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EFFECTS OF RIVER REGULATION ON RIPARIAN BOX ELDER (*ACER NEGUNDO*) FORESTS IN CANYONS OF THE UPPER COLORADO RIVER BASIN, USA

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Abstract: Canyon riparian zone vegetation is vulnerable to effects of upstream river regulation. We studied box elder (*Acer negundo*) dominated canyon riparian forests intensively on the Green and Yampa rivers in Dinosaur National Monument, Colorado, and extensively in four other major rivers of the upper Colorado River Basin to determine the effects of river regulation on riparian tree establishment patterns. We: 1) aged individuals to determine if establishment was correlated with high annual peak flows, 2) mapped cohorts to determine if the areal extent of post-regulation cohorts was reduced on regulated compared to unregulated river reaches, and 3) measured the floodplain position of cohorts in regulated and unregulated rivers to determine if establishment was confined to lower landscape positions under regulated flow regimes. Box elder establishment was highly correlated with annual peak flows, with most recruitment occurring during years with unusually high peak flows. In regulated river reaches recruitment was facilitated by annual peak flows that were below average under a natural flow regime but were unusually high under the post-dam flow regime. The areal extent of post-regulation box elder cohorts was reduced on the regulated river compared to pre-regulation cohorts on all rivers, and recent cohorts on an unregulated river. Post-regulation cohorts on regulated rivers established at lower landscape positions than cohorts on unregulated rivers, resulting in inset floodplain forests on regulated rivers. The reduction in establishment height above the river was directly proportional to the magnitude of post-regulation peak flow reduction. Controlled high magnitude flood releases would facilitate forest regeneration across the full extent of historic forests, and peak flows that would mimic a lower magnitude natural hydrograph would facilitate establishment in the inset floodplain. In an era of increasing consumption of shrinking water supplies, opportunities for high magnitude reservoir releases are likely to diminish, increasing the need for active management of riparian forest ecosystems.

Key Words: dams, Dinosaur National Monument, flood, flow regime, Green River, inset floodplain, Yampa River

INTRODUCTION

Riparian zones are diverse and dynamic ecosystems that provide habitat and migration corridors for a wide range of plant and animal species (Gregory et al. 1991, Naiman et al. 1993, Naiman and Decamps 1997). Seasonal high flows provide an influx of water and sediment to floodplains and maintain the periodic disturbance regime necessary for the establishment and survival of riparian plants (Poff et al. 1997, Bendix and Hupp 2000). Large dams can modify the magnitude, duration, and frequency of flooding, resulting in altered patterns of floodplain water and nutrient availability (Williams and Wolman 1984, Nilsson 1992, Molles et al. 1998) and riparian plant establishment (Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Friedman et al. 1998, Cooper et al. 1999, Merritt and Cooper 2000).

Riparian zones have been heavily impacted by anthropogenic factors including settlement, agriculture, grazing, timber harvesting, gravel mining, groundwater pumping, river regulation, and non-native species invasions (National Research Council 1992). Riparian zones in deep canyons are relatively inaccessible due to their rugged topography, leaving them unaffected by many direct human impacts. The dramatic landscapes and seemingly pristine nature of canyons have led to their protection as national parks and refuges in many parts of the world, particularly in the southwestern United States. Yet canyons are also ideal settings for the construction of large dams, which can dramatically alter river flow regimes for hundreds of km downstream (Rood et al. 1995).

The response of stream channels and riparian vegetation to river regulation is influenced by several factors including pre- and post-dam river flow regimes, channel type, and the species involved. Regulation has been shown to cause multi-threaded channels to narrow and trigger a pulse of woody plant establishment on abandoned channel margins (Nadler and Schumm 1981, Williams and Wolman 1984, Johnson 1994, Scott et al. 1996, Friedman et al. 1998). Along meandering rivers, regulation-induced reductions in stream power have decreased channel migration rates and limited the formation of woody plant establishment sites (Johnson et al. 1976, Bradley and Smith 1986, Rood and Mahoney 1990, Johnson et al. 1992, Friedman et al. 1998). Stabilized river flows, which result from reduced peak and increased base flows, can allow marsh vegetation to develop on islands and bars, and desert shrubs to invade senescing riparian forests (Merritt and Cooper 2000).

Canyon river floodplains are characterized by narrower valley and channel widths, higher stream power, steeper stream gradients, and larger stage changes for given changes in discharge compared to non-canyon river reaches. Seasonal flooding, which facilitates recruitment on high elevation surfaces that are safe from future fluvial disturbances, may be the dominant recruitment pathway (Scott et al. 1996). Woody plant recruitment can occur in pool and eddy margins following high flows and on low elevation gravel bars following successive years of regulation-induced low flows (Shafroth et al. 1998, Cooper et al. 2003).

Existing canyon riparian forests can potentially respond to river regulation that reduces peak flows in two ways: 1) the dominant woody species fail to reproduce and are replaced by other riparian or upland species, or 2) recruitment is confined to lower elevation surfaces, resulting in the development of an inset floodplain forest with similar species composition to the pre-dam forest. Regulation of the Colorado River in the Grand Canyon has resulted in the replacement of forests dominated by native mesquite (*Prosopsis glandulosa* Torr.) with a woody plant community dominated by non-native tamarisk (*Tamarix ramosissima* Ledebour) on newly formed fluvial surfaces (Turner and Karpiscak 1980, Johnson 1991). In the Black Canyon of the Gunnison River, regulation has resulted in establishment of the historically dominant species, box elder (*Acer negundo* L. var. *interius* (Britt.) Sarg.), closer to the river channel on formerly unvegetated sediments, with an increase in forest area (Auble et al. 1994).

