Controls on transpiration in a semiarid riparian cottonwood forest

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Abstract

Cottonwood (*Populus* spp.) forests are conspicuous and functionally important elements of riparian vegetation throughout much of the western U.S. Understanding how transpiration by this vegetation type responds to environmental forcing is important for determining the water balance dynamics of riparian ecosystems threatened by groundwater depletion. Transpiration was measured in semiarid riparian cottonwood (*Populus fremontii*) stands along a perennial and an intermittent reach of the San Pedro River in southeastern Arizona. Sap flow was measured using thermal dissipation probes and scaled to the stand level to investigate stand water use in relation to canopy structure, depth to groundwater and climate forcing. The cottonwood stand located at the perennial stream site had higher leaf-to-sapwood area ratio (0.31 ± 0.04 m^2 cm^{-2}), leaf area index (2.75) and shallower groundwater depth (1.1–1.8 m) than the stand at the intermittent stream site (0.21 ± 0.04 m^2 cm^{-2}, 1.75 and 3.1–3.9 m, respectively). Moreover, total annual transpiration was higher at the perennial stream site (966 mm) than at the intermittent stream site (484 mm). The significant positive and linear correlation between transpiration and vapor pressure deficit indicated high hydraulic conductance along the root–shoot pathway of cottonwood trees at the perennial stream site. During the peak dry period prior to the summer rainy season, the trees at the intermittent stream site exhibited greater water stress as transpiration did not increase beyond its mid-morning peak with increasing vapor pressure deficit, which was likely due to leaf stomatal closure. However, this stress was alleviated after significant monsoonal rains and runoff events had recharged soil moisture and raised groundwater levels. Riparian cottonwood forests are exposed to extreme fluctuations in water availability and transpiration demand throughout the growing season, and their access to shallow groundwater sources determines their structural and physiological responses to drought. Spatial and temporal variation in depth to groundwater induces drought stress in cottonwood threatening their productivity and existence along the river systems throughout much of western U.S.
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1. Introduction

Riparian cottonwood (*Populus* spp.) forests in the western United States are ecologically and hydrologically important features of the arid landscape. Cottonwood trees in these forests have high rates of transpiration due to the trees' access to groundwater and the high evaporative demand of the atmosphere (Schaeffer et al., 2000; Dahm et al., 2002). However, leaf gas exchange physiology of cottonwood is extremely sensitive to local hydrologic conditions. Depth to groundwater and proximity to surface stream flow are key environmental features strongly determining cottonwood stomatal conductance and photosynthesis (Leffler and Evans, 1999; Horton et al., 2001a; Potts and Williams, 2004).

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Transpiration by cottonwood forests can be a substantial component of the total water budget of riparian systems (Goodrich et al., 2000). However, there remains considerable uncertainty in estimates of transpiration in these systems because of landscape-scale variation in forest structure and the heterogeneity of groundwater availability (Schaeffer et al., 2000).

Spatial and temporal heterogeneity in cottonwood forest transpiration is likely to be substantial, but is poorly documented. Yet heterogeneity in water use of vegetation influences ecosystem water balance and key ecological processes. Water use of cottonwood forests, one of the most dominant riparian vegetation types in the Upper San Pedro Basin in southeastern Arizona, USA, has a great influence on the overall productivity and water balance of the riparian corridor (Goodrich et al., 2000; Scott et al., in press). Within this context, it is important to determine the extent to which cottonwood trees control hydrological processes and the effects of seasonal variability and temporal trends in water resources on the physiology of cottonwood trees (Gurnell et al., 2000).

Plants regulate transpiration (E) to maximize photosynthesis, minimize water loss and avoid drought-induced formation of xylem embolisms (Tyree and Sperry, 1989; Whitehead, 1998; Sparks and Black, 1999). Plant structural and physiological traits associated with regulation of transpiration include the amount of leaf and sapwood area (Gholz, 1982; White et al., 1998; Whitehead, 1998; Cinnirella et al., 2002; Schaeffer et al., 2000) and stomatal characteristics and responsiveness to atmospheric moisture (Oren et al., 1999; Medrano et al., 2002; Vose et al., 2003). The hydraulic connection between the roots and the water table also influences transpiration (Cooper et al., 2003), particularly in riparian forests that are sustained by shallow groundwater tables (Tyree et al., 1994; Zhang et al., 1999; Vose et al., 2003).

Plants avoid excessive transpiration during periods of high vapor pressure deficit (D) by regulating stomatal conductance. Cottonwood trees along an ephemeral river system in Arizona were found to be more sensitive to high vapor pressure deficit than other riparian species such as the drought tolerant *Tamarix chinensis* (Horton et al., 2001a). Stomatal conductance and net photosynthesis rate of cottonwood trees decline during drought (Horton et al., 2001a), which may indicate the influence of soil moisture stress on stomatal opening (Unsworth et al., 2004). Reduction in leaf area, accompanied by physiological changes necessary to counterbalance loss in photosynthetic leaf tissue, provides an effective mechanism that can be used

with stomatal closure to prevent excessive water loss (Roberts, 2000).

In this paper, we present the seasonal patterns of cottonwood transpiration at two contrasting riparian sites in order to better understand how the trees transpire in relation to canopy structure, evaporative demand and groundwater depth. Along the San Pedro River in southeastern Arizona, we quantified cottonwood transpiration using sap flow measurements for a cluster of trees located on a perennial section of the river and another located along a reach with intermittent stream flow. Hydrologically, these sites differed in the depth and seasonal fluctuation of the water table. We also computed crop coefficients for cottonwood transpiration to understand mechanisms controlling transpiration and to evaluate suitable proxies for cottonwood transpiration in the absence of direct transpiration measurements.

