Mechanisms of Riparian Cottonwood Decline Along Regulated Rivers

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ABSTRACT

Decline of riparian forests has been attributed to hydrologic modifications to river flows. However, little is known about the physiological and structural adjustments of riparian forests subject to modified flow regimes, and the potential for forest restoration using historic flow regimes is poorly understood. In this paired river study, we compared hydrology, water relations, and forest structure in cottonwood-dominated floodplains of the regulated Green River to those of the unregulated Yampa River. We measured floodplain groundwater levels, soil water availability, cottonwood xylem pressure (ψ_{xp}), and leaf-level stomatal conductance (g_s) to assess current impacts of river regulation on the water status of adult cottonwoods. We also simulated a flood on the former floodplain of the regulated river to evaluate its impact on cottonwood water relations. Canopy and root structure were quantified with estimates of cottonwood leaf area and percent live canopy and root density and biomass, respectively. Regulation of the Green River has lowered the annual peak flow yet raised minimum flows in most years, resulting in a 60%

smaller stage change, and lowered soil water availability by as much as 70% compared to pre-dam conditions. Despite differences in water availability, daily and seasonal trends in ψ_{xp} and g_s were similar for cottonwoods on the regulated and unregulated rivers. In addition, soil water added with the experimental flood had little effect on cottonwood water relations, contrary to our expectations of alleviated water stress. Green River cottonwoods had 10%–30% lower stand leaf area, 40% lower root density, and 25% lower root biomass compared with those for Yampa River cottonwoods. Our results suggest that water relations at the leaf and stem level are currently similar for Yampa and Green River trees due to structural adjustments of cottonwood forests along the Green River, triggered by river regulation.

Key words: riparian; cottonwood; water relations; river regulation; structural adjustments; root dieback; canopy dieback.

INTRODUCTION

Large dams and water diversions have altered the flow of many of the world's rivers to provide water and electricity for urban, agricultural, and industrial uses and to offer flood protection and recreational amenities (Petts 1984; Dynesius and Nilsson 1994; McCully 1996; Postel and Carpenter 1997). The Colorado River and its major tribu-

taries represent one of the world's most regulated river systems (Graf 1985) and its riparian ecosystems have severely declined in most areas (Patten 1998).

Low elevation riparian forests in the Colorado River basin are dominated by Fremont cottonwood [*Populus deltoides* Marshall subsp. *wislizenii* (Watson) Eckenwalder], which forms the forest structure, the majority of biomass, and critical wildlife habitat (Carothers 1977). In a region with low rainfall and high growing season potential

evapotranspiration, cottonwoods depend on shallow floodplain groundwater (<4 m) recharged by the adjacent stream (Smith and others 1991; Busch and others 1992; Kolb and others 1997), which makes them particularly vulnerable to modifications of river flow. Reduced cottonwood growth rates, canopy dieback, and tree death have been attributed to hydrologic modifications produced by dams (Reily and Johnson 1982; Rood and Heinze–Milne 1986; Rood and Mahoney 1990). However, few studies have identified mechanisms linking forest decline to river regulation (Busch and Smith 1995), and our understanding of cottonwood ecophysiology on unregulated as compared to regulated river floodplains is limited (Smith and others 1991; Horton and others 2001). In this work we use a case study to address the characteristics of river regulation that may be responsible for cottonwood dieback and death along many large rivers.

Many researchers have linked cottonwood forest decline to a lowering of floodplain water tables. Reduced stream flows and abrupt water table declines from dam operations led to cottonwood forest dieback along the St. Mary River in Montana (Rood and others 1995). Along a gradient of increasing groundwater depth on an Arizona stream, Horton and others (2001) reported reduced predawn twig pressures and leaf gas exchange and increased canopy dieback. Both short-term (Busch and Smith 1995; Cooper and others 2003a) and long-term (Scott and others 1999) groundwater declines of 1 m or less have caused severe water stress, leaf and twig loss, and tree death.

Contrary to the water table depression theory, dam operations on many large rivers have resulted in similar flows throughout the entire year, with lower peak flows and higher, not lower, minimum stream flows, supporting higher floodplain water tables during most of the year (Cooper and others 2003b). However, the reduction of peak flows has reduced or eliminated the recharge of upper soil layers, creating perpetual drought conditions in floodplain soils. This reduction in soil water recharge has been identified as an alternative cause of riparian cottonwood forest decline (Reily and Johnson 1981; Stromberg and Patten 1991; Smith and others 1998). Although cottonwoods are phreatophytes, they may use primarily soil water even when groundwater is available (McQueen and Miller 1972; Snyder and Williams 2000). In addition, unsaturated zone water acquisition may be necessary during periods of high river stage because the hydraulic conductance of cottonwood roots is severely reduced in saturated and anoxic soils (Pregitzer and Friend 1996). Thus, roots reaching the deep late summer water table are submerged by high water tables in early summer rendering them temporarily physiologically inactive. This introduces an allocation tradeoff between investment in deep roots that access predictable groundwater sources but are typically nutrient poor and often anoxic, or shallow roots that access near surface nutrient pools as well as water from seasonal flooding or stochastic thunderstorms (Pregitzer and Friend 1996).

Along the regulated Green River in western Colorado, dead cottonwoods are abundant and live trees exhibit early leaf yellowing and abscission and have many more dead branches than cottonwoods along the unregulated Yampa River, in the same region. In this study we focus on understanding the impacts of reduced peak flow and soil water recharge on the physiological functioning, morphology, and future of Fremont cottonwood forests in the upper Colorado River region. We hypothesized that a permanent change in peak stream flow due to river regulation would lower soil water recharge and result in lower midday and predawn xylem pressures, decrease stomatal conductance, and lower above- and belowground biomass on adult cottonwoods. We also hypothesized that a simulated flood, which increased soil water availability, would increase cottonwood xylem pressures and daily stomatal conductance.

