the exception that Ψ_{md} of cottonwood was slightly lower in August 2006 than in 2005 ($P = 0.013$; Fig. 2, Table 1).

Sap flux density, sapwood area, and whole-plant hydraulic conductance

The relationship between sap flux density (J_s) and mean weighted (weighted mean of all depths) θ was nonlinear, and therefore J_s was fitted against $\ln(\theta)$. Cross-correlation analysis was performed to test the sensitivity of J_s to θ for both cottonwood and willow independently. Sap flux of cottonwood trees was best coupled to soil moisture when θ dropped below 12%, while J_s of willow was best correlated with soil moisture when θ dropped below 13%. Mean daytime J_s of cottonwood dropped sharply when mean θ fell below 12% ($R^2 = 0.85$, $F_{1,62} = 340.0$, $P < 0.0001$; Fig. 3). In fact, J_s fell by a factor of seven from ~ 70 to $10 \text{ g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 3) as mean θ fell from 12% to 7%. On the other hand, willow was far less sensitive to soil moisture depletion than cottonwood (i.e., the interaction species $\times \theta$; $F_{1,124} = 188.24$, $P < 0.0001$): J_s of willow only fell from 35 to $\sim 25 \text{ g}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ when θ dropped from 13% to 7% ($R^2 = 0.31$, $F_{1,62} = 29.4$, $P < 0.0001$; Fig. 3).

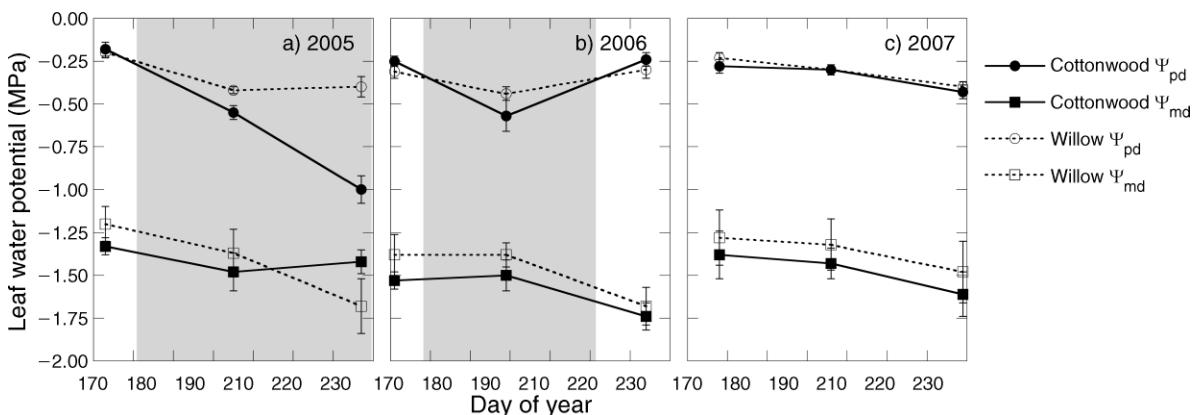


FIG. 2. Predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potential of mature Fremont cottonwood (*Populus fremontii*; $n = 6$) and mature coyote willow (*Salix exigua*; $n = 6$) for trees occurring near the inlet of the Red Butte Canyon reservoir. Data points represent mean \pm SE. Leaf water potentials were measured in mid June, July, and August of each year, 2005–2007 (a–c). Shaded blocks represent periods when volumetric soil moisture (θ) fell below 12% in response to the removal of the reservoir.

TABLE 1. Monthly probability values from least square difference tests of plant traits measured during three consecutive growing seasons on Fremont cottonwood (*Populus fremontii*) and coyote willow (*Salix exigua*) in Red Butte Canyon Research Natural Area, Utah, USA.

Tree species, date	Ψ_{pd}	Ψ_{md}	$\Psi_{pd} - \Psi_{md}$	k_t	$\delta^{13}C$	N_{mass}
Cottonwood						
June						
2005–2006	0.13	0.09	0.32	0.29	0.19	0.73
2005–2007	0.0290*	0.64	0.69	0.09	0.16	0.10
2006–2007	0.43	0.20	0.17	0.0104*	0.91	0.0483*
July						
2005–2006	0.82	0.88	1.00	0.0147*	0.0215*	0.6
2005–2007	0.0037**	0.67	0.23	0.47	0.58	0.79
2006–2007	0.0023**	0.56	0.23	0.07	0.0058**	0.43
August						
2005–2006	<0.0001***	0.013*	<0.0001***	0.09	0.08	0.26
2005–2007	<0.0001***	0.12	0.0002***	0.80	0.0018**	0.0062**
2006–2007	0.0085**	0.27	0.0482*	0.0393*	0.119	0.08
Willow						
June						
2005–2006	0.0124*	0.26	0.68	0.08	0.13	0.25
2005–2007	0.40	0.59	0.76	0.93	0.71	0.63
2006–2007	0.07	0.55	0.92	0.0454*	0.23	0.48
July						
2005–2006	0.49	0.91	0.95	0.0025**	0.87	0.85
2005–2007	0.0046**	0.74	0.60	0.83	0.09	0.61
2006–2007	0.0011**	0.66	0.56	0.0034**	0.06	0.47
August						
2005–2006	0.10	0.96	0.55	0.10	0.50	0.63
2005–2007	1.00	0.26	0.18	0.06	0.06	0.11
2006–2007	0.10	0.28	0.06	0.0010***	0.0128*	0.26

Notes: Measurements include predawn leaf water potential (Ψ_{pd}), midday leaf water potential (Ψ_{md}), predawn leaf water potential minus midday leaf water potential ($\Psi_{pd} - \Psi_{md}$), whole-plant hydraulic conductance (k_t), bulk leaf carbon isotope ratios ($\delta^{13}C$), and leaf nitrogen per unit mass (N_{mass}).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Gray bars in Fig. 4 show periods during the 2005 and 2006 growing seasons when mean θ fell below 12% in response to reservoir removal. A depression in J_s was clearly visible in cottonwood during the 2005 and 2006 growing seasons in response to reservoir draining (Fig. 4). No obvious pattern emerged in willow during periods of reduced soil moisture (Fig. 4). However, mean daytime J_s of willow during May and June (days 147–181) was on average 14% lower in 2006 than in 2005 (Fig. 4), despite a 29% higher mean daytime vpd during this period in 2006 compared to 2005 (data not shown).

