Post-Wildfire Recovery of Riparian Vegetation during a Period of Water Scarcity in the Southwestern USA

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ABSTRACT

Wildland fires occur with increasing frequency in southwestern riparian forests, yet little is known about the effects of fire on populations of native and exotic vegetation. From 2003 to 2006, we monitored recovering woody vegetation in wildfire sites in the bosque (riparian forest) along the Middle Rio Grande of central New Mexico, USA. To examine recovery potential, we estimated densities of native Rio Grande cottonwood (*Populus deltoides* ssp. *wislizenii*) and exotic saltcedar (*Tamarix ramosissima*) in burned plots and estimated mortality rates of resprouts. Exotic vegetation density was higher in most burned sampling plots than in paired unburned plots. Native shrub density was lower in most burned sampling plots than in unburned plots, although the effect sizes were small. Native tree density did not differ between burned and unburned plots, despite relatively high mortality of cottonwood resprouts. All observed cottonwood mortality occurred between 2003 and 2004, following the hottest and driest summer of the study. Cottonwood resprouts had the lowest apparent mortality rate at the site with the lowest depth to groundwater. Saltcedar resprout mortality was low at all wildfire sites, consistent with previous studies showing that this species is less sensitive to drought and better adapted to wildfire than cottonwood and other native species. Our observations suggest that, in the absence of ideal hydrologic and climatic conditions, fire can reduce cottonwood density in the bosque and promote the spread of saltcedar. Increasingly xeric conditions predicted under most climate change scenarios could result in greater recovery of exotic saltcedar over native vegetation.

Keywords: cottonwood, Middle Rio Grande, *Populus deltoides* ssp. *wislizenii*, resprout survival, riparian, saltcedar, *Tamarix ramosissima,* wildland fire

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INTRODUCTION

Riparian forests of the southwestern US have been identified as areas vital to the protection of regional biodiversity and are characterized by woody vegetation adapted to periodic floods (Busch and Smith 1995). Native Rio Grande cottonwood (*Populus deltoides* ssp. *wislizenii*) and exotic saltcedar (*Tamarix ramosissina*) are dominant species in these forests and their relative densities influence the structure of wildlife populations (Carothers *et al.* 1974, Smith *et al.* 2006b, Walker 2008). Cottonwood, saltcedar, and other riparian species are phreatophytic plants, relying on a connection with the water table for growth and survival (Busch and Smith 1995, Scott *et al*. 1999). Numerous studies have shown the importance of floods for successful reproduction and establishment of native (Mahoney and Rood 1998) and exotic (Sher *et al*. 2000) riparian vegetation, but little is known about how interactions of fire, climate, and hydrology affect populations of native and exotic species (Busch 1995, Whelan 1995, Steuver *et al*. 1995, Dwire and Kauffman 2003, Reeves *et al.* 2006, Stromberg *et al*. 2009).

Although fire is beneficial to many organisms in fire-prone ecosystems, many plant species in areas such as riparian forests are not fire-adapted (Whelan 1995). As a result, these organisms have higher post-fire mortality and lower reproductive potential than more fire-adapted species. In southwestern riparian forests, fire is likely occurring with increasing frequency in stands of vegetation already stressed by lowered water tables, altered flood regimes, and exotic species (Busch and Smith 1993, Steuver *et al*. 1995, Ellis 2001, Shafroth *et al*. 2002). Riparian vegetation such as cottonwood has morphological and life history attributes that are adaptations to periodic floods (Johnson *et al*. 1976, Gladwin and Roelle 1998, Tallent-Halstell and Walker 2002), but these adaptations may be unsuitable for recovery from fires (Busch 1995, Lytle and Poff 2004, Nagler *et al*. 2005). Inability of native riparian vegetation to recover from fire as rapidly as fire-adapted, exotic vegetation may cause a conversion from a native-dominated canopy forest to an exotic shrubland (Busch 1995, Nagler *et al*. 2005).

In the Middle Rio Grande basin of central New Mexico, high intensity, high severity wildland fires result in top-killed native and exotic vegetation (Steuver 1997, Ellis 2001, Smith *et al.* 2006a). Native and exotic riparian woody species sprout from their root crowns following fire (Busch and Smith 1993, Ellis 2001, Sprenger *et al.* 2002); a mechanism that may allow quick post-fire recovery (Gom and Rood 1999). There is, however, variation in sprouting probability, resprout condition, and resprout survival among native species and between native and exotic species (Busch and Smith 1993, Gom and Rood 1999, Ellis 2001, Stromberg *et al*. 2009) that may result in altered riparian forest structure and composition following wildfire.

Access to free-flowing water or groundwater has been shown to limit recruitment and survival of riparian vegetation such as cottonwood (Horton *et al.* 2001, Sprenger *et al*. 2002, Lite and Stromberg 2005). In addition, climatic factors such as temperature and precipitation influence the hydrology of a site and the physiological condition of woody vegetation (Cleverly *et al*. 1997, Scott *et al*. 1999, Snyder and Williams 2000). Because abiotic factors such as hydrology and climate affect riparian forest structure and composition, their variation and the nature of their effects must be considered

when predicting post-fire population trajectories of native and exotic species.

To provide an initial assessment of recovery of native and exotic vegetation following wildfire, we measured community composition of woody vegetation in burned and unburned sampling plots and estimated mortality of post-fire resprouts in the Middle Rio Grande bosque. We compared depth to groundwater among fire sites and related this and other variables to variation in survival of resprouted vegetation. Finally, we reviewed predicted effects of climate change on hydrology in the southwestern US and combined this information with our results to describe potential recovery scenarios of native and exotic vegetation.

