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EFFECTS OF MODERATE AND EXTREME FLOW REGULATION ON *POPULUS* GROWTH ALONG THE GREEN AND YAMPA RIVERS, COLORADO AND UTAH

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ABSTRACT

River regulation induces immediate and chronic changes to floodplain ecosystems. We analysed both short-term and prolonged effects of river regulation on the growth patterns of the keystone riparian tree species Fremont cottonwood (*Populus deltoides* ssp. *wislizenii*) at three upper Colorado River Basin rivers having different magnitudes of flow regulation. We compared cottonwood basal area increment on (i) the regulated Upper Green River below Flaming Gorge Dam; (ii) the adjacent free-flowing Yampa River; and (iii) the partially regulated Lower Green River below their confluence. Our goal was to identify the hydrologic and climatic variables most influential to tree growth under different flow regimes. A dendrochronological analysis of 182 trees revealed a long-term (37 years) trend of declining growth during the post-dam period on the Upper Green, but trees on the partially regulated Lower Green maintained growth rates similar to those on the reference Yampa River. Mean annual, mean growing season, and peak annual discharges were the multicollinear flow variables most correlated to growth during both pre-dam and post-dam periods at all sites. Annual precipitation was also highly correlated with tree growth, but precipitation occurring during the growing season was poorly correlated with tree growth, even under full river regulation conditions. This indicates that cottonwoods rely primarily on groundwater recharged by river flows. Our results illustrate the complex and prolonged effects of flow regulation on floodplain forests, and suggest that flow regulation designed to simulate specific aspects of flow regimes, particularly peak flows, may promote the persistence of these ecosystems.

KEY WORDS: *Populus*; flow regulation; floodplain forest; dendrochronology; Flaming Gorge

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INTRODUCTION

The widespread construction of dams over the past century has had a profound effect on rivers and their floodplain ecosystems throughout the world (McCully, 1996; Vörösmarty *et al*., 2005). Changes in river discharge as a result of hydrologic manipulation have drastically altered aquatic and riparian community composition, species richness, ecosystem resilience, and the fluvial geomorphologic processes of flooding, channel migration, and sediment transport (Ward *et al*., 1999; Bunn and Arthington, 2002; Nilsson and Svedmark, 2002). Modification of these fundamental processes has led to undesirable changes to many river and floodplain ecosystems, some changes which may be irreversible (Ward *et al*., 1999).

Dam-induced flow regulation reduces peak discharge and sediment flux, increases base flow, and decouples ecological interactions between rivers and their floodplains, producing wide-ranging geomorphic and ecological changes (Friedman *et al*., 1998; Merritt and Cooper, 2000; Poff *et al*., 2007; Wohl *et al*., 2015). Sediment processes on meandering rivers reflect the balance between erosion and deposition that facilitates riparian tree germination (Hupp and Osterkamp, 1996; Scott *et al*., 1996; Cooper *et al*., 1999). Along dryland rivers, the alluvial aquifer is largely controlled by the water level in the adjacent river (Williams and Cooper, 2005; Rood *et al*., 2013), and tree productivity and survival have been shown to be closely linked to water table depth and soil water availability (Mahoney and Rood, 1998; Cooper *et al*., 1999; Scott *et al*., 2000). Widespread ecological changes follow hydrologic alterations (Poff and Zimmerman, 2010), and a relationship between the extent of flow modification and the degree of species decline has been reported (Kuiper *et al*., 2014).

Across the western USA, floodplain forests are dominated by *Populus* species (Friedman *et al*., 2005). Fremont cottonwood (*Populus deltoides* ssp. *wislizenii*) is the most common native riparian tree in the Upper Colorado River Basin. Cottonwood forest survival depends on the dynamic relationship between tree ecophysiological processes and river hydrologic regimes (Cooper *et al*., 1999; Rood *et al*., 2003; Hultine *et al*., 2010; Johnson *et al*., 2012). Spring

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snowmelt floods elevate the floodplain water table and replenish soil moisture that trees access during the growing season. Although flow regulation can create short-term opportunities for recruitment (Johnson, 1994; Friedman *et al*., 1998), it ultimately reduces the channel migration and sedimentation processes that facilitate cottonwood establishment (Rood and Heinze-Milne, 1989; Johnson *et al*., 2012; Wilding *et al*., 2014).

Cottonwood forest loss occurs when tree mortality exceeds regeneration (Lytle and Merritt, 2004; Andersen *et al*., 2007). An ominous complement to decreased regeneration would be the loss of mature trees. Several studies have documented mature cottonwoods declining following flow regulation (Rood and Mahoney, 1990; Busch and Smith, 1995; Williams and Cooper, 2005), but the hydrological and physiological processes causing this decline are poorly understood and quantified. Models of cottonwood growth following flow regulation have indicated a persistent decline in annual wood production (Stromberg and Patten, 1990), but trees have been shown to adapt by restructuring root and branch morphology (Williams and Cooper, 2005). *P. deltoides* trees can live more than 300 years (Edmondson *et al*., 2014), and healthy floodplain trees provide land and water managers confronting river regulation with time to develop strategies for ecosystem management. Thus, a problem as important as the continued recruitment of seedlings is the survival of mature cottonwoods that provide the structure for floodplain ecosystems and the seed source for recruiting new individuals.

Paired studies investigating similar dammed and undammed rivers can be particularly useful in identifying ecological changes at scales ranging from single trees to whole ecosystems (Rood and Heinze-Milne, 1989; Cooper *et al*., 1999; Shafroth *et al*., 2002; Williams and Cooper, 2005; Merritt and Poff, 2010). We contrast unregulated, regulated, and partially regulated rivers in the Upper Colorado River Basin to determine how cottonwoods respond to flow regulation. We hypothesized that: (*H1*) flow regulation will reduce annual wood production in mature trees; (*H2*) following an initial adjustment period, tree growth will follow one of three paths: (i) recover to baseline growth rate; (ii) grow at a lower rate indefinitely; or (iii) decline to death; and (*H3*) the connection between tree growth and river discharge will decrease under flow regulation, whilst the connection between growth and precipitation will increase. To test these hypotheses, we (i) analysed regression models of annual tree growth increments in response to hydrologic and climatic drivers; (ii) conducted a time series analysis to identify the duration of the observed effects; and (iii) assessed the history of branch dieback to better understand the physiological mechanisms and timing of cottonwood adjustments to river regulation.