We used a multivariate model (ANCOVA) to test the sensitivity of J_s to abiotic variables θ , vpd, Q , and vpd \times Q during the 2005 and 2006 growing seasons. Sap flux of cottonwood in 2005 was well correlated with both soil moisture ($F_{1,59} = 50.97$, $P < 0.0001$) and atmospheric vpd ($F_{1,59} = 19.68$, $P < 0.0001$), and was marginally correlated with photosynthetic active radiation ($F_{1,59} = 3.45$, $P = 0.068$), and the interaction vpd \times Q ($F_{1,59} = 6.02$, $P = 0.0173$; Table 2). In other words, θ had the greatest influence on J_s , but soil moisture depletion did not completely decouple J_s from atmospheric drivers vpd and Q . Conversely, cottonwood J_s was completely decoupled from vpd in 2006 ($F_{1,95} = 1.11$, $P = 0.29$), while it was tightly coupled to θ ($F_{1,95} = 80.37$, $P < 0.0001$; Table 2). Soil moisture in 2005 had no effect on willow J_s ($F_{1,63} = 0.38$, $P = 0.54$). Instead, J_s was coupled

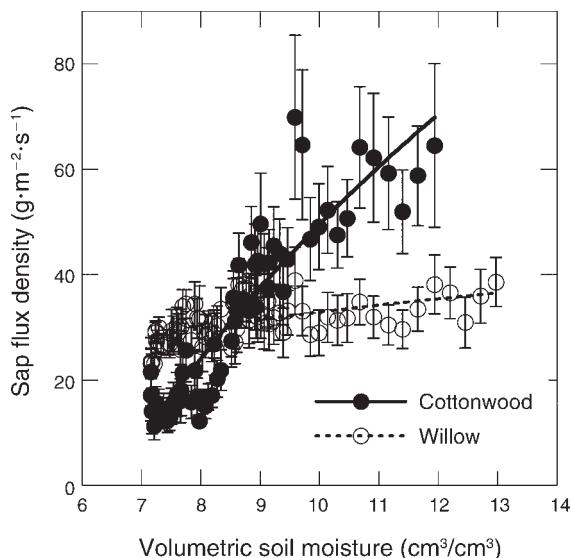


FIG. 3. Stem sap flux density (J_s) of Fremont cottonwood trees ($n = 10$) and coyote willow trees ($n = 10$) in relation to volumetric soil moisture (θ) during the 2005 growing season. A sensitivity analysis showed that J_s of cottonwood was best coupled to soil moisture when θ was below 12% ($R^2 = 0.85$, $P < 0.0001$), while willow was best coupled to θ below 13% ($R^2 = 0.31$, $P < 0.0001$). At higher soil moistures, J_s of both species was primarily coupled to atmospheric vapor pressure deficit (vpd). Error bars represent \pm SE.

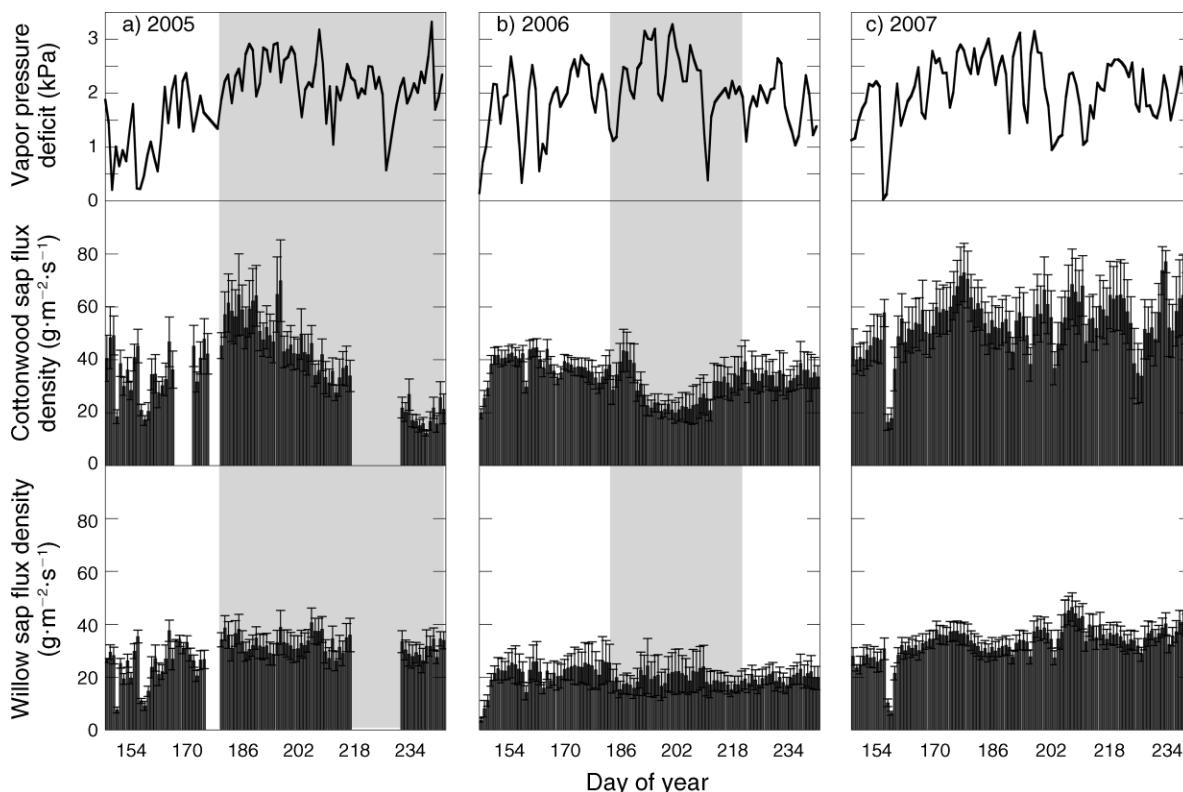


FIG. 4. (Top row) Mean daytime atmospheric vapor pressure deficit (vpd), (middle row) mean daytime stem sap flux density (J_s) of mature Fremont cottonwood trees ($n = 10$ trees), and (bottom row) mean daytime sap flux density of coyote willow trees ($n = 10$ trees) occurring near the inlet of the Red Butte Canyon reservoir near Salt Lake City, Utah, USA. Shaded blocks represent periods when θ fell below 12% in response to the removal of the reservoir. Error bars represent \pm SE.

to atmospheric drivers vpd ($F_{1,63} = 9.01, P = 0.0039$) and Q ($F_{1,63} = 6.82, P = 0.011$; Table 2). In 2006, willow J_s was coupled to θ ($F_{1,95} = 8.19, P = 0.0052$), but was still more highly correlated with vpd ($F_{1,95} = 15.45, P = 0.0002$) and Q ($F_{1,95} = 13.95, P = 0.0003$).

The reservoir was refilled in August 2006, and θ was restored to pre-drained levels before the end of the growing season (Fig. 1). We therefore set out to test if there were any residual effects in 2007 from soil moisture depletion the previous two years by measuring the relationship between J_s and vpd before and after reservoir water removal. The relationship between sap flux density (J_s) and vpd was nonlinear and was

therefore fitted with an exponential saturation model:

$$J_s = b_1(1 - e^{-b_2 \text{vpd}}) \quad (4)$$

where b_1 and b_2 are fitting parameters. The relationship between vpd and mean J_s during June 2007 did not vary in either species from the relationship measured in June 2005, before soil moisture depletion ($P = 0.64$ for cottonwood, and $P = 0.33$ for willow; Fig. 5). Mean J_s in both species was well correlated to vpd during both months (Fig. 5). For cottonwood, $R^2 = 0.70$ in 2005 ($P < 0.0001$) and $R^2 = 0.72$ in 2007 ($P < 0.0001$). In willow, $R^2 = 0.81$ in 2005 ($P < 0.0001$) and $R^2 = 0.75$ in 2007 ($P < 0.0001$).

TABLE 2. F values from ANCOVA of mean daytime sap flux density (J_s) against volumetric soil moisture (θ), mean daytime atmospheric vapor pressure deficit (vpd), mean daytime photosynthetic active radiation (Q), and vpd \times Q .

