



4-29-2005

Nonresponse of native cottonwood trees to water additions during summer drought

Greg Cox

Northern Arizona University, Flagstaff, Arizona

Dylan Fischer

Northern Arizona University, Flagstaff, Arizona

Stephen C. Hart

Northern Arizona University, Flagstaff, Arizona

T. G. Whitham

Northern Arizona University, Flagstaff, Arizona

Follow this and additional works at: <https://scholarsarchive.byu.edu/wnan>

Recommended Citation

Cox, Greg; Fischer, Dylan; Hart, Stephen C.; and Whitham, T. G. (2005) "Nonresponse of native cottonwood trees to water additions during summer drought," *Western North American Naturalist*. Vol. 65 : No. 2 , Article 5.

Available at: <https://scholarsarchive.byu.edu/wnan/vol65/iss2/5>

This Article is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Western North American Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.

NONRESPONSE OF NATIVE COTTONWOOD TREES TO WATER ADDITIONS DURING SUMMER DROUGHT

Greg Cox^{1,2}, Dylan Fischer^{1,3,4,5}, Stephen C. Hart^{1,3}, and T.G. Whitham^{2,3}

ABSTRACT.—Studies have demonstrated that some riparian trees may switch their reliance on surface soil water (unsaturated or vadose zone) to groundwater (saturated zone) sources during the growing season in association with changes in moisture availability. A closely related question is: How do these trees respond to pulse increases in water availability in previously dry zones? We tested the whole-tree physiological response of 6 natural *Populus* genotypes to water additions during the peak of summer drought in northern Utah, USA. We found clear evidence that trees were insensitive to water additions to the surface soil that were twice the magnitude of whole-tree transpiration rates. Our results suggest that some cottonwoods may have little immediate transpiration or leaf conductance response to pulse soil moisture increases. This lack of response may be related to a water-use strategy associated with regional climate patterns (i.e., genetic or environmental programming), cavitation recovery, or other physical determinants of water use such as depth to groundwater. Our data suggest that it is important to consider potential nonresponsiveness to changes in soil water availability when evaluating the impact of climate change on these important and productive ecosystems.

Key words: sap flow, cottonwood, drought, water addition, conductance, water potential, *Populus*.

Studies that examine cottonwood (*Populus* spp.) response to increasing soil moisture are important for several reasons. First, cottonwoods are dominant trees of many western intermountain river ecosystems of the United States. *Populus angustifolia* (narrow leaf cottonwood), *P. fremontii* (Fremont cottonwood), and their natural hybrids are often described as facultative phreatophytes (Snyder and Williams 2000, Horton et al. 2001a, 2001b, 2003; but see Busch et al. 1992). They are generally restricted to riparian areas where they are the dominant plant species and play a major role in ecosystem processes (Driebe and Whitham 2000, Schweitzer et al. 2004, Fischer et al. 2004). Second, it is important to know how riparian species may respond to altered hydrological patterns induced by global change. For example, many modeling efforts predict increased pulse-event summer rainfall in the southwestern U.S. (National Assessment Synthesis Team 2002), but knowledge of intermountain and southwestern riparian species responses to these rainfall events is incomplete. Finally, many studies on cottonwood responses to water additions have been conducted in plantations. Results from these studies have been interpreted in

the context of implications for silviculture (Marron et al. 2002) rather than in terms of the functioning of native forests (Horton et al. 2001a, 2001b). Understanding how cottonwoods respond to changing water availability is important to conservation and restoration for this threatened habitat (cottonwood riparian forests).

Cottonwoods may alternate water source use between groundwater and surface soil moisture (Smith et al. 1991, 1998, Rood et al. 2003) or act as obligate phreatophytes (Busch et al. 1992) by depending entirely on groundwater. For instance, in the spring, cottonwoods may derive water mostly from near-surface sources and in the summer mostly from deeper groundwater sources (Zhang et al. 1999). Cottonwood response to surface moisture may also be dependent on life history and adaptation to local weather patterns. For example, isotope studies in regions where summer precipitation and soil surface moisture are historically unreliable have found evidence that cottonwoods do not use vadose zone water (i.e., Busch et al. 1992, Horton et al. 2003). Thus, it is unclear whether cottonwoods are able to use water sources when water becomes suddenly available where it was previously scarce.

¹School of Forestry, Northern Arizona University, Flagstaff, AZ 86011.

²Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011.

³Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011.

⁴Environmental Studies Program, Evergreen State College, Olympia, WA 98505.

⁵Corresponding author.

Cottonwood trees also have highly adaptable root systems and have been documented to show rapid growth in response to changes in water and nutrient availability (Pregitzer and Friend 1996). These rapid responses suggest that these trees may be capable of responding physiologically to short-term surface water additions through the rapid root growth and uptake of surface moisture. If this were the case, we would expect that short-term water additions and intense pulse summer rainfall events (Loik et al. 2004) would quickly stimulate surface fine root regrowth and tree transpiration and would improve tree water status. A short-term response (within 3 weeks) to surface water is important to consider because it is unlikely that a longer response time could have ecologically important consequences for vegetative response to pulse precipitation events (see Loik et al. 2004). Another key study of a facultative phreatophyte found that water uptake from the surface soil occurred only after 4 weeks of a watering treatment (Devitt et al. 1997).

We hypothesized that increasing water availability in the upper reaches of the soil profile during a drought would increase whole-tree water use and plant water status. To address this hypothesis, we posed 3 questions: (1) Do whole-tree water use and canopy conductance respond to water additions in native cottonwood genotypes? (2) Does cottonwood whole-tree physiology vary differently with changes in surface soil moisture versus measured leaf predawn water potentials? (3) What roles do tree architecture and drought-induced leaf loss play in possible mitigation of the negative consequences of low surface soil moisture?