Box elder occupies a wide range of environments in eastern North America; however, in western North America it is found primarily in river canyons where it may form extensive riparian forests. In contrast to woody riparian plants in the family *Salicaceae* (species of *Salix* and *Populus*), box elder produces large seeds that are released in the fall, over-winter on floodplains, and germinate the following spring (Green 1934). In addition, seedlings can establish on leaf litter and grow in shaded environments (Wilson 1970, Johnson et al. 1976). Box elder is a facultative phreatophyte and is sometimes found in ephemeral drainages that ascend far above the water table. It is unknown whether box elder seed germination and seedling establishment may be tied to seasonal flooding and how river regulation might influence the future of the riparian forests it now dominates.

This study analyzes the effects of river regulation on box elder forests in canyons of the upper Colorado River Basin. The Colorado River Basin is one of the most intensively managed in the world (Graf 1985), with dams on most major rivers flowing from headwater areas in the southern Rocky Mountains. We worked intensively on floodplains of the Green and Yampa rivers within Dinosaur National Monument and extensively on four other large river floodplains in the basin to test the following hypotheses: 1) box elder establishment is dependent on high river flows; 2) the areal extent of post-dam box elder cohorts is reduced on regulated compared with unregulated river reaches, and 3) post-dam box elder cohorts establish in lower landscape positions on regulated rivers relative to unregulated rivers.

STUDY AREA

The Colorado River Basin drains 63.6 million hectares in the western United States and Mexico. We worked along six major snowmelt-driven rivers in the upper basin: the Colorado, Dolores, Green, Gunnison, San Miguel, and Yampa rivers in western Colorado and eastern Utah (Figure 1). Upper basin rivers were chosen for analysis based on accessibility and the presence of box elder populations. Study sites were at 1,500–1,900 m elevation in areas with a semi-arid climate.

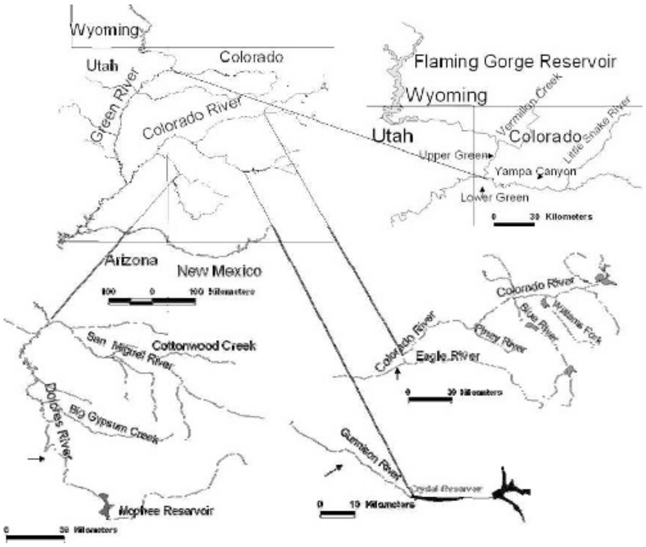

Figure 1. Location of study areas in upper Colorado River Basin. Study sites are indicated by arrows.

Fifteen dams store snowmelt runoff in the upper Colorado River Basin, with most constructed between 1943 and 1968. Trans-basin water projects divert 14% of the mean annual Colorado River flow to the South Platte River Basin (Liebermann et al. 1989). Our Colorado River study site was located in Glenwood Canyon, 10 km below the confluence with the Eagle River, at 1,900-m elevation (Figure 1). The Gunnison River is regulated by Crystal, Morrow Point, and Blue Mesa dams, constructed between 1966 and 1976, and one trans-basin diversion tunnel (Table 1). The study site was located in the upper Gunnison Gorge at 1,700-m elevation, 30 km downstream from Crystal Dam, the lowest dam on the river (Figure 1). Flow at the study site is controlled by dam releases.

McPhee Dam has regulated the Dolores River since 1984 (Table 1). The reservoir is operated for irrigation and hydropower purposes with irrigation diversions directly from the reservoir pool. Consequently, flow from the dam is very low in most years. The study site is in the Dolores River Canyon ~50 km below the dam at 1,900-m elevation (Figure 1). The San Miguel River is a free-flowing tributary of the Dolores River (Table 1). The study site is ~40 km upstream from the Dolores River confluence at 1,700-m elevation (Figure 1).

Flaming Gorge Dam, located 90 km upstream from the upper Green River (Lodore Canyon) study site, has regulated the Green River since 1963. The mean annual peak flow has been reduced from 309 m^3/s to 146 m^3/s, and the magnitude of late summer and winter flows have increased (Table 1). This has reduced seasonal flow variation; however, the mean annual flow of 59 m^3/s has been unaffected. The mean annual flow of the Yampa River is similar to that of the Green River at 60 m^3/s, but it retains seasonal flow variability with a mean annual instantaneous peak flow of 394 m^3/s and low flow of 12 m^3/s (Table 1). The lower Green River (Whirlpool Canyon), located downstream from the Yampa River confluence, has the seasonal flow variability of the Yampa River, but the magnitude of its high and low flows are modified by the Green River's regulated flows (Cooper et al. 1999, Cooper et al. 2003). The three study reaches within Dinosaur National Monument—the Yampa River (Yampa Canyon), the upper Green River (Lodore Canyon), and the lower Green River (Whirlpool Canyon) (Figure 1)—are

Table 1. Date of river regulation onset, mean historic peak annual flow, mean recent peak annual flow, time periods used to derive peak flow means, percent reduction in peak flow, and regulation status for upper Colorado River Basin study rivers. Upper Green River data were used for Lodore Canyon, and lower Green River data were used for Whirlpool Canyon. Years 1929–62 were used to compute historic mean annual peak flow when flow data was available. Years 1964–2004 were used to compute recent annual peak flow unless onset of regulation was after 1964. See text for gauging station numbers and location.