Tree species, year	θ	vpd	Q	vpd \times Q	df
Cottonwood					
2005	50.97***	19.68***	3.45	6.02*	1, 59
2006	80.37***	0.29	13.43**	0.90	1, 95
Willow					
2005	0.38	9.01*	6.82*	0.05	1, 63
2006	8.19*	15.45**	13.94**	0.01	1, 95

* $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$.

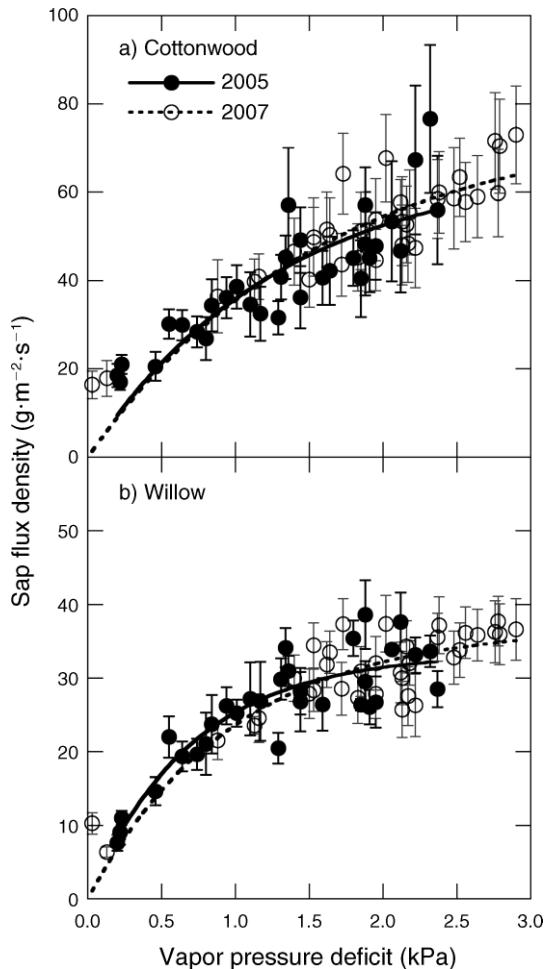


FIG. 5. Stem sap flux density (J_s) in relation to atmospheric vapor pressure deficit (vpd) during late May and June 2005 and 2007 for (a) mature Fremont cottonwood trees ($n = 10$) and (b) mature coyote willow trees ($n = 10$). Error bars represent \pm SE.

On the other hand, late-season differences were detected between years when J_s in August 2004 was compared to August 2007 (Fig. 6). Mean J_s in cottonwood was actually higher in 2007 than in 2004 ($F_{1,52} = 221.68$, $P < 0.0001$). Moreover, the interaction $\text{vpd} \times \text{yr}$ was significant ($F_{1,52} = 4.11$, $P = 0.0482$), meaning that the slopes varied between the two years (Fig. 6a). Unlike the early growing season in June, mean J_s in August was only moderately correlated to vpd: $R^2 = 0.29$ ($P = 0.004$) and $R^2 = 0.36$ ($P = 0.001$) for 2004 and 2007, respectively. Mean J_s in willow was also different between years, but in this case, fluxes were slightly higher in 2004 ($P = 0.039$; Fig. 6b). The model yielded a weak correlation between J_s and the interaction $\text{vpd} \times \text{yr}$ ($P = 0.030$). Mean J_s in 2004 was moderately correlated with vpd: $R^2 = 0.46$ ($P = 0.001$; Fig. 6b). However there was no significant relationship between mean J_s and vpd in 2007 ($R^2 = 0.003$, $P = 0.77$; Fig. 6b).

Seasonal and interannual patterns of whole-plant hydraulic conductance (k_t) were highly variable in both species. Whole-plant conductance was highest in both species in July 2005 and was lowest in August of 2006 (Fig. 7). There were no differences in k_t between measurements in June 2005 and June 2007 for either species (see Fig. 7d), suggesting that the hydraulic pathways of both species recovered after two seasons of decreased soil water levels. Both species had similar whole-plant conductance at the onset and conclusion of the investigation ($P = 0.60$ and $P = 0.83$ for June 2005 and August 2007, respectively). However, species differences were detected during June 2006; cottonwood had 48% higher k_t than willow ($P = 0.006$; Fig. 7b).

There was a significant decrease in the amount of sapwood area to per unit stem diameter from 2004 to 2007 in both cottonwood ($F_{1,19} = 135.5$, $P = 0.0001$; Fig. 8a) and willow ($F_{1,19} = 71.9$, $P < 0.0001$; Fig. 8b). Likewise, the ratio of sapwood area to cross-sectional stem area ($A_s:A_{st}$) was significantly lower in 2007 than in

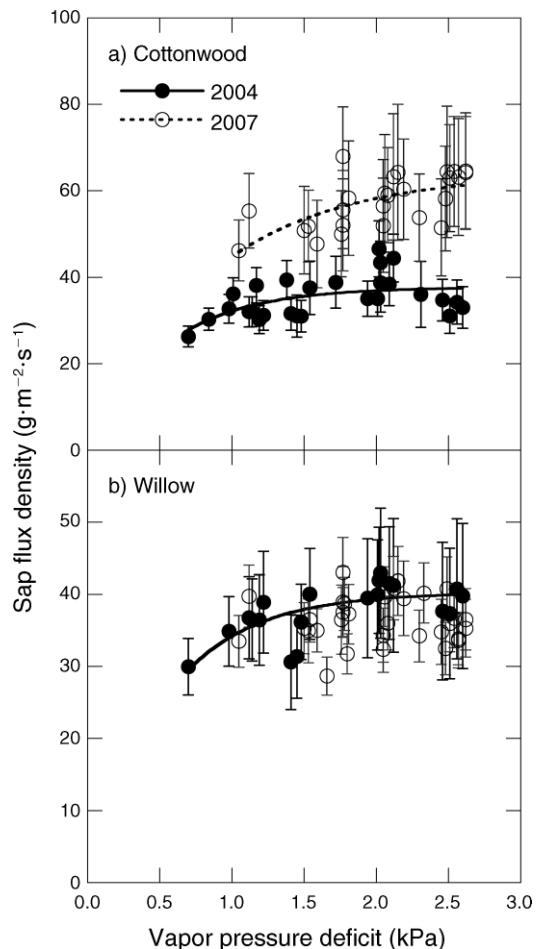


FIG. 6. Stem sap flux density (J_s) in relation to atmospheric vapor pressure deficit (vpd) during August of 2004 and 2007 for (a) mature Fremont cottonwood trees ($n = 10$) and (b) mature coyote willow trees ($n = 10$). Error bars represent \pm SE.