MATERIALS AND METHODS

Study Site

Our study site is a restored riparian area at the Ogden Nature Center (41°11'N, 111°56'W; elevation 1370 m) in Ogden, Utah. The site receives approximately 440 mm of precipitation annually, with an average of 20.1 mm in August. Along the Weber River drainage, surface soil moisture generally declines from late spring into summer and fall (<http://waterdata.usgs.gov/ut/nwis/rt> [accessed 21 July 2004]). Soil moisture is at its lowest when temperatures are at their highest. Mean annual air temperature is 10.4°C, and mean daily air tem-

perature is 32.1°C for August (climatic data summaries for Ogden Sugar House Weather Station; <http://www.wrcc.dri.edu/summary/climsmslc.html> [accessed 21 July 2004]). In August 2002 drought for the area was rated as severe to extreme by the National Drought Mitigation Center (<http://www.drought.unl.edu> [accessed 21 July 2004]). Between 1 August and 5 September 2002 (the period of this study), 1.0 mm of precipitation (19.1 mm below average for August; see above) fell, and average daytime and daily air temperatures were 24.9°C, and 23.6°C, respectively. However, in previous recent years more significant precipitation had been documented during this period. For example, in 2001 we recorded 7.36 mm of precipitation between 1 August and 5 September focused (83%) in 2 individual pulse events.

In 1991 cuttings from *P. fremontii*, *P. angustifolia*, and their hybrids were taken from individuals growing along the nearby Weber River. These cuttings were then planted at 4-m spacing at the Ogden Nature Center in a drainage thought to have been historically occupied by cottonwood riparian forests. Cuttings were from trees of known genotype based on previous RFLP work (see Martinsen et al. 2001 for details). Minirhizotron measurements down to a depth of 45 cm in this "restored" forest versus 7 other natural stands along the Weber River do not indicate a difference in fine root growth morphology (data not shown).

Experimental Watering Treatment

Measurements of sap flux density of the study trees began on 1 August (day of year [DOY] 214), and experimental watering treatments began on 12 August (DOY 226). Experimental watering treatments were begun after we collected sap flux density data for 12 days, allowing for a baseline sap flux density rate to be established for each study tree. Our study trees consisted of 6 *P. angustifolia*, 4 backcross hybrids, and 2 F₁ hybrid genotypes. For each genotype we had 2 tree replicates: one would receive the watering treatment, and the other would serve as the control. Those receiving the treatment were administered extra water via drip irrigation and bucket watering applied to the ground evenly beneath individual tree canopies (see Fig. 1). Treatment trees were clumped together or spatially isolated in an effort to avoid extra water diffusing through

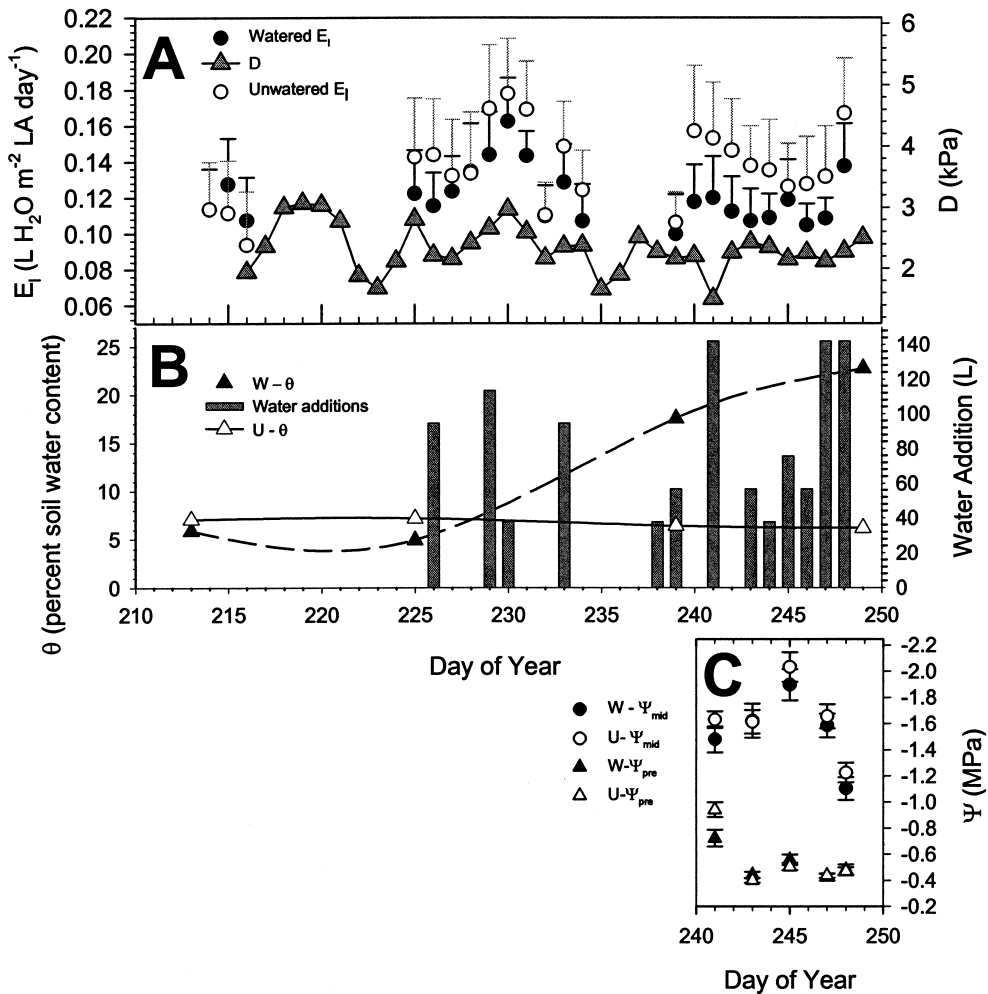


Fig. 1. Physiological responses of watered (W) and unwatered (U) cottonwood trees over time in a common garden environment near Ogden, UT: **A**, leaf-specific transpiration (E_i ; liters $\text{H}_2\text{O m}^{-2}$ leaf area d^{-1}) plotted with vapor pressure deficit (VPD); **B**, gravimetric soil water content (SWC) plotted with the amount of water added (L) to watered trees; **C**, predawn (Ψ_{pre}) and midday (Ψ_{mid}) water potentials. Error bars represent 1 standard error.

the soil to the root zone of the control trees. Watered trees were at least 50 m from unwatered trees and were separated by a 30-cm-deep trench or a road. Watering treatment continued until the end of the study on 5 September (DOY 248). By this time each treatment tree had received 935 L of water more than each control tree; averaged over the entire period that the irrigation treatment was applied, this amount is equivalent to an increase in water addition of $42.5 \text{ L tree}^{-1} \text{ d}^{-1}$. If completely transpired, this would equal about 2 mm d^{-1} for a tree with a crown area of 20 m^2

(median for our watered treatment). This transpirational rate could easily occur at our site given that potential evapotranspiration averaged $5.2 \text{ mm d}^{-1} \pm 0.14$ (s) over the study period.