		Annual Peak Flow					
		Historic		Recent			
River	Regulation Onset	Period	Mean	Period	Mean	Peak Flow Reduction	Regulation Status
Colorado	1943–68	1941–62	333 m^3/s	1964–2004	254 m^3/s	24%	Intermediate
Dolores	1984	1939–52	149 m^3/s	1984–2004	71 m^3/s	52%	High
Upper Green	1963	1929–62	309 m^3/s	1964–2004	146 m^3/s	53%	High
Lower Green	1963	1947–62	653 m^3/s	1964–2004	495 m^3/s	24%	Intermediate
Gunnison	1966–76	1929–62	237 m^3/s	1977–2004	110 m^3/s	54%	High
San Miguel	NA	1941–62	96 m^3/s	1964–2004	86 m^3/s	10%	None
Yampa	NA	1929–62	377 m^3/s	1964–2004	394 m^3/s	0	None

characterized by steep confining bedrock walls, very narrow floodplains, and mean stream gradients of 0.003 m/m (Cooper et al. 2003). The elevation of the study sites ranged from 1,500–1,600 m.

Early explorers along the canyons of the Green and Yampa rivers produced photographic and written evidence of extensive box elder riparian forests (Powell 1875, Dellenbaugh 1908, Hillers 1972, Stephens and Shoemaker 1987). In Lodore Canyon on the Green River above its confluence with the Yampa River, extensive stands of mature and senescent box elders occur on high terraces created by large pre-Flaming Gorge Dam floods (Grams and Schmidt 1999). Using the terminology of Grams and Schmidt (1999), we refer to these as cottonwood-box elder terraces (c-b terrace). River regulation has eliminated flows large enough to inundate the c-b terrace. Adjacent to the c-b terrace and lower in elevation is the intermediate bench (Grams and Schmidt 1999) formed by flows greater than Flaming Gorge Dam power plant capacity (126 m^3/s). Since the closure of Flaming Gorge Dam in 1962, flows exceeding power plant capacity have occurred in 1983, 1984, 1986, 1997, and 1999.

METHODS

Stream Flow

Discharge data for each river reach is available from USGS gauging station records. Gunnison River flows were obtained from below the Gunnison tunnel, Colorado (USGS gauge #9128000) for the period 1929–2004. The Colorado River flow was obtained from the gauge near Dotsero, Colorado (#9070500) for the period 1941–2004. Dolores River flows for the period 1939–52 were obtained from the McPhee, Colorado, gauge (#9167500), and the Bedrock, Colorado, gauge (#9169500) for the period 1971–2004. Dolores flow data for 1952–71 are unavailable. Flows for the San Miguel River were obtained from the Naturita, Colorado, gauge (#9175500) for the period from 1941–62, and the Uravan, Colorado, gauge (#9177000) for the period 1984–2004. The Linwood, Utah, gauge (#9225500) was used for the upper Green River for the years 1929–1962 and the Greendale, Utah, gauge (#9234500) located just below the dam was used for the years 1963–2004. Yampa River flow was calculated by summing the Yampa River flow at Maybell, Colorado (#09251000) and the Little Snake River at Lily Park, Colorado (#09261000) for the period 1922–2004. Flow data for the lower Green River was obtained from the Jensen, Utah, gauge (#09261000) for the period 1947–2004.

Spatial and Temporal Establishment Patterns in Dinosaur National Monument

Spatial and temporal patterns of box elder establishment in regulated and unregulated reaches within Dinosaur National Monument were compared by determining the elevation above river base flow and establishment year for randomly selected trees. Each study reach was divided into five (Lodore and Whirlpool Canyons) or six (Yampa Canyon) equal-length segments. The Yampa Canyon was represented with an additional sample site due to its greater length. When entering each canyon segment by raft, the first suitable stand was chosen for analysis. Suitable stands contained at least 60 juvenile/young adult box elder plants. Juvenile/young adult trees were less than 20 cm in diameter near their base, less than 6 m tall, and typically had single stems with smooth bark and few dead branches. Mature box elders were greater than 20 cm in diameter near the base, greater than 6 m tall, and had multiple live and dead stems. Each box elder in the stand was assigned a number, and individuals were selected for sampling using a random number table. Six to 10 juvenile/young adult box elders were excavated per stand depending on the local population size. Ten mature box elders were also sampled in each stand. The ground elevation at the base of each sample tree was measured relative to the river elevation at low flow using surveying instruments, and the depth to root crown was subtracted from the ground surface elevation to determine the germination surface elevation for each tree. Yampa Canyon sample elevations are relative to river stage at a discharge of 19–28 m^3/s, Lodore Canyon at 22–24 m^3/s, and Whirlpool Canyon at 29–32 m^3/s.

Juvenile/young adult box elders were excavated using hand shovels. On two occasions, excavation revealed that the plant was actually a sprout connected to a mature plant, and substitute plants were selected. The root crown portion of each plant was collected and sectioned into 1- to 5-cm thick slabs, and then sanded to a smooth finish using sequentially finer sandpaper to 30 μm. The slab with the germination point, where the pith originates, was identified as the slab with pith on its top but not bottom side (Scott et al. 1997, Gutsell and Johnson 2002, Cooper et al. 2003, Birken and Cooper 2006). Slabs containing the germination point were then treated with a phloroglucinol solution, which increases annual ring visibility in diffuse porous species such as box elder (Patterson 1961). Rings were counted using a dissecting microscope. False rings were detected by the presence of an incomplete transition between early and late-wood vessels through some portion of the stem. Partial and missing rings were detected by cross-dating between the sections of each sample. Multiple ring counts were taken from different positions on each slab (minimum eight separate counts). Observer error was controlled by periodically conducting independent ring counts using one to three additional researchers. Seventeen trees could not be used due to heartwood rot or inadvertent failure to excavate the root crown.

The largest live stem on mature trees was cored near its base using an increment borer. Most mature trees had many dead stems and live stems were often rotten in the center. Cores were retained if at least 25% of the stem radius could be extracted in an intact core. Trees with only rotten stems were excluded, and a substitute tree was chosen. Cores were mounted on wood blocks, sanded with incrementally finer papers ending with 30-μm sandpaper, and the rings were counted using a dissecting microscope to determine the minimum tree age.