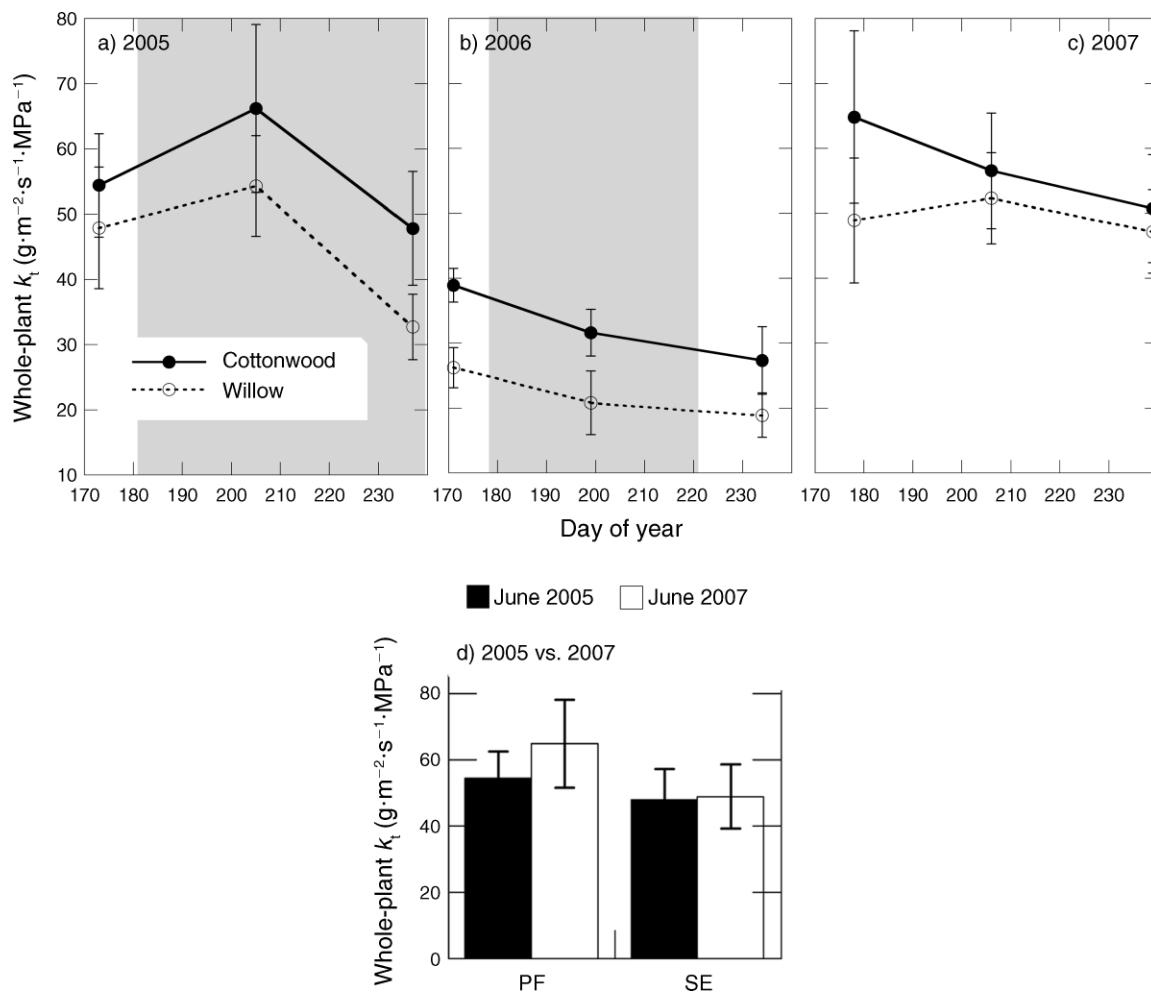


FIG. 7. Whole-plant hydraulic conductance (k_t) of mature Fremont cottonwood ($n = 6$) and mature coyote willow ($n = 6$) trees occurring near the inlet of the Red Butte Canyon reservoir near Salt Lake City, Utah, USA. Hydraulic conductance was measured in mid June, July, and August of each year, 2005–2007 (a–c). (d) Direct comparison of hydraulic conductance in June 2005, before the reservoir was drained (solid bars), and hydraulic conductance in June 2007, after the reservoir was refilled (open bars), for both cottonwood (PF) and willow (SE). Error bars represent \pm SE.

2004 for both species ($F_{1,19} = 20.30$, $P = 0.0003$ for cottonwood; $F_{1,19} = 6.61$, $P = 0.0192$ for willow; Table 3). The lower sapwood area suggested that the stem conductance (k_s) may have declined in both species during decreased soil water levels.

Leaf $\delta^{13}\text{C}$, leaf nitrogen, and tree ring widths

Mean $\delta^{13}\text{C}$ of leaves from both species showed intra- and interannual variation. Mean $\delta^{13}\text{C}$ generally increased in 2005 and 2006 before values progressively decreased in 2007 ($F_{2,17} = 18.29$, $P < 0.0001$, repeated measures of 2007 data; Fig. 9). In cottonwood, for example, $\delta^{13}\text{C}$ was significantly higher (less negative) in July of 2006 than either July 2005 or 2007 (Table 1), and was higher than any other period, indicating that these leaves experienced the greatest drought stress during the investigation (Fig. 9). Willow also had higher leaf $\delta^{13}\text{C}$ values throughout 2006, before decreasing in 2007.

There was no relationship between $\delta^{13}\text{C}$ and leaf nitrogen per unit mass (N_{mass}) of cottonwood leaves ($F_{1,88} = 1.08$, $P = 0.30$, data not shown), indicating that seasonal and interannual variation in $\delta^{13}\text{C}$ was primarily caused by changes in stomatal conductance and not changes in photosynthetic capacity. $\delta^{13}\text{C}$ was weakly correlated with N_{mass} in willow ($F_{1,85} = 4.65$, $P = 0.034$, data not shown). However, N_{mass} did not vary throughout the experiment (Table 1), suggesting that interannual variation in $\delta^{13}\text{C}$ was also driven by variation in plant water status.

Both species exhibited similar leaf $\delta^{13}\text{C}$ values throughout the investigation ($F_{1,18} = 0.16$, $P = 0.69$ from repeated measures), although the interaction time \times species was significant ($F_{8,11} = 3.27$, $P = 0.0363$, from repeated measures). Species differences were only detectable in August 2006, where $\delta^{13}\text{C}$ in willow was 0.9‰ less negative than cottonwood ($P = 0.0453$),

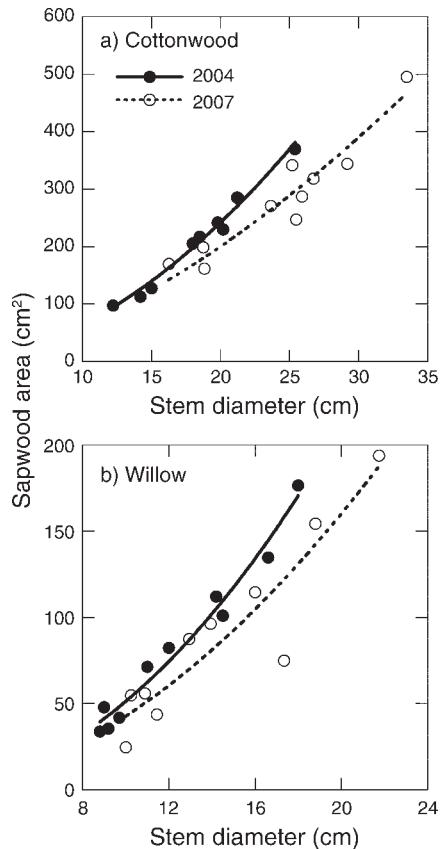


FIG. 8. Sapwood area (A_s) in relation to stem diameter (D) of (a) mature Fremont cottonwood ($n = 10$) and (b) mature coyote willow ($n = 10$) trees occurring near the inlet of the Red Butte Canyon reservoir near Salt Lake City, Utah, USA. Relationships were determined from stem cores collected at the end of the 2004 and 2007 growing seasons.

indicating that willow experienced greater drought stress in late 2006 than cottonwood.

