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Plant diversity in riparian forests in northwest Colorado: Effects of time and river regulation

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Abstract

During the 20th Century the flow of most rivers in the United States was regulated by diversions and dams, with major impacts on riparian forests. Few unregulated rivers remain to provide baseline information for assessing these impacts. We characterized patterns in riparian plant communities along chronosequences on the unregulated Yampa River and the regulated Green River in northwestern Colorado, examining patterns in plant species diversity in relation to the ages of floodplain terraces. On both rivers, mean plant species richness in cottonwood (*Populus deltoides* Marshall subsp. *wislizenzii* (Watson) Eckenwalder) dominated riparian forests declined by more than 50% from young sites (<20 years) to old upland terraces (>250 years). Mean species richness (number of plant species/1000 m^2) was 40% higher on the unregulated Yampa River than on the regulated Green River, and 84% of the variance in total species richness related to age class, river, and tree cover. One-third of the plant species in all plots were exotic and 63% of the variance in exotic species richness was explained by a positive correlation with the richness of native species. On the Yampa and Green Rivers, ecosystem development and river regulation both reduce species richness, and these effects appear to be additive. The methods and insights from this study can be applied to other river systems to investigate the processes that change species diversity over time, and vegetation responses to the major changes in environmental conditions that follow river regulation.

Keywords: Yampa River; Green River; Populus; Cottonwood; River regulation

1. Introduction

The regulation of many of the world's rivers has dramatically altered the processes that influence riparian ecosystems. More than 40,000 large dams regulate river flow throughout the world, and 85% of these were constructed in second half of the 20th

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Century (Postel and Carpenter, 1997). With such a drastic increase in the regulation of river systems worldwide, it is crucial to understand the effects of river regulation on the structure, composition, and processes of riparian ecosystems. River regulation typically reduces sediment load and sediment deposition on floodplains, raises base flows, dampens peak flows, alters water and nutrient availability to riparian vegetation, confines the river into straighter channels, and alters the magnitude, frequency, and duration of floods (Nilsson et al., 1991; Richter et al., 1996; Merritt and Cooper, 2000). Riparian forests are important components of arid and semi arid landscapes, and the changes wrought by river regulation are substantial.

River regulation drastically alters the floodplain environment and may reduce species richness (Nilsson et al., 1991), increasing the relative invasibility of the floodplain by exotic plant species (Decamps et al., 1995). The decline of native woody species, particularly cottonwood (*Populus* spp.), in riparian ecosystems on regulated rivers has been well documented in the southwestern region of the United States (Rood and Mahoney, 1990; Busch and Smith, 1995; Cooper et al., 1999). This decline has been attributed to the modification of flood frequency, duration, and intensity that occurs with river regulation as establishment requirements are satisfied less frequently than they are in an unregulated system (Rood and Mahoney, 1990; Auble et al., 1994; Busch and Smith, 1995).

In the western United States, few unregulated rivers remain as a result of high demand for hydroelectric power, flood control, and water for agriculture and urban uses. The Yampa River is the last relatively unregulated, large river in the upper Colorado River basin, and its hydrologic similarity to the regulated Green River can provide insights to the effects of river regulation on riparian forests (Merritt and Cooper, 2000).

We characterized patterns in plant species diversity in age gradients of floodplain terraces along both rivers, hypothesizing that reduced frequency of floods and sediment deposition would lead to a decline in species richness with age and with river regulation. We also expected that factors fostering high richness of native species would also favor high richness of exotic species (Stohlgren et al., 1999; Stohlgren et al., 2001).

2. Site description and methods

The study sites were located in northwestern Colorado along the floodplains of the Yampa River in Deerlodge Park of the Dinosaur National Monument, and along the Green River in Browns Park National Wildlife Refuge. The Yampa River originates in the Park Range and the White River Plateau of northwestern Colorado, and joins the Green River in the eastern part of Dinosaur National Monument. The Green River originates in the Wind River Range in southwestern Wyoming, flows southward through Utah and Colorado, and joins the Colorado River in Utah. Two large dams regulate the flow of the Green River: the Fontanelle dam and the larger Flaming Gorge dam. The Flaming Gorge dam was completed in December of 1962. Browns Park is located in a wide alluvial valley about 70 km downstream of the Flaming Gorge dam.

Prior to regulation, the mean instantaneous peak discharge of the Yampa River (401 m^3/s) and the Green River (309 m^3/s) were similar, with high interannual variability (descriptions from Merritt and Cooper, 2000). Regulation has had little impact on the mean annual discharge for the Green River (declining from 59 to 56 m^3/s), but the annual and seasonal variability in flow has been greatly reduced since regulation. Regulation of the Green River has also dampened annual peak flows (declining from 309 to 135 m^3/s) and increased the daily average base flow (of the river (increasing from 17 to 56 m^3/s).