Gravimetric soil water content (105°C , 48 hours) was measured 4 times throughout the course of the study. Measurements were taken once at the beginning of the study, once just before treatment began, once midway through treatment, and once again at the end of the study. Soil samples (0–15 cm depth) were taken within the same area of each tree, 0.5 m north

from the bole using a 1-cm-diameter soil corer. The depth of 15 cm was justified because (1) these are rocky riparian soils in which repeatable deeper measurements are difficult, and (2) root distribution in trenches and minirhizotron measurements suggest that about half of surface roots are in the first 15 cm (data not shown).

Whole-tree Physiology

We measured sap flux and transpiration for each study tree ($\text{g H}_2\text{O m}^{-2}$ sapwood s^{-1}) using the Granier sap flux method at the base of the live crown in each study tree from DOY 214 to 248 during 2002 (Granier 1987, Granier and Loustau 1994, Granier et al. 1996, Clearwater et al. 1999). The Granier method uses a heated probe inserted 10 cm above a nonheated probe in the sapwood. Each probe is 2 cm long with a copper constantan wire thermocouple inserted inside at the midpoint. We calculated sap flux density based on the temperature difference between the heated and nonheated probe by Granier's empirical equation (Granier 1987, Clearwater et al. 1999). Sensors were placed at up to 4 depths (0–2 cm, 2–4 cm, 4–6 cm, and 6–8 cm), depending on the diameter of the tree. In all cases we attempted to measure the entire length of the hydroactive xylem from the bark to the heartwood. Sensors were placed at 1 randomly chosen aspect on each tree to randomize over aspect effects. Data were collected every 30 seconds and averages stored every 15 minutes using a Campbell Scientific CR10X data logger and a Campbell Scientific AM416 multiplexer (Logan, UT). Whole-tree sap flux was calculated by apportioning sap flux density rates from each probe to its corresponding sapwood area and summing data from all sapwood areas. Transpiration was expressed as total daily whole-tree leaf specific transpiration rate (E_j ; $\text{L H}_2\text{O m}^{-2}$ LA d^{-1}), which was calculated by dividing whole-tree sap flux by whole-tree leaf area (LA; see below).

On all trees used for sap flux measurements, we measured predawn and midday plant water potentials with a pressure chamber (PMS Instruments, Corvallis, OR; Ritchie and Hinkley 1975) 5 times during the last 10 days of the study. Predawn values provide an estimate of the soil water potential in the rooting zone of the tree, while midday water potentials provide an estimate of tree water stress (Ritchie and Hinkley 1975, Koide et al. 1990). Measure-

ments were taken on mid-canopy branch tips between 0400 and 0600 hours for predawn water potential estimates (Ψ_{pre}) and between 1400 and 1600 hours from sun-exposed parts of the tree for midday water potential (Ψ_{mid}) values. Branches from each tree were measured until 2 measurements within 0.1 MPa were obtained, and these were averaged to obtain a mean value for the tree.

Canopy conductance and whole-tree hydraulic conductance were determined for each study tree. Mean leaf-specific canopy conductance (G_c) was calculated over 15-minute periods for each tree with the following model used by Fischer et al. (2002), which substitutes vapor pressure deficit for the difference in water potential between leaf and air (Montieth and Unsworth 1990):

$$G_c = E_l / (\text{VPD} / A_p), \quad (1)$$

where G_c is canopy conductance, E_l is leaf specific transpiration rate ($\text{L H}_2\text{O m}^{-2}$ LA s^{-1}), VPD is vapor pressure deficit (kPa), and A_p is average atmospheric pressure for the location of the study (~ 86.1 kPa for our site).

Whole-tree hydraulic conductance was calculated in a manner similar to that of Ryan et al. (2000) and Fischer et al. (2002):

$$K_h = E_l / (\Psi_{\text{pre}} - \Psi_{\text{mid}}), \quad (2)$$

where K_h is whole-tree hydraulic conductance ($\text{g H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$). Calculation of K_h was limited to those dates when water potential was measured.

We determined projected leaf area and sapwood area of each study tree. Leaf area was estimated for all trees using an allometric equation based on branch diameter. We developed the equation by removing 3 branches of 3 size classes from each tree at the end of our study. All leaves were removed, dried (72 hours at 70°C), and weighed. A subsample of 10 leaves from each branch was used to determine specific leaf area ($\text{m}^2 \text{kg}^{-1}$) using an Agvis Imaging System (Decagon Devices, Pullman, WA). To estimate projected leaf area, we multiplied dried leaf weights from each branch by specific leaf area. These data were combined with data from a previous study from other trees at the site (Fischer et al. 2004) to construct a more robust equation for estimation of projected leaf area (cm^2) based on the diameters (cm) of removed branches ($r^2 = 0.86$, $P <$

0.01, leaf area = $-32730.66 + 17007.86 * (\text{branch diameter}) + 4634.64 * (\text{branch diameter} - 3.03)^2$). This equation was applied to the diameter at the base of the live crown (DBLC) to yield an estimate of projected leaf area for each tree. To evaluate the accuracy of this approach, we compared this branch-based estimate with whole-canopy leaf area estimates measured on other nearby trees; these 2 approaches gave similar values (data not shown). Sapwood area (SA) was estimated using tree-cores for each tree, taken at the same height and aspect as the sap flux sensors (base of the live crown), and visually distinguishing between light-colored sapwood and dark-colored heartwood.