Tree ring growth

Mean annual tree ring growth was substantially higher in cottonwood than in willow ($F_{1,17} = 13.44$, $P = 0.0002$, from repeated measures; Fig. 10), although annual patterns of mean tree ring growth were similar between species ($F_{3,15} = 1.89$, $P = 0.17$, from repeated measures). Whole-wood tree ring growth in both

cottonwood and willow was substantially reduced during the 2005 and 2006 growing seasons compared to the previous year (Fig. 10), even though mean vapor pressure deficit during the growing seasons (May–September) were similar during the three years (data not shown). Radial growth in cottonwood was 7.7 ± 1.12 and 7.8 ± 0.95 mm in 2005 and 2006, respectively, while radial growth in 2004 was 11.3 ± 1.04 mm (mean \pm SE, for all data shown). Despite the steep drop in 2005 and 2006, mean radial growth rebounded in 2007 to 11.0 ± 1.05 mm, while growing season vpd was actually 8–30% higher in 2007 than either of the previous three years. Mean tree ring growth in willow was 3.2 ± 1.06 and 3.1 ± 0.90 mm in 2005 and 2006, respectively, down from 5.1 ± 0.99 mm the previous year (Fig. 10). Mean radial growth in 2007 rebounded to 4.0 ± 0.99 mm in willow, slightly lower than in 2004 (Fig. 10).

DISCUSSION

Riparian cottonwood/willow (in this case Fremont cottonwood [*Populus fremontii*] and coyote willow [*Salix exigua*]) forests are among the most threatened forest types in the United States (Stromberg 1993, Webb et al. 2007). Accordingly, intensive research has been conducted on the sensitivity of cottonwood and willow to multiple global change processes including climate change, land-use change, and exotic species invasions. Above all, changes in soil water availability appear to have had, or continue to have the greatest negative impact on cottonwood/willow growth, survival, and fitness (Mahoney and Rood 1992, Stromberg 1993, Patten 1998, Scott et al. 1999, Shafroth et al. 2000, Horton et al. 2001a, b, Lite and Stromberg 2005). Despite the wealth of literature on this subject, there is still a considerable lack of information on the whole-plant physiological responses of cottonwood and willow to interannual and intra-annual declines and recovery of water availability (but see Horton et al. 2001a, b). The temporary removal of water from the reservoir described in the present study was analogous to soil water deficits caused by human groundwater pumping, stream diversion, or from long-term drought. Results from this investigation build on previous research of cottonwood and willow sensitivity to soil water deficits, and greatly

TABLE 3. Sapwood depth (L_s), ratio of cross-sectional sapwood area to cross-sectional stem area ($A_s:A_{st}$), and regression coefficients for predictions of cross-sectional sapwood area generated from tree diameters (D).

Tree species, year	D (cm)	L_s (cm)	$A_s:A_{st}$ (cm ² :cm ²)	b_1	b_2	R^2
Cottonwood						
2004	12.20–25.40	5.75 (0.33)	0.77 (0.01)	0.82	1.90	0.98
2007	18.75–33.50	4.94 (0.25)	0.61 (0.03)	1.47	1.64	0.90
Willow						
2004	8.80–16.60	3.14 (0.29)	0.65 (0.03)	0.46	2.04	0.97
2007	10.90–21.75	2.62 (0.30)	0.53 (0.04)	0.54	1.90	0.85

Notes: Tree depth and area measurements are means (with SE in parentheses). The range of tree diameters, measured 1.5 m above the ground, is given. For each year and species, $n = 10$ trees. See Eqs. 2 and 4 for details on regression.

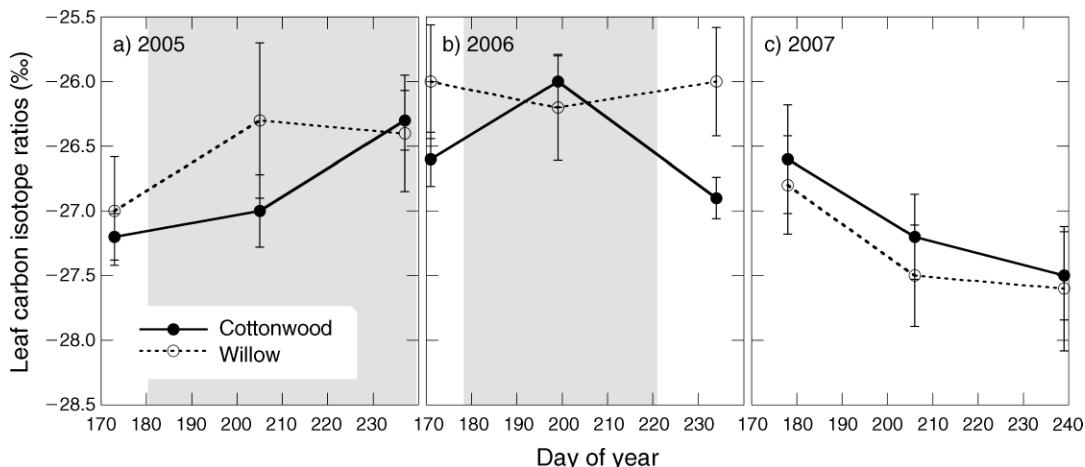


FIG. 9. Bulk leaf carbon isotope ratios ($\delta^{13}\text{C}$) of mature Fremont cottonwood ($n = 10$) and mature coyote willow ($n = 10$) trees occurring near the inlet of the Red Butte Canyon reservoir near Salt Lake City, Utah, USA. Ratios were measured from leaves collected in mid June, July, and August of each year, 2005–2007 (a–c). Error bars represent $\pm\text{SE}$.

improve our ability to predict global change impacts on water cycling and productivity of dominant riparian vegetation. Moreover, this investigation sheds light on the potential ecohydrological feedbacks associated with temporal variation of plant water availability in riparian habitats.

Species response to reservoir water removal

As expected, both species demonstrated a significant negative response to reservoir water removal. However, drying in the upper soil layers initially had a much larger negative impact on cottonwood than on willow (Figs. 3 and 4). Results are consistent with previous reports showing that under certain conditions, cottonwood functions as a facultative phreatophyte, meaning it often acquires at least some of its water for transpiration from shallow, sometimes un-saturated soil layers (Snyder and Williams 2000, Pataki et al. 2005). On the other hand, riparian willow species are obligate phreatophytes that typically only use groundwater even when shallow soil moisture is available (Snyder and Williams 2000).

Leaf water potential measured in 2005 also suggested that cottonwood was initially more negatively impacted by reservoir removal than willow. In June, when θ in shallow soils was still above 14%, mean water potential predawn (Ψ_{pd}) was about -0.2 MPa for both species. In July, mean Ψ_{pd} of cottonwood fell to -0.55 MPa and in August, -1.00 MPa (see Plate 1). Conversely, mean Ψ_{pd} of willow never fell below -0.42 MPa, suggesting that enough moisture was stored in the deep soil to maintain a relatively favorable water balance throughout the 2005 growing season.