STUDY AREA

Study sites

The three study reaches, located in northwest Colorado and northeast Utah, provide an opportunity to compare cottonwood growth and senescence on rivers with similar historic but different modern flow regimes. The Green and Yampa rivers have snowmelt-driven hydrologic regimes, and their pre-dam mean annual discharges were nearly identical (55 and 58 m^3/s; Cooper *et al*., 1999). Flaming Gorge Dam was completed on the Green River in the fall of 1962 for water storage and hydropower generation. The Upper Green River is our regulated study site and is in Browns Park National Wildlife Refuge, located 70 km below Flaming Gorge Dam (1630 m a.s.l.). The Yampa River is our reference study site and is located 50 km southeast of Browns Park in Deerlodge Park in Dinosaur National Monument (1705 m a.s.l.). The Lower Green River site is our partially regulated study site, as it integrates Upper Green and Yampa flows. It is in Deerlodge Park in Dinosaur National Monument's Island Park, 15 km downstream of the confluence of the other two rivers (1510 m a.s.l.; Figure 1). At the Upper Green, we sampled from all of the major floodplain areas below the Refuge headquarters to Grimes Bottom. At the Yampa, we sampled from the Yampa River Canyon upstream to the confluence of the Little Snake River. At the Lower Green, we sampled from the exit of Whirlpool to the entrance to Split Mountain Canyon. Sampled trees were selected to represent the full range of habitats occupied by mature cottonwoods across the floodplains of each site. All trees sampled were at least 40 cm in diameter at breast height, and were thought to be at least 50 years old.

We calculated water year (Oct 1–Sep 30) hydrologic metrics from average daily streamflow records from USGS gages located at or near the three sites: Yampa River at Deerlodge Park, Colorado (Gage 09260050, 1983–1999), Green River near Greendale, Utah (Gage 09234500, 1951–1999), and Green River near Jensen, Utah (Gage 09261000, 1948–1999). The record for the Deerlodge Park stream gage begins with the 1983 water year and is missing data for 1995 and 1996. To extend the Yampa River record back to 1923 and to fill this gap, we summed the daily stream flows at the Yampa River near Maybell, Colorado (Gage 09251000) and the Little Snake River near Lily, Colorado (Gage 09260000), its major tributary. This approach provided a realistic estimate of stream flow as there are no major intervening tributaries or diversions. We extended the flow record for the Green River near Greendale, Utah back to 1933 using an upstream gage with a concurrent record prior to Flaming Gorge Dam (Gage 09225500). These discharge values were calculated using a modified Box–Cox transformation method as outlined by Moog *et al*. (1999). All hydrologic metrics were calculated using R (R Core Team, 2014).

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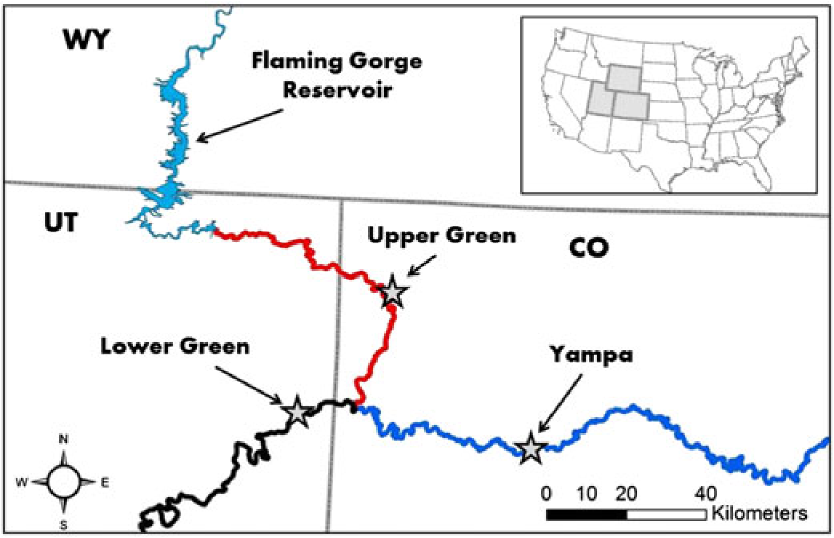

Figure 1. Study site locations (stars) on the unregulated Yampa (dark blue), regulated Upper Green (red), and partially regulated Lower Green (black) rivers in the Colorado River Basin. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

River regulation

We summarized annual flows across sites by comparing median annual hydrographs for pre-dam and post-dam periods (Figure 2). Peak flows were dramatically reduced for both the Upper and Lower Green rivers in the post-dam period (Figure 3, top). Mean annual discharge was similar for pre-dam and post-dam periods in all three rivers (Figure 3, middle), illustrating that Flaming Gorge Reservoir's primary use is seasonal water storage and hydropower generation, not consumptive use. Base flows increased at the Upper and Lower Green from pre-dam to post-dam periods, and increased slightly on the Yampa (Figure 3, bottom). Since 1993, Upper Green River high-flows and low-flows have been released to assist with the recovery efforts for endangered fish species (Cooper and Andersen, 2012). This new flow regime on the Green River may affect cottonwood growth, but our tree samples were collected in 1999 and provided only a brief

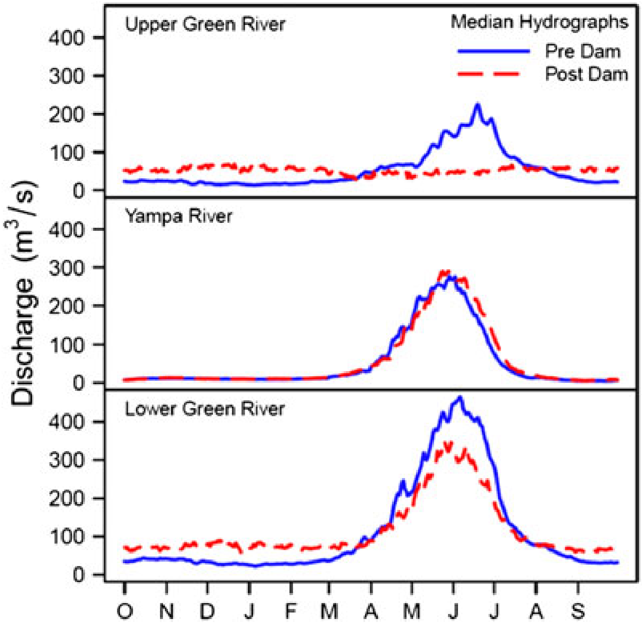

Figure 2. Median annual hydrographs for each site before and after the completion of Flaming Gorge Dam in 1963. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