METHODS

Study Area

The Middle Rio Grande bosque forms one of the most extensive cottonwood galleries in the southwestern US (Howe and Knopf 1991). Historically, regular flood events produced a dynamic mosaic of riparian vegetation in different-aged stands found throughout the valley (Whintey 1996, Scurlock 1998). Following agricultural development and construction of dams and levees, riparian vegetation has been largely confined to lands between the active channel and the levees on either side of the river. Flooding has not occurred outside the levees for 60 years but occasionally occurs within the levees (Molles *et al*. 1998). As with other regulated rivers, cottonwood seedling establishment usually occurs only in the active river channel where seedlings are quickly washed away by high flows or removed with machinery during channel maintenance (Howe and Knopf 1991, Auble and Scott 1998). Although historic return periods of wildland fire in the bosque are not clear, frequency and intensity of fire has likely increased due to human activity, drought, accumulation of woody debris, and increased densities of exotic vegetation (Steuver *et al.* 1995).

Within the levees, Rio Grande cottonwood is the dominant canopy species and Goodding's willow (*Salix gooddingii*) is also found in the canopy. Native understory shrubs include seepwillow (*Baccharis glutinosa*), coyote willow (*Salix exigua*), New Mexico olive (*Forestiera pubescens*), screwbean mesquite (*Prosopis pubescens*), false indigo (*Amorpha fruticosa*), and pale wolfberry (*Lycium pallidum*). Saltcedar, Russian olive (*Elaeagnus angustifolia*), and tree-of-heaven (*Ailanthus altissima*) are exotic species that occur in the understory of the forest. Saltcedar was the most abundant woody species at our study sites.

The primary soil type of the study sites and along most of the Middle Rio Grande floodplain is entisol (Stropki 2003). In general, entisols are soils that lack well developed horizons (Buol *et al.* 1980). They can be good sources of nutrients for plants, but they can also be highly erodible. Soils classified in proximity to our study sites include mixes of sands, loams, silts, and some clays (Maker and Daugherty 1986, Stropki 2003, Stormont *et al.* 2004).

The Middle Rio Grande basin experiences a mild semiarid to continental climate, characterized by low precipitation, high light intensity, low humidity, and a wide range of annual and diurnal temperatures (Western Regional Climate Center 2006). Most precipitation falls during the peak monsoon months of July and August, with the rest somewhat evenly distributed throughout the year (Lenart 2007b). Monsoon strength and area affected typically vary between years (Lenart 2007b). Peak river flows usually occur during the spring snowmelt period. Prior to river regulation, these flows resulted in floods during high snowpack years (Molles *et al.* 1998). Occasional high flows also occur as a result of late summer monsoons and winter and spring Pacific storms (Lenart 2007a).

The shallow groundwater hydrology of the Middle Rio Grande bosque bordering the river is influenced primarily by water flowing in the river and to a lesser degree water flowing in the canals that parallel the river. The undeveloped sandy soils bordering the river (Stropki 2003, Stormont *et al*. 2004) permit rapid infiltration and percolation, such that groundwater levels measured within the levees and bordering the river often reflect changes in river stage (R. Jemison, Forest Service, unpublished data).

We measured vegetation and monitored hydrology at four wildland fire sites (Figure 1). We selected study sites based on accessibility and post-fire management. Because our site selection was not random and lacked temporal replication, we present our results as observations applicable to a specific time period to serve as baseline data for future studies. We