On the other hand, willow appeared to be more negatively affected than cottonwood during the second growing season (2006) of reservoir removal, even though Ψ_{pd} values in 2006 were similar between species. For example, k_t in June 2006 was 48% lower in willow than

in cottonwood despite having similar values during the same period in 2005. Likewise, $\delta^{13}\text{C}$ was 1‰ higher in willow leaves in August compared to cottonwood leaves. Taken together, these results indicate that resistance along the soil–plant hydraulic pathway was higher in willow than cottonwood throughout much of the 2006 growing season. The delayed negative response of willow suggests that the water table was significantly lower during the second year of reservoir water removal. Although depth to groundwater was not measured, it is reasonable to assume that the water table declined while the reservoir was drained given that the height of Red Butte Creek is ~ 3 m lower as it flows through the delta than the height of the reservoir when filled. The apparent partitioning of cottonwood and willow root systems suggests that cottonwood has a greater sensitivity to interannual changes in shallow soil moisture, while willow may be more sensitive to fluctuations in the depth to groundwater.

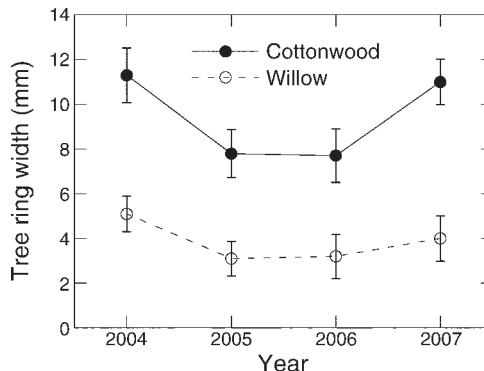


FIG. 10. Whole-tree ring widths of mature Fremont cottonwood ($n = 9$) and mature coyote willow ($n = 10$) trees occurring near the inlet of the Red Butte Canyon reservoir near Salt Lake City, Utah, USA. Error bars represent $\pm\text{SE}$.



PLATE 1. Photos of a mature cottonwood tree taken on 1 September 2005 (photo on left) and 1 September 2006 (photo on right). The cottonwood tree occurred at the inlet of a reservoir near Salt Lake City, Utah, USA, that was drained in the spring of 2005 and remained empty until early August 2006. Total leaf area was noticeably lower in 2005, when the reservoir was drained and predawn leaf water potentials were at their lowest during the study, compared to 2006, when the reservoir was refilled and predawn leaf water potentials were significantly higher than in 2005. Photo credit: K. R. Hultine.

The similar Ψ_{pd} in willow between 2005 and 2006 are somewhat surprising given the large drop in k_t in 2006 relative to 2005. One possible explanation is that a small fraction of willow roots was still equilibrating to a reduced volume of saturated soil in 2006. Under hydrostatic conditions, xylem water potential could equilibrate to the wettest soil layer even if only 20% of the root system is located in the wettest layer (Améglio et al. 1999). If a small fraction of roots were still tapped into wet soils, then it is plausible that k_t would decrease without a measurable drop in Ψ_{pd} .

Whole-wood tree ring analysis (early plus latewood) revealed that radial growth was 22–30% less in cottonwood and 32–40% less in willow in 2005 and 2006 compared to 2004, the year prior to reservoir draining, despite more favorable climate conditions in 2005 and 2006. Spring runoff from Red Butte Creek, an estimate of snow pack, was 77%, and 175% higher in 2005 and 2006, respectively, compared to 2004. Mean growing season vapor pressure deficit (vpd) in 2005 was about the same as 2004: 1.35 and 1.32 MPa for 2004 and 2005, respectively. Taken together, these data show that reservoir water removal had a significant negative

impact on the productivity of both cottonwood and willow.

Species recovery from reservoir water removal

Riparian cottonwood and willow species are highly susceptible to water-stress induced xylem cavitation (Pockman and Sperry 2000). Moreover, they both have diffuse-porous wood anatomy. The significance of diffuse-porous wood is that multiple growth rings contribute to the transport of water from the root system to the canopy. In cases where drought-intolerant, diffuse-porous species are exposed to significant water deficits, xylem embolism may accumulate in previous year's growth rings, thereby inhibiting water transport that would otherwise occur through the xylem. Alternatively, xylem embolism may be partially or completely reversed by refilling of xylem conduits depending on hydrostatic conditions over seasonal or diurnal time scales (Salleo et al. 1996, Holbrook and Zwieniecki 1999, Tyree et al. 1999). We therefore, set out to test whether cottonwood and willow had a physiological "memory" in 2007 of soil water deficits during the two previous growing seasons.

We found no evidence of lower mean J_s , during the early growing season (May–June) in 2007 compared to 2005 for either species. Willow expressed a modest decrease in late-growing season J_s (August) in 2004 compared to 2007, while late-growing season J_s in cottonwood was actually higher in 2007 compared to 2004. These data suggest that long-term water deficits did not result in significant seasonal changes in stomatal control in either species. Likewise, there was no evidence of lower radial growth following reservoir refilling. Again cottonwood had mean radial growth in 2007 that was equal to radial growth in 2004, despite 2007 having less than half the spring runoff than 2004, and mean growing season vpd that was 27% higher than in 2004.

Conversely, sapwood area per stem diameter declined in both species in 2007 relative to initial measurements in 2004. Reduced sapwood may be a function of xylem cavitation in older vessels of the sapwood. For example, older vessels of *Populus tremuloides* near the boundary of the heartwood have the greatest vulnerability within the cross-sectional sapwood matrix to cavitation (Sperry et al. 1991). The occurrence of xylem cavitation and subsequent embolism may initiate heartwood formation in woody stems. Whether differences in area of sapwood to area of stem ($A_s:A_{st}$) in the present study were related to two years of reservoir water removal or changes in allometry during stem radial growth are unclear. What is clear is that a larger cross-sectional A_s permits a higher stem k and thus maintenance of a larger leaf area per unit stem diameter (Gartner 1995).

We did not test for intra-annual changes in leaf area due to the difficulty of estimating leaf area of individual canopies without destructive harvesting. Nor did we explicitly test for intra-annual differences in sap flow due to potential changes in radial J_s at sapwood depths beyond the depth of our thermometric sensors. However, if we assume that J_s was constant with sapwood depth, as previously reported in cottonwoods (Lamb and Muller 2002), then changes in $A_s:A_{st}$ could have a measurable impact on plant transpiration. Potential differences in transpiration are shown for both species in Fig. 11, where sap flux density, measured in June 2005 and 2007, was divided by the ratio of sapwood area to stem area ($J_s:[A_s:A_{st}]$; Table 3), measured in the fall of 2004 and fall of 2007, respectively. Analysis of covariance revealed that mean J_s , normalized for $A_s:A_{st}$ differed between years in cottonwood ($F_{1,62} = 7.23$, $P = 0.0093$), and willow ($F_{1,66} = 47.33$, $P < 0.0001$). Using the regression from Eq. 4 ($R^2 = 0.78$ and $R^2 = 0.73$ for cottonwood in 2005 and 2007, respectively, Fig. 11a; and $R^2 = 0.82$ and $R^2 = 0.79$ for willow in 2005 and 2007, respectively; Fig. 11b), normalized J_s at a mean daytime vpd of 1.5 (a typical value for the reservoir in June) would be 16% and 19% lower in 2007 for cottonwood and willow, respectively. Whether these reductions are enough to result in lower leaf area, productivity, and/or fitness is an open question that warrants further investigation.