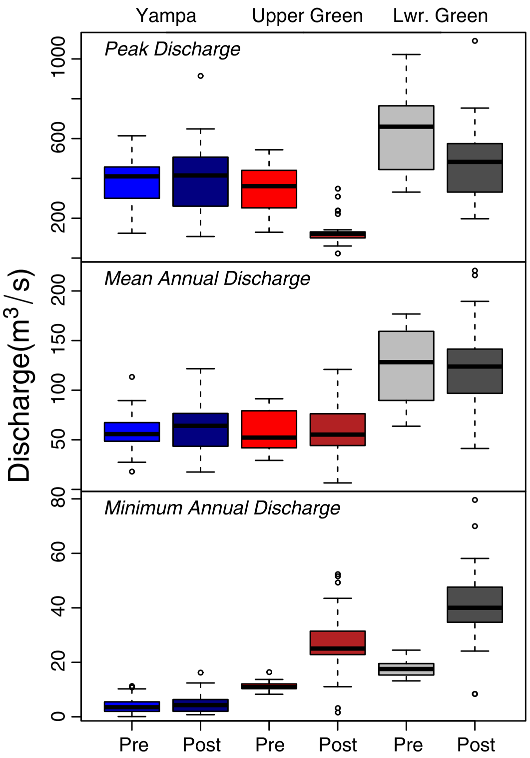

Figure 3. Box plots of selected hydrologic metrics for each site, pre-dam and post-dam. Peak discharge is peak mean daily discharge, mean annual discharge is the average of daily flows in a given year, and minimum annual discharge is the minimum average 7-day flow. Note that the unregulated Yampa River does not have any substantial change between the periods and that mean annual discharge does not change at any site. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

window to assess the effects of the adjusted flow regime. All sites, including the reference Yampa, had high growth after 1993, so we were unable to disentangle the effects of the dam releases from climate. Andrews (1986) reported post-dam channel incision in the Upper Green study reach. However, more recent and comprehensive geomorphic analyses found that although the river channel has narrowed in response to flow regulation, no trends in bed elevation have occurred since damming (Grams and Schmidt, 2005). The Yampa River is one of the last unregulated major tributaries of the Colorado River, and serves as a regional reference for natural flows and floodplain forests for cottonwoods (Cooper *et al*., 1999; Cooper *et al*., 2003a) and other native trees (DeWine and Cooper, 2007).

METHODS

Field sample and data preparation

For analysing the effects of flow regulation on floodplain ecosystem processes, it is highly desirable to have both pre-dam and post-dam data (Poff and Zimmerman, 2010), but these data are rarely available. Dendrochronology provides an opportunity to analyse long-term environmental controls on tree growth because information is preserved in annual growth increments. Cores from riparian cottonwoods can be used to quantitatively connect river discharge to tree growth (Reily and Johnson, 1982; Stromberg and Patten, 1990; Meko *et al*., 2015). We collected cores from 210 Fremont cottonwoods at three sites using a 5.15 × 500 mm Haglof increment borer. The cores were mounted and smoothed with progressively finer sandpaper down to 20 µm, then ring widths were measured using a sliding stage micrometer. Basal area increment (BAI) wood production values were calculated from annual radial growth increments and tree diameter to quantify annual growth. BAI was used because it integrates ring width and tree diameter, and is more consistent than ring width as stem diameter increases (Biondi and Qeadan, 2008). Each tree ring series was divided into pre-dam and post-dam periods, and detrended using cubic smoothing splines with a 0.8 frequency response parameter to capture high frequency growth variations in the dplR package (Bunn, 2010). We only used cores that extended back to at least 1945, which yielded cores from 69, 67, and 46 trees from the Yampa, Lower Green, and Upper Green sites for a total of 182 trees. The Lower Green had the oldest trees (median first year = 1878), followed by Upper Green (1912), and Yampa (1924). The use of BAI as our growth metric guarded against any spurious conclusions resulting from the variations in tree ages across sites. Detrended data from all cores at a site were averaged to identify annual growth rates by site, and we analysed both raw and detrended annual growth values.

Hydro-climatic controls on tree growth

Cottonwood growth in arid and semi-arid regions is limited by water availability that is influenced by soil texture, root distribution, and water table depth. To address Hypotheses 1 and 3, we created multivariate linear regression models with BAI as the response variable. Many hydrologic metrics have been evaluated to characterize flow regimes altered by human activities (e.g. Richter *et al*., 1996). Here, we focus on metrics describing the current water year's mean, maximum, and minimum discharges in addition to precipitation and temperature (Table I). Discharge metrics from the previous year were tested, but they did not substantially change or improve the models so they were left out. River stage can control floodplain water table depth, and stage-discharge relationships can be nonlinear. Using the rating curves for each USGS gage and for five additional sites where we measured stage along the Upper Green, we found linear relationships between stage and discharge across sites

Table I. Physical variables used as predictors in multiple regression models

Metric	Period	Description
$\bar{Q}$	Aug_{y-1}–Jul	Mean annual flow
$\bar{Q}_{grow}$	Apr–Jul	Mean growing season flow
Q_{peak}	Aug_{y-1}–Jul	Maximum average daily flow
Q_{min}	Aug_{y-1}–Jul	Minimum 7-day average flow
Q_{time}	Aug_{y-1}–Jul	Peak discharge day of year
Ppt	Aug_{y-1}–Jul	Annual precipitation
Ppt_{grow}	Apr–Jul	Growing season precipitation
T	Aug_{y-1}–Jul	Mean annual temperature
T_{grow}	Apr–Jul	Growing season mean temperature

Periods selected for each variable are based on previous *P. deltoides* dendrochronological analyses (Reily and Johnson, 1982; Meko *et al*., 2015). 'y − 1' means previous year.

above the very lowest flows that have high roughness (mean $R^2 = 0.98$), including an average relationship of $stage\ (cm) \propto 0.798 * discharge\ (m^3/s)$ at our five Upper Green gauges. We regressed BAI against Q, sqrt(Q), and log(Q), and found no consistent improvement with either transformation. Bivariate plots for BAI and each predictor revealed no apparent threshold or non-linear responses. These lines of evidence suggest that a linear relationship exists between river stage (and hence groundwater elevation) and discharge at these sites.