Box Elder Stand Mapping

Box elder stands in Dinosaur National Monument were mapped in the field onto United States Geological Survey (USGS) digital orthophoto quarter quadrangles (30108 NW and 30108 SW) with 1-m resolution. The total canopy cover of mature (established prior to the 1960s) and juvenile/young adult (established after or during the 1960s) within each polygon was visually estimated in the field. Size/age relationships were developed using the dendrochronological techniques described in the preceding section. We only included box elder stands that occurred on the main stem of each river and ignored those on tributary drainages. Polygons were digitized using Arcview 3.0 (ESRI 1996), the area of each polygon was calculated, multiplied by the cover of each size class, and summed to produce total areal cover (ha) for both pre- and post-1960s cohorts on each study reach. The ratio of pre-1960s to post-1960s box elder stands on each study reach was calculated and compared.

Spatial Establishment Patterns in the Upper Colorado River Basin

The relative elevations of box elders established before and after the 1960s was analyzed for the Gunnison, Colorado, Dolores, and San Miguel rivers using the size/age relationships described prior. Because we did not perform ring counts on these trees, trees in the 15- to 25-cm diameter range that could fit into either age class were excluded from analysis. Study sites were confined to public land and selected based on accessibility and the presence of box elder populations with multiple age/size classes. Within each study reach, two to five stands were chosen for analysis depending on accessibility. Each box elder in the stand was assigned a number, and individuals were selected for sampling using a random number table. In each stand the ground surface elevation of 10 mature and juvenile trees (total $n = 280$) was measured relative to river base-flow elevation.

Statistical Analysis

Nonlinear Poisson regression analysis was used to determine the relationship between the annual peak discharge for each river reach and the number of plants established each year in Dinosaur National Monument. The discrete Poisson distribution, which approximates the normal distribution at high counts, is most appropriate for analyzing count data (*n* trees established per year) (McCullagh and Nelder 1989). The Poisson analysis employs the log link function to ensure negative count data will not occur and a scaling factor can be used to control overdispersion of the data (Stokes et al. 2000, Merritt and Wohl 2002). Overdispersion can occur when the observed variance is larger than the nominal variance for a particular distribution. This is a common situation in the analysis of discrete counts because the variance is fixed by a single parameter, the mean. The relationship between peak discharge and number of plants established was overdispersed because we found no recruitment in most years and high recruitment in a few years. Overdispersion was managed by setting the scaling parameter to one during the estimation procedure of the Poisson regression. The independent variables used in this analysis were peak flow (m^3/s) for a given year (P_0), as well as peak flow in the previous (P_{-1}) and subsequent year (P_{+1}). The dependent variable was number of plants established in a given year. The nonlinear models were fitted using maximum likelihood estimation and the parameters of the model were estimated numerically through an iterative fitting process. The deviance divided by the degrees of freedom and pseudo-R^2 were used to assess the strength of the model in predicting the number of seedlings established for a given flow magnitude. A good model fit is indicated by a deviance divided by degrees of freedom (DEV/df) of 1, while DEV/df > 1 indicates overdispersion. The pseudo-R^2 is an analog of r^2 in linear regression, but is calculated as the proportion of the variance explained in a model including the explanatory variable vs. a model fitted using only the intercept; pseudo-R^2 = ($DEV_{\beta o} - DEV_{\beta o-\beta 1x1}$)/$DEV_{\beta o}$). The significance of peak flow magnitude determining the number of samples established was assessed using likelihood ratio tests for type III analysis.

Repeated measures ANOVA was used to test for the effects of river reach and period of establishment (pre-1963 versus post-1963) on plant elevation above the river channel in Dinosaur National Monument. Repeated measures analysis was deemed appropriate because using a split-plot experimental design, measurements were taken for two correlated response variables (pre- and post-dam establishment elevations) for each experimental unit (river reach). Analyses were performed using PROC MIXED in SAS version 8.0, with sample site nested within study reach (random effect) and the era of establishment as the two response variables measured for each unit (SAS 1999). Linear contrasts were used to test the *a priori* hypothesis that the difference between pre- and post-dam establishment elevations was correlated with degree of regulation, and therefore was highest in Lodore Canyon, intermediate in Whirlpool Canyon, and lowest in Yampa Canyon. Pairwise differences between era of establishment for each canyon were analyzed using differences of least squares means (α = 0.05).

Change in box elder establishment elevation on the Gunnison, Colorado, San Juan, Dolores, Yampa, and Green River reaches was standardized by using the ratio between the elevation, relative to the river, of trees established before the 1960s and the elevation of trees established after the 1960s ($Elevation_{recent}/Elevation_{historic}$, abbreviated as EL_{chg}). This approach allows the comparison of change in establishment pattern on different size rivers. ANOVA was used to test for the effects of river on establishment elevation. Analysis was performed using PROC GLM with patch nested within river. Linear contrasts were used to test the *a priori* hypothesis that the EL_{chg} was highest in the unregulated river reaches (Yampa, San Miguel), intermediate in the partially regulated river reaches (Whirlpool, Colorado), and lowest in the highly regulated river reaches (Lodore, Gunnison, Dolores). Pairwise differences between period of establishment for each canyon were analyzed using Tukey's HSD procedure, with the familywise type I error rate controlled at α = 0.05.