Study Area

The study was conducted in northwestern Colorado on unconfined floodplains of the Green River in Browns Park (regulated, R) within Browns Park National Wildlife Refuge, and the Yampa River in Deerlodge Park (not regulated, NR), in Dinosaur National Monument (Figure 1). Study reaches were located between upstream and downstream canyons within two of the largest Fremont cottonwood forests in the upper Colorado River basin. The R study site is located 70 km downstream from Flaming Gorge Dam, which since 1963 has reduced Green River peak flows from an annual average of 309 to 126 m^3/s, increased late summer and winter low flows, and produced an annual hydrograph with little seasonal variation (Figure 2, peak flows illustrated are low due to year-to-year variation). The Yampa River is the last largely unregulated major tributary of the Colorado River and provides the only regional reference system for Fremont
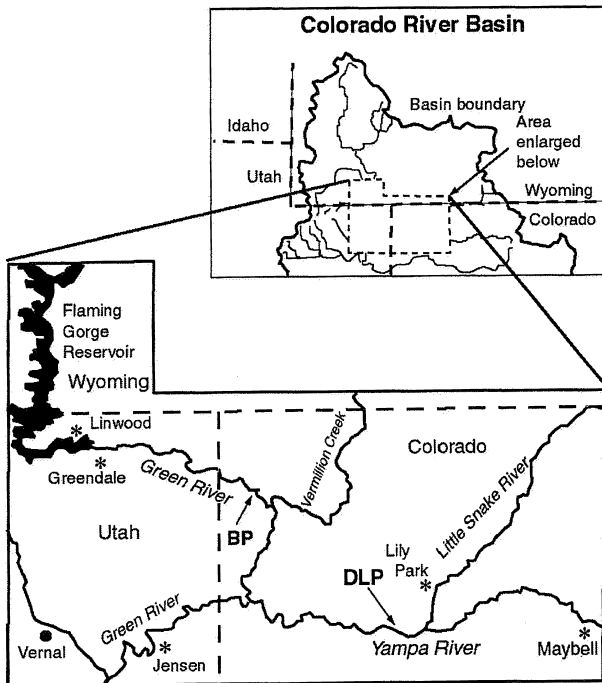
Figure 1. Map of the study region documenting locations of the Green and Yampa Rivers, Flaming Gorge Dam, the Browns Park (BP, regulated) and Deerlodge Park (DLP, not regulated) study sites, gauging stations, and weather stations.

Figure 2. Mean daily flow for the Yampa River from 1922 to 1999, the Green River from 1929 to 1962, and the Green River from 1963 to 1999.

METHODS

River Flow, Stage, Precipitation, and Water Table Depth

Mean daily flow and instantaneous annual peak flow data were obtained from USGS gauging stations. For the Yampa River at NR we summed flows from upstream gauges on the Little Snake River at Lily Park, Colorado (USGS gauge #09260000), and Yampa River at Maybell, Colorado (#09251000). The Green River at Linwood, Utah (#09225500), was used to represent R flows from 1929 to 1962, however, this gauge was inundated by Flaming Gorge reservoir filling. We used the Green River near Greendale, Utah (#09234500) to represent R flows from 1963 to the present.

We measured river stage at one staff gauge in each study area and groundwater levels in four to six monitoring wells in each study stand every 10–12 days during the 1998 and 1999 growing seasons. A rating curve was developed for each site by regressing mean daily flow against measured river stage and was used to estimate historic river stage. Daily precipitation data were obtained from the Maybell, CO, weather station, located 30 km east of NR, and the Browns Park, CO, station, located 5 km north of the R study site (National Climatic Data Center 2000).

Experimental Flood

We simulated historic R floodplain soil saturation from high river flows by pumping from the Green River onto the surface of the two R treatment stands (R1T and R2T) with a CP-12 Crisafulli Pump (Crisafulli Pump Co., Glendive, MT). The pump

cottonwoods growing in a natural flow regime (Cooper and others 1999, 2003b). The Yampa River peak flow is driven by snowmelt in the high Rocky Mountains and typically occurs in late May to early June.

Elevations at R and NR are 1630 and 1705 m above sea level. Their climates are semiarid with mean annual precipitation of 218 and 321 mm for R and Maybell (the station closest to NR). About one-third of the annual precipitation falls between 1 June and 30 September. The mean daily June, July, August, and September temperatures are 17, 20, 20, and 14°C at R and 16, 19, 18, and 13°C at Maybell, CO.

Two mature (>100 years old) cottonwood stands were selected for study at each study site, NR1 and NR2 in Deerlodge Park, and R1 and R2 in Browns Park. The two Browns Park stands were each split, with half being untreated (R1C and R2C) and the other half (R1T and R2T) treated with experimental floods. Stands were approximately 3–5 ha in size and included the range of soils and understory vegetation that typify each area. Stand density, understory composition, and the number of study trees examined are summarized in Table 1.
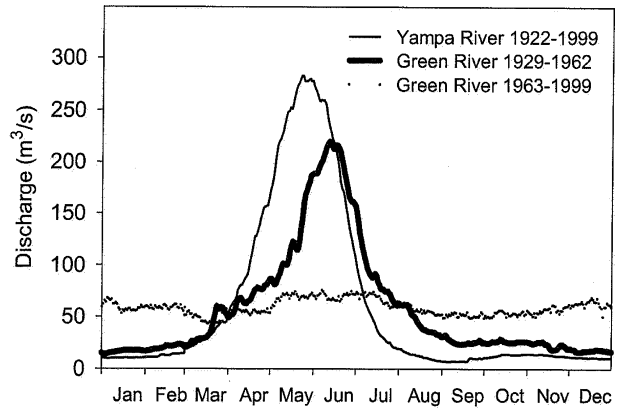
Table 1. Stand Density, Composition, and Number of Trees per Study Stand

Site	Density	Understory vegetation	n trees (control/treatment)
R1	29	*Sporobolus cryptandrus* (sand dropseed); *Anisantha tectorum* (cheatgrass); *Sporobolus airoides* (alkali sacaton)	5/5
R2	35	*Sarcobatus vermiculatus* (greasewood); *Chrysothamnus nauseosus* (rabbitbrush)	5/5
NR1	9	*Poa pratensis* (bluegrass); *Distichlis stricta* (saltgrass)	6/—
NR2	50	*Poa pratensis* (bluegrass); *Distichlis stricta* (saltgrass)	9/—

discharged about 0.15 m³/s and was run for 9–15 hours over 1–3 days with an application of about 50–80 cm of water to each stand. Small berms and shallow ditches were constructed to evenly distribute the water throughout the treated stands. The treatment was timed to match the historic annual peak flow in middle to late June.

Controlled Flood from Flaming Gorge Dam

During 1999, high snowmelt runoff down the Green River filled Flaming Gorge Reservoir necessitating a controlled flood release. This flood, with a maximum discharge of 310 m³/s, was nearly identical in magnitude to the predam mean annual peak and was the second highest flow since dam completion.

Available Soil Water

Soil water content in the top 1.5 m of soil was measured with a neutron probe (Model 503DR, Campbell Pacific Nuclear Corp., Martinez, CA) following the procedure of Gardner (1986). Three to five seamless aluminum tubes were installed in each study stand. Measurements of soil water content were made in 20-cm increments from the soil surface every 10–12 days from June through early September 1998 and 1999. Gravimetric soil water content (θ_g) was calculated using a linear regression calibration for soils in R and NR determined to be $\theta_g = 13.6*PCR + 0.46$, where θ_g = gravimetric soil water content in percent, and PCR = neutron probe count ratio ($r^2 = 0.86$, $P < 0.0001$, standard error of regression = 2.7). Bulk density and particle size distribution of major soil layers were determined from soil cores following the procedures of Blake and Hartage (1986) and Gee and Bauder (1986). We calculated volumetric soil water content (θ_v in percent) from θ_g multiplied by bulk density. From θ_v we summed total plant available water in the top 1.5 m of soil. Volumetric water content at wilting point $\theta_{v(wp)}$ was determined for each soil textural class from pressure chamber methods (Klute 1986) and assigned to soil layers by texture. Plant available water (AW in cm) was estimated for each soil layer as AW = $(\theta_v - \theta_{v(wp)})*b$, where b is layer thickness in cm.