We performed multiple regression analyses for each of the three sites for pre-dam (1947–1962 at the Lower Green; 1933–1962 at the Upper Green and Yampa) and post-dam (1963–1999) periods to determine the physical variables most correlated to tree growth. Analysis start dates varied according to available flow records. Partially to account for the shorter duration at the Lower Green River, subsequent analyses were performed to support the regression models. All predictors were standardized using a z-score transformation and regressed against BAI for each site and time period. All subset regressions were performed using the R package LEAPS (Lumley and Miller, 2009). Mallow's Cp was used as the model selection criterion because of the heavy penalty it places on additional variables, thus favouring parsimonious models. Flow variables used are in Table I.

The relative strength of each predictor is frequently reported as a coefficient in multiple regression analysis equations. However, when predictors are multicollinear, this can produce oversimplified and potentially inaccurate interpretations (Courville and Thompson, 2001). We summarized the selected models, including the calculation of beta weights and structure coefficients (Kraha *et al*., 2012; Nathans *et al*., 2012). Regression equations are not reported because all variables were standardized before model selection occurred, rendering only their relative values interpretable. To complement the parsimonious models, multiple regressions were run for full models using all nine predictors to fully explore each variable's correlation to BAI. We performed a commonality analysis that partitions a model's R^2 across all predictors, a procedure that provides more information than the binary presence or absence of predictors in a regression model (Budescu, 1993; Nathans *et al*., 2012). General dominance rankings for all predictors are also reported from dominance analysis, which quantifies the variance explained by each predictor in all possible subsets to determine its relative significance (Budescu, 1993; Nathans *et al*., 2012).

Prolonged effects of regulation on tree growth

We addressed Hypotheses 1 and 2 by comparing BAI across sites and over time to determine the duration over which tree growth is influenced by flow regulation. Although the study sites were similar, their pre-dam growth rates differed. We defined the mean growth over the 15 years before damming as each site's baseline growth rate. This period fairly represents the correlation between Yampa and Upper Green flows during the entire 1933–1962 period, and it represents the magnitude and distribution of Yampa flows measured from 1923 to 1999. The baseline growth rate was subtracted from each year's BAI to generate values comparable across sites. After this standardization, we assigned Yampa BAI as the reference growth rate and compared this to the Upper and Lower Green growth using repeated ANOVAs. Because comparing each year separately across sites would either increase the likelihood of a Type I error or introduce a severe multiple-test penalty, we combined years into seven 7- to 8-year periods: 1949–1955, 1956–1962, 1963–1969, 1970–1976, 1977–1984, 1985–1992, and 1993–1999 for analysis. The first two periods were pre-dam, and the last five were post-dam. If a period's ANOVA was significant, pairwise cross-group comparisons were conducted using a Tukey's HSD adjustment.

Branch dieback

Under water-stressed conditions, cottonwoods are known to sacrifice branches as a survival mechanism (Rood *et al*., 2000; Scott *et al*., 2000). Upon field visits, we observed widespread branch sacrifice at the Upper Green River. In an effort to develop a method to reconstruct the timing of tree branch dieback, we harvested dead branches from the canopy of two typical mature trees from the Upper Green River (Figure 4). Cross-sections were taken at the lowest portion of each dead branch, mounted, sanded, and measured to 0.01 mm precision for dendrochronological analysis. Rings were cross-dated using two cores collected from the same tree's trunk to identify the year of branch death. Because of a small sample size, we discuss the

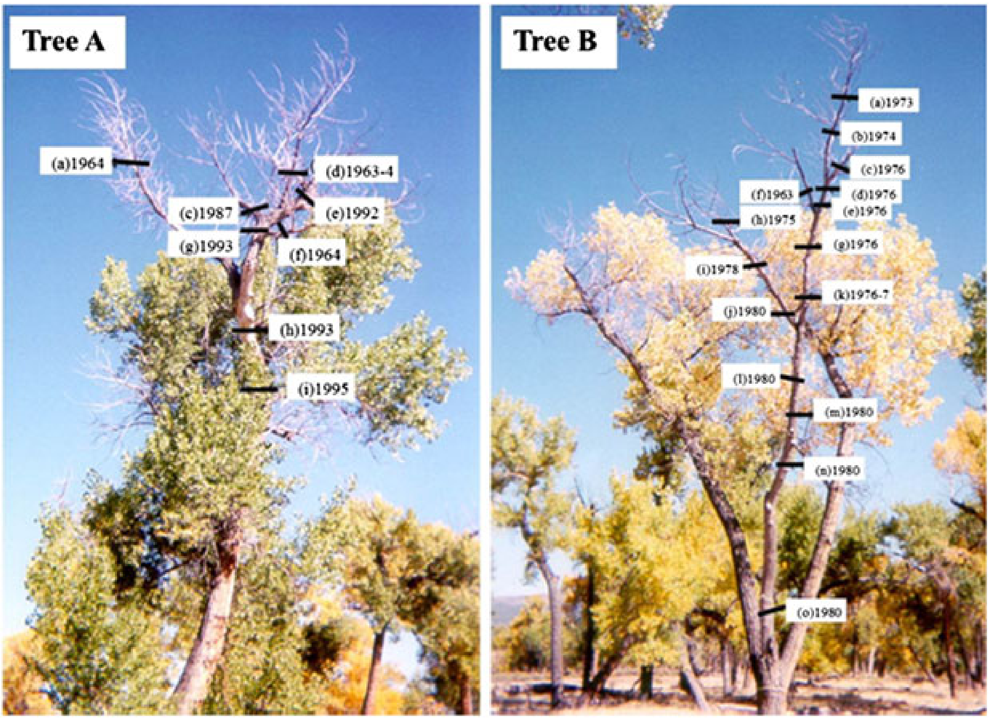

Figure 4. Autumn photographs of the two Upper Green River cottonwoods dissected in 1999. Lines with dates identify branches that were sampled and cross-dated. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

general findings instead of presenting quantitative relationships between branch growth and river discharge.