Linear regression was used to analyze the effects of river regulation on the mean relative elevation of recent vs. historic box elder establishment for each study river. Historic annual peak flow was derived from USGS gauging stations for the years 1929–62

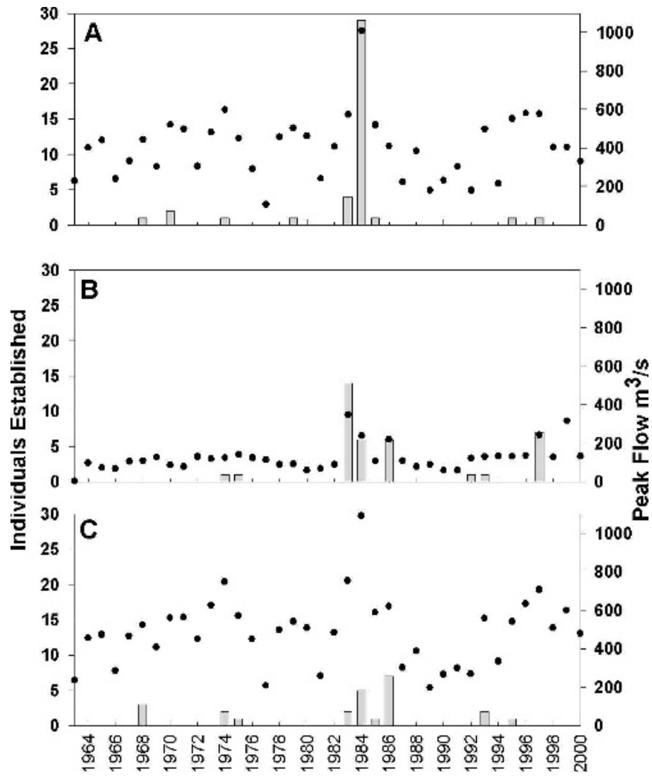

Figure 2. Timing of plant establishment for A) Yampa Canyon, B) upper Green (Lodore Canyon), C) lower Green (Whirlpool Canyon), and associated annual peak flows (m^3/s). Bars indicate number of plants established, and dots indicate annual peak flow (see text for USGS gauging station locations).

(Table 1). Recent peak flow was derived using data for the years 1964–2004, with the exception of the Dolores and Gunnison rivers, for which the years 1984–2004 and 1977–2004 were used (Table 1). The recent mean annual peak flow was divided by the historic peak annual peak flow to arrive at the $Flow_{recent}/Flow_{historic}$ ratio, abbreviated as FL_{chg}. SAS version 8.0 was used for all statistical analysis (SAS, 1999).

RESULTS

Temporal Establishment Patterns in Dinosaur National Monument

Seventy one percent of the 41 juvenile/young adult box elders sampled in Yampa Canyon established in 1984 when the largest flood on record occurred (peak flow = 915 m^3/s). Box elders also established in eight other years: 1968 (peak flow 444 m^3/s), 1970 (522 m^3/s), 1974 (599 m^3/s), 1979 (505 m^3/s), 1983 (575 m^3/s), 1985 (521 m^3/s), 1995 (553 m^3/s), and 1997 (578 m^3/s) (Figure 2). All establishment years featured peak flows higher than the 1963–2000 mean

Table 2. Results of Poisson regression analysis relating annual peak flow (P, units = m^3/s) to box elder recruitment in a given year along Dinosaur National Monument sampling reaches. Peak flow of the preceding (P_{-1}) and following year (P_{+1}) did not improve the model fit for any of the reaches; therefore, only peak flow of the establishment year (P_0) was included. The period of years evaluated 1964–2002 (n = 38), did not differ among sampling sites. However, the subset of years within that period during which recruitment was detected (N_{RY}) and the total number of sampled plants (N_{SP}) varied. Degrees of freedom (df) are calculated as the number of observations (n = 38) minus the number of parameters included in the Poisson model. The χ^2 and P-values for annual peak flow are tabulated. Pseudo-R^2 and deviance divided by degrees of freedom (DEV/df) measurements of predictive strength are also given. Deviance divided by degrees of freedom (DEV/df) = 1 indicates an excellent model fit, DEV/df > 1 indicates overdispersion and DEV/df < 1 indicates underdispersion. Statistical significance is based on likelihood ratio tests from type III analysis.

	Annual Peak Flow						
Study Reach	N_{RY}	N_{SP}	Df	(χ^2)	(P-value)	Psuedo-R^2	DEV/df
Yampa	9	41	36	373.4	< 0.0001	0.91	0.50
Upper Green	8	37	36	95.9	< 0.0001	0.71	1.10
Lower Green	9	24	36	26.67	< 0.0001	0.41	1.28

annual peak flow of 403 m^3/s. A Poisson regression analysis explained 91% of the variability of Yampa River recruitment when only peak flow in the establishment year (P_0) was included (Table 2). Peak flow of the preceding (P_{-1}) and following year (P_{+1}) did not improve the model fit. A DEV/df value of 0.50 indicates the model was somewhat limited by under-dispersion (Table 2), but the annual peak flow was significantly related to establishment ($\chi^2 = 373.4$, df = 36, P < 0.0001).

Box elder established in eight post Flaming Gorge Dam years in Lodore Canyon. However, 89% of the 37 sample trees established in 1983, 1984, 1986, and 1997, years in which controlled dam releases produced unusually large flows of greater than power plant capacity (Figure 2). The largest post-dam flood (in 1983) resulted in the establishment of 38% of all sample trees. Box elder also established in 1974, 1975, 1992, and 1993. The Poisson regression analysis explained 71% of the variability in box elder establishment when only peak flow in the year of establishment (P_0) was included (Table 2). Peak flow of the preceding (P_{-1}) and following year (P_{+1}) did not improve the model fit. A DEV/df value of 1.10 indicated a good model fit and annual peak flow was significantly related to establishment ($\chi^2 =$ 95.9, df = 36, P < 0.0001).

Box elder established in Whirlpool Canyon during nine years between 1963 and 2003. Seven samples were from 1986, five from 1984, three from 1968, two each from 1974, 1983, and 1993, and one each from 1975, 1985, and 1995 (Figure 2). Every sample tree established in a year when peak flow exceeded the post-dam mean annual peak flow on the lower Green River (486 m^3/s). Seventy-five percent of trees established during years when peak flow exceeded 600 m^3/s. The years 1983–86 had annual peak flows well above the mean for the lower Green River, and 63% of all samples established during these years. Poisson regression analysis explained 41% of the variability in recruitment when peak flow in the establishment year (P_0) was included; peak flow of the preceding (P_{-1}) and following year (P_{+1}) did not improve the model fit. A DEV/df value of 1.28 indicated a fairly good model fit (Table 2), and annual peak flow was significantly related to establishment ($\chi^2 = 26.67$, df = 36, P < 0.0001). The analyses from Lodore, Whirlpool, and Yampa canyons support hypothesis one: box elder establishment is dependent on high flows.