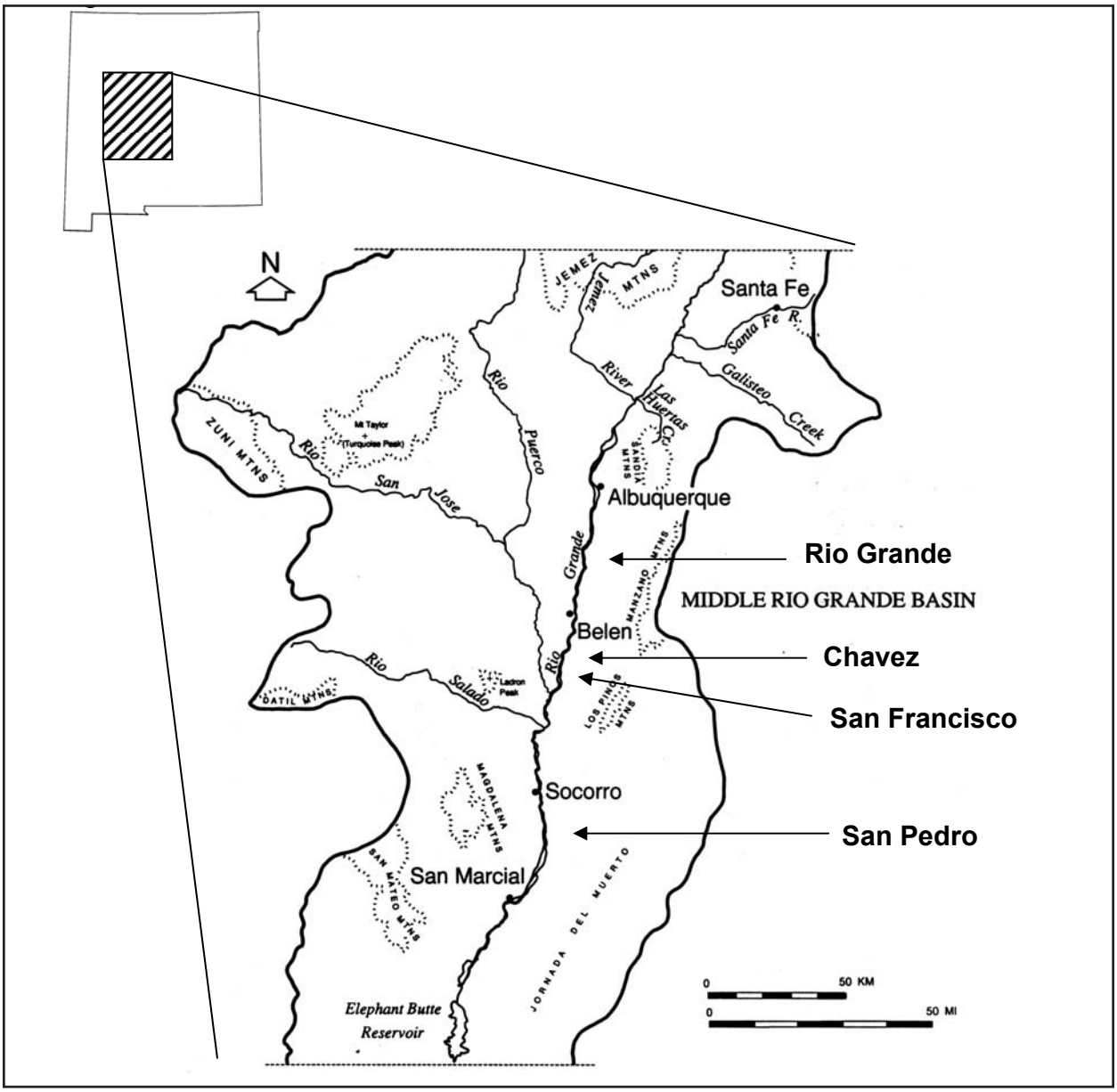


Figure 1. Location of study area and wildfire sites along the Middle Rio Grande, New Mexico.

selected four sites, detailed below, that burned in different years and contained burned and resprouting vegetation that was not cleared or salvaged by work crews following fire (Table 1). Three sites, San Francisco; Chavez; and Rio Grande Complex (RGC), are on land managed by the Middle Rio Grande Conservancy District; the San Pedro fire site is located at Bosque del Apache National Wildlife Refuge. The San Pedro site is composed of two plots, one located adjacent to the river channel within the levees, and another located in the historic floodplain outside of the levees.

Vegetation Composition

We established a sampling transect running the length of each wildfire site to describe the composition of post-fire woody vegetation. Along each transect, we established sampling points every 150 m. Following protocols described by Finch *et al*. (2006), we established one or two 4 m diameter sampling plots placed 25 m from each sampling point in randomly assigned directions. We identified all the woody species in each plot and counted the number of individuals. To describe community composition, we calculated species richness and density of plants assigned to three functional groups: native shrubs, native trees, and exotic shrubs. We placed species that contributed to canopy structure (cottonwood and Gooding's willow) into the category of native trees. Species that typically grow below the canopy were designated native or exotic shrubs. We collected data at vegetation sampling points in the Chavez, RGC, and San Pedro wildfire sites in 2004, and in the San Francisco Fire in 2008.

To determine if the vegetative composition of burned sites differed from unburned sites, we compared species richness and density of functional groups at each burned site with data from a paired unburned site. We paired data from the Chavez Fire site with data collected at vegetation sampling plots at the same site measured in 2000 and 2001 prior to the fire in 2002. We did not collect data at the other sites prior to burning, so we used data collected for another study (Finch *et al.* 2006) at unburned sampling plots for burned-unburned site comparisons. Because we used data from unburned sampling plots opportunistically, we lacked true "control" sites needed to infer ef-

Table 1. Characteristics of wildfire study sites in the Middle Rio Grande, New Mexico observed between 2003 and 2006.

	San Francisco	Chavez	Rio Grande Complex	San Pedro (floodplain)	San Pedro (channel)
Year of fire	2003	2002	2000	1996	1996
Area of site (ha)	20	9.4	31.4	0.6	22.1
Number of vegetation sampling plots	14	10	12	6	16
Year of vegetation sampling in fire plots	2008	2004	2004	2004	2004
Number of unburned sampling plots	16	16	16	0	16
Year(s) of vegetation sampling in unburned plots	2004	2000-2001	2004	2000-2001	2000-2001
Number of cottonwood resprouts marked in 2003	15	15	10	9	9
Number of saltcedar resprouts marked in 2003	20	15	6	8	15

fects of fire on riparian vegetation. Instead, we compared composition of burned and unburned sites during the period in which data were collected. We collected unburned sampling plot data between 2000 and 2004 (Table 1). We assumed that vegetation composition of unburned sampling plots was similar to that of paired wildfire plots prior to burning because unburned plots were located on the same side of the river and were no more than 5 km from paired wildfire sites. We did not measure vegetation composition of burned and comparison plots during the same years (Table 1). This should not be a confounding factor in comparisons of burned and unburned community composition because most vegetation mortality and resprouting occurred during the year of each fire (D.M. Smith, University of Oklahoma, personal observation), mortality of mature vegetation is low, and seedling regeneration rarely occurs within the forest (Howe and Knopf 1991, Molles *et al.* 1998).

Resprout Mortality

We established resprout mortality sampling points at each fire site to compare mortality rates among species and functional groups. We monitored mortality of all woody species, but placed special emphasis on cottonwood and saltcedar because the presence of these species has a large effect on the physiognomy of riparian forests and associated animal communities (Carothers *et al.* 1974, Walker 2008). We use the term "resprout" to refer to individual genets that sprouted from the stumps of top-killed trees and shrubs. We identified trees or shrubs as top-killed when there were no green leaves in the canopy. We were able to distinguish resprouts from seedlings because resprouts were growing from the stump or root crowns of trees and shrubs, usually in areas where seedling establishment does not occur. All resprouts were marked in 2003, but the age of cohorts differed among sites because wildfires burned in different years.