2. Methods

2.1. Study sites

Study sites were located on the floodplain of the San Pedro River in the San Pedro Riparian National Conservation Area (SPRNCA) in southeastern Arizona. A cluster of cottonwood trees was monitored at two sites with contrasting groundwater depth levels (Table 1). The Boquillas site (1180 m elevation, 31.6986°N 110.1808°W) was located along an intermittent reach of the river and the groundwater depth ranged from 3.1 to 3.9 m (mean = 3.3 m) during this study. In contrast, the Lewis Springs site (1250 m elevation, 31.5533°N, 110.1391°W) was located along a perennially flowing reach of the San Pedro River and the groundwater depth ranged from 1.1 to 1.8 m (mean = 1.6 m). The climate in the San Pedro Basin is semiarid with large fluctuations in water availability and diurnal and annual air temperature. Approximately 350 mm of precipitation falls annually with about 60% of that occurring during the summer monsoon from July–September (Scott et al., 2004). Cottonwood trees usually leaf out in early April, about one month before the last nocturnal frost of the spring. The pre-monsoon period of May and June is usually very dry (midday $D > 5$ kPa) and hot (maximum temperature $>35\,°C$). The frequent afternoon thunderstorms and river flooding during the annual summer monsoon relieve the intense drought. Cottonwood trees in the river basin become dormant in early November and transpiration typically ends after the first hard frost of autumn (Goodrich et al., 2000). The cottonwood stands along

Table 1
Structural characteristics of cottonwood clusters at Lewis Spring ($n = 9$) and Boquillas ($n = 10$) sites along the San Pedro River in southeastern Arizona

Site	Diameter (cm)	Height (m)	Canopy area[a] (m^2)	SWA[b] (cm^2)	Leaf Area/SWA[***] ($m^2\ cm^{-2}$)
Boquillas	61	27	1037	1223 ± 231	0.21 ± 0.02
Lewis Springs	49	25	421	797 ± 243	0.31 ± 0.04

[a] Canopy area refers to the planar area of the canopy as seen from aerial photographs (Schaeffer et al., 2000).
[b] Sapwood area.
[***] A_L:A_S ($\pm$S.E.) significant at $P = 0.10$.

most of the San Pedro generally grow within the active floodplain and upon highly permeable alluvium, consisting primarily of sand and gravel (Pool and Coes, 1999)

2.2. Basal sap flow measurements

Sap flow of four cottonwood trees, a diffused porous species, within each cluster was measured using constant heat flow Granier-type probes (TDP-30 and TDP-80, Dynamax, Inc., Houston, TX). Thermocouple needles 1.2 and 1.65 mm in diameter (TDP-30 and TDP-80, respectively) were installed as a vertically aligned pair 4 cm apart within the sapwood of each tree. The system measures the temperature difference between two probes inserted radially in the xylem, one constantly heated and the other unheated. Sets of these probes were implanted on the north and south side of each tree at 1.75 m above the ground.

Sap flow was measured continuously from April 5 to November 9, 2003 using a datalogger (CR10x datalogger, Campbell Scientific Inc., Logan, UT). Plastic putty was installed around the needles for water protection and foam quarter-spheres were tightly secured on both sides of the needles to protect the wire from bending stress and to provide thermal insulation to the needles. Reflective bubble wrap was installed around the tree bole for additional insulation.

The Granier (1987) method was used to calculate the dimensionless parameter (K) as:

$$K = \frac{\partial T_m - \partial T}{\partial T} \qquad (1)$$

where ∂T is the measured difference in temperature between the heated needle, referenced to the lower non-heated needle and ∂T_m is the value of ∂T when there is no or minimum sap flow. Average sap flow velocity [V, cm s^{-1}] was calculated as (Granier, 1987):

$$V = 0.0119K^{1231} \qquad (2)$$

Sap flow velocity was then converted to sap flow rate [J_s, cm^3 h^{-1} or g cm^{-2} h^{-1}] from:

$$J_s = SWA \times V \times 3600) \qquad (3)$$

where SWA is the sapwood area (cm^2) and 3600 is in s h^{-1}.

2.3. Scaling

Cottonwood stand transpiration, E (mm day^{-1}), was calculated based on individual tree sap flow, total sapwood area and crown area of the cluster (Wulls-chleger et al., 1998). At the end of the season, sapwood area (SWA) was determined from increment cores taken as close as possible to the probe insertions at each side of the tree. Sapwood was identified from heartwood by color change from lightly colored to darkly colored and water saturated heartwood. Total canopy area and diameter of all the trees in the cluster were measured at both sites (Table 1). The sapwood area-to-diameter relationship was used to estimate the total sapwood area of all the trees in the cluster (Schaeffer et al., 2000).

For trees instrumented with TDP-30, sap flow was assumed to be constant over the radial sapwood profile since radial profile information was lacking for our study site. However, using the TDP-80, sap flow rate per tree (J_s) was scaled based on the sapwood area that covers the position of the two thermocouples per probe. Scaling of sap flow from those trees instrumented with probes to the whole patch of trees involves several sources of uncertainty such as estimates of sapwood area and within-tree and between-tree variation in sap flow.

J_s from the north and south side of each thermocouple position was averaged and multiplied by the sapwood area corresponding to the depth of the thermocouple in the sapwood ($\hat{J}_s$). $\hat{J}_s$ from the two thermocouple positions was then added and the sum was divided by the total sapwood area of the tree ($\bar{J}_s$). $\bar{J}_s$ from the instrumented trees in the cluster was averaged and multiplied by the total sapwood area of the entire cluster to get the total water use of the stand (kg d^{-1}).

Total water use of the entire cottonwood cluster was divided by projected canopy area (m^2) to determine ground-area based transpiration, E (kg m^{-2} d^{-1} or mm d^{-1}). The projected canopy area of the clusters was estimated digitally using aerial photographs.

2.4. Leaf area index, meteorological and groundwater depth measurements

Leaf area index (LAI) was measured using a plant canopy analyzer (LAI 2000, LiCor, Lincoln, NE) in October 2003. LAI readings were taken from the four cardinal directions around the base of each tree within the cluster. Air temperature, relative humidity, solar radiation, wind speed, air pressure and precipitation were measured at nearby meteorological towers located 3 km from the Boquillas intermittent stream site and 0.3 km from the Lewis Springs perennial stream site. Depth to groundwater (Z_{GW}) at each site was measured in piezometers located close to the sites. Water levels were measured manually on a weekly basis at the intermittent stream site and every 30 min with a well transducer at the perennial stream site.