Box Elder Stand Area in Dinosaur National Monument

Lodore Canyon had the greatest total area of mature box elder forest, 27.5 ha, compared with 22.8 ha for the much longer Yampa Canyon and 6.2 ha for Whirlpool Canyon. The area of pre-1960s forest was 0.96 ha/km for Lodore Canyon, 0.31 ha/km for Yampa Canyon, and 0.44 ha/km for Whirlpool Canyon (Figure 3A). The area of young box elder forest was not proportionate to the area of pre-1960s forest. Yampa Canyon had the largest area of post-1960s forest, 11.7 ha, which was 0.17 ha/km, while Whirlpool Canyon had 2.5 ha at 0.18 ha/km, and Lodore Canyon had the lowest area 2.5 ha at 0.09 ha/km. Yampa Canyon had the highest ratio of post-1960s to pre-1960s box elder forest per river km (post/pre ratio) at 0.51, followed by Whirlpool Canyon at 0.41. The post/pre ratio for Lodore Canyon was much lower at 0.09. These data support hypothesis two: the areal extent of recently established (post-1960s) box elder cohorts is reduced on regulated compared with unregulated river reaches.

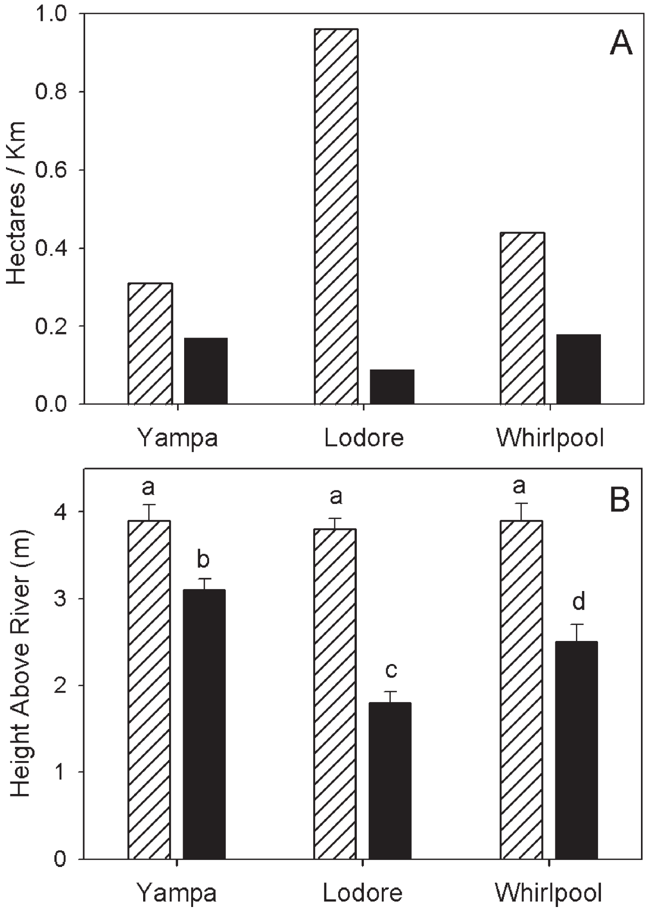

Figure 3. A) Hectares of box elder forest established per river km pre- (crosshatched bars) and post-1963 (filled bars) for study reaches in Yampa, Lodore, and Whirlpool canyons. The ratio of post/pre-regulation forest area was 0.51, 0.09, and 0.41 for Yampa, Lodore, and Whirlpool canyons, respectively. B) Height above river for box elders established pre- (crosshatched bars) and post-1963 (filled bars) (onset of Green River flow regulation) for study reaches in Yampa, Lodore, and Whirlpool canyons. Means with the same letter are not significantly different ($P > 0.05$).

Spatial Establishment Patterns in Dinosaur National Monument

In Lodore Canyon, pre-1963 box elders occurred high above the river on the c-b terrace, while juvenile-young adult box elders occurred only on the intermediate bench. Box elders in the Yampa Canyon were not vertically segregated by age class and occurred adjacent to, above, and below the elevation of mature trees, although the mean elevation of post-1963 trees was significantly lower than the pre-1963 mean for each study reach ($P = 0.0002$, $df = 163$) (Figure 3B) because of the presence of relatively young plants on low to middle elevation bars. In Whirlpool Canyon vertical segregation of mature and juvenile box elders exists, but not of the magnitude occurring in Lodore Canyon.

Study canyon and period of establishment (pre-1963 versus post-1963) were both highly significant ($P < 0.0001$) predictors of establishment elevation. Mean pre-1963 establishment elevations above the base flow water surface elevation were not significantly different ($P > 0.05$, $df = 163$) between the three study reaches: 3.9 ± 0.18 m for the Yampa, 3.9 ± 0.20 m for Whirlpool, and 3.8 ± 0.12 m for Lodore canyons (Figure 3B). However, the mean post-1963 establishment elevation was significantly different between study reaches ($P < 0.05$, $df = 163$), and was highest in Yampa Canyon, 3.1 ± 0.13 m, lower in Whirlpool, 2.5 m ± 0.20 m, and lowest in Lodore, 1.8 ± 0.13 m.

The difference between pre- and post-establishment elevations was greatest in Lodore Canyon, intermediate in Whirlpool, and lowest in Yampa. The difference was significantly greater in Lodore Canyon than in Yampa Canyon ($t = 3.83$, $df = 163$, $P < 0.001$); however, it was not significantly greater in Lodore than in Whirlpool ($t = 1.84$, $df = 163$, $P = 0.068$), or in Whirlpool than in Yampa ($t = 1.43$, $df = 163$, $P = 0.156$). These data support hypothesis three: post-dam box elder cohorts on regulated rivers occur in lower elevation landscape positions relative to those established under natural flow regimes. This has resulted in the formation of an inset floodplain forest.