We determined whole-tree leaf loss over the course of the study for each study tree. On DOY 229, before significant drought-induced leaf loss, a litter bucket was placed under the canopy of each tree. At the end of the study, we collected litter in each bucket, dried (72 hours at 70°C) it, and then weighed it. Using the mass of each sample and the specific leaf area values, we calculated leaf area loss. Crown area of each tree was estimated using perpendicular measurements of crown diameter and using the average of the values to calculate crown area. This value was divided by bucket area, and the result was multiplied by leaf area from each bucket to estimate total crown leaf loss during the course of the study.

Air temperature and relative humidity were measured in an open field near the study site using a Campbell Scientific CS500 air temperature and humidity measurement probe (Logan, UT, USA). We collected weather data every 30 seconds and averaged it hourly with a Campbell Scientific CR10X data logger (Logan, UT). We calculated vapor pressure deficit (VPD) from ambient temperature and relative humidity measurements, assuming relative humidity inside the leaves was 100% (Montieth and Unsworth 1990).

All statistical analyses were done with the SAS JMP-IN statistical package (Version 4.0.4, SAS Institute, Cary, NC), with an α of 0.05. Relationships among tree characteristics and physiological and environmental parameters were analyzed using least-squares linear regression. Paired *t* tests of overall means were used to evaluate irrigation treatment effects on physiological variables; repeated measures analyses of variance (RM ANOVAs) on daily

and weekly averages were also used to evaluate irrigation effects.

RESULTS

Mean daily transpiration (E_1) was similar between watered trees and unwatered trees prior to experimental water additions ($P = 0.95$, Fig. 1A), as was mean daily canopy conductance (G_c ; $P = 0.93$; data not shown). Gravimetric soil water content also was similar between watered and unwatered trees prior to the watering treatment ($P = 0.06$; Fig. 1B).

Water addition significantly increased the gravimetric soil water content ($P = 0.03$). During the study period gravimetric soil water content under watered trees increased significantly from 5.9% ($\pm 0.41 s_{\bar{x}}$) to 22.7% ($\pm 0.98 s_{\bar{x}}$; $P = 0.03$); during the same period, gravimetric soil water content among unwatered trees decreased significantly from 7.0% ($\pm 0.67 s_{\bar{x}}$) to 6.2% ($\pm 0.41 s_{\bar{x}}$; $P = 0.02$; Fig. 1B). Although supplemental watering was effective in increasing surface soil moisture, E_1 ($P = 0.47$; Fig. 1A), G_c ($P = 0.84$; Fig. 2B), and whole tree hydraulic conductance (K_h ; $P = 0.63$) were not significantly different between watered and unwatered trees. Both Ψ_{pre} and Ψ_{mid} also were similar between watered and unwatered trees (Ψ_{pre} : $P = 0.83$, Ψ_{mid} : $P = 0.62$), with Ψ_{pre} averaging about -0.54 MPa and Ψ_{mid} approximately -1.58 MPa during the measurement period (Fig. 1C).

We found a significant inverse linear relationship between Ψ_{pre} and G_c ($P = 0.02$, $r^2 = 0.44$; Fig. 2A). However, there was no relationship between soil gravimetric water content and G_c ($P = 0.47$; Fig. 2B). Similarly, we found a significant inverse relationship between Ψ_{pre} and E_1 ($P = 0.04$, $r^2 = 0.35$; Fig. 2C), but there was no significant relationship between gravimetric soil water content and E_1 ($P = 0.34$; Fig. 2D). Relationships between VPD and E_1 were significant ($P < 0.05$, Fig. 3A) for both watered trees ($r^2 = 0.33$) and unwatered trees ($r^2 = 0.21$), as were relationships between VPD and G_c ($P < 0.01$, $r^2 = 0.42$ [watered] and 0.44 [unwatered]; Fig. 3B). Slopes of response curves for G_c versus VPD relationships had overlapping 95% confidence intervals between watered and unwatered trees and thus were not considered different.

Both E_1 and G_c were not significantly correlated with either DBLC ($P = 0.17$ and 0.20,

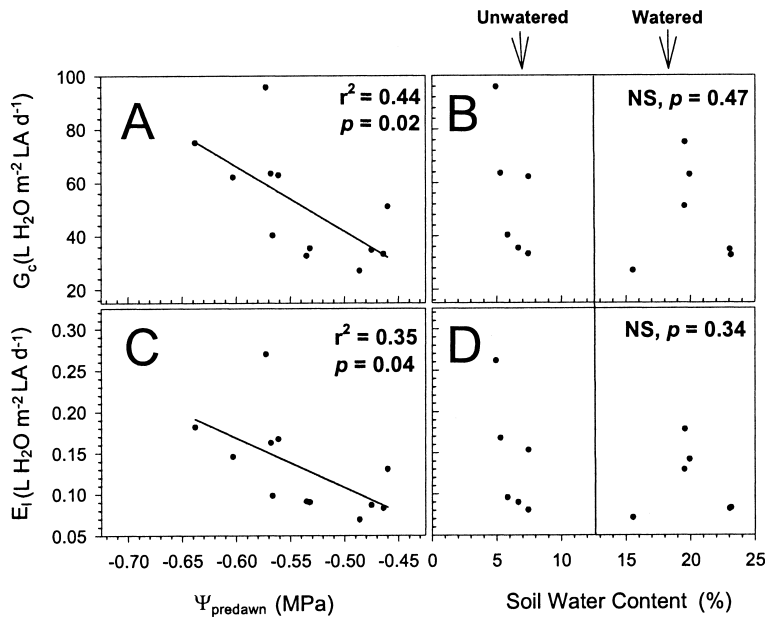


Fig. 2. Soil and plant water relations during irrigation. Canopy conductance (G_c ; $L H_2O m^{-2} d^{-1}$) versus predawn water potential (Ψ_{pre} , **A**) and gravimetric soil water content (%), **B**). Leaf-specific transpiration (E_l ; $L H_2O m^{-2} leaf area d^{-1}$) versus predawn water potential (Ψ_{pre} , **C**) and gravimetric soil water content (%), **D**). For panels **B** and **D**, watered trees are represented on the right and unwatered trees on the left.

respectively) or LA:SA ratios ($P = 0.12$ and 0.18 , respectively; Fig. 4A). Whole-tree hydraulic conductance (K_h) was unrelated to DBLC ($P = 0.14$); however, a significant ($P = 0.02$, $r^2 = 0.43$) inverse power ($y = m * x^{-b}$) relationship was found between K_h and the LA:SA ratio (Fig. 4B). E_l was also related to K_h , but this is likely driven by the calculation of K_h (eq. 2).

