Responses of Riparian Cottonwoods to Alluvial Water Table Declines

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ABSTRACT / Human demands for surface and shallow alluvial groundwater have contributed to the loss, fragmentation, and simplification of riparian ecosystems. *Populus* species typically dominate riparian ecosystems throughout arid and semiarid regions of North American and efforts to minimize loss of riparian *Populus* requires an integrated understanding of the role of surface and groundwater dynamics in the establishment of new, and maintenance of existing, stands. In a controlled, whole-stand field experiment, we quantified responses of *Populus* morphology, growth, and mortality to water stress resulting from sustained water table decline following in-channel sand mining along an ephemeral sandbed stream in eastern Colorado, USA. We measured live crown volume, radial stem growth, annual branch increment, and mortality of 689 live *Populus deltoides* subsp. *monilifera* stems over four years in conjunction with localized water table declines. Measurements began one year prior to mining and included trees in both affected and unaffected areas. *Populus* demonstrated a threshold response to water table declines in medium alluvial sands; sustained declines ≥ 1 m produced leaf desiccation and branch dieback within three weeks and significant declines in live crown volume, stem growth, and 88% mortality over a three-year period. Declines in live crown volume proved to be a significant leading indicator of mortality in the following year. A logistic regression of tree survival probability against the prior year's live crown volume was significant (-2 log likelihood $= 270$, χ^2 with 1 $df = 232$, $P < 0.0001$) and trees with absolute declines in live crown volume of ≥ 30 during one year had survival probabilities <0.5 in the following year. In contrast, more gradual water table declines of ~ 0.5 m had no measurable effect on mortality, stem growth, or live crown volume and produced significant declines only in annual branch growth increments. Developing quantitative information on the timing and extent of morphological responses and mortality of *Populus* to the rate, depth, and duration of water table declines can assist in the design of management prescriptions to minimize impacts of alluvial groundwater depletion on existing riparian *Populus* forests.

Riparian corridors occupy important landscape positions between upland and aquatic ecosystems and are uniquely productive, physically dynamic, and biologically diverse (Brinson and others 1981, Gregory and others 1991, Naiman and others 1993). Depletions of surface and shallow alluvial groundwater have contributed to the loss, fragmentation, or severe ecological impairment of these systems (Dynesius and Nilsson 1994, Stromberg and others 1996). Species of *Populus* are the most abundant trees of riparian ecosystems throughout arid and semiarid regions of North America. *Populus*-dominated stands provide unique structural habitat (Brinson and others 1981) and are vulnerable to reductions in surface and groundwater availability.

Declines in *Populus* forest cover have been observed where severe drought or land and water management activities have decreased water availability by reducing surface flows or depleting alluvial groundwater aquifers (Albertson and Weaver 1945, Groeneveld and Griepentrog 1985, Rood and Heinze-Milne 1989, Rood and others 1995, Stromberg and others 1996). For example, approximately 1125 km of once perennial streams in Kansas are now intermittent, in part a consequence of groundwater pumping in the High Plains Aquifer (Layher 1986, Luckey and others 1988), and flow depletion along the Arkansas River is associated with loss of riparian trees (Kromm and White 1992). Similarily, large areas of riparian forest have been lost to groundwater pumping and associated flow depletion in the southwestern United States (Stromberg 1993). Human activities that directly or indirectly influence alluvial groundwater sources include damming and diversion of rivers and streams, groundwater pumping, and channel incision resulting from altered flows of water and sediments, bank stabilization, and instream gravel mining (Bravard and others 1997, Kondolf 1994, 1997, Rood and others 1995, Stromberg and others 1996, 1997).

KEY WORDS: Colorado; Water stress; Groundwater; Gravel mining; *Populus deltoides;* Riparian; Water table declines

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Effective management of riparian *Populus* ecosystems requires an integrated understanding of surface and alluvial groundwater dynamics in relation to reproduction and maintenance of existing stands. Controlled, whole-plant experiments are needed to quantify relationships between the severity of water stress and integrated patterns of tree response (Braatne and others 1992). To date, quantitative information on the extent and timing of functional responses and mortality of *Populus* to groundwater depletion have rarely been temporally matched with quantitative information on the rate, depth, and duration of water table declines in the field (Stromberg and others 1996). Establishing such relationships can assist management efforts to minimize impacts of alluvial groundwater depletion on existing riparian *Populus* ecosystems.

Our objectives were to quantify changes in morphology, growth, and mortality of mature riparian *Populus deltoides* subsp. *monilifera* in response to measured declines in the alluvial water table. In a controlled, whole-stand field experiment using 689 live trees, we measured the response of live crown volume, radial stem growth, annual branch increment, and stand mortality to sustained water table declines resulting from in-channel sand mining. Measurements began in 1990, one year prior to mining, and ended in the third year following mining.

Water Relations of *Populus*

Despite widespread occurrence in arid and semiarid landscapes, *Populus* species require continually moist substrates for establishment (Read 1958, Friedman and others 1995), are susceptible to drought-induced cavitation of xylem vessles (Tyree and others 1994), and suffer higher mortality during drought than several eastern deciduous forest species (Kaylor and others 1935, Albertson and Weaver 1945). Ruderal traits of *Populus* contribute to the persistence of this drought-sensitive species in drought-prone regions (Friedman et al. 1997); these traits include small wind dispersed seeds, rapid germination and growth, and the ability to tolerate flooding and physical disturbance. *Populus* is generally restricted to alluvial soils with shallow groundwater (Meinzer 1927, Robinson 1958).