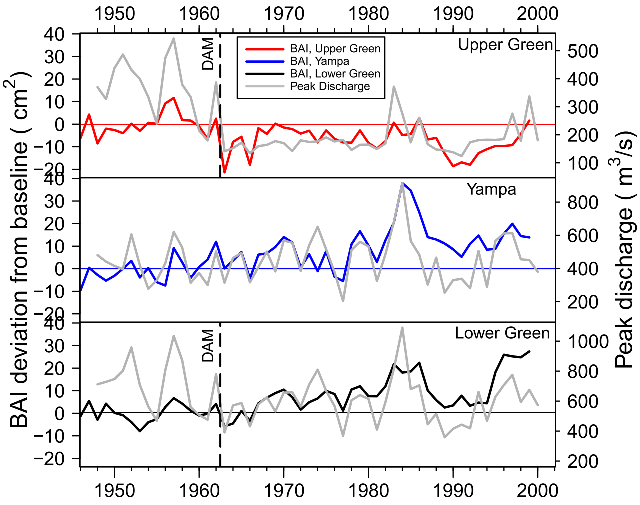

Figure 5. Mean cottonwood basal area increment (BAI; coloured lines) and peak annual discharge at each study site. The left y-axis is each site's BAI scaled so that the 15-year period preceding Flaming Gorge Dam is the baseline growth rate (horizontal line). The vertical line before 1963 indicates when Flaming Gorge Dam was completed. This figure is available in colour online at wileyonlinelibrary.com/journal/rra

RESULTS

Long-term effects of river regulation on tree growth

At the Upper Green River, flow regulation reduced the mean annual BAI from 41.9 to 34.5 cm^2/year after damming (Figure 5), and growth rates for trees at that site were lower in each of the five post-dam sub-periods compared with the Yampa (Table II). In contrast, the mean annual BAI increased at the Lower Green (28.4 to 37.9 cm^2/year) and Yampa (35.1 to 45.7 cm^2/year; all $p < 0.01$). Tree growth on the Lower Green did not significantly differ from the Yampa during four of the five post-dam periods, suggesting that moderate river regulation had little influence on wood production.

1963 and 1966 had the two lowest growth rates of all 37 post-dam years at the Upper and Lower Green rivers. These years occurred during the 1962–1967 filling of Flaming Gorge Reservoir (Cooper and Andersen, 2012). The maximum annual and mean growing season discharges at the Upper Green in 1963 were extremely low compared with the pre-dam years (26% and 3%), resulting in a drastic change in tree water availability and decreased growth (Figure 5). Relatively high growth occurred in some post-dam years. For example, after damming, the highest Upper Green cottonwood growth occurred in 1983, 1986, and 1999, three of only five years when the dam releases exceeded the turbine power plant capacity of 130 m^3/s

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Table II. Cross-site comparison of the effects of flow regulation on tree BAI

Sites compared	1949–1955	1956–1962	1963–1969	1970–1976	1977–1984	1985–1992	1993–1999
Yampa vs. Upper Green	na	na	<0.001*	0.002*	<0.001*	<0.001*	<0.001*
Lower Green vs. Upper Green	na	na	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
Yampa vs. Lower Green	na	na	0.21	0.70	0.87	0.05*	0.30
Effect size	0.01	0.00	0.76	0.58	0.58	0.85	0.81

Effect sizes for each ANOVA are reported, and *p*-values are reported for pairwise comparisons with Tukey HSD adjustment for each time period where the ANOVA was significant ($p < 0.05$). Pre-dam growth was the same across sites. The Upper Green River had significantly lower growth throughout the post-dam period.
*$p < 0.05$.

(Cooper and Andersen, 2012). 1984 and 1985 were the two highest growth years on the Yampa, but not on either Green River reach.

Environmental controls on tree growth

Regression models, commonality analysis, and dominance analysis combined to reveal that peak and mean discharges, followed by annual precipitation, were the physical variables most closely correlated with BAI under all levels of regulation (Tables III and IV). We hypothesized that the four regression models for free-flowing rivers (all three rivers pre-dam and the Yampa post-dam) would have the same predictors in similar proportions, but the models were confounded by multicollinearity and varied. The strongest predictor in each regression model, regardless of regulation status, was peak annual, mean annual, or mean growing season discharge. Although post-dam models at both the Upper and Lower Green included growing season weather variables, commonality and dominance analyses indicated that their influence was low. Commonality and dominance analyses revealed similar information, and only dominance analysis results are reported (Table IV). Variance inflation

Table III. The best models for annual BAI production selected from all subset regressions for each study site during pre-dam and post-dam periods

Site	Predictor	Beta weight	Structure coef.	Mallows' Cp	Adj. R^2	*p*-value
			Pre-dam			
Yampa	Q_{peak}	0.42	0.95	−1.21	0.47	<0.001
	Ppt	0.35	0.92			
Lower Green	$\bar{Q}_{grow}$	0.53	1	−1.17	0.23	0.04
Upper Green	Q_{peak}	0.45	0.79	−1.39	0.41	<0.001
	Ppt	0.42	0.75			
			Post-dam			
Yampa	$\bar{Q}_{grow}$	0.67	0.97	−1.22	0.58	<0.001
	Q_{min}	0.21	0.63			
Lower Green	$\bar{Q}$	0.68	0.98	2.10	0.61	<0.001
	Ppt_{grow}	0.18	0.71			
Upper Green	$\bar{Q}$	0.55	0.94	−0.90	0.39	<0.001
	T_{grow}	−0.23	−0.56			

Predictors are the variables retained in the models, beta weights are relative weighting of each predictor, structure coefficients are correlations to predicted BAI, Mallows' Cp was the selection criterion, and adjusted R^2 and *p*-values are reported for model interpretation.

Table IV. Dominance analysis results revealed the strength of relationships between predictors and BAI. General dominance values, or the average amount of variance explained by a predictor in all possible subsets, are reported

		Pre-dam		*Post-dam*	
	Predictor	Dominance value	Rank	Dominance value	Rank
Yampa	$\bar{Q}$	0.08	3	0.13	2
	$\bar{Q}_{grow}$	0.08	4	0.14	1
	Q_{peak}	0.12	2	0.13	3
	Q_{time}	0.03	8	0.00	9
	Q_{min}	0.01	9	0.06	5
	Ppt	0.14	1	0.06	4
	Ppt_{grow}	0.04	6	0.05	6
	T	0.03	7	0.04	7
	T_{grow}	0.04	5	0.03	8
Lower Green	$\bar{Q}$	0.09	4	0.17	1
	$\bar{Q}_{grow}$	0.12	1	0.17	2
	Q_{peak}	0.09	5	0.11	3
	Q_{time}	0.02	8	0.02	8
	Q_{min}	0.01	9	0.06	5
	Ppt	0.11	3	0.06	6
	Ppt_{grow}	0.04	6	0.08	4
	T	0.12	2	0.01	9
	T_{grow}	0.04	7	0.03	7
Upper Green	$\bar{Q}$	0.08	4	0.12	1
	$\bar{Q}_{grow}$	0.09	3	0.10	2
	Q_{peak}	0.10	2	0.06	3
	Q_{time}	0.02	8	0.04	5
	Q_{min}	0.02	9	0.03	8
	Ppt	0.11	1	0.04	4
	Ppt_{grow}	0.07	5	0.04	7
	T	0.02	6	0.01	9
	T_{grow}	0.02	7	0.04	6

Higher values represent stronger predictors of growth, and the values are ranked for interpretation.