Supplemental watering had no detectable effect on leaf abscission during drought; percent leaf area lost was similar between watered and unwatered trees ($P = 0.29$; data not shown). Furthermore, we found no significant relationships between percent leaf area lost and K_h , G_c , or E_l ($P = 0.90$, 0.39 , and 0.53 , respectively). However, leaf area loss was negatively correlated with Ψ_{pre} ($r^2 = 0.37$, $P = 0.04$), suggesting that low water availability may have led to leaf loss. Study trees lost between 0% and 29% of their leaf area during the course of the study (mean leaf loss = 9%, median leaf loss = 4%), and leaf area varied from 75.2 m^2 to 505.2 m^2 among study trees (Table 1).

DISCUSSION

Previous research has suggested that at certain times of the year cottonwood trees access

water from the unsaturated (vadose) zone (i.e., part of the soil profile above the groundwater table and the capillary fringe zone), acting as facultative phreatophytes (Smith et al. 1991, Snyder and Williams 2000). Other research suggests that the principal source of water for tree uptake may shift through a growing season (Zhang et al. 1999), and cottonwood trees are known to have plastic and adaptable root systems (Pregitzer and Friend 1996). However, significant evidence exists to support an alternative hypothesis that cottonwoods exhibit response to surface water commensurate with the climatic history of their region. For example, Busch et al. (1992) did not find evidence of soil moisture uptake at a study site that has historically unreliable summer precipitation patterns, and this suggested phreatophytic behavior. Conversely, Snyder and Williams (2000) found evidence of soil moisture uptake at a study site where summer monsoonal pulse rainfall events are common. Our study site has a historically predictable summer drought, and our results are consistent with this regional climate hypothesis.

Despite (1) successful increases in soil moisture within the upper 15 cm of soil (Fig. 1), (2) observations that most study trees showed some

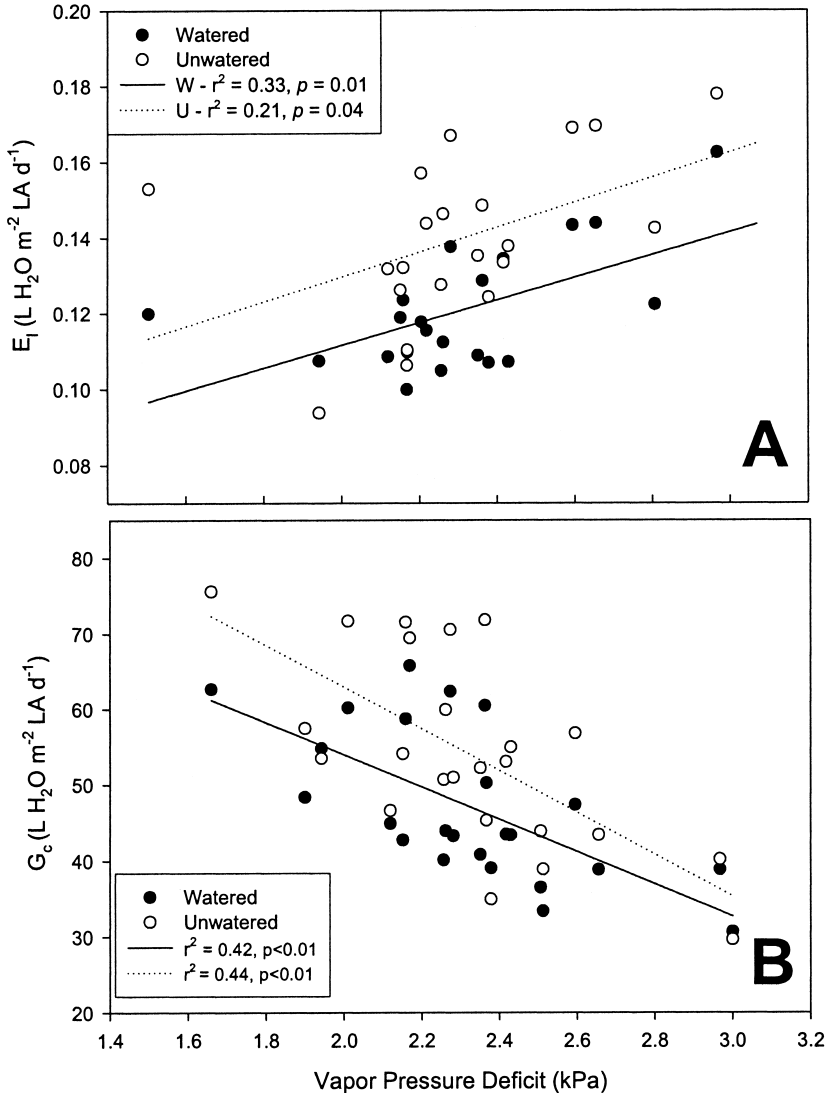


Fig. 3. Environmental control of whole-tree physiology: **A**, leaf-specific transpiration (E_l) versus vapor pressure deficit (VPD) for watered (filled circles) and unwatered trees (unfilled circles); **B**, leaf-specific canopy conductance (G_c) versus vapor pressure deficit (VPD) for watered (filled circles) and unwatered trees (unfilled circles).

signs of water stress (e.g., yellowing of leaf tips and loss of leaves), and (3) environmental conditions conducive to water availability limiting growth (e.g., lack of recent precipitation, high VPD, summer drought), our results indicate that watered trees did not increase their rates of leaf-specific transpiration, canopy conductance, or whole-tree hydraulic conductance relative to trees that did not receive supplemental water (Fig. 2). Averaged over the entire experimental period, watered trees received 42.5 L

more water per day than unwatered control trees (Fig. 1). Sap flux measurements scaled to the whole-tree level indicate that both watered and unwatered trees transpired an average of 24.7 L water d^{-1} . Hence, water additions should have been more than enough to stimulate transpiration rates that were low compared with other studies (Zhang et al. 1999, Schaeffer et al. 2000, Nagler et al. 2003). Similarly, canopy conductance was relatively low in all trees over our study period (e.g., Zhang et al. 1999, Horton

TABLE 1. Selected characteristics of trees monitored in this study. Clone codes serve as markers for individual genotypes but otherwise have no relation to cross type. Cross types are A (*Populus angustifolia*), B (backcross hybrids), and F₁ (F₁ hybrids).