On coarse substrates in dry regions, early establishment and growth of *Populus* spp. seedlings may require water tables within 1–2 m of the establishment surface (McBride and Strahan 1984, Mahoney and Rood 1992, Segelquist and others 1993, Stromberg and others 1996). Following establishment, root growth allows young trees to survive gradual water table declines. Depth to the water table may increase as a result of subsequent floodplain accretion or channel incision (Everitt 1968, Hereford 1986), and *Populus* species have been observed at sites where depth to the water table is 7–9 m (Robinson 1958); however, mature riparian *Populus* are typically found in riparian settings where depth to the water table is $\leq$3.5 m (Busch and others 1992, Scott and others 1997, Stromberg and others 1997).

The response of a plant to gradually increasing water stress involves progressive and integrated physiological and morphological responses, beginning with stomatal closure, reduced leaf and canopy development, and ending with death (Bradford and Hsiao 1982, Braatne and others 1992). Mild water stress can reduce plant productivity by limiting CO_2 assimilation through stomatal closure, lowering net photosynthesis, and through the death of leaves and fine roots. Under more severe drought conditions, trees exhibit reduced radial stem increments, wilting and abscission of leaves, and branch death. Tree mortality may follow directly or secondarily as the result of insects or other pathogens (Albertson and Weaver 1945). Because these changes occur at different levels of water stress and on different time scales, accurate quantification of longer-term water stress is problematic (Pallardy et al. 1991).

In water-stressed *Populus* species, Smith and others (1991) found significantly reduced stomatal conductance and reduced midday leaf water potential (Ψ_1) for *P. trichocarpa* compared with nonstressed trees. These trends were particularly pronounced for juvenile trees. Busch and Smith (1995) found moderately higher rates of stomatal conductance and transpiration and slightly higher predawn and midday Ψ_1 in comparing *Populus fremontii* and *Salix gooddingii* from a gaining reach with those from a losing reach of the Bill Williams River, Arizona. Riparian *Populus* can exhibit morphological and growth responses to chronic water stress, including reduced leaf size, increased leaf thickness, reduced leaf area, reduced annual stem elongation, and reduced radial stem increments (Smith and others 1991, Stromberg and Patten 1991, Busch and Smith 1995). Under conditions of acute water stress associated with severe climatic drought or water table declines, *Populus* display more extreme morphological responses such as crown dieback, and ultimately stand mortality (Ellison and Woolfolk 1937, Albertson and Weaver 1945, Stromberg 1993, Rood and others 1995).

Study Site

The study site was a 4.8-km reach of Coal Creek, an ephemeral, sandbed stream within the South Platte River drainage in the Colorado Piedmont province of central Colorado (Figure 1). A tributary of Sand Creek,

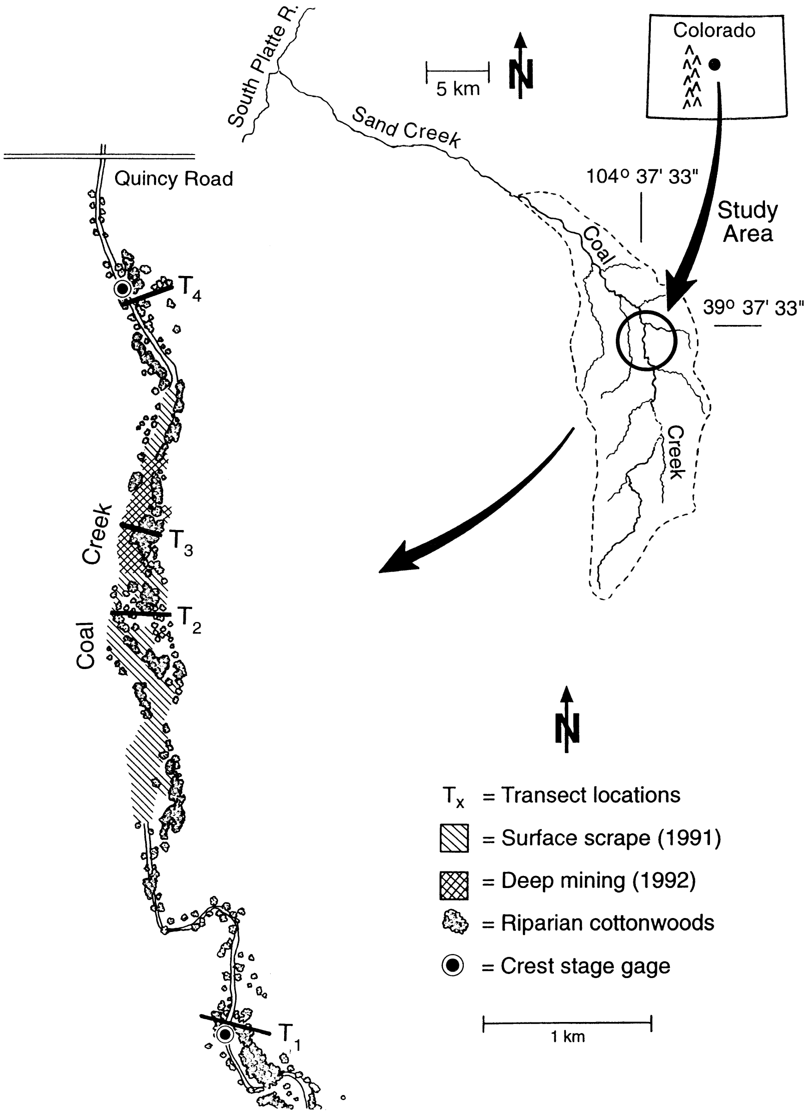

Figure 1. General location of the Coal Creek Study area, including its position within the watershed, and a detail of the study reach with locations of transects, gauges, cottonwood stands, and mining activity.

Coal Creek drains approximately 124 km^2 of short-grass prairie 30 km southeast of Denver, Colorado, USA, and flows north from the base of the Palmer Divide, which separates the South Platte and Arkansas River basins. Coal Creek is an ungauged ephemeral stream that typically flows for a few days in spring or for brief periods after locally heavy rain. Most of the water in the basin moves down valley as shallow alluvial groundwater.