We located resprout sampling points by randomly selecting a distance from the levee road for each point. The levee road generally runs north and south, and all sites were located on the west bank of the river, so all sampling points lay east of the levee road. To sample as much of the burned area as possible, we spaced sampling points at least 50 m apart. We arrived at each point by walking perpendicular to the levee road toward the river channel until we reached a randomly selected distance from the levee. At each point, we marked the location with flagging tape and recorded its position with a handheld GPS device. We established a 10 m diameter plot centered at each point. We used numbered aluminum tags to mark a resprout of each species found within the plots. We marked the largest stem of the resprout of each species that was closest to the center of the plot. To aid in relocation of marked stems, we recorded the distance and direction of each stem to the sampling point. After marking each stem, we returned to the levee road and traveled 50 m to the north or south to locate the next sampling point. To estimate annual and overall mortality rates, we attempted to relocate each marked stem in June through August of 2004 and 2005, and in May of 2006. Condition of each relocated genet was recorded as "found live" or "found dead." When possible, we checked to ensure that individuals described as "found dead" did not grow back in subsequent years. When a tagged stem was not relocated, we revisited the site later in the season to search for it again. If we failed to locate a stem a second time, its condition was described as "not found" and we returned to search for it in subsequent seasons.

Hydrology

We obtained discharge data for the Middle Rio Grande that was measured at gauging stations near the northern and southern ends of our study area in Albuquerque (US Geological Survey 2006: Gauge 08330000) and San Aca-

cia (US Geological Survey 2006: Gauge 08354900). Data were recorded throughout our study period.

To compare groundwater depth between wildfire sites, we installed groundwater wells at the north and south ends of each site. We installed two pairs of wells at the San Pedro site; one pair in the plot inside the levees and one pair in the floodplain plot outside of the levees. We installed one pair of wells at each of the other sites at half the distance to the river channel from the levee road. We hand-augured wells to depths of 4 m. Wells were constructed with galvanized casings and stainless steel screens 1.3 m to 1.7 m in length. Each well contained an In-Situ miniTROLL data logger (In-Situ, Inc., Fort Collins, Colorado) within 0.5 m of the bottom of the well. Each data logger recorded pressure, which was converted to groundwater depth in cm, at 15 min intervals each day from August 2004 through July 2005.

Climate

We obtained rainfall and temperature data for the region during our study from the Western Regional Climate Center (WRCC 2006) and National Oceanic and Atmospheric Administration Southern Region Headquarters (NOAA SRH 2008). We calculated averages from weather stations at Albuquerque, Los Lunas, Bernardo, and Bosque del Apache (WRCC 2006). We obtained historical climate records from these stations to determine if temperature and precipitation were above or below regional averages. We reviewed literature pertaining to predicted effects of climate change on hydrologic conditions in the southwestern USA to determine if observed climate and hydrology represent expected future conditions.

Data Analysis

We compared mean depth to groundwater between fire sites for the year sampled and for the month of June 2005. We chose this month because it occurs during the growing season for woody plants in the bosque, and this was the month with the highest river flows during the study. We calculated daily means from each well, mean daily values from the north and south well at each site, and monthly means for each site incorporating the north and south wells. We made pairwise comparisons by calculating effect sizes (difference in means between two sites) and tested the strength of effect sizes by constructing 95 % confidence intervals. If effect size intervals did not contain zero, we interpreted differences to be the result of a considerable effect of site (Colegrave and Ruxton 2003). We calculated water level fluctuation for each fire site as the difference in maximum and minimum depths to groundwater measured during the period between August 2004 and July 2005 (Lite and Stromberg 2005).

We calculated mean species richness and mean density of native shrubs, exotic shrubs, and native trees at wildfire and unburned sites. We adjusted number of plants per sampling plot to number per hectare. We calculated effect sizes and associated confidence intervals to determine if species richness or densities differed between paired wildfire and paired unburned sampling plots.

We compared overall annual mortality rate among cottonwood, saltcedar, and all woody species placed into three functional groups. We also compared the annual mortality rate of cottonwood resprouts among wildfire sites. Because we were uncertain about the fates of resprouts that were not relocated, we calculated an annual mortality rate assuming survival of non-relocated stems and another assuming mortality of non-relocated stems. This resulted in two rates estimated for each species and site: a conservative, minimum estimate of mortality and a more liberal, apparent mortality estimate. We used the following equation to estimate minimum annual mortality rate (Sheil and May 1996):

$$M(m) = [1 - (1 - S_D/N)^{1/t}] \quad (1)$$

where S_D is the number of known mortalities at the end of the study period, N is the number of stems marked at the beginning of the study, and t is number of years in the study period. Apparent annual mortality rate was estimated with the following equation:

$$M(a) = [1 - (1 - S_F/N)^{1/t}] \quad (2)$$

where S_F equals the number of known mortalities plus the number of stems that were not relocated.

RESULTS

Hydrology

The highest river flows during the study period occurred during May and June of 2005, following a winter of above average precipitation (Figures 2 and 3). During this time, much of the bosque was flooded, including the river channel plot of the San Pedro site and the entire RGC site. The floodplain plot of the San Pedro site was flooded in 2003 as a result of refuge management activities. To our knowledge, the Chavez and San Francisco sites were not flooded at any time during the study. Lowest river flows of the study period occurred during the summers of 2003 and 2004 when all water was diverted from the river channel into conveyance canals (Figure 2).

From August 2004 to July 2005, mean depth to groundwater varied among sites (Table 2). Depth to groundwater was highly variable at the San Pedro wildfire site, which had a maximum depth of 357.6 cm in 2004 and a minimum depth of 39.3 cm in 2005 (Figure 4). The RGC fire site had a consistently shallow depth to groundwater (<150 cm), particularly in 2005 (Figure 4). The Chavez and Bernardo sites had consistently moderate depths to groundwater (100 cm to 300 cm) despite fluctuating river flows (Figures 3 and 4). During the month of June 2005, which had the highest stream flows, depth to groundwater was similar at the Chavez and San Francisco sites, but varied between the others (Table 2).