2.5. Calculation of resistances and crop coefficient

To assess the seasonal variations in stand-level canopy resistance, r_c (s m^{-1}), the Penman–Monteith equation (Montieth and Unsworth, 1990) was inverted to become:

$$r_c = \left[\frac{\Delta}{\gamma} \left(\frac{A - \lambda E}{\lambda E} \right) - 1 \right] r_a + \frac{\rho_a C_p D}{\gamma \lambda E} \qquad (4)$$

where Δ is the slope of the saturation vapor pressure and temperature curve (kPa $^{\circ}$C^{-1}), γ the psychrometric constant (kPa $^{\circ}$C^{-1}), λE the latent heat flux (W m^{-2}), A the available energy (W m^{-2}), r_a the aerodynamic resistance (s m^{-1}), ρ_a the density of moist air (kg m^{-3}), C_p the specific heat for dry air under constant pressure (1013 J kg^{-1} $^{\circ}$C^{-1}) and D is the vapor pressure deficit (kPa). Parameters such as Δ, ρ_a, γ and D were calculated from air temperature, relative humidity and air pressure measured from nearby meteorological stations. Since canopy available energy measurements were not available, A was estimated by using measured incoming solar radiation and a formula for reference crop available energy developed for southern Arizona (Brown, 1989). The canopy aerodynamic resistance was dominated by and assumed equal to the boundary layer resistance, which was estimated following the methods described by Goodrich et al. (2000). Since wind speeds and leaf dimensions were nearly equal between sites,

the magnitude of r_a was influenced mainly by the difference in LAI between the sites.

The canopy aerodynamic resistance was estimated following the methods described by Goodrich et al. (2000). Stomatal resistance, r_s, was determined by:

$$r_s = r_c \text{LAI} \qquad (5)$$

where we assume that LAI at the perennial (LAI = 2.75) and intermittent stream sites (LAI = 1.75) were constant throughout the growing season.

A crop coefficient, k_c was calculated as:

$$k_c = \frac{E}{ET_0} \qquad (6)$$

where E (mm d^{-1}) is the transpiration from actual sap flow measurements and ET_0 is reference crop evaporation (mm d^{-1}). k_c is simply referred to as E/ET_0 in this paper. ET_0 is an estimate of evaporation that would occur from short, well-watered grass that fully covers the ground. ET_0 was calculated using a modified Penman–Monteith equation developed for southern Arizona (Brown, 1989) and is defined as:

$$ET_0 = \frac{\Delta}{\Delta + \gamma} A + \frac{\gamma}{\Delta + \gamma} f(U_2)D \qquad (7)$$

where A is the same available energy as above except in units of mm d^{-1}. Two wind functions ($f(U_2)$; mm h^{-1} kPa^{-1}) are used to compute ET_0—one for daytime conditions ($A > 0$) and one for nighttime conditions ($A \leqq 0$). These wind functions are as follows:

$$f(U_2) = 0.03 + 0.0576(U_2); \quad A > 0, \ \text{Daytime} \qquad (8)$$
$$f(U_2) = 0.125 + 0.0439(U_2); \quad A < 0, \ \text{Nighttime} \qquad (9)$$

where U_2 (m s^{-1}) is the mean hourly wind speed obtained at a height of 2 m.

3. Results

3.1. Seasonal variation in meteorological conditions

Because the meteorological conditions at both the intermittent and perennial stream sites were very similar, they can be adequately summarized graphically by using just one site (Fig. 1). Diurnal temperature ranges were typically 22 $^{\circ}$C with the highest temperature (42 $^{\circ}$C) recorded in July and lowest temperature (-9 $^{\circ}$C) recorded in November. The last hard frost of spring (defined by minimum temperature ≤ 3 $^{\circ}$C) occurred on DOY 132 and the first hard frost of fall was on DOY 295. Monsoon rains began on DOY 192
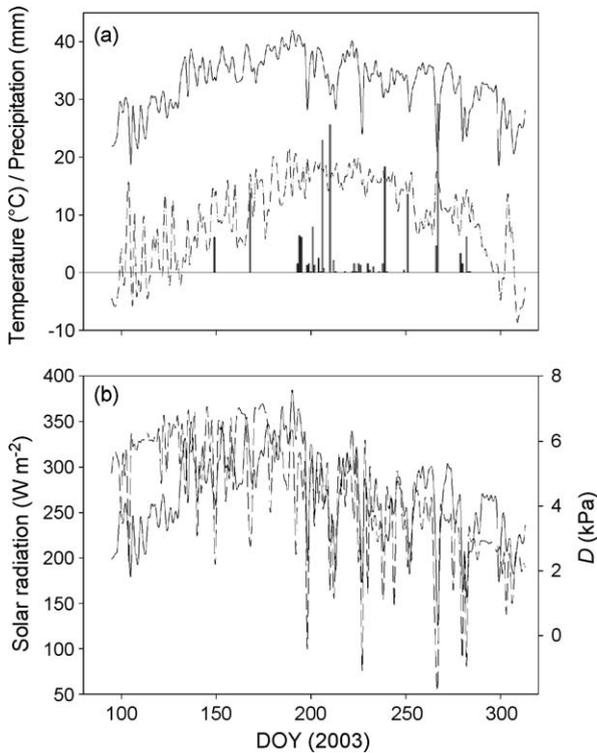
Fig. 1. Seasonal variations in environmental conditions: (a) maximum (solid line) and minimum (broken line) air temperature (°C) and precipitation (mm; bar); (b) vapor pressure deficit (D, kPa; solid line) and solar radiation (W m⁻²; broken line); during the 2003 growing season at the intermittent stream site.

and resulted in reduced D. The end of the monsoon is harder to define as rainy periods with dry interstorm periods continued throughout July–October. Maximum D was often greater than 5 kPa during the pre-monsoon and was reduced to less than 5 kPa during the peak of the monsoon. Average daily solar radiation peaked in June and was reduced for the rest of the season due to the reduction in extraterrestrial forcing and greater percentage of cloudy days.

Monthly distribution of rain events was not similar between sites due to localized and patchy occurrence of the summer convective storms (data not shown). At the Boquillas site (intermittent stream site), the highest monthly amount of rainfall (52 mm) was observed in August while it was in July (80 mm) for the Lewis Springs site (perennial stream site). The total amount of rainfall, however, was almost the same for both sites throughout the duration of sap flow measurements from April to October 2003 (intermittent, 186 mm and perennial, 188 mm). Approximately 80% of the total growing season rainfall occurred in the months of July, August and September. The first precipitation event of the monsoon was on DOY 192 at the intermittent stream

site (2.0 mm event) and at DOY 193 at the perennial stream site (1.5 mm event).