At Deerlodge Park and Browns Park, the rivers meander within largely unconfined floodplains (one to several kilometers wide) of thick fluvial deposits. The basin geology of the Yampa River in Deerlodge Park includes Weber sandstone, limestone, and Mancos shale. The basin geology of the Green River in Browns Park includes sandstone and shale of the Uinta Mountain Group and the Lodore Formation.

The climate, elevation, and biota of Deerlodge Park and Browns Park are similar, though mean annual precipitation is higher for Deerlodge Park along the Yampa River (280 mm) than at Browns Park along the Green River (210 mm). The average maximum and minimum temperatures during the growing season (May to September) at Deerlodge Park are 26 and 4 °C, and Browns Park is slightly warmer (28 and 5 °C). Deerlodge Park (1700 m elevation) is about 75 m higher than Browns Park (1635 m). The riparian

forests along both rivers are dominated by Fremont cottonwood (*Populus deltoides* Marshall subsp. *wislizenzii* (Watson) Eckenwalder) (Weber, 1987).

We used a chronosequence approach to examine patterns in plant species diversity along both rivers (Adair et al., 2004). After cottonwood trees establish on newly deposited geomorphic surfaces, subsequent recruitment of cottonwoods is low (Stromberg et al., 1991), and the age of the cottonwood stand match the time when primary succession began on the floodplain surface. Subsequent floods raise the surface of the fluvial feature by >2 m in 200 years.

Fluvial surfaces along the Green and Yampa Rivers were classified into age classes based on the age of the dominant cottonwoods and floodplain characteristics (described by Adair et al. (2004)). The ages at breast height (1.3 m) of the largest three to five cottonwood trees present at a site were estimated by tree cores, and sites were grouped into four age classes: <20 years (cottonwood establishment), 20–120 years (mature cottonwood forests), 120–250 years (old-growth cottonwood forests), and older than 250 years (upland terraces). The geomorphology of upland terrace sites included primarily fluvial deposition of sediment, but some alluvial deposition likely occurred in some cases. The upland terraces were too old to retain cottonwood trees.

We established three to six replicates of each of the four age classes along both rivers, for a total of 20 sites on the Yampa River and 16 sites on the Green River (four of the original 20 Green River sites burned in a wildfire in 2000). One 1000 m^2 plot was used to determine species richness at each site. Vegetation sampling was performed in the early summer from June 26 to July 19, 2001 when plants were close to peak phenology. Plant species that could not be identified in the field using the taxonomic key of Weber (1987) were collected and identified using the herbarium of Colorado State University. Of the 191 total species encountered, only three species could not be identified using taxonomic keys or the herbaria due to the phenological stage of the specimens. Taxonomic nomenclature was taken from USDA Natural Resource Conservation Service's PLANTS Database for the year 2000 (NRCS, 2001). Soils information (terrace elevation, clay fraction, sand fraction, available soil nitrogen, total soil nitrogen, total soil carbon, and soil potassium, magnesium, calcium, and sodium) acquired along a 75 m transect that ran through the middle of each plot was taken from Adair et al. (2004).

We analyzed patterns with three approaches: regression analysis (linear and non-linear) of the number of species (total and exotic) in relation to river and terrace age, Jaccard's coefficients of similarity among terrace ages on each river, and canonical correspondence analysis between species composition and environmental factors. Environmental factors were age class, river (Green or Yampa), overstory tree cover, terrace elevation, clay fraction, sand fraction, available soil nitrogen, total soil nitrogen, total soil carbon, and total soil potassium, magnesium, calcium, and sodium. Overstory tree cover was defined as cottonwood cover; terrace elevation was defined as the elevation of the soil surface above the river channel; clay fraction and sand fraction were taken as the percentage of mass for each particle size class; available soil nitrogen was taken as the annual net N mineralization (g/m^2) to a depth of 20 cm; total soil nutrient variables (nitrogen, carbon, potassium, magnesium, calcium, and sodium) were taken as the total amount of the individual soil nutrients (g/m^2) to a depth of 20 cm.

All statistical analyses, except for the canonical correspondence analysis (CCA), were performed using MINITAB (version 12.1, MINITAB Inc., 1998) and an α level = 0.10 was used to determine significance. All regression models were selected based on the forward selection procedure as described by Kleinbaum et al. (1998). The regression models reported here satisfied the basic assumptions of regression analysis (i.e. linearity, normality, homoscedasticity, and independence among treatments) and included only the variables with a partial F statistic greater than the F critical value ($P > F$: $\alpha = 0.10$).