Climate

During our study, New Mexico was in the midst of a multi-year drought, with the summer of 2003 being part of the peak period

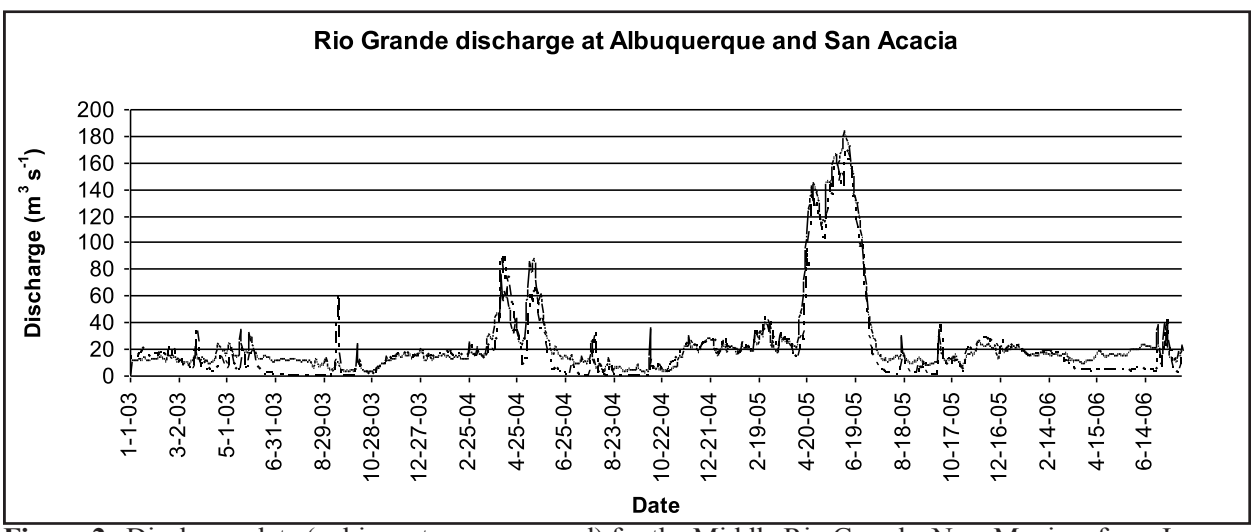


Figure 2. Discharge data (cubic meters per second) for the Middle Rio Grande, New Mexico, from January 2003 through July 2006. Measurements were made near Albuquerque (USGS Gauge 08330000; solid line) and San Acacia (USGS Gauge 08354900; dashed line).

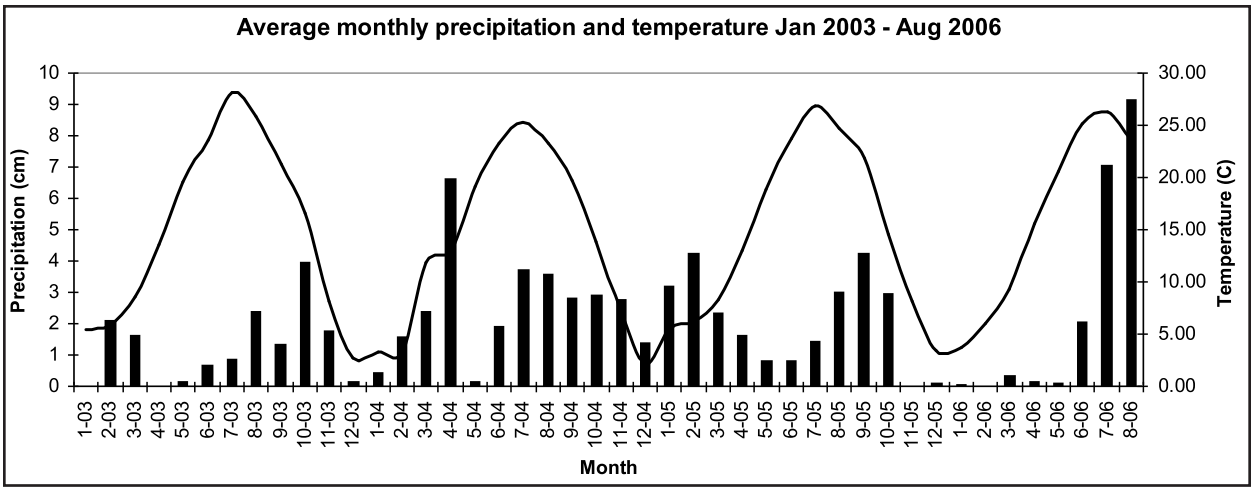


Figure 3. Average monthly precipitation (bars) and temperatures (line) in the Middle Rio Grande, New Mexico, from January 2003 through August 2006 (NOAA 2008). Values represent means from stations at Albuquerque, Los Lunas, Bernardo, and the Bosque del Apache National Wildlife Refuge.

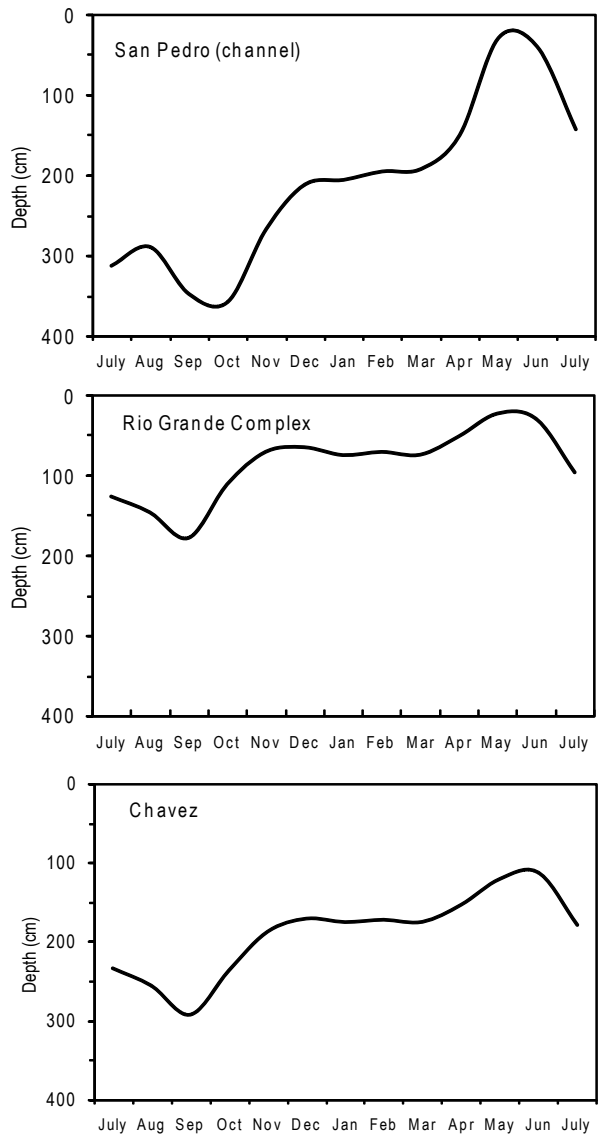
Table 2. Hydrologic characteristics of wildfire sites measured between 2004 and 2005 along the Middle Rio Grande, New Mexico. Groundwater depth values that do not share a letter indicated considerable effect sizes (confidence intervals do not contain zero).