Xylem Pressure

Predawn (ψ_{pd} MPa) and midday (ψ_{md} in MPa) xylem pressures were measured at 0300–0600 and 1100–1500 h in terminal twigs located approximately 7 m above the ground. Measurements were made within 30 s of cutting using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR) approximately biweekly from early June through early September 1998, and during five sample periods during the 1999 growing season.

Stomatal Conductance

Leaf-level stomatal conductance (g_s in mmol m^{-2} s^{-1}) was measured with a null-balance porometer (LI-1600, Li-Cor Inc., Lincoln, NE) in each stand every 15 days from mid-June through early September 1998 between 0900 and 1100 and 1200 and 1500 h. Although the porometer measures total leaf conductance, we refer to these observations as ''stomatal'' conductance, ignoring conductance through the cuticle or mesophyll. Measurements were taken only when *PAR* was more than 1200 μmol m^{-2} s^{-1}. On select days in 1999, we measured g_s and ψ_{xp} approximately every hour from dawn to dusk on at least 3 trees in each stand. We measured 5 full-sun and fully developed leaves located 2–3 m aboveground, accessed with a ladder, on each of 3 trees per stand. Photosynthetically active radiation (*PAR* in μmol m^{-2} s^{-1}), leaf (T_l in °C) and cuvette (T_c in °C) temperatures, and relative humidity (*RH* in percent) were also measured with the porometer. Vapor pressure deficit (*D* in kPa) was calculated from the saturation vapor pressure associated with the T_l and RH.

Stand Biomass

Canopy light interception and the percentage live canopy were used to characterize stand-level leaf area and biomass. Intercepted *PAR* was measured with a 1-m ceptometer (Model SF-80, Decagon Devices, Inc., Pullman, WA) in August within one hour of solar noon under the cottonwood canopy but above the understory vegetation as described in Norman and Campbell (1989). Measurements were made in four directions every 10 m on two 100-m transects in NR and R control stands. The average of 20 measurements was recorded for each direction at each point yielding four averages for every point along transects. Intercepted *PAR* was calculated as the percent of total incident *PAR* measured in open areas, and provides an estimate of cottonwood leaf area.

A visual assessment of tree crown volume was conducted following the approach of Scott and others (1999). The number of live and dead branches greater than approximately 15 cm in diameter was counted for each tree in each stand.

Root Distribution

Cottonwood root distribution was quantified in four trenches in control plots at R and two at NR excavated 1.5 m from the base of mature cottonwood trees. Trenches were 3 m deep, 2 m wide, and 3 m long, oriented perpendicular to the radial axis of the bole. Three 1-m-wide vertical profiles were established on the proximal face of each trench, as described in Caldwell and Virginia (1989), and each profile was divided into 25-cm-depth increments from the soil surface to the base of the trench. Cottonwood roots that intercepted the trench wall were counted according to six diameter classes: 0–5, 5–10, 10–30, 30–60, 60–100, and 100+ mm. Larger roots had patchy vertical and horizontal distributions and were infrequently encountered so the smallest size class (0–5 mm) was used in data analysis. To distinguish cottonwood roots from those of understory vegetation, we noted root characteristics for representative individuals by tracing roots back to the crown.

Cottonwood fine root biomass was quantified by collecting three horizontal soil samples from each depth increment in each profile ($n = 3$). Cores were 20-cm-long sections collected using a 3.18-cm-diameter PVC pipe pounded into the proximal face of each trench (Caldwell and Virginia 1989). Fine roots were separated by elutriation, and cottonwood roots were manually separated from other plant roots. Root samples were dried at 70°C for 24 h, weighed, ashed at 600°C for 6 h, and reweighed (Nelson and Sommers 1982). The ash-free dry root mass was calculated as the difference between the initial dry mass and the ashed dry mass.

Statistical Analyses

Available soil water and xylem pressure data were analyzed using repeated-measures analysis of variance (ANOVAR) (SAS Institute, Cary, NC), which tests for the time-averaged response between sites and replicates within sites (between-subjects effects), and the change in response over time (within-subjects effects). Observations were paired by minimizing the time between pairings while maximizing the number of comparisons. The mean time between paired dates was 4 days with a maximum of 10 days. The *river effect* tests for differences between R and NR ($n = 2$), The *subsite effect* tests for differences between stands nested within sites ($n = 2$). The *flood effect* tests for differences between R treatment and control stands. The *time effect* tests for differences over time. We adopted the Huyhn–Feldt adjustment to probabilities when a violation of compound symmetry of the variance–covariance matrix was found (Potvin and others 1990). The data were also grouped into three periods (P1, P2, P3) reflecting their seasonal timing, as well as timing relative to the experimental flood, where P1 was before treatment and P2 and P3 span the first and second months following treatment. Least-squares-means multiple-comparisons tests were used to identify significant ($\alpha < 0.05$) differences on paired dates. We used two-sample *t*-tests to identify significant differences between treated and untreated g_s for morning and afternoon observations. We also used two-sample *t*-tests to identify significant differences between sites for intercepted *PAR*, percent live canopy, percent live branches, root density, and fine root biomass (SYSTAT 7.0, SPSS Inc., Chicago, IL).