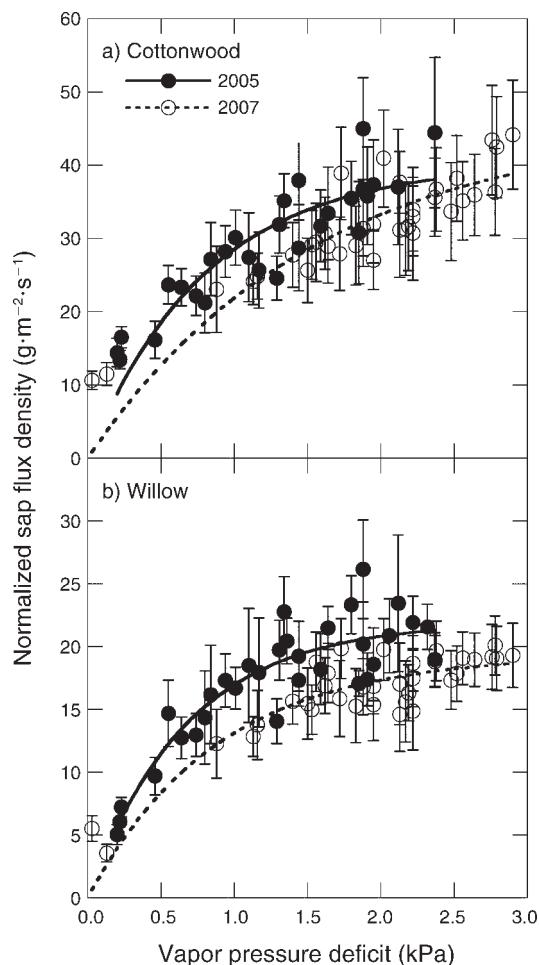


FIG. 11. Stem sap flux density (J_s), normalized by the ratio of cross-sectional sapwood area to cross-sectional stem area ($A_s:A_{st}$) in relation to atmospheric vapor pressure deficit (vpd) during late May and June 2005 and 2007. Sap flux data in 2005 were normalized by $A_s:A_{st}$ measured in the fall of 2004, and sap flux data in 2007 were normalized by $A_s:A_{st}$ measured in the fall of 2007. (a) J_s of mature Fremont cottonwood trees ($n = 10$). (b) J_s of mature coyote willow trees ($n = 10$). Error bars represent \pm SE.

Implications of streamflow alteration on cottonwood and willow

Climate change coupled with increased water demands to support expanding human enterprise in the western United States is expected to increase the seasonal variability of stream discharge and reduce mean annual stream flow. Streamflow may have larger consequences on the success of cottonwood and willow than any other single hydrologic parameter, given its linkage to both shallow soil moisture and groundwater stability. For example, reliable streamflow had a greater positive impact on cottonwood and willow abundance along the San Pedro River in southeastern Arizona, USA than any other hydrologic parameter, including interannual groundwater fluctuations and groundwater depth (Lite and Stromberg 2005). Likewise, tree ring

$\delta^{13}\text{C}$ ratios and subsequent physiological performance of mature cottonwood trees have been linked to streamflow regimes (Leffler and Evans 1999, Potts and Williams 2004). Results from the present study showed that two consecutive years of adjacent surface water removal had a significant negative impact on cottonwood and willow productivity and physiology. Nevertheless, both species apparently recovered, although with reduced $A_s:A_{st}$ that may result in lower whole-plant water use and carbon uptake even during periods of high water availability. The strong linkage between surface moisture and tree ecophysiology and water use suggests that alterations in streamflow will likely have cascading impacts on riparian ecosystem cycling of water, carbon, and nutrients (Schade et al. 2002, Scott et al. 2004, 2006, Huxman et al. 2005, Williams et al. 2006), even if the population structure of cottonwood/willow forests remains static.

Results from this investigation show a clear physiological response of Fremont cottonwood and coyote willow to long-term soil water removal and recovery. Convergent patterns of sap flux, leaf $\delta^{13}\text{C}$, whole-plant conductance, and radial growth emerged between species. However, cottonwood was in general more sensitive to shallow soil water depletion over short timescales (days to weeks), while willow showed a greater sensitivity to multiple-year depletion in soil water. Both species demonstrated the potential for recovery in response to long-term soil water deficits. These data shed light on the linkage between hydrology and ecophysiological processes of threatened riparian forests given potential land use and climate change impacts on freshwater resources.

ACKNOWLEDGMENTS

The authors thank D. Breshears, J. Cleverly, and an anonymous reviewer for their helpful comments, which greatly improved the final version of the manuscript. The authors also thank M. Buhanan, K. Burtch, T. Jackson, A. Macharia, K. B. Milne, K. M. Milne, K. Sohm, A. West, and W. Ike for technical assistance. This research was supported by the Andrew W. Mellon Foundation.

LITERATURE CITED

- Améglio, T., P. Archer, M. Cohen, C. Vaanocogne, F. Daudet, S. Dayau, and P. Cruziat. 1999. Significance and limits in the use of predawn leaf water potential for tree irrigation. *Plant and Soil* 207:155–167.
- Baird, K. J., J. C. Stromberg, and T. Maddock III. 2005. Linking riparian dynamics and groundwater: an ecophysiological approach to modeling groundwater and riparian vegetation. *Environmental Management* 36:551–564.
- Busch, D. E., N. L. Ingraham, and S. D. Smith. 1992. Water uptake by woody riparian phreatophytes of the southwestern United States: a stable isotope study. *Ecological Applications* 2:450–459.
- Butler, J. J., G. J. Kluitenberg, D. O. Whitmore, S. P. Loheide, W. Jin, M. A. Billinger, and X. Y. Zhan. 2007. A field investigation of phreatophyte-induced fluctuations in the water table. *Water Resources Research* 43:W02404.
- Cleverly, J. R., S. D. Smith, A. Sala, and D. A. Devitt. 1997. Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: the role of drought. *Oecologia* 111:12–18.
- Cooper, D., D. D'Amico, and M. Scott. 2003. Physiological and morphological response patterns of *Populus deltoides* to alluvial groundwater pumping. *Environmental Management* 31:215–226.
- Donovan, L. A., D. J. Grisé, J. B. West, R. A. Rapport, N. N. Alder, and J. H. Richards. 1999. Predawn disequilibrium between plant and soil water potentials in two cold-desert shrubs. *Oecologia* 120:209–217.
- Ehleringer, J. R. 1991. $^{13}\text{C}/^{12}\text{C}$ fractionation and its utility in terrestrial plant studies. Pages 187–200 in D. C. Coleman and B. Fry, editors. *Carbon isotope techniques*. Academic Press, New York, New York, USA.
- Ehleringer, J. R., L. A. Arnow, T. Arnow, I. B. McNulty, and N. C. Negus. 1992. Red Butte Canyon Research Natural Area: history, flora, geology, climate, and ecology. *Great Basin Naturalist* 52:95–121.
- Enquist, B. J. 2002. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. *Tree Physiology* 22:1045–1064.
- Gartner, B. L. 1995. Patterns of xylem variation within a tree and their hydraulic and mechanical consequences. Pages 125–149 in B. L. Gartner, editor. *Plant stems: physiology and functional morphology*. Academic Press, San Diego, California, USA.
- Gazal, R. M., R. L. Scott, D. C. Goodrich, and D. G. Williams. 2006. Controls on transpiration in a semiarid riparian forest. *Agricultural and Forest Meteorology* 137:56–67.
- Granier, A. 1987. Evaluation of transpiration in a Douglas fir stand by means of sap flow measurements. *Tree Physiology* 3:309–320.
- Holbrook, N. M., and M. A. Zwieniecki. 1999. Embolism repair and xylem tension. Do we need a miracle? *Plant Physiology* 120:7–10.
- Horton, J. L., T. E. Kolb, and S. C. Hart. 2001a. Responses of riparian vegetation to interannual variation in groundwater depth in a semi-arid river basin. *Plant, Cell and Environment* 24:293–304.
- Horton, J. L., T. E. Kolb, and S. C. Hart. 2001b. Physiological response to groundwater depth varies among species and with river flow regulation. *Ecological Applications* 11:1046–1059.
- Hultine, K. R., S. E. Bush, A. G. West, and J. R. Ehleringer. 2007a. Population structure, physiology and ecophysiological impacts of dioecious riparian tree species in western North America. *Oecologia* 154:85–93.
- Hultine, K. R., S. E. Bush, A. G. West, and J. R. Ehleringer. 2007b. The effect of gender on sapflux-scaled transpiration in a dominant riparian tree species: box elder (*Acer negundo*). *Journal of Geophysical Research* 112 G03S06.
- Huxman, T. E., B. P. Wilcox, D. B. Breshears, R. L. Scott, K. A. Snyder, E. E. Small, K. Hultine, W. T. Pockman, and R. B. Jackson. 2005. Ecophysiological implications of woody plant encroachment. *Ecology* 86:308–319.
- Lamb, L., and E. Muller. 2002. Sap flow and water transfer in the Garonne River riparian woodland, France: first results and poplar and willow. *Annales des Sciences Forestieres* 59:301–315.
- Leffler, A. J., and A. S. Evans. 1999. Variation in carbon isotope composition among years in the riparian tree: *Populus fremontii*. *Oecologia* 119:311–319.
- Lite, S. J., and J. C. Stromberg. 2005. Surface water and groundwater thresholds for maintaining *Populus-Salix* forests, San Pedro River, Arizona. *Biological Conservation* 125:153–167.
- Mahoney, J. M., and S. B. Rood. 1992. Response of a hybrid poplar to water table decline and different substrates. *Forest Ecology and Management* 54:141–156.
- McCabe, G. J., and M. P. Clark. 2005. Trends and variability in snowmelt runoff in the Western United States. *Journal of Hydrometeorology* 6:476–482.

- Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lattenmaier. 2005. Declining mountain snowpack in western North America. *Bulletin of the American Meteorology Society* 86:39–49.
- Nagler, P., A. Jetton, J. Fleming, K. Didan, E. Glenn, K. Morino, J. Erker, J. Milliken, and S. Gloss. 2007. Evapotranspiration in a cottonwood (*Populus fremontii*) restoration plantation estimated by sap flow and remote sensing methods. *Agricultural and Forest Meteorology* 144:95–110.
- Paltineanu, I. C., and J. L. Starr. 1997. Real-time soil water dynamics using multisensor capacitance probes: laboratory calibration. *Soil Science Society of America Journal* 61:1576–1585.
- Pataki, D. E., S. E. Bush, P. Gardener, D. K. Solomon, and J. R. Ehleringer. 2005. Ecohydrology in a Colorado River riparian forest: implications for the decline of *Populus fremontii*. *Ecological Applications* 15:1009–1018.
- Pataki, D. E., R. Oren, and W. K. Smith. 2000. Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. *Ecology* 81:2557–2566.
- Patten, D. T. 1998. Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* 18:498–512.
- Pockman, W. T., and J. S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran Desert vegetation. *American Journal of Botany* 87:1287–1299.
- Potts, D. L., and D. G. Williams. 2004. Response of tree ring holocellulose $\delta^{13}\text{C}$ to moisture availability in *Populus fremontii* at perennial and intermittent stream reaches. *Western North American Naturalist* 64:27–37.
- Potvin, C., M. J. Lechowicz, and S. Tardiff. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology* 71:1389–1400.
- Rood, S. B., J. H. Braatne, and F. M. R. Hughes. 2003. Ecophysiology of riparian cottonwoods: streamflow dependency, water relations and restoration. *Tree Physiology* 23:1113–1124.
- Salleo, S., M. A. Lo Gullo, D. De Paoli, and M. Zippo. 1996. Xylem recovery from cavitation-induced embolism in young plants of *Laurus nobilis*: a possible mechanism. *New Phytologist* 132:47–56.
- Schade, J. D., E. Marti, J. R. Welter, S. G. Fisher, and N. B. Grimm. 2002. Sources of nitrogen to the riparian zone of a desert stream: implications for riparian vegetation and nitrogen retention. *Ecosystems* 5:68–79.
- Schaeffer, S. M., D. G. Williams, and D. C. Goodrich. 2000. Transpiration of cottonwood/willow forest estimated from sap flux. *Agricultural and Forest Meteorology* 105:257–270.
- Scott, M. L., P. B. Shafroth, and G. T. Auble. 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environmental Management* 23:347–358.
- Scott, R. L., E. A. Edwards, W. J. Shuttleworth, T. E. Huxman, C. Watts, and D. C. Goodrich. 2004. Interannual and seasonal variation in fluxes of water and CO_2 from a riparian woodland ecosystem. *Agriculture and Forest Meteorology* 122:65–84.
- Scott, R. L., T. E. Huxman, D. G. Williams, and D. C. Goodrich. 2006. Ecohydrological impacts of woody plant encroachment: seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment. *Global Change Biology* 12:311–324.
- Shafroth, P. B., J. C. Stromberg, and D. T. Patten. 2000. Woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands* 18:577–590.
- Smith, S. D., A. B. Wellington, J. L. Nachlinger, and C. A. Fox. 1991. Functional responses of riparian vegetation to streamflow, diversion in the eastern Sierra Nevada. *Ecological Applications* 1:89–97.
- Snyder, K. A., and D. G. Williams. 2000. Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. *Agricultural and Forest Meteorology* 105:227–240.
- Sperry, J. S., A. Perry, and J. E. M. Sullivan. 1991. Pit membrane degradation and air-embolism formation in ageing xylem vessels of *Populus tremuloides* Michx. *Journal of Experimental Botany* 42:1399–1406.
- Stromberg, J. C. 1993. Fremont cottonwood-Gooding willow riparian forests: a review of their ecology, threats, and recovery potential. *Journal of the Arizona-Nevada Academy of Science* 26:97–111.
- Stromberg, J. C. 1998. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. *Journal of Arid Environments* 40:133–155.
- Tyree, M. T., S. Salleo, A. Nardini, M. A. Lo Gullo, and R. Mosca. 1999. Refilling of embolized vessels in young stems of laurel. Do we need a new paradigm? *Plant Physiology* 120:11–20.
- Webb, R. H., S. A. Leake, and R. M. Turner. 2007. The ribbon of green: change in riparian vegetation in the southwestern United States. University of Arizona Press, Tucson, Arizona, USA.
- Williams, D. G., R. L. Scott, T. E. Huxman, D. C. Goodrich, and G. Lin. 2006. Sensitivity of riparian ecosystems in arid and semiarid environments to moisture pulses. *Hydrological Processes* 20:3191–3205.