	San Francisco	Chavez	RGC	San Pedro (floodplain)	San Pedro (channel)
Mean depth to groundwater (m) 2004-2005	1.58 a	1.87 b	0.82 c	2.12 d	2.05 e
Mean depth to groundwater (m) June 2005	1.12 a	1.13 a	0.28 b	1.58 c	0.39 d
Max. groundwater fluctuation (m) 2004-2005	2.08	1.93	1.81	2.66	3.70
Years flooded	None	None	2005	2003	2005

(Lenart 2007a). Summer precipitation in 2003 was below average in the months of June, July, and August (Figure 3) and temperatures measured during this time were the highest on record (Figure 3). Spring precipitation was above average in 2004, as was winter precipitation in 2005, leading to high river flows (Figure 2). The year 2006 was characterized by below average winter precipitation and above average monsoon rainfall (Figure 3).

Vegetation Composition

Species richness was similar between sampling plots in burned and unburned sites, with exotic shrubs having the highest densities of any functional group at each site (Table 3). Native shrub cover was similar between paired sampling plots at all wildfire sites except for the San Pedro Fire, which had higher density of native shrubs than did unburned plots. Density of exotic shrubs was higher in plots measured post-fire at the Chavez site than during pre-fire conditions in 2000 and 2001. Exotic shrub density was higher in fire plots at the RGC and San Francisco sites as well, though the effect size confidence intervals contained zero. The San Pedro Fire plots had lower density of exotic shrubs than did unburned plots, but the effect size confidence intervals also contained zero. Native tree density was similar between unburned and wildfire plots at all sites.



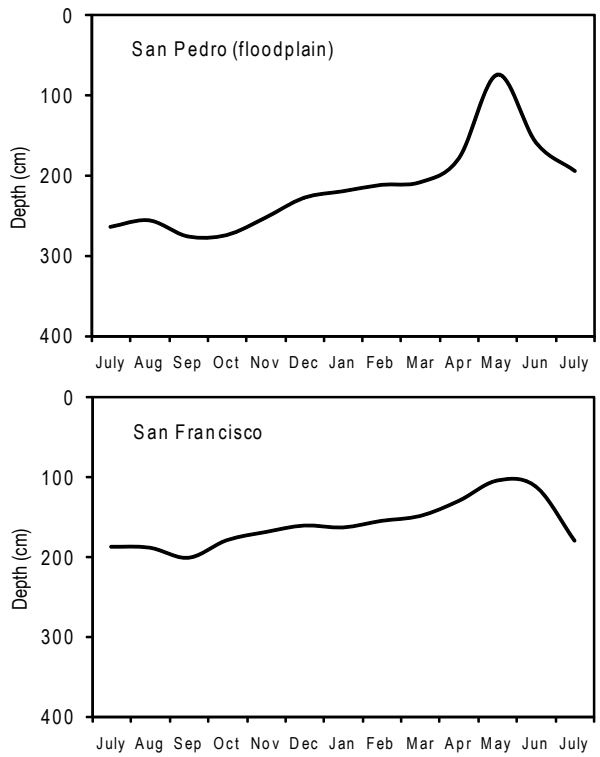


Figure 4. Average monthly depth to groundwater at five burned sites along the Middle Rio Grande, New Mexico, measured from August 2004 to July 2005. One pair of wells was installed at each site except San Pedro where one pair was installed in a plot located between the western levee and the river channel and another pair was located in the flood plot outside the levees.

Resprout Mortality

In 2003, we marked 365 resprouts and we relocated most tagged stems during three subsequent years (Table 4). We were unable to locate most stems at the San Pedro Fire site in 2005 due to heavy flooding. Some of the cottonwood resprouts marked in 2003 were found dead during the summer of 2004, but all of the cottonwoods we checked in 2005 and 2006 were live (Table 4). One saltcedar death was observed in 2006, and mortality of other species was more evenly distributed across years (Table 4). Minimum and apparent mortality rates were similar for native and exotic functional groups (Table 5), indicating that post-fire mortality occurred for a variety of woody species.

Minimum annual mortality of cottonwoods across plots was 4.1% and apparent annual mortality was 10.6%. Cottonwood resprouts at the San Francisco site had the highest annual mortality rate of any site (Table 6). Minimum annual saltcedar mortality rate was 0.3% and the apparent annual rate was 7.4%.

Table 3. Mean species richness, native shrub density, exotic shrub density, and native tree density measured in sampling plots located in wildfire and associated unburned sites along the Middle Rio Grande. Differences with effect size confidence intervals that do not contain zero are marked with an asterisk (*).