A balanced design of randomly selected plots from each age class on each river was produced to examine the relative contribution of each age class to total species richness, unique species richness (species found at one river but not the other river), and to determine the degree of species overlap among age class. Three plots from each age class on each river were selected to provide 12 plots on each river in the balanced design. Analysis of variance was used to compare total species richness, unique species richness, and species overlap among the various age classes on the two rivers.

The relationships between plant community composition and environmental characteristics (age class,

terrace elevation, river, overstory tree cover, clay fraction, and total soil nitrogen) were analyzed using canonical correspondence analysis (CCA) with PC-ORD (version 4.14, MJM Software; McCune and Mefford, 1999). Canonical correlation examines associations between sets of data, rather than associations between a single dependent variable and one or more independent variable as in regression analysis. All the default options were selected in the CCA as described by Stohlgren and Bachand (1997) and Monte Carlo permutation tests were performed to test the significance of the first axis (McCune and Mefford, 1999).

Jaccard's similarity index (J) was used to compare the similarity of plant species composition within and between each age class along both rivers

$$J = A/(A + B + C)$$

where A is the number of species common to both areas, B the number of species in area 1 but not in area 2, and C the number of species in area 1 but not in area 2 (Krebs, 1989). The index ranges from 0 to 1, with 1 indicating complete overlap of all species, and 9 indicating no species in common.

3. Results and discussion

Total richness of native and exotic plant species declined with the age of floodplain terraces on both rivers, declining by 53% from the youngest to the oldest age class (Fig. 1). The species richness of plots along the regulated Green River averaged about 40% less than along the unregulated Yampa River. The age of the floodplain terraces accounted for about 93% of the variance in total species richness along the Yampa River, compared with 72% along the Green River. Across both rivers, 84% of the variation in total plant species richness, and 75% of exotic species richness, was associated with variables of age class, river, and tree cover, with richness declining with time and increasing tree cover.

Exotic species comprised at least one-third of all species across all plots, and 63% of the variance in exotic species richness was explained by a positive relationship with native species richness alone (Fig. 2). We found no evidence that river regulation may increase increase invasibility of the floodplain by exotic plant species (as was found by Decamps et al., 1995).

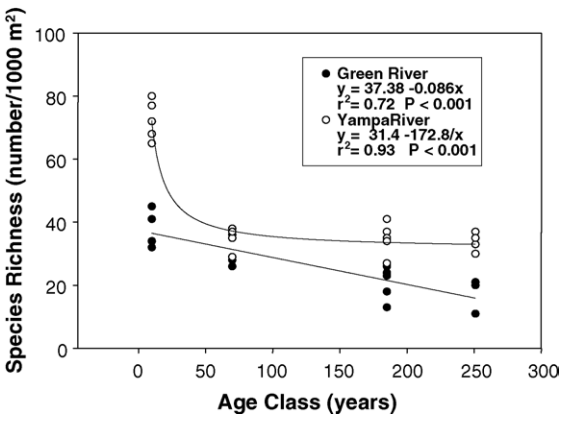

Fig. 1. Total species richness declined monotonically with age along the regulated Green River. Along the unregulated Yampa River, diversity in the youngest age class was almost double that of the later classes.

Using an equivalent number of randomly selected plots from each age class, a total of 155 species were encountered in the vegetation surveys of 12 plots on the Yampa River, whereas only 93 species were encountered in 12 plots on the Green River. Eight-eight percent of the species found along the Green River were also found on the Yampa River, but only 53% of the Yampa River species were found on the

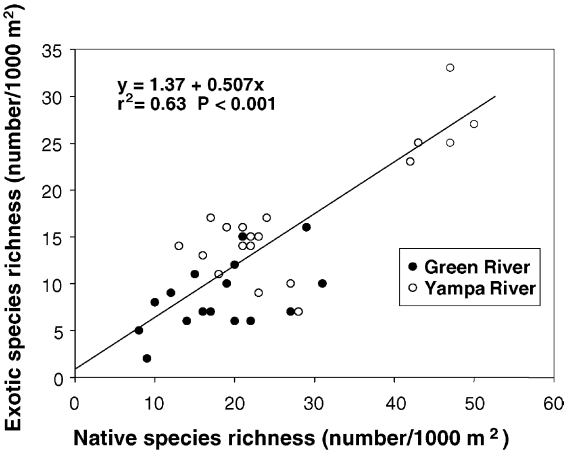

Fig. 2. The richness of exotic species increased linearly with the richness of native species across all age classes on along both rivers.