3.2. Vapor pressure deficit and transpiration

During the peak of the pre-monsoon drought (around DOY 185), mean maximum D ($\overline{D_{\max}}$) was 6 kPa at the intermittent and perennial stream sites (Fig. 2). D and E followed the same trend throughout the days. At the intermittent stream site, however, declines in E coincided with the peaks in D during the day. Separation of 30 min $\bar{J}_s$ values into morning (07:00–12:00 h) and afternoon (12:30–17:00 h) periods at both sites during the peak of the drought period shows unique responses of cottonwood trees to D (Fig. 3). In the morning, a positive, linear relationship between D and $\bar{J}_s$ exists at the perennial stream site. However, during the same morning period, there was already evidence of stomatal closure at D greater than 3 kPa at the intermittent stream site. In the afternoon, $\bar{J}_s$ at the perennial stream site was still linearly related to the even greater values of D, but $\bar{J}_s$ was not correlated to any change in D at the intermittent stream site.

The trees responded differently after the summer monsoon rainfall had recharged soil moisture and the alluvial aquifer (Fig. 2) than before the rainy period. From July 29 to August 13, after a total of 31 and 32 mm of precipitation had fallen at the intermittent and perennial stream sites, respectively, $\overline{D_{\max}}$ (=5 kPa) was similar to that during the pre-monsoon season in July. $\bar{J}_s$ increased at both sites during the monsoon season with a much greater increase at the intermittent than at the perennial stream site. There was still evidence of stomatal limitation at the intermittent stream site in response to high D during the course of the day during the rainy period (Fig. 3c and d). On a daily basis, E increased with D at the perennial stream site ($r^2 = 0.61$; Fig. 4a). However, at the intermittent stream site, E was not correlated to D. Leaf-area-normalized E (E/LAI) at the perennial stream site was higher than the intermittent stream site when D was greater than 3 kPa (Fig. 4b).

3.3. Total growing season transpiration

Daily total transpiration of the cottonwood cluster at the perennial stream site was higher than that at the intermittent stream site throughout the growing season (Fig. 5). A marked decline in E at the intermittent stream site was observed during the peak of the pre-monsoon drought. Leaves of cottonwood trees fully leafed out by DOY 91 and completely senesced by DOY 309. In order to determine total growing season
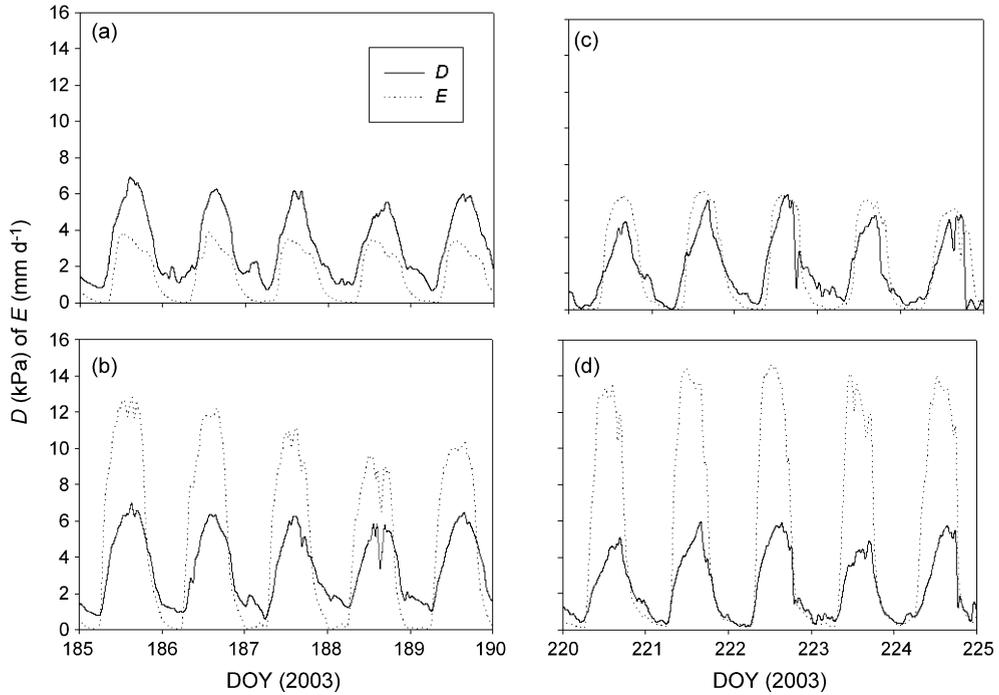
Fig. 2. Thirty-minute average vapor pressure deficit, D (kPa), and measured transpiration, E (mm d^{-1}), at the (a and c) intermittent and (b and d) perennial stream sites during the pre-monsoon, July 4–9, 2003 (DOY 185–190) (a and b) and monsoon, August 8–13, 2003 (DOY 220–225) (c and d) season.
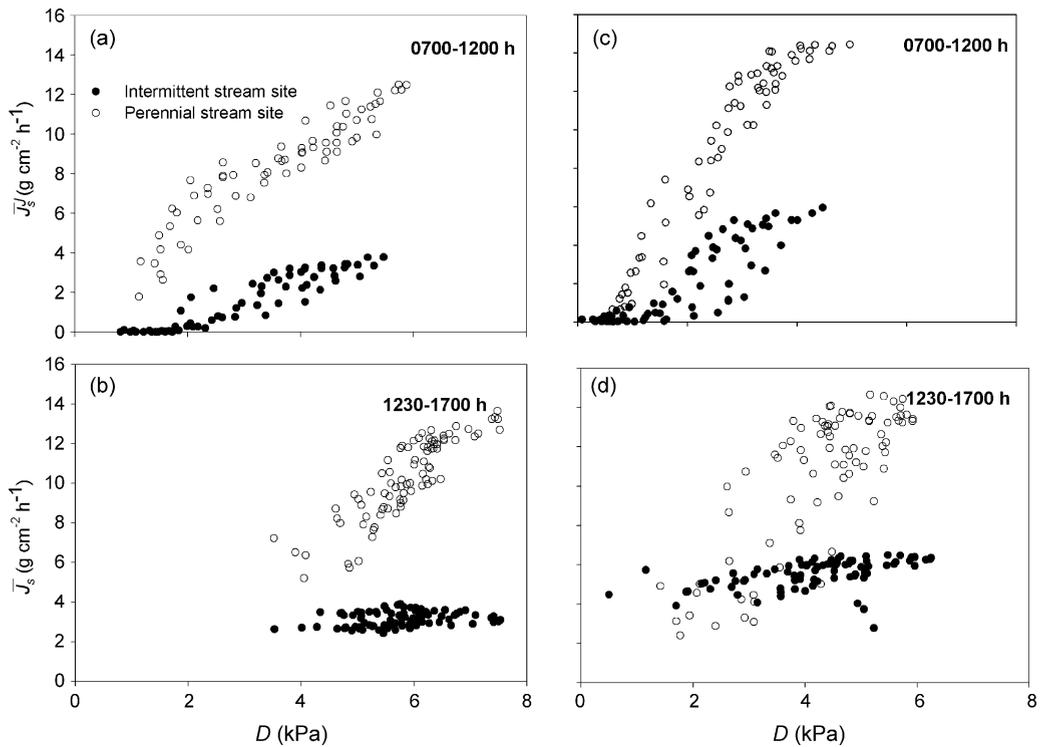