	San Francisco[a]		Chavez		Rio Grande		San Pedro	
	Burned (SE)	Un-burned (SE)	Burned (SE)	Un-burned (SE)	Burned (SE)	Un-burned (SE)	Burned (SE)	Un-burned (SE)
Species richness (spp. plot^{-1})	1.86 (0.27)	2.07 (0.31)	2.20 (0.25)	2.06 (0.25)	2.00 (0.22)	2.44 (0.34)	2.55 (1.21)	2.44 (1.49)
Native shrub density (# ha^{-1})	42 (22)	258 (112)	200 (122)	562 (196)	86 (0.30)	262 (102)	1618 (516)*	38 (22)*
Exotic shrub density (# ha^{-1})	2428 (744)	1728 (334)	2020 (466)*	676 (190)*	1714 (596)	750 (186)	2454 (620)	3626 (1068)
Native tree density (# ha^{-1})	128 (58)	142 (76)	460 (236)	512 (130)	28 (28)	162 (54)	472 (234)	300 (90)

[a] Species richness and densities at the Chavez site were recorded in 2000 and 2001 prior to burning in 2002. Other unburned sampling plots were measured in areas adjacent to wildfire sites.

Table 4. Percentages of resprouts marked in 2003 along the Middle Rio Grande, New Mexico, that were found live, found dead, or not found during the next three years.

		2004			2005[a]			2006		
	n	Found live	Found dead	Not found	Found live	Found dead	Not found	Found live	Found dead	Not found
		%								
Cottonwood	58	72	16	12	52	0	33	63	0	21
Saltcedar	64	94	0	6	58	0	42	73	1.5	25
Native shrubs	63	87	6	6	57	0	37	65	8	14
Exotic shrubs	97	91	3	6	53	4	40	66	5	22
Native trees	83	76	11	13	51	1	37	64	0	24

[a] Many resprouts were not relocated in 2005 due to flooding at the San Pedro wildfire site.

Table 5. Annual mortality rate of resprout functional groups measured in wildfire sites from 2003 to 2006 along the Middle Rio Grande, New Mexico.

		Annual mortality rate (%)	
Functional group	*n*	Minimum	Apparent
Exotic shrub	97	3.2	9.9
Native shrub	63	5.6	10.2
Native tree	83	3.2	10.6

Table 6. Annual mortality rate of cottonwood resprouts from 2003 to 2006 at wildfire sites along the Middle Rio Grande, New Mexico.

		Annual mortality rate (%)	
Site	*n*	Minimum	Apparent
San Francisco	15	14.5	20.4
Chavez	15	0.0	17.3
Rio Grande	10	2.5	2.5
San Pedro	18	1.4	4.4

DISCUSSION

Our comparisons of vegetation communities in burned and unburned sites show that native and exotic species are capable of recovering from fire through resprouting. Our estimation of mortality rates, however, showed that many of these resprouts failed to survive the post-fire period. Resprout mortality rates did not vary between functional groups, and species richness was similar between wildfire and unburned sites; therefore, post-fire sites should retain native shrubs, exotic shrubs, and native trees, though their relative densities may be altered by fire.

We observed high mortality of tagged cottonwoods between 2003 and 2004 and failed to relocate several other resprouts. Our overall mortality rate of 4.1% to 10.6% for cottonwoods was higher than that measured for adult cottonwoods at unburned sites along other rivers (0% to 2%, Scott *et al.* 1999; 4% to 5% Horton *et al.* 2001) and was likely higher than mortality rates of cottonwoods at adjacent unburned sites. We assume that inability to relocate cottonwoods was due to mortality because live cottonwood resprouts were relatively easy to find in this forest. We therefore believe that our apparent cottonwood mortality rate is closer to the true rate than the minimum mortality rate.

The fact that most known cottonwood mortality occurred in the recently burned site during the peak of a drought indicates a number factors that could limit resprout survival of this species. Most observed mortalities occurred during the first year following fire at the San Francisco site. This observation suggests that survival of cottonwood resprouts is lowest during the first year post-fire, as previous studies examining short-term resprout survival of eastern cottonwood (*Populus deltodies*) and Fremont cottonwood (*P. fremontii*) have shown (Busch and Smith 1995, Gom and Rood 1999, Ellis 2001, Rood *et al*. 2007, Stromberg *et al*. 2009). During our study, annual mortality rate of cottonwood resprouts was high in sites burned after 2000 (>15%) and low in plots burned in 2000 or earlier (<5%). Because only one site with a recent fire (<1 yr since burn) was available for study in 2003, we could only monitor mortality of one cohort during its first year post-fire, and therefore we could not fully separate site and time-since-fire effects on survival. We observed cottonwood mortality at additional sites between the summers of 2003 and 2004; therefore, mortality could also be attributed to the fact that 2003 was the driest year of our study. The fact that most mortalities occurred during the peak of a drought at the most recently burned site could also indicate that resprouts are most vulnerable to drought during their first year, but additional research is needed to test these hypotheses. Due to our small number of sampling sites, additional research is needed to disentangle the effects of climate, spatial, and temporal variables on cottonwood resprout survival as additional wildfires occur.

We were unable to relate survival among years with fluctuation in groundwater depth because we installed the wells in 2004 and most mortality occurred between 2003 and 2004. Our hydrology measurements, however, revealed differences in water table fluctuations and river connectivity among sites that were reflected in characteristics of cottonwood resprouts. The mean depth to groundwater in June 2005 was above the threshold of 2.5 m identified by Lite and Stromberg (2005) that allows native vegetation to be dominant over saltcedar. Fluctuations in groundwater depth, however, exceeded 0.46 m and this degree of fluctuation can result in mortality of cottonwoods (Lite and Sromberg 2005). The RGC site consistently had the lowest depth to groundwater and least fluctuation in depth. Cottonwood resprouts at this site had the lowest apparent annual mortality rate of any site and produced flowers and seeds sooner (6

years post-fire) than those in the San Pedro site (9 yr to 10 yr; D.M. Smith, University of Oklahoma, unpublished data) where groundwater depth fluctuated greatly. Though preliminary, these results suggest that mesic conditions at burned sites result in high survival and more rapid sexual reproduction of cottonwoods than those at drier sites. Most of our fire sites differed in their depth to groundwater and flooding frequency, and we expect that in the Middle Rio Grande bosque, recovery of native vegetation varies with the hydrology of burned sites.