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factors for all predictors in all models ranged from 1.19 to 2.28, indicating that highly correlated predictors were excluded from the final models. The consistently higher ranking of annual precipitation compared with growing season precipitation across sites indicated the importance of pre-growing season soil moisture accumulation from inputs such as local snowmelt.

To assess the strength of each of the nine multicollinear predictors, we also performed commonality and dominance analyses on full regression models that used all predictors. Commonality analysis confirmed that mean growing season, mean annual, and peak annual discharges consistently explained the most variance in BAI across sites and time periods (mean $R^2 = 0.42$, 0.41, and 0.38, respectively). Dominance analysis supported commonality analysis, indicating that mean growing season flow, peak annual flow, and annual precipitation explained the most variance in BAI across sites and periods (Table IV). Even under full and partial regulations, flow variables were more correlated to tree growth than was growing season precipitation, and similar physical variables affected tree growth under new flow regimes.

Branch dieback

Within-tree dendrochronology provided a novel technique for analysing tree responses to water stress. Cross-dating with the trunk allowed us to reconstruct patterns of branch dieback and confirmed that all sampled branches from the two trees died after the closing of Flaming Gorge Dam (Figure 4). Younger, distal branches were the first to die in both trees. The mean annual BAI during the 3 years immediately post-damming was only 45% of the pre-dam average, and three of the seven branches on Tree A died between 1963 and 1965. From 4 years after damming until branch death, the annual wood production increased to 59% of pre-dam values, but no branch regained its pre-dam growth rate. Another major period of branch death occurred in 1993, following low river flows from 1987 to 1992. The branches on Tree B died during the low flow years of 1976 and 1980. We explored quantitative relationships between branch growth and death versus flow metrics, but our small sample size renders qualitative interpretation more appropriate. If widely applied, this method should be capable of building an understanding of tree dieback and its relationship to river flows.

DISCUSSION

Flaming Gorge Dam began regulating Green River discharge in 1963 by reducing peak flows, preventing overbank flooding, lowering early summer water tables, and limiting wetting of the cottonwood root zone (Cooper and Andersen, 2012). These changes eliminated the hydrologic regime that facilitated cottonwood establishment and sustained tree growth (Cooper *et al.*, 2003a; Lytle and Merritt, 2004). Dendrochronological analyses allowed us to demonstrate that BAI was more highly correlated with river flow than with local precipitation. A sustained decline in cottonwood growth has occurred on the Upper Green River, which couples with a paucity of tree regeneration to indicate that the native forests are unlikely to persist. River regulation resulted in chronically lower growth rates throughout a tree's post-dam life, and trees did not experience a short period of low growth followed by morphological and physiological adjustments that allowed a resumption of pre-dam growth rates. These conclusions apply only to the trees that survived the extreme drought conditions during the filling of Flaming Gorge Dam, which reduced the 1963 mean growing season discharge to 3% of its pre-dam average and resulted in the death of many branches and trees (Cooper and Andersen, 2012).

Regression models of site-specific and time-specific tree growth indicated that peak discharge, mean discharge and annual precipitation were the most important physical predictors of cottonwood growth across the range of flow conditions. Multicollinearity likely led to the models differing more than expected, but subsequent analyses clarified the relationships between each predictor and tree growth (Table III). The Upper Green's post-dam regression model explained less variance than the models for the Lower Green and Yampa, possibly because of limited post-dam flow variance and unnatural character of discharges.

We had anticipated that post-dam tree growth on the Upper Green River would have an increased correlation with growing season precipitation, as occurred after river regulation with riparian *Celtis reticulata* in Arizona and Utah (Salzer *et al.*, 1996), *P. trichocarpa* in California (Stromberg and Patten, 1990), and *P. deltoides* in Colorado (Coble and Kolb, 2012). However, we found a slightly decreased correlation on the Upper Green (Table III). This may be because the mean annual precipitation of our study sites averages only 21 cm (Cooper and Andersen, 2012), or because the greatly reduced post-dam peak flows caused root dieback higher in the soil profile and limited tree response to shallow soil water replenishment (Williams and Cooper, 2005). Our findings support the conclusion that in our study area, most water used by mature cottonwoods is derived from groundwater instead of unsaturated soil water, a pattern also found in *P. fremontii* in Arizona where less than 16% of transpired water came from shallow soil water even after a rainstorm (Snyder and Williams, 2000).

Our analyses of annual growth from 182 trees, and branch growth from two trees, indicated that flow regulation has triggered a long-term decline in cottonwood growth on the Upper Green River throughout the post-dam period. The modestly different tree age structures across sites should not influence our conclusions drawn from the BAI measurements. Upper Green River cottonwoods that survived the dramatic hydrologic transition to the post-dam period responded by sacrificing branches, which lowered transpiration, an adjustment that would also limit photosynthesis and reduce growth (Tyree *et al*., 1994; Rood *et al*., 2000; Scott *et al*., 2000). Hundreds of dead cottonwoods litter the Upper Green River floodplain, indicating that many trees were unable to adjust to reservoir filling and the novel post-dam flow regime. Cottonwoods are known to be highly sensitive to drought-induced xylem cavitation (Tyree *et al*., 1994), and under-reduced water availability *P. deltoides* have been shown to sacrifice branches before tree death (Scott *et al*., 1999). In a *P. deltoides* floodplain forest in eastern Colorado, early leaf senescence and twig shedding occurred 2–3 weeks after groundwater levels were lowered, indicating rapid tree responses to reduced groundwater availability (Cooper *et al*., 2003b). Similar processes likely occurred at the Upper Green River in 1963, resulting in large-scale losses of branches and whole trees, and decreased growth rates in surviving trees.

Reduced ring widths indicate that the post-dam Upper Green River floodplain provided poor growing conditions for cottonwood trees. This was likely caused by reduced soil water recharge from the small annual river stage changes and competition with desert shrubs and grasses that now dominate the understory beneath the cottonwoods (Merritt and Cooper, 2000). Branch and root sacrifices are mechanisms that may have helped trees survive the onset of regulation, but also left trees with reduced growth capacity that persisted throughout the post-dam study period. The altered flow and sediment regimes have changed the channel geometry and floodplain vegetation of the Upper Green River (Merritt and Cooper, 2000) and, along with the reduction in peak flows, have nearly eliminated cottonwood seedling establishment (Cooper *et al*., 2003a). Because of the lack of recruitment, continued decrease in the growth of mature cottonwoods, and periodic fires that have burned through the dried floodplain and killed many stands of trees, the Upper Green River likely will lack cottonwood-dominated forests in the future.