Fig. 3. Relationship of average sap flow rate ($\bar{J}_s$, g cm^{-2} h^{-1}) of cottonwood trees and vapor pressure deficit (D, kPa) at the intermittent (closed circle) and perennial (open circle) stream sites in the (a and c) morning (07:00–12:00 h) and (b and d) afternoon (12:30–17:00 h) periods during the (a and b) pre-monsoon (DOY 185–190) and (c and d) monsoon (DOY 220–225) season in 2003.
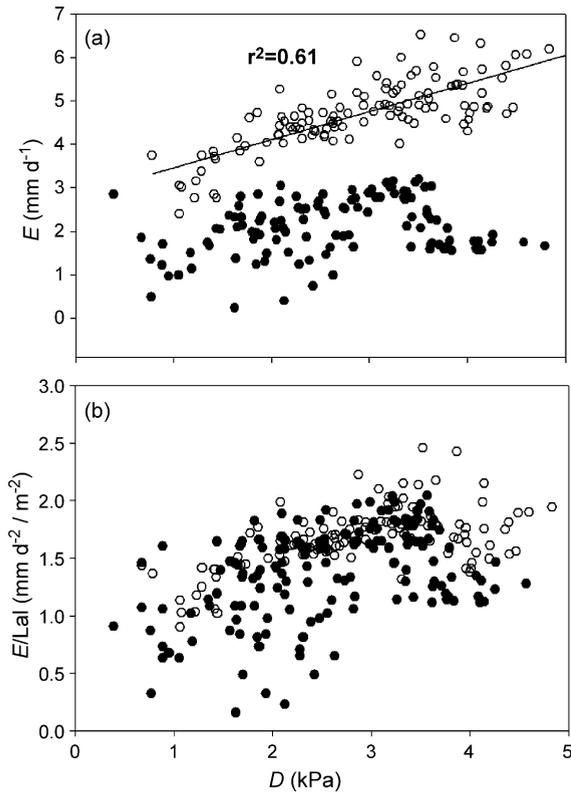
Fig. 4. Relationship of vapor pressure deficit, D (kPa) and (a) measured transpiration, E (mm d^{-1}) and (b) leaf-area-normalized E (E/LAI) at the intermittent (closed circle) and perennial (open circle) stream sites. Regression model is significant at $P = 0.05$.
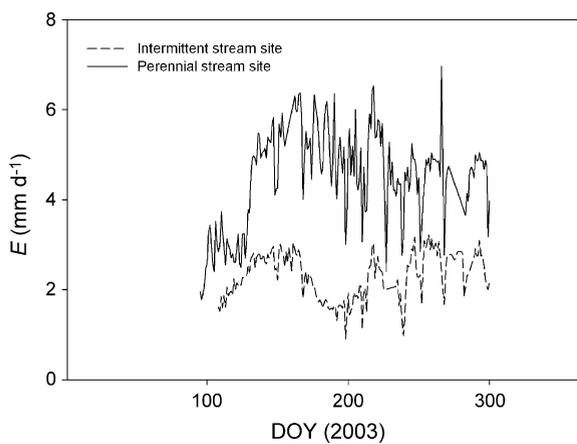

Fig. 5. Daily cottonwood transpiration (E, mm d^{-1}) at the intermittent (broken line) and perennial (solid line) stream sites. Decline in E caused by a localized leaf infestation of caterpillars occurred at the perennial stream site on DOY 102. Full recovery from herbivory was indicated by new leaves development and the return of high transpiration rates around DOY 130.
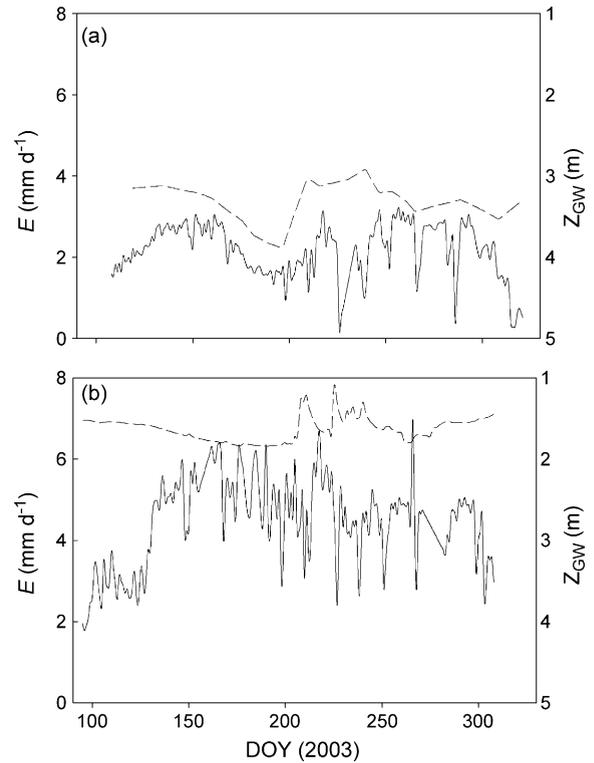

Fig. 6. Seasonal cottonwood transpiration, E (mm d^{-1}) (solid line) and depth to groundwater, Z_{GW} (m) (dashed lines) at the (a) intermittent and (b) perennial stream sites.

transpiration we summed all daily values after first using linear interpolation to fill small data gaps and between the start of measurements (DOY 95, perennial stream site; DOY 108, intermittent stream site) and the beginning of transpiration, which we assumed was zero on DOY 91 (i.e., assuming a linear ramp up in transpiration from DOY 91 until the first day of measurements). Total growing season E at the intermittent stream site was 484 and 966 mm at the perennial stream site. During the early part of the growing season, approximately 11 days after budbreak, there was a localized leaf infestation of caterpillars that occurred at the perennial stream site. A decline in E started at the onset of the herbivory on DOY 102 and continued until DOY 112 when the cottonwood trees were most defoliated (Fig. 5). Declines in E were observed throughout the duration of infestation. The trees appeared to be fully recovered from herbivory by ∼DOY 130 when high transpiration rates had resumed.