East of the Front Range of the Rocky Mountains, the South Platte River drainage is located within the Denver Basin, a large, asymmetrical syncline. Strata overlying the structural formation of the Denver Basin are primarily sedimentary and range in age from Paleozoic to Recent. The principal bedrock of the study area is the Dawson Arkose, which is composed of Arkosic sandstone, shale, mudstone, conglomerate, and local coal beds of upper Cretaceous and Paleocene age (Duke and Longenbaugh 1966). Because strata of the Denver Basin are relatively impermeable, the alluvial aquifer at Coal Creek is isolated from deeper regional aquifers (Bjorklund and Brown 1957). Logs from ten test borings at the study site indicate a medium hard claystone to very hard claystone/sandstone bedrock at an average depth of 4.95 m (SD ± 1.8 m) (A. G. Wassenaar, Inc. unpublished report). The alluvium consists of poorly graded, slightly silty medium sands (0.297–1.19 mm diameter) with some clay to clayey sand lenses.

A mature cottonwood forest dominated by *Populus deltoides* subsp. *monilifera* occurs along Coal Creek where the alluvial water table occurs within ~1–3 m of the ground surface. The riparian zone of Coal Creek is dominated by mature cottonwoods with three diameter classes centered around 80 cm, 50 cm, and 1 cm. The trees range in age from a few to approximately 150 years; most were established prior to 1930, apparently following large floods (J. Friedman unpublished data).

In 1990, a local sand and gravel mining firm proposed to excavate sand from the active channel within a portion of the study reach. In cooperation with the miner, we designed a controlled, multiyear study of the effects of water table decline on mature *Populus*.

Methods

Field Methods

In October 1990, prior to deep mining of Coal Creek, four belt transects 150 m wide were established perpendicular to the channel. Two transects were located within the proposed area of sand excavation, and two additional transects were located upstream and downstream of the mining area to serve as controls (Figure 1). The transects were numbered sequentially from upstream to downstream and were extended across the entire bottomland. Because of adjacent land-clearing, the width of transect 1 was reduced to 130 m. The belt transects were divided into a series of discrete fluvial geomorphic surfaces of relatively uniform elevation, hereafter referred to as surfaces. Elevations of the corners of a surface were surveyed using a rod and level. Active channel cross sections were resurveyed twice at each transect.

Three to four groundwater wells were installed along the center line of each transect using hand-driven sand points for shallow (<5 m) wells and a truck-mounted drill for deeper wells. All wells were surveyed relative to a common benchmark, and depth to the water table was monitored in the wells from August 1990 to November 1994 using a steel tape. Water table depths were measured once or twice monthly during the growing season (April–October) and once per month for the remainder of the year. For each year, average growing season depth to water was calculated at each surface by interpolation between the two nearest wells.

Sand mining occurred in three stages; in October of 1990, approximately 0.5–1 m of sand was skimmed from the surface of the channel at transect 3 (Figure 1). This activity continued slowly upstream over the next year to a point between transects 1 and 2; no alluvial groundwater was exposed as a result of this activity. In December 1991, a shallow trench (<0.5 m) was dug within the active channel from transect 2, downstream to a point above transect 4. From late June through August 1992, deep mining of the channel at transect 3 locally lowered the channel bed up to 2 m.

In June 1991, all trees within the belt transects and >2.54 cm diameter at breast height (dbh, 1.3 m) were numbered with aluminum tags. Measurements of live crown volume, stem growth, and mortality were initiated in August. Stem diameters of all tagged, live trees were measured in September 1991, October 1993, and November 1994 by averaging three stem diameter readings at permanently marked positions 125, 130, and 135 cm above the ground. Live crown volume of each tree was measured annually from 1991 through 1994 between August and September. This measurement was a visual determination of the percentage of potential crown volume occupied by live foliage and branches. We report the average of crown volume measurements from two independent observers. Survivorship of all tagged trees was determined at the end of each growing season by comparing the number of live trees (live crown volume >0) in 1992, 1993, and 1994 to the number of live trees in 1991. Dead trees were excluded in calculating the average stem growth and crown volume. In December 1994, annual branch elongation for the previous seven-year period was measured in all transects on two randomly selected live trees on each surface. Five live branches with at least seven years of growth were collected from each selected tree, and the increments between annual bud scale scars were measured. Branch elongation values were normalized by determining each year's percent deviation from the premining average (1988–1991). The five deviation values per year per tree were averaged to arrive at a single average value per tree.

We performed a secondary set of measurements to examine the effects of water table decline on leaf xeromorphy. In September 1994, individual leaf area (square centimeters) and specific leaf mass (milligrams per square centimeter) were measured on leaves from 24 trees. Across all transects, a total of eight trees were randomly selected from each of three classes of water table change: (1) $+0.5$ to -0.25 m; (2) -0.26 to -1.0 m; and (3) < -1.0 m. Fifty leaves were collected per tree: 25 leaves from five branches removed from the side of the crown and 25 leaves from five branches removed from the top of the crown. The leaves were photocopied and areas were measured using a planimeter. Dry mass was determined by weighing leaves that had dried in an oven at 60°C for 72 h.