CONCLUSIONS

Floodplain forests are critical components of semi-arid landscapes. Whilst previous research has focussed on the effects of flow regulation on cottonwood regeneration, there has been less emphasis on the long-term effect of flow regulation on existing trees. The Yampa–Green River system is one of the few places in North America where a comparison of similar riparian ecosystems under fully, partially, and unregulated flow conditions can occur. Flow regulation has triggered a persistent decline in tree growth on the Upper Green River, whilst the partially regulated Lower Green River and the unregulated Yampa River supported similar growth rates. In the post-dam period, mean growing season, mean annual, and peak annual discharges were the physical drivers most highly correlated with tree growth under all levels of regulation. Cottonwood growth patterns across sites suggest that managing flow releases to resemble the historic flow regime may help maintain existing floodplain forests. Preservation of existing floodplain forests would allow land and river managers time to develop strategies for restoring flood regimes, channel dynamics, and cottonwood regeneration which are ultimately necessary for these ecosystems to persist.

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REFERENCES

Andersen DC, Cooper DJ, Northcott K. 2007. Dams, floodplain land use, and riparian forest conservation in the semiarid Upper Colorado River Basin, USA. *Environmental Management* **40**: 453–475. DOI:10.1007/s00267-006-0294-7.

Andrews ED. 1986. Downstream effects of Flaming Gorge Reservoir on the Green River, Colorado and Utah. *Geological Society of America Bulletin* **97**: 1012–1023. DOI:10.1130/0016-7606(1986)97<1012:DEOFGR>2.0.CO;2.

Biondi F, Qeadan F. 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Research* **64**: 81–96. DOI:10.3959/2008-6.1.

Budescu DV. 1993. Dominance analysis: a new approach to the problem of relative importance of predictors in multiple regression. *Psychological Bulletin* **114**: 542–551. DOI:10.1037/0033-2909.114.3.542.

Bunn AG. 2010. Statistical and visual crossdating in R using the dplR library. *Dendrochronologia* **28**: 251–258. DOI:10.1016/j.dendro.2009.12.001.

Bunn SE, Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* **30**: 492–507. DOI:10.1007/s00267-002-2737-0.

Busch DE, Smith SD. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the Southwestern U.S. *Ecological Monographs* **65**: 347–370. DOI:10.2307/2937064.

Coble AP, Kolb TE. 2012. Riparian tree growth response to drought and altered streamflow along the Dolores River, Colorado. *The Western Journal of Applied Forestry* **27**: 205–211. DOI:10.5849/wjaf.12-001.

Cooper DJ, Andersen DC. 2012. Novel plant communities limit the effects of a managed flood to restore riparian forests along a large regulated river. *River Research and Applications* **28**: 204–215. DOI:10.1002/rra.1452.

Cooper DJ, Andersen DC, Chimner RA. 2003a. Multiple pathways for woody plant establishment on floodplains at local to regional scales. *Journal of Ecology* **91**: 182–196.

Cooper DJ, D'Amico DR, Scott ML. 2003b. Physiological and morphological response patterns of *Populus deltoides* to alluvial groundwater pumping. *Environmental Management* **31**: 215–226. DOI:10.1007/s00267-002-2808-2.

Cooper DJ, Merritt DM, Andersen DC, Chimner RA. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the Upper Green River, USA. *Regul. Rivers Res. Manag.* **15**: 419–440. DOI:10.1002/(SICI)1099-1646(199909/10)15:5<419::AID-RRR555>3.0.CO;2-Y.

Courville T, Thompson B. 2001. Use of structure coefficients in published multiple regression articles: β is not enough. *Educational and Psychological Measurement* **61**: 229–248. DOI:10.1177/0013164401612006.

DeWine JM, Cooper DJ. 2007. Effects of river regulation on riparian box elder (*Acer negundo*) forests in canyons of the Upper Colorado River Basin, USA. *Wetlands* **27**: 278–289.

Edmondson J, Friedman J, Meko D, Touchan R, Scott J, Edmondson A. 2014. Dendroclimatic potential of plains cottonwood (*Populus deltoides* subsp. *monilifera*) from the Northern Great Plains, USA. *Tree-Ring Research* **70**: 21–30. DOI:10.3959/1536-1098-70.1.21.

Friedman JM, Auble GT, Shafroth PB, Scott ML, Merigliano MF, Freehling MD, Griffin ER. 2005. Dominance of non-native riparian trees in western USA. *Biological Invasions* **7**, 747–751. doi:10.1007/s10530-004-5849-z

Friedman JM, Osterkamp WR, Scott ML, Auble GT. 1998. Downstream effects of dams on channel geometry and bottomland vegetation: regional patterns in the Great Plains. *Wetlands* **18**: 619–633.

Grams PE, Schmidt JC. 2005. Equilibrium or indeterminate? Where sediment budgets fail: sediment mass balance and adjustment of channel form, Green River downstream from Flaming Gorge Dam, Utah and Colorado. *Geomorphology* **71**: 156–181. DOI:10.1016/j.geomorph.2004.10.012.

Hultine KR, Bush SE, Ehleringer JR. 2010. Ecophysiology of riparian cottonwood and willow before, during, and after two years of soil water removal. *Ecological Applications* **20**: 347–361. DOI:10.1890/09-0492.1.

Hupp CR, Osterkamp WR. 1996. Riparian vegetation and fluvial geomorphic processes. *Geomorphology, Fluvial Geomorphology and Vegetation* **14**: 277–295. DOI:10.1016/0169-555X(95)00042-4.

Johnson WC. 1994. Woodland expansions in the Platte River, Nebraska: patterns and causes. *Ecological Monographs* **64**: 45–84. DOI:10.2307/2937055.

Johnson WC, Dixon MD, Scott ML, Rabbe L, Larsen G, Volke M, Werner B. 2012. Forty years of vegetation change on the Missouri River Floodplain. *BioScience* **62**: 123–135. DOI:10.1525/bio.2012.62.2.6.

Kraha A, Turner H, Nimon K, Zientek LR, Henson RK. 2012. Tools to support interpreting multiple regression in the face of multicollinearity. *Frontiers in Psychology* **3**. DOI:10.3389/fpsyg.2012.00044.