3.4. Depth to groundwater and transpiration

Depth to groundwater (Z_{GW}) at the intermittent stream site was greater than at the perennial stream site (Fig. 6).
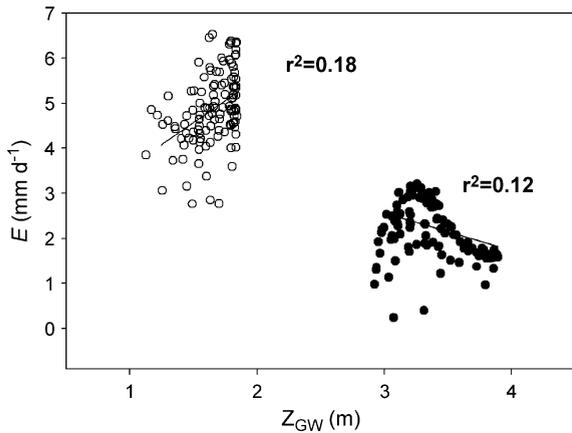
Fig. 7. Relationship of measured transpiration, E (mm d^{-1}) and depth to groundwater, Z_{GW} (m) at the intermittent (closed circle) and perennial (open circle) stream sites. Regression model is significant at $P = 0.05$.
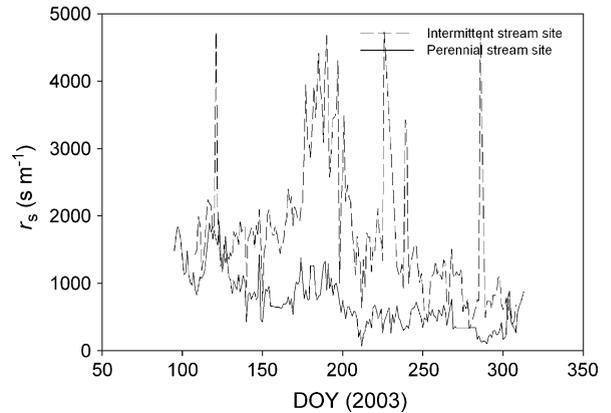

Fig. 8. Stomatal resistance (r_s, s m^{-1}) at the intermittent (broken line) and perennial stream (solid line) sites throughout the growing season in 2003.

At the intermittent stream site, Z_{GW} increased from 3.1 m during the early part of the spring season to 3.9 m during the peak of the drought period. At the perennial stream site, Z_{GW} had a gradual but much smaller decline during the pre-monsoon drought, and the largest increases were the result of groundwater recharge from river flood events during the monsoon season. The depth at the beginning of the spring season was 1.5 m and increased to only 1.8 m at the peak of the drought period (a decline which was 0.5 m less than at the intermittent site).

At the perennial stream site, the small fluctuations in groundwater depth did not appear to strongly influence transpiration (Fig. 7a). Perhaps unexpectedly, there was a general tendency for increased E with increased Z_{GW}, but this tendency was likely not casual as pre-monsoon period with the greatest evaporative demand coincided with the maximum groundwater depths. At the intermittent stream site, there was a stronger relationship between E and Z_{GW}; lower rates of transpiration corresponded with greater depths to groundwater (Fig. 7).

The inverted Penman–Monteith equation was used to assess the seasonal variation in stomatal resistance (r_s) of cottonwood forest. r_s at the intermittent stream site was higher than at the perennial stream site with maximum r_s attained at the peak of the drought period (Fig. 8). Leaf defoliation (DOY 102–112) at the perennial stream site also caused r_s to increase. It was also evident that even the perennial stream site also exhibited some water stress during the pre-monsoon season as r_s decreased following monsoon rains and flood flows.

3.5. Modeling transpiration

In order to determine if a simple modeling approach would adequately predict E, we examined the functional dependence of E/ET_0 on D and Z_{GW} at both sites (Fig. 9). Larger daily average D, which occurred during the pre-monsoon season, had the effect of decreasing E/ET_0 (Fig. 9). Likewise, as depth to groundwater increased, the crop coefficient was reduced. In general, variations in D accounted for more of the variability in E/ET_0 than did variations in Z_{GW}. Nevertheless, there was a well-defined decrease in E/ET_0 for Z_{GW} greater than $\sim$3.5 m. Fig. 10 shows the average E/ET_0 throughout the growing season. E/ET_0 is higher at the perennial than the intermittent stream site. The average crop coefficient at the intermittent stream site was 0.43 ± 0.14 and 0.74 ± 0.24 at the perennial stream site. The ratio between intermittent and the perennial mean crop coefficient (0.58) was slightly less than the ratio of the site LAI's (0.64), likely due to the greater water stress exhibited at the intermittent stream site.

4. Discussion

Spatial and temporal heterogeneity of water availability in riparian ecosystems along the San Pedro River in southeastern Arizona has marked influences on the physiology of the cottonwood forests. Canopy structure, atmospheric demand and depth to groundwater played significant roles in the seasonal fluctuations in transpiration of cottonwood trees in this riparian ecosystem. Understanding the mechanisms by which trees respond to these factors is important to accurately assess and manage water budgets of this riparian system.