Statistical Methods

Our overall statistical analysis is presented in terms of comparisons between transects. Two of the transects (1 and 4) were relatively distant from the mining operation and had little or no decline in water table levels. We pooled surfaces from these transects into a control group and used pairwise T tests to compare with the mined transects (2 and 3). In most cases sample sizes and variances were unequal. In these cases we used an approximate T statistic for unequal variances with

Table 1. Premining condition of transects[a]

	Transects			
	Controls		Mining affected	
Premining condition (1991)	1	4	2	3
Surface (N)	12	7	10	5
Density (trees/ha)				
Mean	1088	412	671	856
Range	75–2028	59–570	95–2175	516–1240
Standard deviation	625	173	655	334
Stem size (cm^2/tree)				
Mean	2372	7350	2940	3781
Range	605–4901	3895–11,382	908–5573	2744–4814
Standard deviation	1349	2851	1475	749
Depth to groundwater (m)				
Mean	2.40	2.15	2.48	2.53
Range	1.52–3.61	1.29–3.16	2.06–2.94	2.45–2.66
Standard deviation	0.69	0.73	0.28	0.08

[a]Means are averages of all surfaces with trees for each transect.

Saitterthwaite's approximation for degrees of freedom. We conducted two types of transect comparisons. Premining conditions of the transects were compared by examining 1991 differences in average surface values of depth to water table, density of cottonwood trees, and size of cottonwood trees. We made a total of eight premining pairwise tests and used a Bonferroni-adjusted significance level of 0.00625 for these tests.

Response over the interval from the end of the growing season in 1991 to the end of the growing season in 1994 was examined by making between-transect comparisons of surface values for water table level, *Populus* survivorship, radial stem growth increase of surviving trees, normalized branch increment of surviving trees, and percent live crown volume of surviving trees. We made a total of ten pairwise comparisons of mining response and used a Bonferroni-adjusted significance level of 0.005 for these tests.

A maximum likelihood logistic regression was fit to the binary survival of individual trees across all transects in 1993 using an iterative reweighted least squares algorithm (Proc Logistic of SAS Ver. 6.09, SAS 1990). The independent variable in this regression was the absolute change in live crown volume index between 1991 and 1992, excluding those trees dying in 1992. One-way analysis of variance was used to examine differences in leaf area and specific leaf mass between trees in three defined water table classes.

Results

Premining Conditions

In June 1991, 698 live and 57 standing dead trees were located and tagged. Stem density and stem size (cross-sectional area) of live trees in the mining-affected transects (2 and 3) were intermediate between control transects 1 and 4 (Table 1). Average transect densities ranged from 412 to 1088 trees/ha for transects 4 and 1, respectively, and individual surface densities ranged from 59 trees/ha for a surface on transect 4 to 2175 trees/ha for a surface on transect 2. The T tests indicated no significant difference in initial density between transect 3 and the pooled controls ($T = -0.058$, $df = 22$, $P = 0.954$) or between transect 2 and the pooled controls ($T = 0.695$, $df = 27$, $P = 0.49$). Average stem size on individual surfaces ranged from 605 cm^2/tree for a surface on control transect 1 to 11,382 cm^2/tree for a surface on control transect 4. Average values for the mining affected transects 3 and 2 were 3781 and 2940 cm^2/tree, respectively, whereas control transect 1 had slightly smaller stems at 2372 cm^2/tree and control transect 4 had somewhat larger stems at 7350 cm^2/tree. Average stem sizes across surfaces were not significantly different between transect 3 ($T = 0.53$, $N = 22$, $P = 0.60$) or transect 2 ($T = 1.47$, $df = 26.8$, $P = 0.15$) and the pooled controls.

Average depths to the water table were similar for the transects before mining (Table 1), and the water table surface remained level across the valley bottom at each transect. Both control transects had surfaces with shallower (1.29 and 1.52 m for transects 4 and 1, respectively) and deeper water tables (3.16 and 3.61 m for transects 4 and 1, respectively) than either of the mining-affected transects (extremes of 2.06 and 2.94 both on transect 2). There were no significant differences in the average 1991 depths to the water table between transect 3 ($T = 1.34$, $df = 19.7$, $P = 0.20$) or

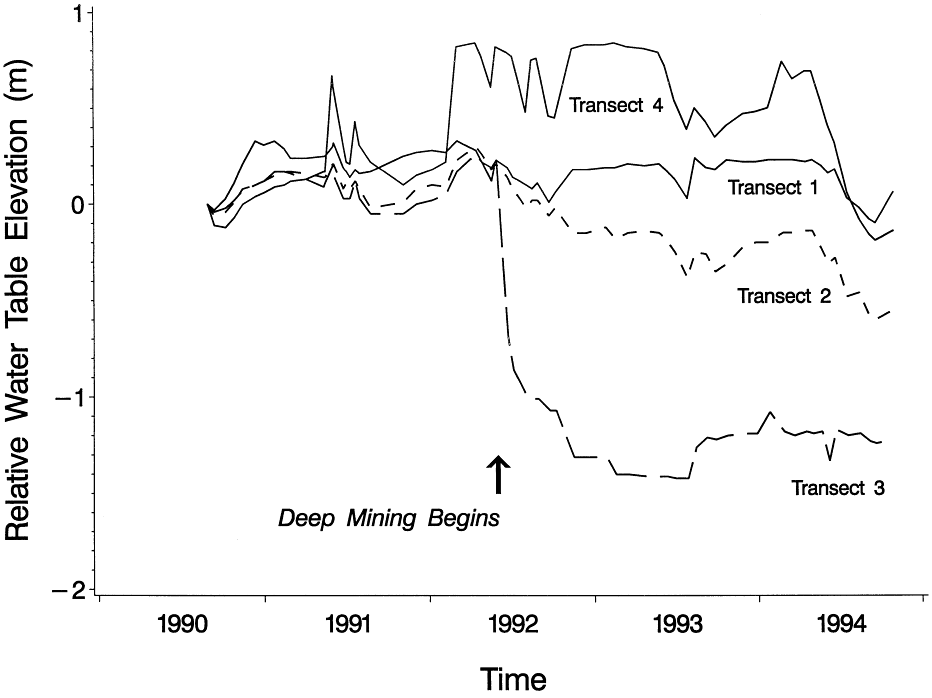

Figure 2. Change in water table elevation relative to initial, premining elevation measured on 14 August 1990 for selected wells at each transect. Control transects are represented by solid lines and mining-affected transects are represented by dashed lines.

transect 2 ($T = 0.90$, $df = 26$, $P = 0.38$) and the pooled controls.