RESULTS

River Flow, Stage, and Water Table

During 1998 and 1999 Yampa River peak flows were close to the long-term average of 395 m³/s (Figure 3). The 1998 Green River peak flow equaled Flaming Gorge Dam power plant capacity of 126 m³/s, which is the postdam mean annual peak flow and is significantly lower than the predam mean of 309 m³/s. However, the 1999 controlled Flaming Gorge Dam release produced a peak flow of 310 m³/s. Minimum Green River flows during the growing season are about 1.5 times
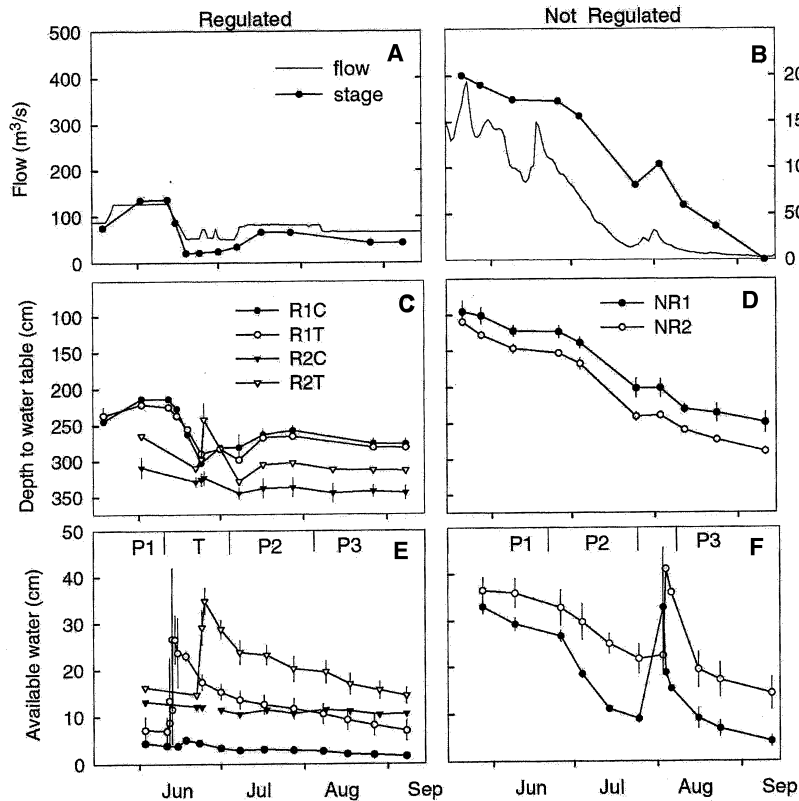
Figure 3. Seasonal trends in flow and calculated river stage (**A, B**), depth to water table (**C, D**), and available water in the upper 1.5 m of soil (**E, F**) at R and NR in 1998. The error bars represent ± 1 SE.

higher in the postdam than predam periods ($P = 0.001$). Additional analyses of Green and Yampa River flows are presented elsewhere (Cooper and others 1999, 2003b).

River stage on both rivers was controlled by flow (Yampa River stage = 15.4*flow$^{0.46}$, $r^2 = 0.97$, $P < 0.0001$, standard error of the regression = 7.7; Green River stage = 0.76*flow - 29.5, $r^2 = 0.99$, $P < 0.0001$, standard error of the regression = 6.7). The power function for the Yampa River (NR) stage-flow relationship is consistent with the seasonal change in river channel width (Merritt and Cooper 2000). The broad channel and vertical banks of the Green River at Browns Park (R) result in a linear stage-flow relationship. Total Green River stage change at Browns Park (R) in 1998 was about 71 cm and about 143 cm in 1999, and Yampa River stage change was approximately 200 cm in both study years. Using the stage-flow relationship and mean daily flow, Green River stage change in 1998 was about 40% of its predam range.

Floodplain water table depth was correlated with river stage at both NR (depth = −0.84*stage + 268, $r^2 = 0.98$, $P < 0,0001$, standard error of the regression = 7.1) and R (depth = −0.89*stage + 281, $r^2 = 0.90$, $P < 0.0001$, standard error of the regression = 17.0). In 1998, the change in water table depth during the growing season was 140–180 cm at NR, but only 35–60 cm at R (Figure 3). However, in 1999 the water table change at R was about 140 cm.

Available Soil Water

Maximum available soil water in the upper 1.5 m of NR soils ranged from 30 to 37 cm, coinciding with the timing of peak river stage, and decreased approximately 75% during the growing season (time effect, P1, $P = 0.082$, P2, $P < 0.001$, and $P < 0.001$) (Figure 3). Summer precipitation had little effect on floodplain-soil water at either study site, other than following a rare intense thunderstorm on 3 August 1998 that generated a localized flash flood down an ephemeral stream inundating a portion of the study site. Maximum available soil water in R control plots R1 and R2 in 1998 was only 4 and 13 cm, and declined 1–3 cm from May through September (Figure 3).

NR stands had 16–26 cm (approximately 2–9 times) more available soil water than R stands in 1998 during the early and middle periods of the growing season (ANOVAR, P1, river effect, $P < 0.001$; P2, river effect, $P = 0.003$). Significant differences in available water between sites did not persist into the late summer (P3, river effect, $P = 0.193$). Higher water tables from the 1999 dam
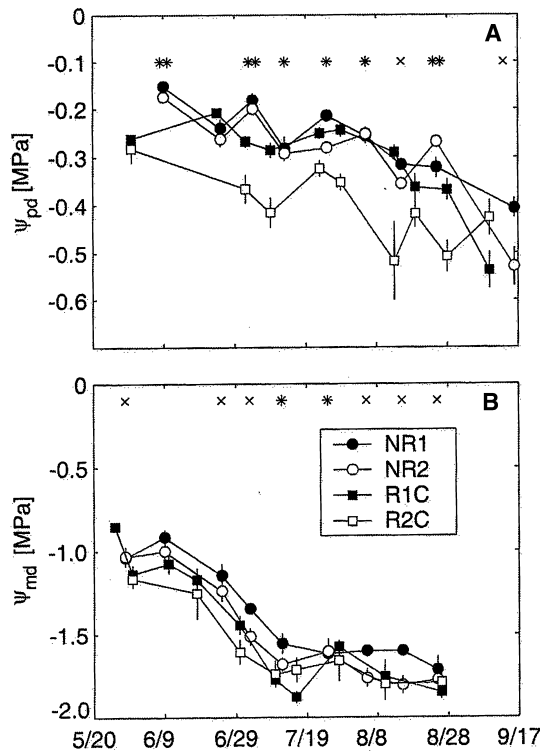
Figure 4. (**A**) Predawn (ψ_{pd}) and (**B**) midday (ψ_{md}) xylem pressures for NR1, NR2, R1C, and R2C in 1998. Error bars represent ± 1 SE. Least-square-means results for site contrasts are indicated above paired data, with x, *, and ** indicating not significant, significant at $\alpha < 0.05$, and significant at $\alpha < 0.001$, respectively.

Figure 5. (**A**) Predawn (ψ_{pd}) and (**B**) midday (ψ_{md}) xylem pressure for control and treatment (open) stands in 1998. Error bars represent ± 1 SE.

release increased AW at R by 20–30 cm, making it similar to NR.

Prior to the R experimental flood, NR stands had more available soil water than R stands (P1, Flood effect $P < 0.001$) (Figure 3). Flooding increased available soil water at R soils to within 1 cm of those at NR, and no post-treatment statistical differences in available water between sites were found (flood effect between sites, P2, $P = 0.282$, P3, $P = 0.861$).