Kuiper JJ, Janse JH, Teurlincx S, Verhoeven JTA, Alkemade R. 2014. The impact of river regulation on the biodiversity intactness of floodplain wetlands. *Wetlands Ecology and Management* **22**: 647–658. DOI:10.1007/s11273-014-9360-8.

Lumley T, Miller A. 2009. Leaps: regression subset selection.

Lytle DA, Merritt DM. 2004. Hydrologic regimes and riparian forests: a structured population model for cottonwood. *Ecology* **85**: 2493–2503. DOI:10.1890/04-0282.

Mahoney JM, Rood SB. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. *Wetlands* **18**: 634–645. DOI:10.1007/BF03161678.

McCully P. 1996. Silenced rivers: the ecology and politics of large dams. xvi + 350 pp.

Meko DM, Friedman JM, Touchan R, Edmondson JR, Griffin ER, Scott JA. 2015. Alternative standardization approaches to improving streamflow reconstructions with ring-width indices of riparian trees. The Holocene 0959683615580181.

Merritt DM, Cooper DJ. 2000. Riparian vegetation and channel change in response to river regulation: a comparative study of regulated and unregulated streams in the Green River Basin, USA. *Regulated Rivers Research & Management* **16**: 543–564. DOI:10.1002/1099-1646(200011/12)16:6<543::AID-RRR590>3.0.CO;2-N.

Merritt DM, Poff NLR. 2010. Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers. *Ecological Applications* **20**: 135–152. DOI:10.1890/08-2251.1.

Moog DB, Whiting PJ, Thomas RB. 1999. Streamflow record extension using power transformations and application to sediment. *Water Resour. Res.* **35**: 243–254. DOI:10.1029/1998WR900014.

Nathans LL, Oswald FL, Nimon K. 2012. Interpreting multiple linear regression: a guidebook of variable importance. *Practical Assessment, Research & Evaluation* **17**: 2.

Nilsson C, Svedmark M. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Management* **30**: 468–480. DOI:10.1007/s00267-002-2735-2.

Poff NL, Olden JD, Merritt DM, Pepin DM. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Science* **104**: 5732–5737. DOI:10.1073/pnas.0609812104.

Poff NL, Zimmerman JKH. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* **55**: 194–205. DOI:10.1111/j.1365-2427.2009.02272.x.

R Core Team. 2014. R Development Core Team. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reily P, Johnson W. 1982. The effects of altered hydrologic regime on tree growth along the Missouri River in North Dakota. *Canadian Journal of Botany-Revue* **60**: 2410–2423.

Richter BD, Baumgartner JV, Powell J, Braun DP. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* **10**: 1163–1174. DOI:10.1046/j.1523-1739.1996.10041163.x.

Rood SB, Ball DJ, Gill KM, Kaluthota S, Letts MG, Pearce DW. 2013. Hydrologic linkages between a climate oscillation, river flows, growth, and wood $\Delta^{13}C$ of male and female cottonwood trees: hydrological linkages for riparian cottonwoods. *Plant, Cell & Environment* **36**: 984–993. DOI:10.1111/pce.12031.

Rood SB, Braatne JH, Hughes FMR. 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. *Tree Physiology* **23**: 1113–1124. DOI:10.1093/treephys/23.16.1113.

Rood SB, Heinze-Milne S. 1989. Abrupt downstream forest decline following river damming in southern Alberta. *Canadian Journal of Botany* **67**: 1744–1749. DOI:10.1139/b89-221.

Rood SB, Mahoney JM. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environmental Management* **14**: 451–464.

Rood SB, Patiño S, Coombs K, Tyree MT. 2000. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. *Trees* **14**: 248–257.

Salzer MW, McCord VAS, Stevens LE, Webb RH. 1996. The dendrochronology of *Celtis reticulata* in the Grand Canyon: assessing the impact of regulated river flow on tree growth, in: Tree Rings, Environment, and Humanity. Department of Geosciences, University of Arizona, Tucson, AZ, pp. 273–281.

Scott ML, Friedman JM, Auble GT. 1996. Fluvial process and the establishment of bottomland trees. *Geomorphology, Fluvial Geomorphology and Vegetation* **14**: 327–339. DOI:10.1016/0169-555X(95)00046-8.

Scott ML, Lines GC, Auble GT. 2000. Channel incision and patterns of cottonwood stress and mortality along the Mojave River, California. *Journal of Arid Environments* **44**: 399–414. DOI:10.1006/jare.1999.0614.

Scott ML, Shafroth PB, Auble GT. 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environmental Management* **23**: 347–358. DOI:10.1007/s002679900191.

Shafroth PB, Stromberg JC, Patten DT. 2002. Riparian vegetation response to altered disturbance and stress regimes. *Ecological Applications* **12**: 107–123. DOI:10.1890/1051-0761(2002)012[0107:RVRTAD]2.0.CO;2.

Snyder KA, Williams DG. 2000. Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. *Agricultural and Forest Meteorology* **105**: 227–240. DOI:10.1016/S0168-1923(00)00193-3.

Stromberg JC, Patten DT. 1990. Riparian vegetation instream flow requirements: a case study from a diverted stream in the Eastern Sierra Nevada, California, USA. *Environmental Management* **14**: 185–194. DOI:10.1007/BF02394035.

Tyree MT, Kolb KJ, Rood SB, Patiño S. 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. DOI:10.1093/treephys/14.5.455.

Vörösmarty CJ, Bos R, Balvanera P. 2005. Fresh water. Ecosystems and Human Well-Being: Current STate and Trends. Vol. 1, 165p.

Ward JV, Tockner K, Schiemer F. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers: Research and Management* **15**: 125–139.

Wilding TK, Sanderson JS, Merritt DM, Rood SB, Poff NL. 2014. Riparian responses to reduced flood flows: comparing and contrasting narrowleaf and broadleaf cottonwoods. *Hydrological Sciences Journal* **59**: 605–617. DOI:10.1080/02626667.2014.880786.

Williams CA, Cooper DJ. 2005. Mechanisms of riparian cottonwood decline along regulated rivers. *Ecosystems* **8**: 382–395. DOI:10.1007/s10021-003-0072-9.

Wohl E, Bledsoe BP, Jacobson RB, Poff NL, Rathburn SL, Walters DM, Wilcox AC. 2015. The natural sediment regime in rivers: broadening the foundation for ecosystem management. *BioScience* **65**: 358–371. DOI:10.1093/biosci/biv002.

DOI: 10.1002/rra