Clone	Status	Diameter at base of live crown (cm)	Cross type	Leaf area (m ²)	Sapwood area (cm ²)	Leaf area: sapwood area (m ² cm ⁻²)
wc-5	Unwatered	13.9	A	75.2	149.1	0.50
wc-5	Watered	17.6	A	125.1	167.5	0.75
1008	Unwatered	21.3	A	187.7	203	0.92
1008	Watered	16.4	A	107.5	105.6	1.02
t-15	Unwatered	19.3	A	152.3	161.8	0.91
t-15	Watered	20.5	A	173.1	173	1.00
996	Unwatered	22.5	B	210.7	225.9	0.93
996	Watered	17.7	B	126.6	105.8	1.20
11	Unwatered	18.3	B	136	99.9	1.36
11	Watered	22.9	B	218.7	221.7	0.99
1994	Unwatered	34.2	F ₁	505.2	704.9	0.72
1994	Watered	30.7	F ₁	403.8	775.2	0.52

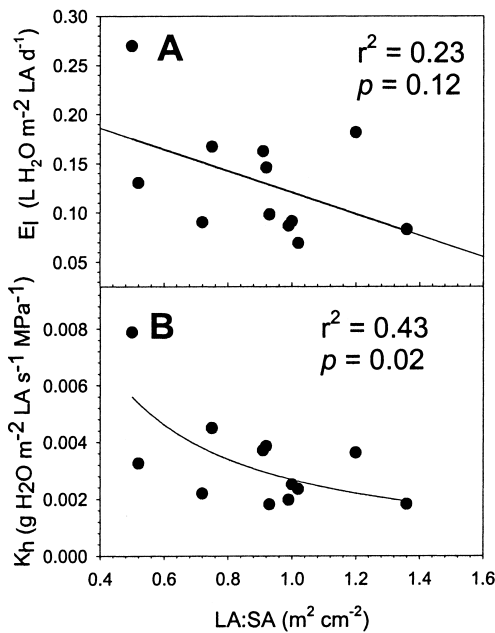


Fig. 4. Architectural controls of whole-tree physiology; **A**, leaf-specific transpiration (E_i) versus leaf area to sapwood area ratio (LA:SA); **B**, whole-tree hydraulic conductance (K_h) versus LA:SA.

et al. 2001a; but see Fischer et al. 2004), but hydraulic conductance was not exceptionally low compared with other angiosperms (Becker et al. 1999). Dickmann et al. (1994) also found no difference in net photosynthesis rates between irrigated and nonirrigated cottonwood saplings, and our results are consistent with responses of *Populus* clones to a 40% reduc-

tion in soil moisture in a study by Braatne et al. (1992). We conclude that during the height of summer drought, any uptake of increased soil moisture was insufficient to influence important physiological variables such as hydraulic conductance, canopy conductance, or transpiration. This may be consistent with factors other than water limiting both photosynthesis and, by default, water use as has been found in at least 1 other species in our region (Snyder et al. 2004).

We speculate there are several other possible explanations for the lack of response to water additions in our study trees. First, greater loss of leaf area in unwatered trees relative to watered trees may have partially compensated for lower water availability to the trees, reducing any differences in leaf-specific transpiration rates. However, we found no difference in leaf area loss between watered and unwatered trees, suggesting that this potential mechanism cannot account for the lack of physiological responsiveness to water additions in our study trees. Nevertheless, we recognize that our measure of leaf area lost due to drought was somewhat coarse, and so we cannot entirely rule out this possible mechanism for the lack in physiological response of the cottonwood trees to water additions.

Second, xylem dysfunction in the roots of study trees might have impaired uptake of water supplied to the trees by irrigation treatments. Cottonwoods are mostly drought intolerant, limited to riparian corridors, and dependent on groundwater, and they typically have

high vulnerability to cavitation (Blake et al. 1996). On day 245 of the study, Ψ_{mid} of study trees averaged -2.0 MPa (Fig. 1); this value corresponds to approximately a 70% loss of hydraulic conductivity in stems due to xylem embolism according to one *P. angustifolia* vulnerability curve (Tyree et al. 1994), and potentially 100% loss in some tissues according to Blake et al. (1996). Because we did not assess the origin of the water transpired by trees in our current study, we cannot conclude unequivocally that they did not take up surface soil moisture. However, since Ψ_{mid} values indicate high levels of stem xylem embolism (but see Blake et al. 1996) and since roots are more susceptible to xylem embolism than stems (Sperry and Saliendra 1994, Hacke and Sauter 1996, Sperry and Ikeda 1997), it is probable that xylem dysfunction occurred during our study period. If significant xylem dysfunction did occur in surface roots, and if embolism repair in cavitated roots was too slow to reestablish function, then this might account for the lack of physiological response in cottonwoods to the irrigation treatment in our study.

Finally, it is possible that our irrigation treatments, which lasted 3 weeks, may not have been long enough to elicit a physiological response. For instance, Devitt et al. (1997) found a physiological response to surface irrigation in trees from arid environments after 4 weeks. However, given that sporadic pulse precipitation events are common and short-lived in the region (Loik et al. 2004), it is unlikely that a 4-week response time to increased surface moisture is ecologically meaningful unless early precipitation events are harbingers of prolonged wet periods. Thus, a lack of response within the time frame used in our study may be ecologically equivalent to a lack of response.