Mining Effects on Alluvial Water Table Dynamics

Surfaces within transects exhibited consistent changes in water table levels over the mining interval from 1991 to 1994 (Figure 2). Control transect 4 had a 0.01-m rise in water table level, while individual surfaces ranged from a rise of 0.04 m to a decline of 0.01 m. The water table at control transect 1 declined an average of 0.12 m, while declines on individual surfaces ranged from 0.11 to 0.14 m. Transects affected by mining (2 and 3) had greater water table declines. Average declines were 0.47 m (surface ranges = 0.45–0.49 m) for transect 2 and 1.12 m (surface ranges = 1.08–1.21 m) for transect 3. Changes in water table elevation were significantly different from the pooled controls for both transect 2 ($T = 25.2$, $df = 21.1$, $P = 0.0001$) and transect 3 ($T = 31.8$, $df = 22$, $P < 0.0001$).

Quantitative Response of Measured Variables to Changes in Water Table

Tree survival rates and stand structure were significantly affected by sustained declines in the alluvial water table surface ≥1 m. In transect 3, average survival over the interval 1991–1994 was 12% (surface range 3%–76%) and was significantly lower ($T = 5.6$, $df = 4$, $P = 0.0049$) than the pooled controls (transects 1 and 4). In contrast, transect 2, which experienced a water table decline of ≤0.5 m, survival averaged 94% (surface range 75%–100%) and was not significantly different from the pooled controls ($T = 1.9$, $df = 9.8$, $P = 0.086$). Average survival was 98% in control transect 1 (surface range 92%–100%) and 100% in control transect 4 (Figure 3).

Tree morphological and growth variables responded differentially to water table declines. Average changes in live crown volume, from September 1991 to November 1994, declined significantly at transect 3 ($T = 6.37$, $df = 4.4$, $P = 0.0025$) but not at transect 2 ($T = 0.53$, $df = 11.4$, $P = 0.60$) compared with the pooled controls (transects 1 and 4) (Figure 3). Similarily, stem growth was significantly reduced in transect 3 ($T = 3.9$, $df = 12.5$, $P = 0.002$) but not in transect 2 ($T = 0.85$, $df = 27$, $P = 0.405$) in comparison to the pooled controls (Figure 3). On the other hand, normalized branch increments decreased significantly in transect 2 ($T = 5.05$, $df = 25$, $P < 0.0001$) but not in transect 3 ($T = 1.2$, $df = 20$, $P = 0.24$) (Figure 3). Water table declines had no significant effect on leaf size ($P = 0.38$, Table 2) or average specific leaf mass ($P = 0.28$, Table 2).

Temporal Patterns of Tree Responses to Water Table Declines

At the end of three years (1994), 88% of the trees had died at the site with the greatest and most rapid water table declines (transect 3, Figure 3). The greatest mortality was observed in the second year following initiation of mining (1993). Mortality was presaged by declines in live crown volume (Figure 4A and B). A

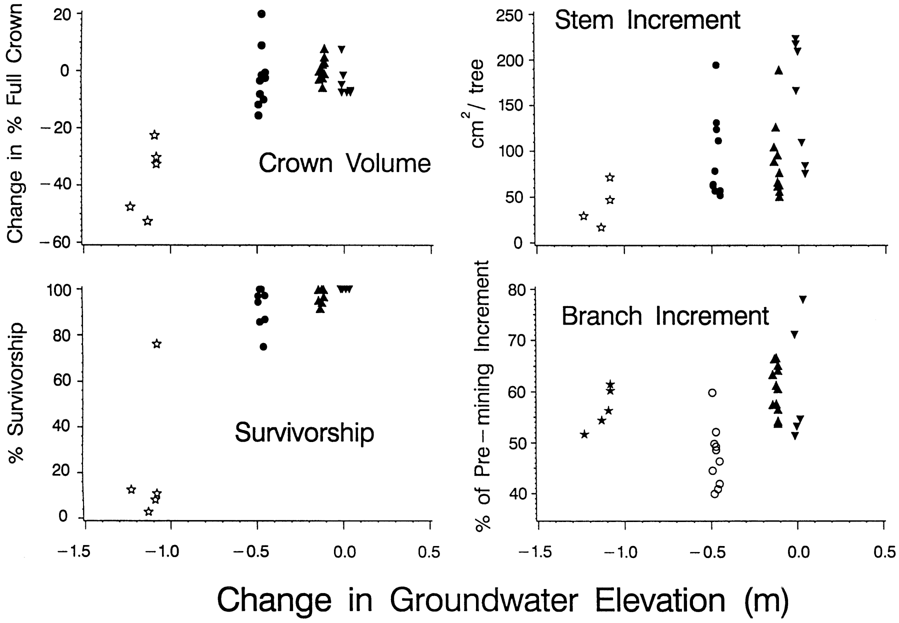

Figure 3. Cottonwood responses over the mining interval versus change in groundwater level. Symbols represent averages for geomorphic surfaces (surfaces) within each transect as follows: ▲ = 1, ○ = 2, ☆ = 3, ▼ = 4,. Control transects 1 and 4 are always solid, mining affected transects 2 and 3 are open if significantly different than the pooled controls. All values are based on the difference between measurements at the end of the premining growing season, 1991, and the end of the growing season in 1994. Stem increment is thus a three-year total and branch increment is a three-year total as a percentage of a premining three-year total. Growth responses apply only to trees that survived the entire mining period.

logistic regression of the probability of tree survival in 1993 against the prior year's change in live crown volume (Figure 5) was highly significant (−2 log likelihood = 270, χ^2 with 1 $df = 232$, $P < 0.0001$). Trees with increases or no prior year change in the live crown volume had negligible mortality (probability of survival >97%), whereas trees with prior year declines in canopy volume of ≥30 had survival probabilities less than 0.5.