Xylem Pressure

Predawn xylem pressure declined from June to September 1998 in R control and NR stands (time effect, $P < 0.001$) (Figure 4). The range of ψ_{pd} was similar between sites, −0.13 to −0.78 MPa at R and −0.10 to −0.68 MPa at NR. However, on 6 of 8 paired dates ψ_{pd} was 0.01–0.30 MPa lower for R compared with NR trees, and the river effect was as much as 0.01 MPa lower for R (P1 and P2, $P < 0.001$, and P3, $P = 0.010$). In addition to the river effect, R2 had significantly lower ψ_{pd} than R1, by 0.06–0.23 MPa, during the early (subsite effect, $P < 0.023$) and middle (subsite effect, $P < 0.001$) periods.
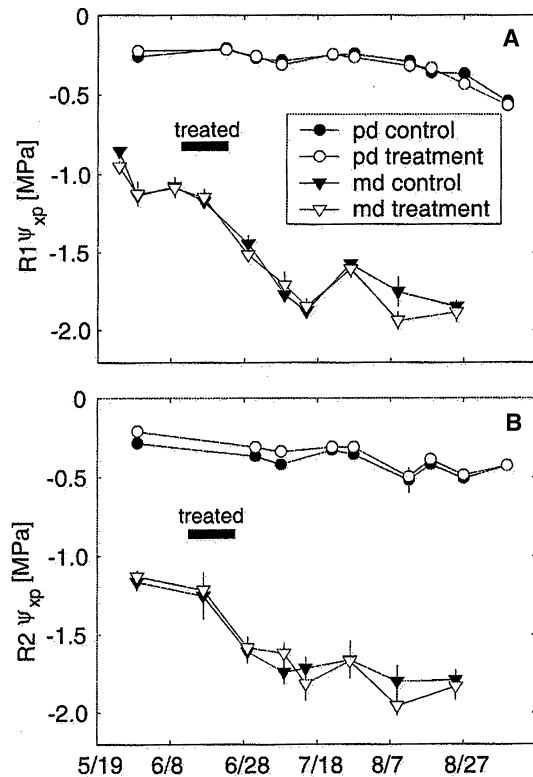
Midday xylem pressure declined during the growing season (time effect, $P < 0.001$) (Figure 4), and the range of ψ_{md} was similar between stands, −0.75 to −2,15 MPa at R and −0.75 to −2.03 MPa at NR. On 2 of 8 paired dates trees in R control stands had significantly lower ψ_{md} during the midsummer period than trees in NR; however, river effect was not significant (PI, $P = 0.282$, P2, $P = 0.011$, P3, $P = 0.627$).

Our experimental floods at R during 1998 (Figure 5) and 1999 had no effect on either ψ_{pd} or ψ_{md} ($P > 0.214$), indicating that increasing soil water content at R treatment stands to NR levels had no effect on cottonwood water status. Furthermore, the controlled flood produced by the Flaming Gorge Dam release in 1999 had little effect on control plot cottonwood water relations despite elevating water tables and recharging soil water (Figure 6).

All study trees experienced ψ_{xp} well below the reported cavitation threshold of −1.05 to −1.6 MPa (Pockman and others 1995; Blake and others 1996; Leffler and others 2000) and the minimum ψ_{xp} of −1.40 to −1.65 MPa reported for *P. deltoides* (Pallardy and Kozlowski 1981; Smith and others 1991). *Populus deltoides* is reported to experience an
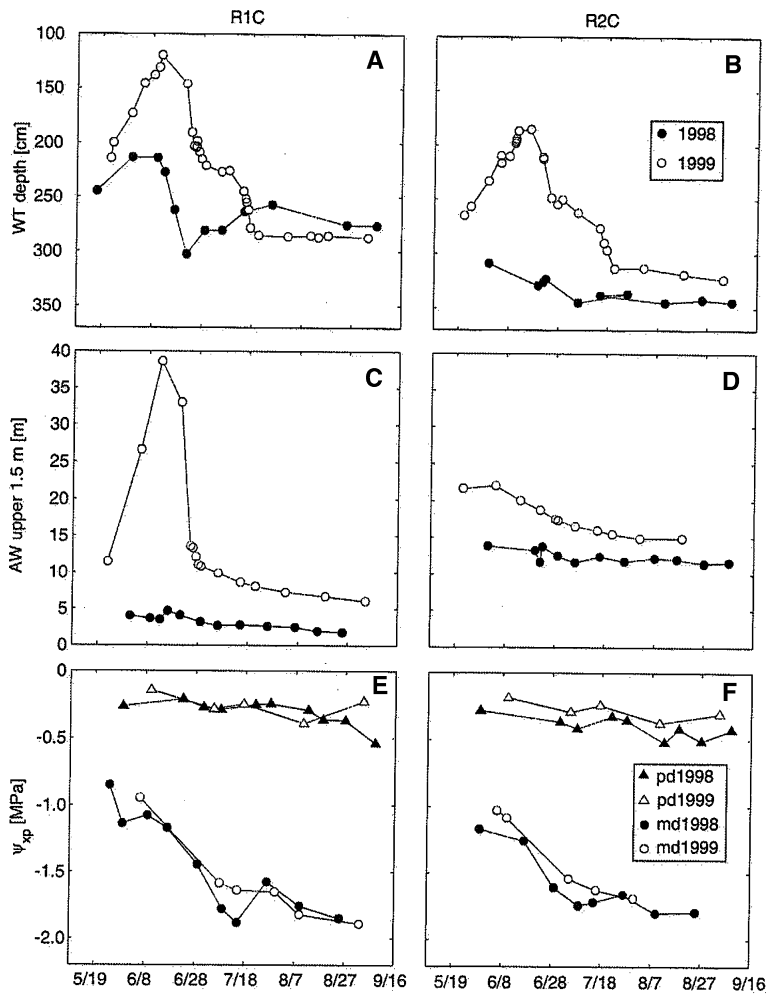
Figure 6. Seasonal trends in water table depth (WT), available water (AW), and xylem pressure (ψ_{pd}, ψ_{md}) in 1998 and 1999 at R control stands.

80% and 100% loss of hydraulic conductivity at ψ_{xp} −1.7 and −1.8 to −2.5 MPa, respectively (Cochard and others 1992; Tyree and others 1994; Pockman and others 1995; Blake and others 1996). However, the values in our study were within the range reported by Horton and others (2001) who documented midday ψ_{xp} as low as −2.5 MPa for *P. deltoides* ssp. *wislizenii* growing in sites with a water table less than 2 m below the soil surface. ψ_{md} for our study trees were typically near −1.8 MPa in July and August. This may represent a threshold for local populations of *Populus deltoides* ssp. *wislizenii*, which appear to be less vulnerable to cavitation than other *P. deltoides* populations and provides further support for the phenotypic plasticity documented by Sparks and Black (1999).

Stomatal Conductance

Between 0900 and 1100 h g_s increased at all sites during June and early July, despite the seasonal decrease in available water and increase in water table depth (Figure 7), The range of g_s was similar for all sites, although morning g_s was 10–40 mmol m^{-2} s^{-1} higher at NR than at R during July. Consistent with lower ψ_{pd} in R2, morning g_s was also lower, by as much as 30–100 mmol m^{-2} s^{-1} than other stands.