Hydrologic conditions at some sites appeared conducive to cottonwood reproduction. At each site, average depths to groundwater were above established thresholds for survival of native vegetation, and flooding occurred at some sites, resulting in high soil moisture during the cottonwood seed dispersal period (D.M. Smith, personal observation). Fire removes competing vegetation and litter, mimicking flooding by providing opportunities for establishment of riparian vegetation (Dwire and Kauffman 2003, Wolf *et al*. 2007). There is clearly potential for cottonwood seedling establishment following fire, but additional research is necessary to evaluate germination and survival of seedlings in wildfire sites.

Saltcedar resprouts had low mortality rates at all sites and, of 64 saltcedar resprouts monitored for this study, we confirmed the mortality of only one. We were unable to relocate many tagged saltcedar stems but, in contrast with cottonwoods, we assume that these stems survived, but were not relocated because the high density of stems made it difficult to find the tags. Moreover, we observed few dead saltcedar resprouts at any wildfire site. For these reasons, we believe that our minimum annual mortality estimates reflect the true mortality rates of saltcedar at each site. Saltcedar has been shown to have higher survival rates than native vegetation under dry conditions (Cleverly *et al*. 1997, Busch and Smith 1993) and this appears to be the case with saltcedar resprouts that survived during dry conditions at our sites. Exotic shrubs, including saltcedar, were abundant at all sites and their densities were higher in most wildfire sampling plots than in unburned comparison plots. These findings suggest that wildfire could increase cover of exotic species at wildfire sites, as noted by Busch (1995).

Climate potentially affects survival of cottonwood resprouts through several mechanisms. Dry, hot summers could stress individual resprouts, stunting growth and leading to mortality. Periods of drought also cause depletion of water tables, on which riparian vegetation depends for growth and survival. There is evidence that cottonwoods can use rainfall to survive periods of fluctuating groundwater depth, but other species, such as Goodding's willow, are entirely dependant on groundwater (Snyder and Williams 2000). During the summer of 2003, surface flows ceased at our study sites because water was diverted for irrigation and the monsoon season did not occur during the usual months (D.M. Smith, personal observation). During this time, we observed early leaf drop in cottonwood resprouts and adults, indicating high water stress. The growing seasons following 2003 had more rainfall, shallower depths to groundwater, and later leaf drop (D.M. Smith, personal observation), which may have resulted in lower rates of cottonwood resprout mortality. Again, these observations lacked replication and future studies are needed across a range of climatic variables to relate hydrology and precipitation to post-fire resprout survival.

Though much of the climatic variation we observed has occurred historically, predicted climate change scenarios call for conditions that are not conducive to recovery of native vegetation following wildfire. To survive and reproduce, cottonwood resprouts require reliable connection to groundwater, stable temperatures, and flood events that are synchronized

with seed release (Mahoney and Rood 1998, Horton *et al.* 2001, Lytle and Poff 2004). Under most climate change predictions, the southwestern US is expected to see reduced snowpack (Mote *et al.* 2005) and early onset of spring runoff (Cayan *et al.* 2001, Stewart *et al.* 2005), which would result in unusually low river flows, much of which are diverted to agriculture and other human uses (Christiansen *et al*. 2004, Hoerling and Eischeid 2007). In addition, longer and more frequent droughts are expected to occur (Lenart 2007a). These changes would make conditions observed in 2003 more frequent, possibly leading to increased mortality of cottonwood and other native species.

Under some predicted climate change scenarios, monsoon rains will become less frequent but stronger than average, resulting in late summer floods (Lenart 2007b). Though these floods may result in low depth to groundwater and saturated soils, which increase survival of native vegetation (Talent-Halstell and Walker 2002), they would likely occur too late to allow seedling germination. In addition, early runoffs predicted under climate change scenarios would occur before cottonwoods release seeds. Because saltcedar resprout seed production begins several years earlier than cottonwoods and can begin earlier in the summer and extend beyond the seed release period of cottonwoods (Di Tomaso 1998; Cooper *et al.* 1999; D.M. Smith, unpublished data), such flooding events in recently burned wildfire sites will likely result in establishment of saltcedar and little to no establishment of cottonwood, especially in areas flooded in late summer, when cottonwood trees are not dispersing seeds. Additional research is necessary to determine germination potential and viability of saltcedar seedlings in soils of wildfire sites to determine if these climate change scenarios will benefit saltcedar at the expense of cottonwood.

Under a variety of post-fire scenarios, resprouting cottonwoods and other native vegetation species at our sites have a competitive disadvantage to exotic species. Although cottonwood resprouts are capable of growing to adult size and reproducing in some areas (D. M. Smith, unpublished data), cottonwood density could decrease in other areas due to high mortality of resprouts. Additional research is needed to better explain variation in resprout survival among species, fire sites, and years. The low mortality rate of saltcedar resprouts in comparison to cottonwood indicates that caution should be used when prescribing fire where these two species occur. Following wildfire, native resprouts should be protected from additional disturbances to limit genet mortality. Management actions that support connection between river channel and floodplain, including increased peak river flow and decreased river bank armoring, should be implemented to promote mesic conditions in the bosque (Crawford *et al.* 1993). These conditions result in increased cottonwood growth and promote seedling establishment of native vegetation (Molles *et al.* 1998, Sher *et al*. 2000). During years of low precipitation, groundwater declines should be prevented to aid survival of native resprouts. Following wildfire, managed flooding should not occur outside of the seed dispersal period of cottonwood or other native plants, otherwise newly exposed germination sites will be colonized by exotic species such as saltcedar. Additional research incorporating flooding frequency, fire intensity, seed viability, germination rates, and seedling survival into population models is needed to predict post-fire population growth of native and exotic vegetation.

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