The most immediate visible responses of *Populus* to rapid initial water table declines ≥1 m at transect 3 included leaf desiccation and branch dieback within three weeks. This response was reflected in decreases in live crown volume that persisted as progressive year-to-year declines for surviving trees over the study period (1991–1994). In contrast, live crown volume values for transect 2 and control transects 1 and 4 remained essentially unchanged through the same period.

Overall pre- and postmining differences in branch and stem growth contained considerable year-to-year variation. For example, at the transect mostly heavily affected by mining (transect 3), branch growth in 1992 on surviving trees increased relative to the premining average; however, growth declined sharply in 1993 and 1994. By comparison, branch growth remained below premining averages at the other transects (transects 1, 2, and 4) from 1992–1994. On the other hand, stem growth for surviving trees at transect 3 averaged 1 cm^2/yr in the first two years after mining (1992–1993) and increased to 10 cm^2/yr in 1994. In contrast, consistently higher rates of annual stem growth were observed at the other transects, ranging from 19 to 56 cm^2/yr at transects 2 and 4, respectively.

Discussion

Drought Response Patterns of Riparian *Populus* to Water Table Declines

Our experimental results demonstrated that *Populus* forests are vulnerable to relatively small declines in shallow alluvial water tables. Sustained, gradual water table declines of ≤0.5 m in the alluvial sands of Coal Creek were associated with reduced branch growth but little mortality; abrupt declines ≥1 m produced leaf desiccation and branch dieback within three weeks and significant reductions in live crown volume (Figure 4A and B), stem growth, and 88% mortality over a three-year period. Significant branch dieback, measured as a reduction in live crown volume, occurred relatively quickly following rapid water table declines at transect 3 and served as a significant predictor of tree mortality in the following year (Figure 5). Branch dieback is a common response of trees to water stress (Albertson and Weaver 1945) and may enhance tree survival during severe drought by reducing transpirational surface area (Zimmerman 1978, Bradford and Hsiao 1982, Braatne and others 1996). However, acute water stress associated with rapid water table declines can induce cavitation of xylem vessels and subsequent branch dieback (Tyree and others 1994). *Populus* spp. are particularly vulnerable to losses in hydraulic conductivity resulting from drought-induced cavitation of xylem vessels, and cavitation has been implicated in the decline of *Populus* forests downstream of some dams and diversions (Tyree and others 1994).