Afternoon g_s varied little from June to mid- July, increased in late July, and decreased in August (Figure 7). Stomatal conductance was 25%–50% higher in the morning than in the afternoon, indicating stomatal regulation following the mid-morning peak. NR and R stands had similar afternoon g_s in June and July, but later in the summer trees at R1 had higher afternoon g_s. Overall, there was no consistent effect of river regulation on g_s.

As with xylem pressure, our experimental flood had little effect on R cottonwood g_s compared with control trees (Figure 8). Most differences between treatment and control trees were less than 25 mmol m^{-2} s^{-1} and leaf-level measurements of assimilation and conductance indicate that this would account for only 1.2 μmol m^{-2} s^{-1} of

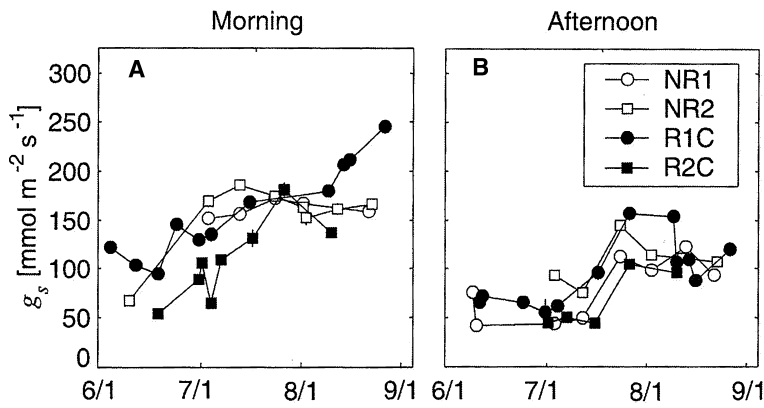**Figure 7.** (**A**) Morning (0900–1100 h) and (**B**) afternoon (1200–1500 h) stomatal conductance (g_s in mmol m^{-2} s^{-1}) at R1C, R2C, NR1, and NR2 for June–September 1998. The error bars represent ± 1 SE.
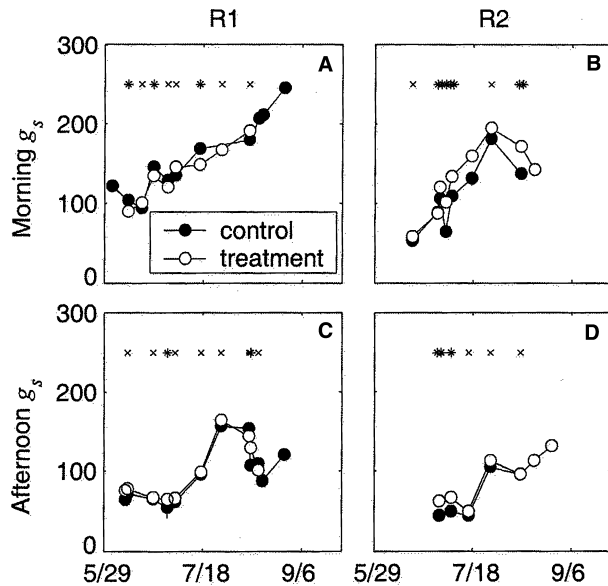

Figure 8. Morning (**A, B**), and afternoon (**C, D**), stomatal conductance (g_s in mmol m^{-2} s^{-1}) for control and treatment stands in R1 and R2 from June to September 1998. Results of t-tests comparing treatment and control trees are shown above each set of paired data with x, *, and ** indicating not significant, significant at $\alpha < 0.05$, and significant at $\alpha < 0.001$, respectively. Error bars represent ± 1 SE.

Figure 9. Daytime stomatal conductance (g_s circle) (**A, B, C**), xylem pressure (ψ_{xp} triangle) (**D, E, F**), and vapor pressure deficit (D, square) (**G, H, I**), on representative days in June, July, and August 1999 at R (closed) and NR (open).

assimilated carbon, less than 7% of the mean midday assimilation rate of approximately 19 μmol m^{-2} s^{-1} (data not shown).

The daytime pattern of g_s during the 1999 growing season clearly illustrates a seasonal increase in maximum daily g_s (Figure 9). Mean daily maximum g_s was 114 ± 7, 225 ± 11, and 283 ± 9 mmol m^{-2} s^{-1} in June, July, and August at R, and 130 ± 5, 226 ± 13, and 260 ± 5 mmol m^{-2} s^{-1} at NR. The seasonal increase in maximum daily and total daily g_s suggests that cottonwoods continued to increase daily carbon gain even as available soil water declined, possibly due to greater
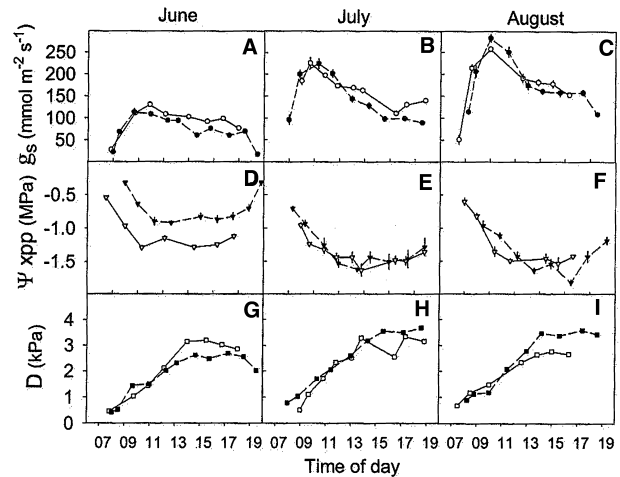
nitrogen availability or increased groundwater use. Furthermore, the lack of substantial differences in leaf-level g_s between R and NR indicates that the hydrologic regime created by the regulated Green River during the study period was not, on a daily basis, increasing cottonwood water stress. ψ_{xp} decreased and D increased from June to July, with little difference between daytime trends during July and August (Figure 9).

Available soil water did not explain the seasonal variation in g_s but ψ_{md} was inversely related to g_s at the R control ($r = -0.46$) and treatment ($r = -0.96$) stands (Figure 10). Stomatal conductance of NR cottonwoods had less seasonal variability than that of R cottonwoods, and ψ_{xp} was not correlated with g_s at NR ($r = 0.049$). To control for environmental conditions that may influence the comparisons described above, we binned g_s into D classes and con-
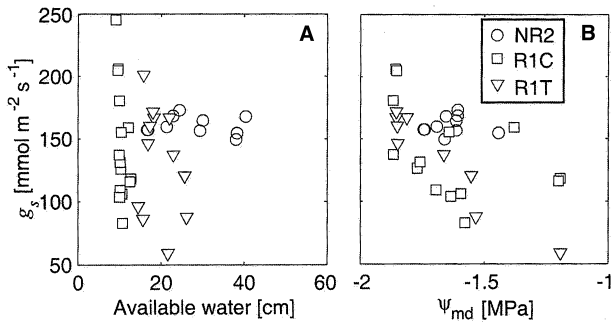
Figure 10. (**A**) Mean morning stomatal conductance (g_s) plotted as a function of available water (AW), and (**B**) g_s as a function of midday xylem pressure (ψ_{md}) for NR2, R1C, and R1T stands.

ducted a boundary line analysis (Figure 11). The response of g_s to D was similar across sites and across treatments confirming that river and flood effects were small or absent. In addition, for each D bin, the lowest boundary line conductances were associated with periods with relatively wet upper soils.