Green River. About 70% of all species on both rivers were found in the plots of the youngest age class.

The Yampa River had the greater number of unique species (species found at one river but not the other river) with 73 of 155 species being unique to the Yampa River plots (using an equivalent number of plots from each age class). Only 11 of the species encountered on the Green River were not found in our plots on the Yampa River. Most of the species that were unique to one river occurred in the youngest age class.

Mean species overlap differed between the plots on the Yampa River and the Green River ($F = 28.7$, d.f. = 1, $P < 0.001$) and among age classes ($F = 6.0$, d.f. = 2, $P < 0.05$). The mean number of species that one age class had in common with the next age class declined as age increased and was lower on the Green River than on the Yampa River (Fig. 3). On average, 77% of the species found in a particular age class on the Green River were also found on the same age class on the Yampa River, but only 47% of the species found in a particular age class on the Yampa River were found on the same age class on the Green River.

The first two canonical axes of the CCA explained 20.3% of the cumulative variance ($P < 0.01$; Fig. 4). Monte Carlo permutation tests showed the first canonical axis was highly significant (eigenvalue = 0.541, d.f. = 35, $P < 0.01$) and the environmental factors correlated with axis 1 were age class ($r = 0.98$), terrace elevation ($r = 0.66$), total soil nitrogen ($r = 0.58$), and clay fraction of the soil ($r = 0.57$). The raw correlation value for the environmental variable for river ($r = 0.03$) was not significant for the first axis but river correlated significantly with axis 2 ($r = 0.92$) as did overstory tree cover ($r = 0.38$) (Table 1).

The Jaccard coefficients within the same age class and between age classes on each river showed no clear trends in similarities among plots within each age class or between age classes between the Yampa and Green Rivers, or with age (Table 2).

The development of riparian Populus forests commonly includes an increase in terrace elevation, surface height above the water table, and distance from the river channel (Stromberg et al., 1991). As these forests develop in semi-arid environments, water availability may become more limiting. Total, native, and exotic plant species richness declined with age on the floodplains of both rivers. Water limitation and a decline in flood disturbance could explain the decline in species richness as succession progresses on the Green and Yampa Rivers. We do not expect increasing N limitation could explain the decline in plant species diversity, as N supply increased sharply as diversity decreased with age (Adair et al., 2004).

Previous research of on the development of floodplain forests found an increase in species richness with boreal forest development (Reiners et al., 1971) as well as an oscillating overall increase in species richness with time (Nanson and Beach, 1977). This trend contrasts with the patterns for the Yampa and Green Rivers, and more studies are needed to determine if age-related trends in species richness consistently differ between humid boreal and semi-arid temperate systems.

Our case study had only one regulated river and one unregulated river, so we cannot test statistically for the

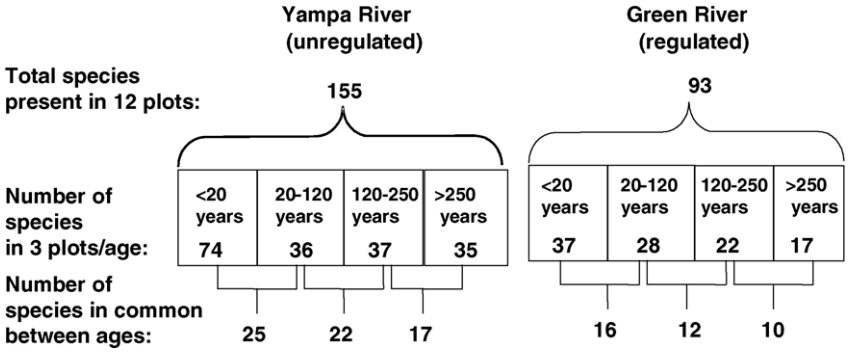

Fig. 3. Mean species richness and mean species overlap between each age class on the Green and Yampa Rivers.