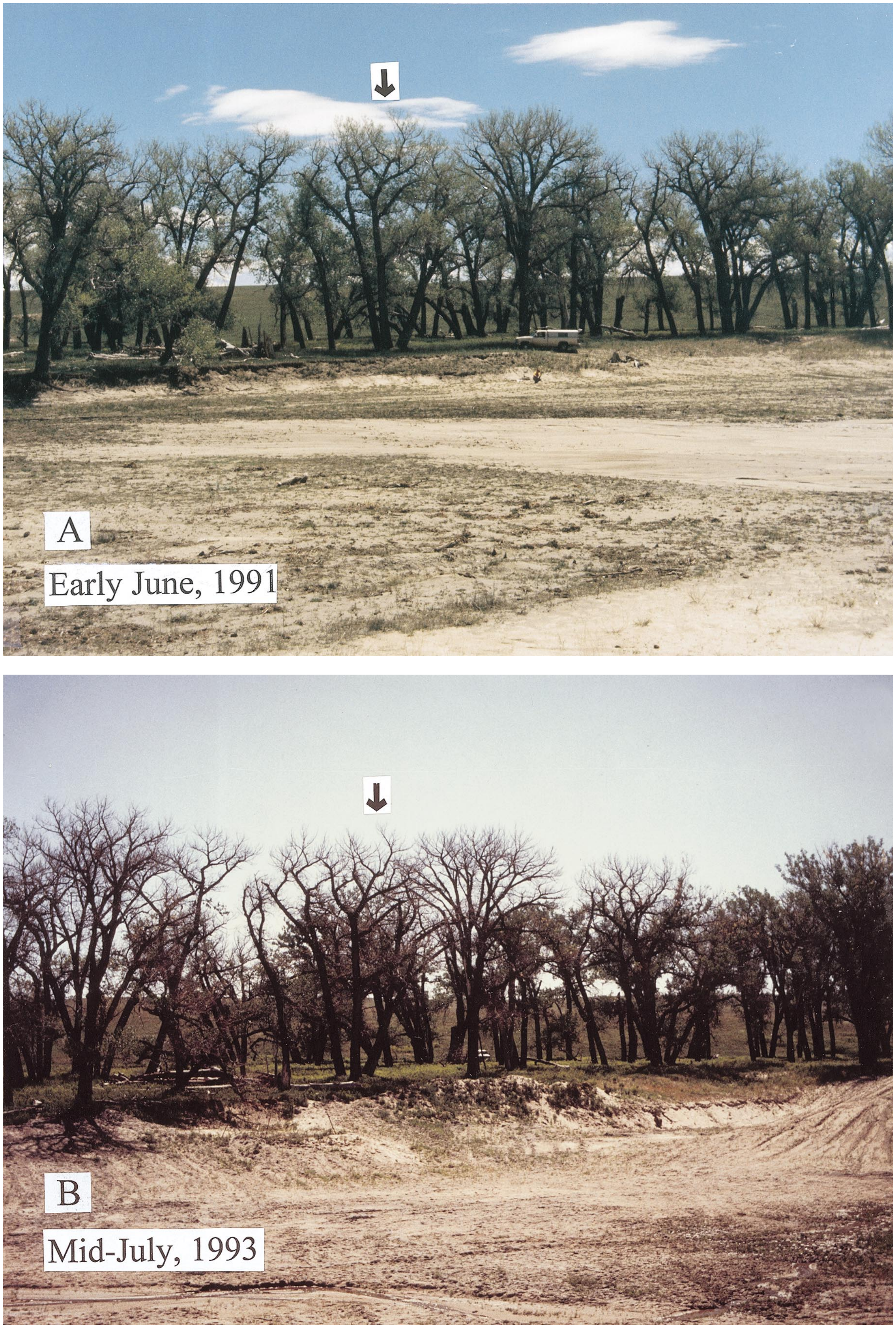

Figure 4. (**A**) Mature *Populus deltoides* subsp. *monilifera* at transect 3 just prior to mining of alluvial sands from the channel in early June 1991. Trees are in early leaf-out condition. (**B**) Transect 2 in mid-July 1993 following removal of in-channel sands and lowering of the alluvial water table ≥1 m. Note reduction in live crown volume of affected trees.

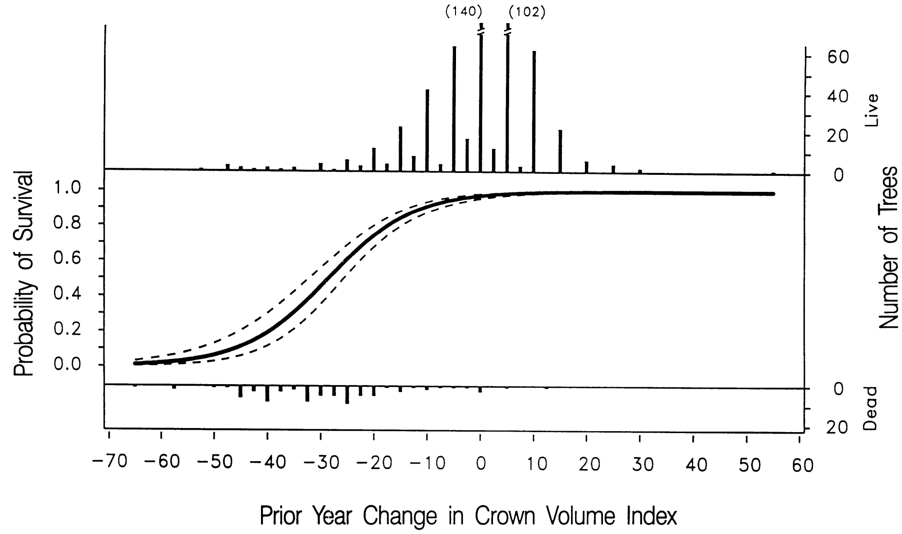

Figure 5. Tree survival in 1993 as a function of change in crown volume index between 1991 and 1992. Solid line is probability of survival (P) in 1993 determined by maximum likelihood regression logit $(P) = 3.561 + 0.125 \cdot (\text{CLIFF})$, where logit $(P) = \ln[p/(1\text{-}p)]$ and CLIFF = live crown volume in 1992 − live crown volume in 1991. Dashed lines are 95% confidence intervals around the survival probability. Binary responses for individual trees ($N = 633$) are tallied above and below the regression line with the two off-scale values given in parentheses.

Annual branch increment was the only measured variable that showed a significant response to gradual water table declines ≤ 0.5 m at transect 2, suggesting this growth variable is a sensitive indicator of smaller, sublethal declines in the water table. *Populus* species exhibit free or indeterminate shoot elongation, which includes expansion of preformed shoots as well as initiation and elongation of new shoot elements (Kozlowski and others 1991). In *Populus,* indeterminate shoot growth is strongly influenced by site water conditions (Liphschitz and Waisel 1970), and branch growth increments of riparian cottonwoods have been shown to be significantly correlated with stream flows (Willms and others 1998). At transect 3, a short-term increase in average annual branch growth in 1992 was associated with branch dieback and reductions in live crown volume and accounts in part for the fact that the average three-year branch increment was not significantly different from that of the pooled controls (Figure 3). This apparent growth release in surviving branches may be related to within-tree improvements in water status resulting from selective branch dieback (Zimmerman 1978, Hinkley and others 1981) and emphasizes the importance of interpreting the response of a single morphological variable in the context of integrated whole-plant responses to water stress (Braatne and others 1992).

Table 2. Comparison of specific leaf mass and leaf area for changes in water table depths between 1991 and 1994

Water table change (m) 1991–1994	Specific leaf mass (mg/cm^2) ±SE	Leaf area (cm^2) ±SE
+0.5 to −0.25	10.6 ± 0.2	33.5 ± 1.9
−0.26 to −1.0	10.7 ± 0.4	31.3 ± 2.2
>−1.0	11.4 ± 0.4	30.0 ± 0.8
F	1.36	1.01
$P > F$	0.28	0.38

In contrast to branch elongation, there were no significant reductions in radial stem growth at transect 2 ($T = 0.85$; $P = 0.405$), despite the fact that the final year of the study (1994) was the warmest and driest in 30 years of record at nearby Byers, Colorado. Similarly, Reily and Johnson (1982) observed no significant stem growth declines in *Populus* associated with dam-related reductions in spring peak flows and assumed reductions in spring water table levels. However, reduced flows in that case were correlated with apparent increased reliance of growth on precipitation and temperature (Reily and Johnson 1982). Increased sensitivity of growth to precipitation and temperature would make trees more vulnerable to periods of low precipitation and high temperatures (Smith and others 1991). In more humid regions, *Populus* is likely to be less sensitive to water table declines because there is less evapotranspiration with more frequent and abundant addition of moisture from precipitation to the unsaturated soil zone.