Aboveground and Belowground Biomass

The percent of *PAR* intercepted by the NR cottonwood canopy was 11%–33% higher than that of the R canopy ($P < 0.05$) (Table 2), indicating a higher leaf area index at NR. NR stands also had up to 16% more live branches than did R stands. However, these data likely underestimate branch dieback at R, where the forest floor was littered with large limbs that previously died and fell. In contrast, few such branches were found in NR. Additionally, R stands had approximately 9%–19% less live canopy than did NR stands (Table 2).

Cottonwood root density was highest at 0.75–1.50-m depth at NR and 1.75–2.25-m depth at R (Figure 12). The density of roots in the upper 2.25 m of soil was more than double at NR (129 ± 22 roots/m^2) than at R (50 ± 11 roots/m^2), with significant differences from 0.50 to 1.75 m below the soil surface ($P < 0.05$). Root density was not significantly different at depths greater than 1.75 m. Soil depths with highest root density at NR corresponded to the average peak water table elevation for the previous 10 years, approximately 75 cm, as shown with a boxplot (Figure 12B), as well as loam-textured soil layers with high water-holding capacity. In contrast, the vertical distribution of roots at R was relatively uniform with depth. Cottonwood fine root biomass declined with depth at both sites, but was nearly 4 times greater at NR (75.8 ± 19.8 g/m^3) than at R (20.1 ± 7.8 g/m^3) at 0–1.50-m depth.
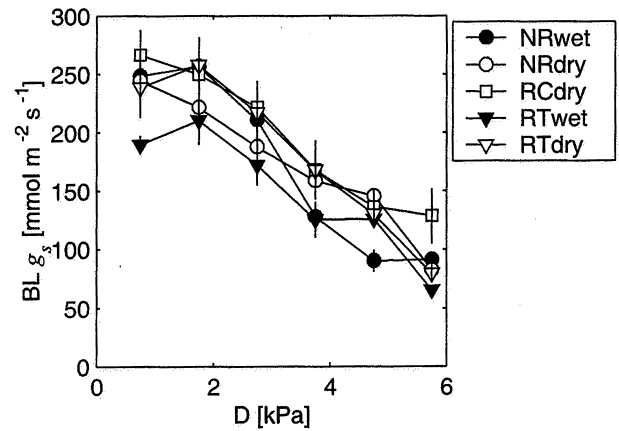

Figure 11. Boundary line stomatal conductance (BL g_s) bin-averaged over a range of leaf to air vapor pressure deficit (D) for NR wet, NR dry, R control dry, R treatment wet, and R treatment dry conditions, where wet includes observations made when available water in the upper 150 cm (AW) of soil was greater than 20 cm, and dry conditions include observations made when AW was less than 20 cm.

DISCUSSION

We hypothesized substantially lower g_s and ψ_{xp} for R cottonwoods due to reduced soil water availability along the Green River. In contrast, the lack of ecophysiological differences between cottonwoods at R and NR was striking, suggesting that at the leaf and twig level, all cottonwoods in the region functioned similarly. We also hypothesized that both the experimental flood and higher Green River flow in 1999 would increase cottonwood g_s and ψ_{xp} as a result of increased soil water availability. However, the lack of an ecophysiological response to either led us to reject this hypothesis. We concluded that the lower root density and fine root biomass, as well as reduced canopy area and larger numbers of dead branches for R cottonwoods, indicated that a structural adjustment of cottonwood had occurred in response to decreased peak flows and lower unsaturated zone soil water availability. These data suggest that cottonwoods adjusted their stem and root structures to maintain leaf-level functioning. The root dieback in previous decades prevented trees from responding ecophysiologically to temporary increases in stream flow and unsaturated zone soil water. Provided this context, we discuss how river regulation could have altered floodplain hydrology, there by exciting structural and functional adjustments in cottonwoods.

Seasonal variation in floodplain soil water availability and water table depth requires riparian cottonwoods to have widely spreading and well-

Table 2.   Mean Intercepted *PAR*, Live Branches, and Live Canopy

Site	Intercepted *PAR*	Live branches	Live canopy
R			
1	27 (4)[a]	53 (4)[a]	55 (5)[a]
2	48 (3)[b]	58 (2)[a]	50 (3)[a]
NR			
1	59 (3)[c]	69 (3)[b]	69 (4)[a]
2	60 (3)[c]	64 (5)[b]	64 (6)[a]

All values are percentages and the standard errors are shown in parentheses. Letters indicate significant dierences at α < 0.05.

distributed roots for drought avoidance (Pregitzer and Friend 1996). Large spatial and temporal fluctuations in water availability present an allocation tradeoff associated with investment in deep versus shallow roots. Lines (1999) reported that cottonwoods invest a greater proportion (up to 50%) of roots in the upper 1 m of soil in sites where the water table is more than 3 m below the surface compared to sites with shallower water tables. Along the San Pedro River, Fremont cottonwoods obtained a greater fraction of water from soil water as compared to groundwater sources at sites with deeper water tables, particularly following summer rain events (Snyder and Williams 2000). These studies indicate the potential importance of near-surface soil water contributing to cottonwood water use.

Estimates of annual riparian cottonwood transpiration indicate that soil water may contribute a large fraction of the water used. Riparian cottonwood stands in the western U.S. transpire 3–6 mm of water per day (Hinckley and others 1994; Goodrich and others 2000; Schaeffer and others 2000), and if this rate is applied to our study areas, growing season transpiration would be about 40–80 cm. This is 10–20 times the maximum available soil water measured at R in 1998. However, soils at NR are recharged with approximately 30 cm of water each summer, which has the potential to supply a significant fraction of the total used annually by cottonwoods.

Upper soils provide an important rooting medium for cottonwoods, as they have the finest texture and highest water-holding capacity, as well as high nutrient availability (Adair 2001). The rooting structure of cottonwoods at R facilitates water acquisition primarily from the water table and its capillary fringe, with little ability to acquire water from upper soil horizons. Because *Populus* spp. root hydraulic conductance is strongly reduced in flooded soils (Pregitzer and Friend 1996), deep roots may play a role in acquiring water from the water table in the late summer but are likely to be inactive in the spring and early summer when the water table is higher. Thus, during high Green River flows, water acquisition by deep cottonwood roots may be largely curtailed, increasing tree vulnerability to drought stress. Greater soil water availability during summer at NR than at R may allow NR cottonwoods to support a higher leaf area and reduce premature foliage abscission and branch dieback. Furthermore, low root density in the upper soil horizons of R floodplains appears to have rendered cottonwoods unable to utilize the water added due to the experimental flood treatment or the Flaming Gorge Dam controlled flood.