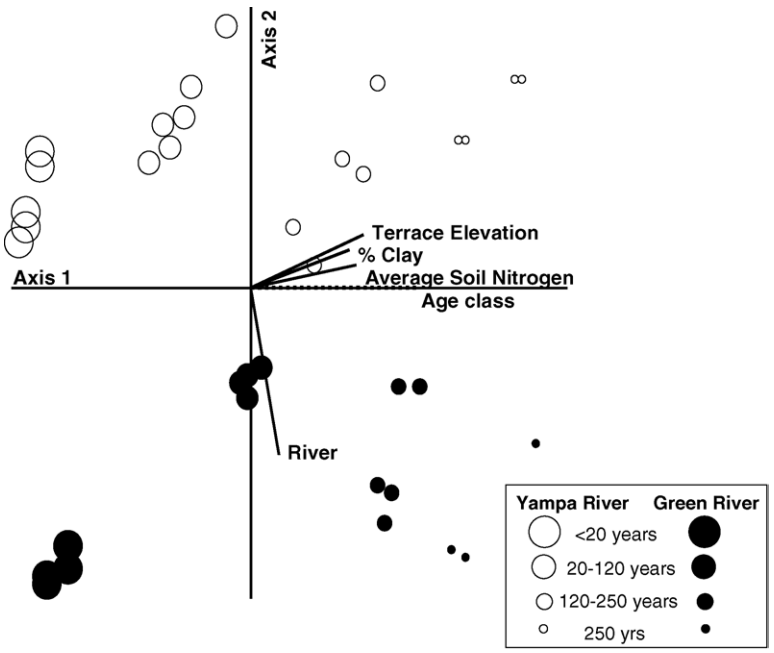

Fig. 4. Canonical correspondence analysis (CCA) showed that terrace elevation, clay, and soil N tended to increase with age (associated largely with axis 1), and that vegetation composition differed strongly between rivers (associated with axis 2).

Table 1
Mean unique species richness for each age class on the Yampa and Green Rivers

River	Age class (years)				
	<20	20–120	120–250	>250	All ages
Yampa (unregulated)	22 (74)	5 (36)	6 (37)	11 (35)	11 (46)
Green (regulated)	2 (37)	1 (28)	1 (22)	2 (17)	1 (26)

The mean number of species present in each age class is in parentheses.

Table 2
Mean Jaccard coefficients (1 = complete similarity in vegetation composition, 0 = no species in common) for plant communities within the same age class and between age classes on the floodplains of the free flowing Yampa River and the regulated Green River

River, age class	<20 years	20–120 years	120–250 years	>250 years
Yampa River				
<20 years	0.45 (0.01)	0.35 (0.01)	0.25 (0.01)	0.16 (0.02)
20–20 years		0.46 (0.05)	0.37 (0.02)	0.25 (0.04)
120–50 years			0.43 (0.02)	0.33 (0.03)
>250 years				0.25 (0.02)
Green River				
<20 years	0.49 (0.02)	0.30 (0.02)	0.29 (0.01)	0.16 (0.01)
20–20 years		0.39 (0.05)	0.40 (0.03)	0.21 (0.03)
120–50 years			0.43 (0.06)	0.28 (0.02)
>250 years				0.43 (0.05)

Values are means (standard errors).

effects of river regulation per se. Given the similarities between these reaches of the Yampa and Green Rivers, we expect that the major hydrologic effects of river regulation account for the major differences in diversity. This inference is consistent with other studies of regulated and unregulated paired rivers, where species richness was lower along regulated rivers (Nilsson et al., 1991; Jansson et al., 2000). Jansson et al. (2000) found lower species richness for most species groups on four regulated rivers than on four paired unregulated rivers, and in no case was species richness higher on the regulated rivers.

The linear increase in exotic species with an increase in native species showed that hotspots of native plant diversity were also hotspots for invasion (Fig. 2). This common pattern occurs in riparian zones (Planty-Tabacchi et al., 1996) and other environments as well (Stohlgren et al., 1999; Stohlgren et al., 2001). Riparian zones may serve as havens, corridors, and sources for exotic plant invasions (Stohlgren et al., 1998a) due to high resource supplies and the heterogeneity of the environment created by allogenic and autogenic processes. The areas with the highest exotic species diversity on the Yampa and Green Rivers were also areas with the highest number of unique species. These areas should be of concern for future monitoring and management efforts by land managers and conservation biologists to preserve unique habitats as well as the local and regional species pools.

Age class appeared to be a primary driver of community composition. The first axis of the CCA ordination matrix correlated best with the age gradient (Fig. 4). Age class was also the most significant variable related to total species richness in the linear regression models. Increases in terrace elevation, clay fraction, and total soil nitrogen were all closely aligned with an increase in age class (time) and it is difficult to parse any individual influence of these covarying factors.

The key management implications from our study are that plant diversity of riparian forests should be expected to decline over time as a result of natural processes that raise the floodplain surface above the river. River regulation appears to have an ''additive'' effect in reducing the plant species diversity for all age classes; various manipulations of flow regimes (including periodic flood-level flows) may be needed to sustain plant species diversity in riparian forests. The landscape-scale invasion of exotic species may be influenced by the flow regimes that initiate the establishment of riparian forests, and the details of hydrologic impacts on exotic species need further description and experimentation.

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