Climatic factors such as temperature, vapor pressure deficit and solar radiation are important regulators of transpiration which interact with water availability and the physiological and phenological status of plants
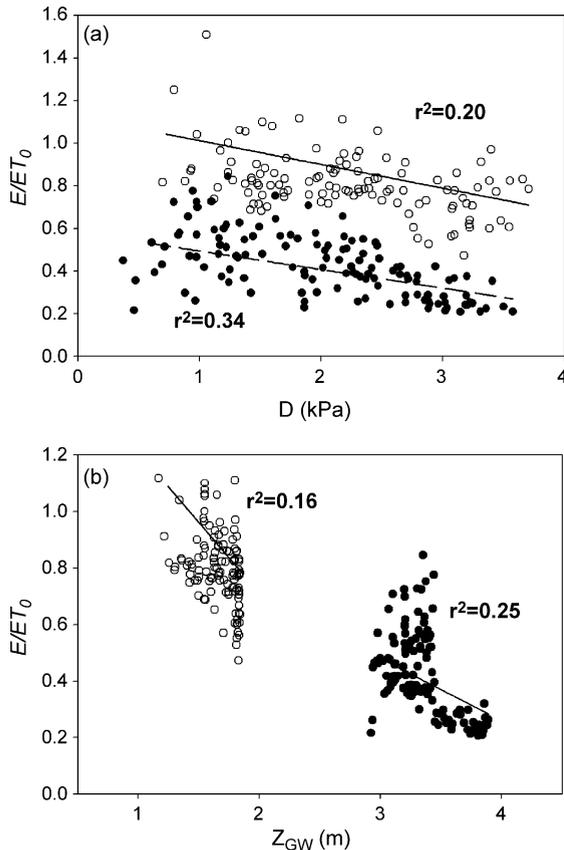
Fig. 9. Relationship of the ratio of measured transpiration and crop coefficient (E/ET_0; E is the measured transpiration in mm d^{-1} and ET_0 is the reference crop evaporation in mm d^{-1}) and (a) vapor pressure deficit, D (kPa) and (b) depth to groundwater, Z_{GW} (m) at the intermittent (closed circle) and perennial (open circle) stream sites. Regression model is significant at $P = 0.05$.
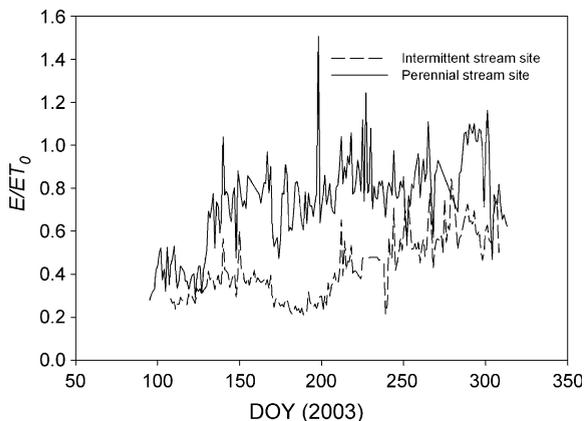

Fig. 10. Mean crop coefficient (E/ET_0) at the intermittent (broken line) and perennial stream (solid line) sites throughout the growing season in 2003.

(Vose et al., 2003). At the peak of the dry period, there was evidence of stomatal closure in response to high D at the intermittent stream site (Fig. 2). Stomatal midday depression is indicative of stomatal regulation of E as leaf water potential declines through the morning (O'Grady et al., 1999; Horton et al., 2001a). Soil water limitation at the intermittent stream site may have caused the decline in hydraulic conductivity during the growing season and reduced their stomatal sensitivity to D. In contrast, there was less apparent stomatal closure during the day in response to D at the perennial stream site throughout the season. This is supported by a significant positive linear relationship between E and D at the perennial stream site that indicates low resistance to water transport (Fig. 4). E appeared to be controlled by water transport capacity and amount of foliage in cottonwood trees at the perennial stream site (Cinnirella et al., 2002). The lack of a significant relationship between $\bar{J}_s$ and D at the intermittent stream site implies control of stomatal movement to avoid excessive transpiration in the afternoon when D tends to be high (Fig. 3).

Cottonwood trees at the intermittent stream site had lower annual water use that was approximately 50% less than the water use at the perennial stream site. Goodrich et al. (2000) estimated cottonwood consumptive water use using limited 1997 synoptic-period sap flow observations of cottonwood stands along a larger perennial reach of the San Pedro River. Our 2003 estimates of the annual cottonwood forest E at the perennial stream site was 20% more water on a per canopy area basis than their 1997 estimates. It is likely that the Goodrich et al. (2000) estimates of cottonwood forest transpiration were lower than that found in the current study due to the shorter growing season in 1997 (by about 30 days) and their lack of nighttime sap flow measurements. We found that sap flow, in fact, continued past sunset and gradually declined to zero between 19:00 and 20:00 h. Nocturnal sap flow accounted for approximately 10–25% of the daily totals. Dahm et al. (2002) also provided an estimate of annual evapotranspiration (980 mm) of a mature cottonwood stand with a closed canopy along the Middle Rio Grande in New Mexico which was similar to our estimate of total annual water use (966 mm) of cottonwood forests at the perennial stream site.

Seasonal fluctuation in water use of cottonwood trees at the intermittent stream site was closely related to the fluctuations of the groundwater table (Fig. 6). From the onset of transpiration to the peak stress of the pre-monsoon period (April–June), the depth to groundwater increased by 0.8 m at the intermittent stream site and

only 0.3 m at the perennial stream site. Transpiration at the intermittent site was considerably reduced after declines of about 0.5 m (Z_{GW} = 3.5 m, Figs. 7 and 9) Similarly, other studies have showed that cottonwood forests were vulnerable to small declines in shallow alluvial water tables (Stromberg et al., 1996; Scott et al., 1999; Horton et al., 2001b,c; Cooper et al., 2003). With less than a 0.5 m decline in Z_{GW}, cottonwood trees exhibited reduced branch growth and little mortality while greater than 1 m decline in Z_{GW} produced leaf desiccation, branch die back, loss of canopy vigor and substantial mortality (Stromberg et al., 1996; Scott et al., 1999).

Stromberg (1993) concluded that cottonwood trees on the San Pedro river basin in Arizona do not occur at sites where Z_{GW} is greater than ∼3 m. Juvenile cottonwood trees, on the other hand, usually occur in areas where Z_{GW} ranges between 0 and 2 m (Stromberg et al., 1996). Mortality of cottonwood trees was observed when Z_{GW} increased above a threshold of 2.5–3.0 m along Hassayampa River, Arizona (Horton et al., 2001b). Because the trees at the intermittent stream site were likely operating on the edge of their range of suitable habitat, the increase in Z_{GW} during the pre-monsoon drought probably reduced the trees' access to groundwater which led to observed decreases in transpiration. During the pre-monsoon season, cottonwood trees at the intermittent stream site were also observed to experience premature shedding of some leaves due to drought stress (personal observation). Flood events in the nearby stream at the onset of the monsoon season recharged the alluvial aquifer causing the groundwater table to rise and E to recover. The relationship between E and Z_{GW} (Fig. 7) implies a greater dependency of E on fluctuations in Z_{GW} at the intermittent stream site than at the perennial stream site where Z_{GW} was shallow enough to sustain high E during the summer. Cottonwood, an obligate phreatophyte, obtains 80–100% of its water from groundwater, with the proportion increasing as the soil in unsaturated zone dries out (Snyder and Williams, 2000; Horton et al., 2001c).