Spatial Establishment Patterns in the Upper Colorado River Basin

The ratio of tree establishment elevations for the pre- and post-1960s time period (EL_{chg}) was lowest in regulated rivers (Figure 4). River was a statistically significant predictor of EL_{chg} ($P < 0.0001$). The unregulated San Miguel and Yampa rivers, 0.96 ± 0.03 and 0.79 ± 0.02, respectively, had higher EL_{chg} values than the other rivers studied ($\alpha = 0.05$). Whirlpool Canyon and the Colorado River had identical EL_{chg} values, 0.69 ± 0.03, and were significantly different from all other rivers, excluding the Dolores River ($\alpha = 0.05$). The EL_{chg} ratio was lowest for the highly regulated Dolores River (0.64 ± 0.03), Gunnison River (0.49 ± 0.03), and Lodore Canyon (0.47 ± 0.03). The Gunnison River EL_{chg} value was not significantly different from the other highly regulated rivers ($\alpha = 0.05$). The Lodore Canyon EL_{chg} value was significantly lower than all of the other rivers excluding the Gunnison ($\alpha = 0.05$).

EL_{chg} was significantly higher for unregulated than partially regulated ($P < 0.0001$) and highly

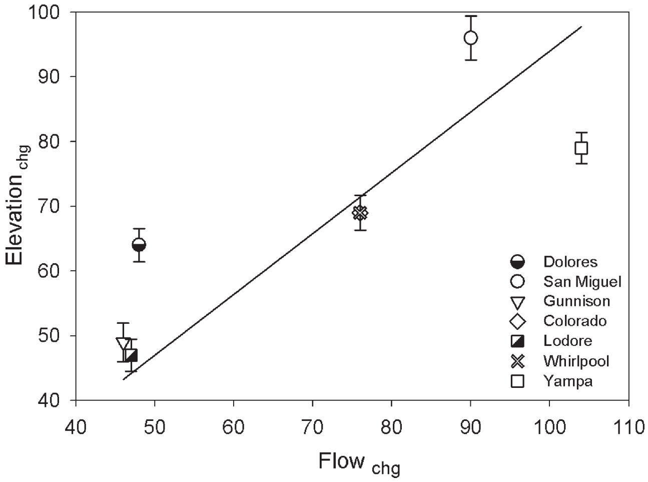

Figure 4. Regression of the recent proportion of historic peak flow magnitudes (FL_{chg}) and the proportion of the historic floodplain elevation (EL_{chg}) occupied by box elder trees established after the 1960s for upper Colorado River Basin river reaches ($F = 11.74$, $P = 0.0187$, $R^2 = 0.701$). Error bars indicate ± 1 SE. Note that lower Green and Colorado values are identical and the symbols are superimposed upon each other.

regulated rivers ($P < 0.0001$). Likewise, EL_{chg} was significantly lower for highly regulated than partially regulated rivers ($P = 0.0002$). FL_{chg} was a significant predictor of EL_{chg} ($F = 11.74$, $P = 0.0187$, $R^2 = 0.701$) (Figure 4) for all river reaches. These analyses support hypothesis three: post-dam box elder cohorts on regulated rivers will be in lower elevation landscape positions relative to those established under natural flow regimes.

DISCUSSION

Flood Flows and Box Elder Establishment

The positive association between the annual peak flow magnitude and box elder establishment indicates that box elder establishment is strongly dependent on high flows and is adversely affected by river regulation that reduces peak flows. The large proportion of Yampa Canyon juvenile box elders (71%) that established during the very large 1984 flood suggests that large, rare floods can lead to the recruitment of large numbers of riparian trees in canyon environments, as has been documented for alluvial settings (Friedman et al. 1996, Yin 1998). In regulated river reaches of the Green River, recruitment was facilitated by annual peak flows that would have been below average under a natural flow regime, but are well above average under the post-dam flow regime. Flaming Gorge Dam flows of greater than power plant capacity resulted in the establishment of 89% of all sampled trees in Lodore Canyon. In both Yampa and Lodore canyons, few or no trees established in years of low and moderate peak flow, indicating that high flows are the primary mechanism for box elder recruitment. Our results are likely due to the hot and arid conditions in the study canyons. Flooding may facilitate recruitment by creating sufficiently moist floodplain soils to allow germination and seedling establishment.

The high correlation between box elder establishment and peak flow magnitude differs from the findings of Friedman and Auble (1999) in the Black Canyon of the Gunnison River in Colorado. They examined the magnitude and duration of floods needed to remove or kill box elders and attempted to determine the establishment year of box elders using cores taken from the ground surface, slabs taken from the ground surface, and slabs taken from the root crown. However, they were not able to date box elder establishment to a given year. We know of no other study that has attempted to relate box elder establishment to river flow regime using dendrochronology; however, Johnson et al. (1976) tentatively attributed low densities of juvenile box elders on the Missouri River in North Dakota to a regulation-induced reduction in peak flow. Previous studies, which examined the effects of flow regime and peak flow regulation on woody plant establishment, were focused on early successional *Populus*, *Salix*, and *Tamarix* species (Scott et al. 1997, Cooper et al. 2003, Birken and Cooper 2006). This study demonstrates that large seeded species with distinctly different ecological characteristics also can be affected by river regulation.