This lack of responsiveness in cottonwoods to surface water additions may reflect an evolutionary constraint on soil water uptake due to a long regional history of low summer precipitation in northern Utah. For example, lack of significant response to soil moisture may be a successful carbon allocation strategy of cottonwoods. The timing of our irrigation treatments corresponded with a period of seasonally dry soils, when infrequent rains only temporarily elevate soil moisture. A long-term evolutionary response, maximizing carbon allocation and limiting unnecessary growth (i.e., easily cavi-

tated root tissues; Sperry and Saliendra 1994, Hacke and Sauter 1996, Sperry and Ikeda, 1997), may be avoidance of embolism repair in such tissues during seasonal drought periods. This level of genetic specificity would not be surprising given the extensive documented genetic variation in cottonwood water-stress tolerance, root growth, and water use (Tschaplinski and Blake 1989a, 1989b, Blake et al. 1996, Pregitzer and Friend 1996, Fischer et al. 2004). When surface soil moisture levels are more consistently high, whole-tree response to soil moisture increases may be more common.

We found a significant relationship between average daily E_1 and Ψ_{pre} , and average daily G_c and Ψ_{pre} . However, in both cases the relationship was opposite of our hypothesized relationship; both E_1 and G_c decreased rather than increased with increasing Ψ_{pre} values (Fig. 2). This pattern may be partially due to the high transpiration rates of some cottonwood trees and their poor stomatal regulation (Stettler et al. 1996, Fischer et al. 2004); the relatively high transpiration rates may have led to progressively poor whole-plant water status (as measured by lower Ψ_{pre} values), reflecting that some cottonwood trees seem to operate with a small margin of safety from cavitation events (Blake et al. 1996). Furthermore, these statistically significant negative correlations may be somewhat spurious given that they were fairly weak ($r^2 = 0.35$ and 0.44 , respectively) and occurred over a fairly narrow range of Ψ_{pre} values (-0.45 to -0.65 MPa).

Our results suggest that, while some species may show strong physiologic responses to pulse increases in soil moisture (Donovan and Ehleringer 1994, Cui and Caldwell 1997; also see Ogle and Reynolds 2004, Schwinning and Sala 2004), some cottonwood trees may exhibit little immediate physiological response to increases in soil moisture from precipitation events. This lack of response may be related to a water-use strategy associated with regional climate patterns, cavitation recovery, or other physical determinants of water use such as depth to groundwater. Cottonwood riparian forests represent some of the most biologically productive ecosystems in the West, and our data suggest that it is important to consider potential nonresponsiveness to changes in soil water availability when evaluating the impact of climate change on these important and productive ecosystems.

ACKNOWLEDGMENTS

We thank the Ogden Nature Center for supporting our common garden facilities and the Mill Creek Youth Center juvenile detention facility for helping logistically. We thank National Science Foundation grant DEB-0078280 and a Research Experience for Undergraduates award under NSF grant DEB-0078280 for financial support. We also thank Nathan Lojewski, Kevin Simonin, Gina Wimp, Jen Schweitzer, Tom Kolb, A.J. Thompson, and the Hart and Whitham laboratories for field assistance, consultation, and providing comments on earlier versions of the manuscript. Finally, we thank R.W. Baumann and 2 anonymous reviewers for thoughtful reviews of this manuscript.

LITERATURE CITED

- BECKER, P., M.T. TYREE, AND M. TSUDA. 1999. Hydraulic conductances of angiosperms versus conifers: similar transport sufficiency at the whole-plant level. *Tree Physiology* 19:445–452.
- BLAKE, T.J., J. SPERRY, T.J. TSCHAPLINSKI, AND S.S. WANG. 1996. Water relations. Pages 401–422 in R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley, editors, *Biology of Populus* and its implications for management and conservation. NRC-CNRC, Ottawa, ON.
- BRAATNE, J.H., T.M. HINCKLEY, AND R.F. STETTLER. 1992. Influence of soil water on the physiological and morphological components of plant water balance in *Populus trichocarpa*, *Populus deltoides* and their F₁ hybrids. *Tree Physiology* 11:325–339.
- BUSCH, D.E., N.L. INGRAHAM, AND S.D. SMITH. 1992. Water uptake in woody riparian phreatophytes of the southwestern United States: a stable isotope study. *Ecological Applications* 2:450–459.
- CLEARWATER, M.J., F.C. MEINZER, J.L. ANDRADE, G. GOLDSTEIN, AND N.M. HOLBROOK. 1999. Potential errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree Physiology* 19:681–687.
- CUI, M., AND M.M. CALDWELL. 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant and Soil* 191:291–299.
- DEVITT, D.A., J.M. PIORKOWSKI, S.D. SMITH, J.R. CLEVERLY, AND A. SALA. 1997. Plant water relations of *Tamarix ramosissima* in response to the imposition and alleviation of soil moisture stress. *Journal of Arid Environments* 36:527–540.
- DICKMANN, D.I., K.S. PREGITZER, AND P.V. NGUYEN. 1994. Net assimilation and photosynthate allocation of *Populus* clones grown under short rotation intensive culture: physiological and genetic responses regulating yield. Final report, ORNL/Sub/86-95903/4. Oak Ridge National Laboratory, Oak Ridge, TN. 36 pp.
- DONOVAN, L.A., AND J.R. EHLERINGER. 1994. Water stress and use of summer precipitation in a Great Basin shrub community. *Functional Ecology* 8:289–297.
- DRIEBE, E., AND T.G. WHITHAM. 2000. Cottonwood hybridization affects tannin and nitrogen content of leaf litter and alters decomposition. *Oecologia* 123:99–107.
- FISCHER, D.G., T.E. KOLB, AND L.E. DEWALD. 2002. Changes in whole-tree water relations during ontogeny of *Pinus flexilis* and *Pinus ponderosa* in a high-elevation meadow. *Tree Physiology* 22:675–685.
- FISCHER, D.G., S.C. HART, T.G. WHITHAM, G.D. MARTINSEN, AND P. KEIM. 2004. Ecosystem implications of genetic variation in water-use of a dominant riparian tree. *Oecologia* 139:188–197.
- GRANIER, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology* 3:309–320.
- GRANIER, A., AND D. LOUSTAU. 1994. Measuring and modeling the transpiration of a maritime pine canopy from sap-flow data. *Agricultural and Forest Meteorology* 51:309–319.
- GRANIER, A., P. BIRON, N. BREDA, J.-Y. PONTAILLER, AND B. SAUGIER. 1996. Transpiration of trees and forest stands: short and long term monitoring using sapflow methods. *Global Change Biology* 2:265–274.
- HACKE, U., AND J.J. SAUTER. 1996. Drought-induced xylem dysfunction in petioles, branches, and roots of *Populus balsamifera* L. and *Alnus glutinosa* (L.) Gaertn. *Plant Physiology* 111:413–417.
- HORTON, J.L., T.E. KOLB, AND S.C. HART. 2001a. Physiological response to groundwater depth varies among species and with river flow regulation. *Ecological Applications* 11:1046–1059.
- _____. 2001b. Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant, Cell and Environment* 24:293–304.
- HORTON, J.L., S.C. HART, AND T.E. KOLB. 2003. Physiological condition and water source use of Sonoran Desert riparian trees at the Bill Williams River, Arizona, USA. *Isotopes in Environmental and Health Studies* 39:69–82.
- KOIDE, R.T., R.H. ROBICHAUX, S.R. MORSE, AND C.M. SMITH. 1990. Plant water status, hydraulic resistance and capacitance. Pages 161–178 in R.W. Pearcy, J.R. Ehleringer, H.A. Mooney, and P.W. Rundel, editors, *Plant physiological ecology: field methods and instrumentation*. Kluwer Academic Publishers, Dordrecht.
- LOIK, M.E., D.D. BRESHEARS, W.K. LAUENROTH, AND J. BELNAP. 2004. A multi-scale perspective of water pulses in dryland ecosystems: climatology and hydrology of the western USA. *Oecologia* 141:269–281.
- MARRON, N., D. DELAY, J.-M. PETIT, E. DREYER, G. KAHLEM, F.M. DELMOTTE, AND F. BRIGNOLAS. 2002. Physiological traits of two *Populus × euramericana* clones, Luisa Avanzo and Dorskamp, during a water stress and re-watering cycle. *Tree Physiology* 22:849–858.
- MARTINSEN, G.D., T.G. WHITHAM, R.J. TUREK, AND P. KEIM. 2001. Hybrid populations selectively filter gene introgression between species. *Evolution* 55:1325–1335.
- MONTIETH, J.L., AND M. UNSWORTH. 1990. *Principles of environmental physics*. Edward Arnold, London. 291 pp.
- NAGLER, P.L., E.P. GLENN, AND T.L. THOMPSON. 2003. Comparison of transpiration rates among saltcedar, cottonwood and willow trees by sap flow and canopy temperature methods. *Agricultural and Forest Meteorology* 116:73–89.