Significant reductions in leaf area and increases in leaf thickness have been observed concomitantly with significant reductions in annual branch growth in chronically water stressed *Populus* (Smith and others 1991, Busch and Smith 1995); however, we found no clear xeromorphic modification of leaves. Although leaves showed a tendency toward xeromorphy with increasing water table declines (Table 2), these changes were not significant and may have been overridden by more radical morphological adjustments such as crown dieback in response to severe water stress at transect 3.

Populus stands on alluvial sites with shallow groundwater are vulnerable to water table declines due in part to the limited soil volume for tree roots above the water table. The form of root systems in some deciduous tree species is variable and influenced by site conditions (Biswell 1935); for *Populus*, overall root structure is responsive to the site specific distribution of soil moisture (Yeager 1935). *Populus* is reported to extend roots into the water table or tension saturated zone (capillary fringe) above the water table surface (Meinzer 1927), and trees growing on shallow groundwater sites exhibit shallow, laterally spreading root structures in close association with the tension saturated zone (Condra 1944, Sprackling and Read 1979). At Coal Creek, all trees were associated with a shallow water table surface (≤3.2 m) that exhibited little inter- or intraannual variation in depth. Rapid lowering of the water table in early June at transect 3 produced visible water stress in trees within three weeks. Under conditions of drought, shallowly rooted trees exhibit greater water stress (more negative water potentials) than more deeply rooted trees (Hinkley and others 1978, Oosterbaan and Nabuurs 1991). During the drought years 1933–1941, mortality of shallow-rooted *Populus* on floodplains and surfaces occurred within the first few months of severe drought and following rapid water table declines (Albertson and Weaver 1945).

Some drought-tolerant species are able to adjust to water limitations imposed by water table decline through modification of aboveground structure (Stromberg and others 1993) or by growing roots through drained soils to access deeper, saturated soil (Sorenson and others 1991). However, *Populus* in this study were unable to adjust to water stress associated with rapid decline of the water table in coarse alluvial sands. As the water table and associated tension-saturated zone decline, water drains from the soil by gravity, leaving behind water bound by capillarity to soil pore spaces. Because of a high proportion of noncapillary pore space, the plant-available water content of unsaturated, coarse soils is typically three to four times less than that of finer textured soils (Brady 1974). Rapid water table declines in coarse alluvial soils have been correlated with reduced transpiration and growth of *Populus* cuttings (Mahoney and Rood 1992). Water table declines ≥1 m at Coal Creek were linked with progressive structural changes in mature *Populus* including leaf desiccation, branch dieback, reduced stem growth, and subsequent mortality, suggesting that these trees were unable to reestablish root contact with deeper saturated soils. Similarly, mortality of mature *Populus* following water table declines in coarse floodplain soils was attributed to an inability of trees to root more deeply because of limited soil water following drawdown (Condra 1944, Groeneveld and Griepentrog 1985). In contrast, the greater water storage capacity of fine-textured soils may serve as a buffer against rapid water table declines, allowing some groundwater-dependent plants to extend roots and access stored water in deeper soil layers (Sorenson and others 1991).

The rate, depth, and duration of water table decline and the water holding characteristics of the soil interact with water demand (i.e., temperature, humidity, wind speed) to influence the intensity and duration of water stress in groundwater-dependent plants. Furthermore, because *Populus* root systems appear to be tailored to site-specific groundwater environments (Yeager 1935), the historical stability of the water table would influence root distribution, which may in turn condition the response of trees to subsequent water table changes (Oosterbaan and Nabuurs 1991). Thus, trees growing in association with a formerly stable water table may be more sensitive to declines than trees formerly associated with a more variable water table environment. This study was a manipulative field experiment where whole-plant responses of mature *Populus* were assessed in the context of sustained declines in a formerly stable water table, in medium alluvial sands. Clearly, other combinations of antecedent water table environments, meteorological conditions, drawdown patterns, and soil characteristics are possible and beyond the scope of this study. For example, the extent to which a gradual decline in the water-table at Coal Creek to similar depths would have mitigated observed water stress is unknown. Furthermore, anecdotal evidence suggests that rapid, deep water table declines of short duration may provide sufficient residual soil moisture to allow some survival of riparian *Populus* (M. L. Scott personal observation). Additional controlled studies of whole-tree and whole-stand responses, over a range of conditions, would be desirable.

From a management perspective, this study is important because it represents conditions of water table decline and water stress that mature riparian *Populus* forests would experience as the result of in-channel gravel mining, channel incision, surface water diversion, or groundwater pumping. Our results suggest that mature *Populus* forests associated with sandy alluvial soils and a relatively stable groundwater environment are vulnerable to groundwater depletion and would be directly threatened by human activity resulting in a sustained lowering of the water table ≥1 m. More gradual declines of ∼0.5 m produced measurable reduction only in annual branch increments; however, such trees may be more vulnerable to subsequent periods of low precipitation and high temperatures. Developing quantitative information on the extent and timing of morphological changes, growth responses, and mortality of *Populus* to the rate, depth, and duration of water table declines can aid monitoring efforts designed to detect and minimize the impacts of alluvial groundwater depletion and resulting water stress on existing riparian *Populus* forests. For example, based on these findings, monitoring annual branch growth appears to be the single best indicator of sublethal water stress in *Populus* (and see Willms and others 1998). Furthermore, leaf senescence, desiccation, and shedding are an effective way of detecting the onset of severe water stress, and monitoring of live crown volume can be used to predict impending mortality under conditions of prolonged water stress.

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