Riparian Forest Area

Lodore Canyon supports the largest area of pre-1960s box elder cohorts in the study area; however, limited post-dam recruitment threatens the persistence of this forest. In contrast, Yampa and Whirlpool canyons support stands of box elders that established both before and after the construction of Flaming Gorge Dam. In the Gunnison River Canyon, a discontinuous box elder forest increased in area due to tree establishment in lower landscape positions following river regulation (Auble et al. 1994, Elliot and Parker 1997). High velocity pre-regulation Gunnison River floods scoured virtually all vegetation from the canyon bottom. River regulation decreased flood magnitudes and allowed vegetation to establish on formerly bare surfaces (Auble et al. 1994). Unlike the Gunnison River Canyon, conditions in the lower gradient Lodore Canyon were conducive to the formation and maintenance of extensive box elder riparian forests before river regulation. However, post-regulation conditions do not appear to be conducive to extensive forest formation possibly because the lower magnitude flood pulses trigger recruitment only on the narrow intermediate bench, which occupies approximately half the area of the c-b terrace (Grams 1997).

Inset Floodplains and Post-Regulation Flow Variability in Dinosaur National Monument

Flaming Gorge Dam operations have resulted in the isolation of mature Lodore Canyon box elder on high c-b terraces, which are now disconnected from fluvial geomorphic and hydrological processes. We found no box elder recruitment on c-b terraces in Lodore Canyon. Before the Flaming Gorge Dam was constructed, the c-b terrace was inundated by floods with a ~25-year recurrence interval; however, this surface was last inundated in 1957 by a flood peak of 544 m^3/s(Grams and Schmidt 2002). The largest post-dam bypass flow, in 1983, peaked at 348 m^3/s, which was far too small to reach the c-b terrace. The largest stems on trees cored on the c-b terrace are at least 80–100 years old, and many were senescing. Under current river management and climatic conditions, these deciduous forests will be replaced by semi-desert woodlands, a situation analogous to the replacement of cottonwood forest by desert shrubs along upstream alluvial Green River reaches below Flaming Gorge Dam (Merritt and Cooper 2000).

The floodplain forest, which is developing on the intermediate bench in Lodore Canyon, is dominated by both box-elder and tamarisk and occurs on bars inset into the relict pre-dam c-b terrace. The intermediate bench forest exists solely due to recruitment triggered by post-dam floods that exceeded power plant capacity (131 m^3/s), the annual peak flow in most post-dam years. The intermediate bench begins to be inundated at flows greater than 240 m^3/s and is fully inundated at 300 m^3/s (Grams and Schmidt 2002). Flaming Gorge Dam's two bypass tubes combined with power plant capacity flow produce a flow of 244 m^3/s, which can only inundate the lower portion of the intermediate bench. Since dam operations began in late 1962, releases of 244 m^3/s or higher have occurred three times and facilitated the establishment of 51% of the sampled box elder in Lodore Canyon. Flows greater than 244 m^3/s can be produced only by combining power plant capacity flows, bypass tube flows, and releases from the service spillway, which has a design capacity of 938 m^3/s. The spillway has been utilized twice since dam operations began in 1983 and 1999 when flows of 348 m^3/s and 317 m^3/s were produced. We found no establishment from 1999; however, the largest post-dam box elder recruitment cohort established in 1983. The lack of box elder establishment in 1999 may have resulted from the very short duration of that flood.

Management Implications and Conclusions

Two management scenarios are suggested for the maintenance of box elder riparian forests in Lodore and other upper Colorado River Basin canyons featuring strongly regulated flows and similar geomorphic settings. The first scenario considers the pre-dam c-b terrace forest an unsustainable relict of the rivers natural flow regime. Periodic spring floods exceeding power plant capacity could be used to simulate a flow regime with some of the variability of pre regulation conditions, but with lower peak flows than occurred historically. Box elders established during four of the five post-dam controlled floods on the Green River, indicating that bypass flows can be used to promote tree establishment on the inset intermediate bench, but this bench is narrow, and the area of forest that could be supported is much lower than occurred historically. Total forest area would decline as the mature pre-dam forest senesces.

An alternative scenario is to periodically use the dam's spillway to produce flows sufficient to inundate the c-b terrace and facilitate box elder establishment at the full range of historic establishment elevations. Photographic evidence of c-b terrace inundation following a flood of 550 m^3/s in 1917 (Grams and Schmidt 2002) suggests that the c-b terrace could be inundated by flows released from the turbines, bypass tubes, and a portion of the spillway capacity. Such high flows could be infrequent, for example, only following a series of high snowmelt years when Flaming Gorge Reservoir is near capacity, as occurred in the mid-1980s and the mid-1990s. This may reflect natural recruitment patterns that we observed on the Yampa River, where the flood of record in 1984 led to the establishment of a very high proportion of all young box elder on the entire river. High flows intended to mimic the natural hydrograph should peak in late May to early June at 500–550 m^3/s and gradually decline to base flow in early to mid-July.

River regulation-induced inset floodplain formation was found in canyons along the Gunnison, Dolores, Green, and Colorado rivers, indicating that river regulation is an important driver of geomorphic and ecological reorganization of riparian zones in the upper Colorado River Basin. The native woody riparian forest species have not been eliminated, but occur in lower floodplain positions, often in association with tamarisk. The magnitude of reduction in height above the channel for recent versus historic box elder cohorts is directly proportional to the degree of annual peak flow reduction (Figure 4). The maintenance of these riparian forests is dependent on the post-dam flow variability driven by infrequent, higher-than-average peak flows. Managing post-dam flows to increase variability would increase recruitment and native riparian forest cover, with the floodplain size determined largely by the magnitude of spring peak flows with sufficient duration to allow seedling establishment above the river channel. The higher flows of the early to mid-1980s, which led to the establishment of most box elders, resulted from concerns over dam safety, rather than water needs for ecosystem restoration and maintenance. Benefits to riparian ecosystems were considered in the late 1990s releases. If the climate becomes warmer and drier and the human population in the southwestern U.S. continues to increase, ever-greater demands on available water resources likely will limit the availability of water for bypass flows that produce controlled floods. However, the tight coupling of river peak flow and box elder establishment, as well as its control on the area and elevation occupied by box elder dominated riparian forests, is a clear indication of the necessity of periodic high peak flows to maintain these ecosystems.

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