- NATIONAL ASSESSMENT SYNTHESIS TEAM. 2002. Climate change impacts on the United States: potential consequences of climate variability and change. U.S. Global Change Research Program, 400 Virginia Avenue SW, Suite 750, Washington, DC.
- OGLÉ, K., AND J.F. REYNOLDS. 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia* 141:282–294.
- PREGITZER, K.S., AND A.L. FRIEND. 1996. The structure and function of *Populus* root systems. Pages 331–354 in R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley, editors, *Biology of Populus* and its implications for management and conservation. NRC-CNRC, Ottawa, ON.
- RITCHIE, G.A., AND T.M. HINCKLEY. 1975. The pressure chamber as an instrument for ecological research. *Advances in Ecological Research* 9:165–254.
- ROOD, S.B., J.H. BRAATNE, AND F.M.R. HUGHES. 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. *Tree Physiology* 23:1113–1124.
- RYAN, M.G., B.J. BOND, B.E. LAW, R.M. HUBBARD, D. WOODRUFFE, E. CIENCIALA, AND J. KUCERA. 2000. Transpiration and whole tree conductance in ponderosa pine trees of different heights. *Oecologia* 124:553–560.
- SCHAEFFER, S.M., D.G. WILLIAMS, AND D.C. GOODRICH. 2000. Transpiration of cottonwood/willow forest estimated from sap flux. *Agricultural and Forest Meteorology* 105:57–270.
- SCHWEITZER, J.A., J.K. BAILEY, B.J. REHILL, GREGORY D. MARTINSEN, S.C. HART, R.L. LINDROTH, P. KEIM, AND T.G. WHITHAM. 2004. Genetically based trait in a dominant tree affects ecosystem processes. *Ecology Letters* 7:127–134.
- SCHWINNING, S., AND O.E. SALA. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. *Oecologia* 141:211–220.
- 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.
- SMITH, S.D., D.A. DEVITT, A. SALA, J.R. CLEVERLY, AND D.E. BUSCH. 1998. Water relations of riparian plants from warm desert regions. *Wetlands* 18:687–696.
- 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.
- SNYDER, K.A., L.A. DONOVAN, J.J. JAMES, R.L. TILLER, AND J.H. RICHARDS. 2004. Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. *Oecologia* 141:325–334.
- SPERRY, J.S., AND T. IKEDA. 1997. Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiology* 17:275–280.
- SPERRY, J.S., AND N.Z. SALIENDRA. 1994. Intra- and inter-plant variation in xylem cavitation in *Betula occidentalis*. *Plant, Cell, and Environment* 17:1233–1241.
- STETTLER, R.F., P.E. HEILMAN, AND M.D. BRADSHAW. 1996. *Biology of Populus*. 1st edition. NRC Research Press, Ottawa, ON. 542 pp.
- TSCHAPLINSKI, T.J., AND T.J. BLAKE. 1989a. Water-stress tolerance and late-season organic solute accumulation in hybrid poplar. *Canadian Journal of Botany* 67:1681–1688.
- _____. 1989b. Correlation between early root production, carbohydrate metabolism, and subsequent biomass production in hybrid poplar. *Canadian Journal of Botany* 67:2168–2174.
- TYREE, M.T., K.J. KOLB, S.B. ROOD, AND S. PATIÑO. 1994. Vulnerability to drought induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? *Tree Physiology* 14:455–466.
- ZHANG, H., J.I.L. MORISON, AND L.P. SIMMONDS. 1999. Transpiration and water relations of poplar trees growing close to the water table. *Tree Physiology* 19:563–573.

Received 12 January 2004
Accepted 14 September 2004