Previous studies addressing ecophysiological responses of *Populus* to hydrologic modifications documented reduced stomatal conductance and xylem pressure with increased depth to groundwater (Busch and Smith 1995; Horton and others 2001). However, Smith and others (1991) reported similar stomatal conductance for adult *P. deltoides* on diverted and undiverted reaches. In this study, we found a seasonal increase, not a decrease, in stomatal conductance despite increasing depth to groundwater and/or decreasing soil water availability, indicating little to no current ecophysiological effect of river regulation. The seasonal increase in g_s was likely due to developmental factors. Leaf mass, length, area, and vessel architecture are dynamic from initiation to abscission on cottonwoods (Larson and Isebrands 1971), such that seasonal changes in leaves may have enabled increased stomatal conductance. Increased water temperatures or transition from an anoxic to oxic rooting environment may have reduced root abscisic acid signaling, potentially increasing stomatal conductance (Pregitzer and Friend 1996). In either case, it suggests a seasonal increase in transpiration associated with the same or greater vapor pressure deficit, which could explain the seasonal decrease in midday xylem pressure. Nightly recovery from low midday xylem pressure appeared to be adequate to sustain high stomatal conductance throughout the growing season. Overall, R and NR
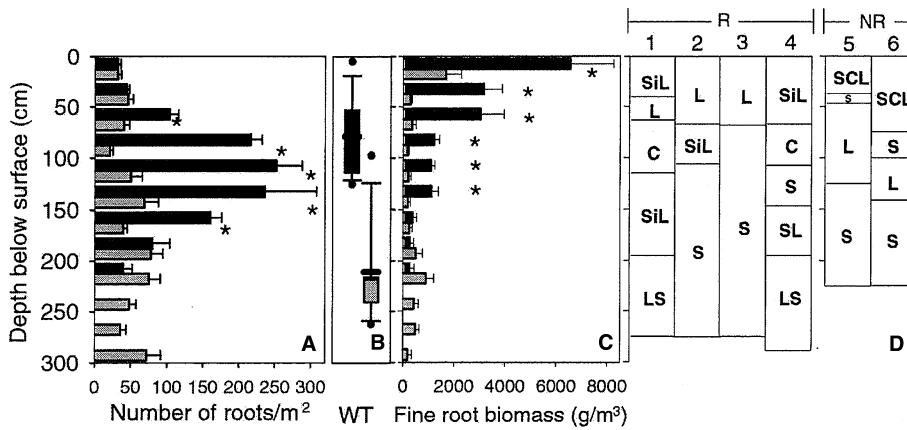
Figure 12. Small root density distribution (**A**), box stand of predicted peak water table from 1990 to 1999 (**B**), root biomass distribution (**C**), and soil texture profiles for 4 trenches at R and 2 at NR (**D**). Bars represent ± 1 SE. Asterisks indicate a significant difference at α < 0.05 for *t*-tests between R and NR at corresponding depths below the surface.

cottonwoods did not appear to be water-stressed, aside from typical afternoon stomatal limitation. Considering the difference in canopy and root structure between R and NR cottonwood stands, it indicates that hydrologic modifications from river regulation may have resulted in leaf and root dieback that maintains leaf-level ecophysiology.

The condition of current cottonwood forests at Browns Park (R) and examination of predam aerial photos (Merritt and Cooper 2000) indicate that the predam forests supported a greater leaf area and higher tree density. Lower leaf area, larger numbers of dead branches, and much lower root density and fine root biomass in upper soils for R compared with those of NR cottonwoods cannot be a function of predam site hydrologic differences, which were few. However, in 1963, the first year of filling Flaming Gorge Reservoir, the peak Green River summer flow was 4 m³/s, or approximately 1% of the mean annual predam peak of about 300 m³/s, and a tiny fraction of the 1962 peak flood of 428 m³/s. From 1964 to 1967 peak early summer flows were only 98, 73, 67, and 107 m³/s. These extreme reductions in peak flow, river stage, floodplain water table levels, and soil water recharge during 1963–1967 likely produced such severe water stress in cottonwoods that a massive dieback of leaves, branches, roots in the upper soil profile, and whole trees occurred. Such ''branch sacrifice'' has been identified as an adaptive response to drought, potentially improving the water relations of remaining branches as leaf area comes into balance with water available to the roots (Rood and others 2000; Horton and others 2001). Root dieback has also been proposed as a possible consequence of cottonwood water stress (Rood and others 1995; Pregitzer and Friend 1996), but little data on cottonwood root systems are available. Although not conclusive, our data support the theory that in the decade following the initiation of river regulation, cottonwoods sus-

tained a reduction in above- and belowground biomass, which has maintained tree water relations within ecophysiological constraints and prevented a total collapse of the Browns Park (R) riparian forest ecosystem.

We earlier documented that desert shrubs, including rabbitbrush (*Chrysothamnus nauseosus* (Pallas) Britton) and greasewood (*Sarcobatus vermiculatus* (Hooker) Torrey), have invaded the Browns Park (R) floodplain since 1963 (Merritt and Cooper 2000). These shrubs are highly sensitive to soil saturation (Groeneveld and Crowley 1988) and can survive only due to the cessation of high peak flows and flooding. In addition, marshes have developed on formerly bare Green River sand bars in the postdam years due to the stabilized flows, which have created perennially saturated soils (Merritt and Cooper 2000). This community type, dominated by spikerush (*Eleocharis macrostachya* Britton) and bulrush (*Schoenoplectus pungens* (Vahl) Palla and *S. lacustris* (L.) Palla), did not occur in the predam period and represents a novel vegetation type (*sensu* Johnson 2002). Marshes have developed for similar reasons in the Grand Canyon on the Colorado River (Stevens and others 1995).

Little cottonwood recruitment has occurred at Browns Park (R) during the postdam years (Cooper and others 2003b) and the riparian forests are not being replaced. Our results suggest that although cottonwood trees can survive the radical changes in hydrologic regime created by the operations of dams such as Flaming Gorge, the pre-existing cottonwood forest ecosystems cannot survive. If current trends continue, it is possible that these riparian forests will largely disappear within 60–75 years following dam closure. The perpetuation of cottonwood riparian forests along the Green River will require dynamic flows, with regular floods to create landforms suitable for cottonwood establishment, and an annual peak flow that recharges

floodplain soil water to support normal tree leaf area and longevity.

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