Cottonwood trees usually possess lateral surface roots and moderately deep roots (about 3 m) that extend into the saturated zone (Stromberg, 1993). Plants with their roots in saturated soil typically show gradual reductions in E as drought progresses while plants growing in deep water sources show large reductions in E in response to drought (Breda et al., 1993; Dawson, 1996; Oren et al., 1996). Hence, transpiration of cottonwood trees at the perennial stream site likely responded less to changes in soil moisture because of

their direct access to the groundwater table (Oren and Pataki, 2001). At the intermittent stream site, however, decline in the groundwater table caused large reductions in E that may be associated with the loss of hydraulic conductivity that also facilitated a reduction in stomatal conductance. At the onset of the monsoon, E at both sites responded to groundwater recharge by precipitation and runoff events. Hourly maximum E at the intermittent stream site increased by 50% compared to only 15% increase in E at the perennial stream site (Fig. 2). The increase in E after the groundwater recharge may be attributed to the relaxation of hydraulic resistance in the soil and soil–root interface and reversal of stem and root embolism (Oren et al., 1996; Oren and Pataki, 2001).

Changes in canopy structure during drought often alleviate the direct effects of water stress on stomatal conductance and photosynthesis (Cinnirella et al., 2002). The differences in LAI between the intermittent and perennial stream sites account for most of the differences in the magnitude of E when the water table was high (Fig. 9). Our study shows that cottonwood trees at the intermittent stream site had lower LAI than at the perennial stream site. Previous studies conducted at the same sites support this result and further reveal that LAI is more variable in intermittent stream than in the perennial stream sites (Schaeffer, 1998; Schaeffer et al., 2000). Low LAI may be attributed to the deep water table at the intermittent stream site. Hence, in order to sustain transpiration with a limited amount of water, cottonwood trees and other riparian vegetation reduce their leaf area (Cooper et al., 2003). In warm and dry sites, trees respond to increased transpiration demand by reducing the ratio of leaf area to conducting sapwood area (A_L:A_S) (Whitehead, 1998; Cinnirella et al., 2002). Our results agreed with this finding because at the perennial stream site, having shallow Z_{GW} and ample water supply throughout the growing season, cottonwood had significantly higher A_L:A_S than at the intermittent stream site.

Modeling E using the crop factor approach revealed that E/ET_0 is inversely related to D and Z_{GW} at both sites (Fig. 9). E/ET_0 is more related to variations in D and Z_{GW} at the intermittent stream site which may imply that E at the intermittent stream site was more regulated by LAI and stomata than at the perennial stream site. The average E/ET_0 at the perennial stream site was consistently higher than the intermittent stream site throughout the season. The differences in LAI between the two sites explained much of the differences in magnitude of E/ET_0. Transpiration often varies due to differences in sensitivity to drought (Oren and Pataki,

2001). Decline in E while D remains high may indicate increasing stomatal closure (Unsworth et al., 2004). In June and July, maximum stomatal resistance of cottonwood trees at both intermittent and perennial steam sites increased which may indicate that soil moisture stress was starting to influence maximum stomatal opening. Stomatal resistance at the intermittent stream site was consistently higher than the perennial stream site throughout the growing season (Fig. 10).

Our study provides full growing season estimates of riparian cottonwood E at two contrasting sites that differ in groundwater depth. Determining sources of spatial and temporal heterogeneity of cottonwood E is crucial in characterizing actual consumptive water loss from this vegetation and its role in the overall riparian water budget (Cleverly et al., 2002). For example, occurrence of floods during the monsoon season, fluctuation in ground water depth and the surface flow volume contribute to the spatial and temporal variations in transpiration of cottonwood forests (Stromberg, 1993). The extent and timing of structural and morphological changes (i.e., seasonal variation in LAI and $A_L:A_S$) and growth responses of cottonwoods to the rate, depth and duration of water table decline interact with water demand (i.e., temperature, humidity and wind speed) influence the intensity and duration of water stress in this riparian vegetation (Scott et al., 1999). The loss of young age classes and death of mature cottonwood trees as a result of water table decline (Stromberg et al., 1996) and the replacement of native species (*Populus fremontii* and *Salix gooddingii*) by more drought tolerant *T. chinensis* (Schaeffer et al., 2000; Horton et al., 2001b) pose a great threat to the existence of riparian cottonwood forests. Recognizing these variabilities as they relate to the riparian hydrology and functions will contribute substantially to a better estimate of water budget of this riparian system (Scott et al., in press).

In summary, riparian cottonwood trees are often exposed to large fluctuations in environmental forcing throughout the growing season; their accessibility to shallow groundwater sources dictates their structural and physiological responses to drought. A cottonwood stand located at the perennial stream site had a higher ratio of leaf area to sapwood area, leaf area and shallower depth to groundwater than the cottonwood stand at an intermittent stream site. Correspondingly, total daily sap flow and total annual water use were higher at the perennial stream site than the intermittent stream site. Variations in transpiration at the intermittent stream site were related to fluctuations in the depth to groundwater. A significant linear relationship between transpiration and vapor pressure deficit indicates a high hydraulic conductance along the root–shoot pathway of cottonwood trees at the perennial stream site. During the peak dry period, the cottonwood stand at the intermittent stream site exhibited daytime stomatal depression in response to high D. However, transpiration increased with no apparent daytime stomatal closure after significant monsoonal rain and runoff events that recharged groundwater at both sites. Riparian cottonwood trees are very much dependent on shallow groundwater sources and hence relatively small changes in water table depth through time make them more susceptible to drought stress. Understanding the different unique attributes and behaviors of cottonwood forests in different parts of this riparian area is important to accurately estimate the water budget of the whole riparian corridor.

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