

Impacts of Wildfire on the Composition and Structure of Riparian Forests in Southern California

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ABSTRACT

In southern California, wildfire is a ubiquitous agent shaping plant communities. Although fire impacts have been widely studied in chaparral-covered uplands, few data are available regarding fire and riparian vegetation. This study provides an example of the impact of a severe fire on riparian habitat. Plant species found in southern California gallery forests are typically adapted to maintaining populations following flood disturbances; we seek to determine whether structural and compositional changes following fire here demonstrate a similar quasi-equilibrium response. We sampled 65 quadrats on 11 transects along two streams in the Los Padres National Forest to characterize tree species size-class distributions before and after the 2002 Wolf Fire. We tested whether species exhibited differential patterns of survivorship and regeneration following the fire, and also tested for spatial

variability in mortality within the floodplain. *Alnus rhombifolia* dominated the pre-fire forest, but experienced severe mortality in the fire and showed very limited resprouting after 3 years. Other prominent taxa (*Populus*, *Salix*, *Quercus* spp.) also lost considerable standing basal area, but had substantially greater rates of resprouting, resulting in a dramatically altered post-fire vegetation composition and structure. Fire impacts did not vary with landform position, leading to a distinctive homogenizing disturbance that contrasts with the spatially zoned and relatively stabilizing compositional influence that flood events have in this same riparian setting.

Key words: riparian vegetation; riparian habitat; fire; disturbance; *Alnus*; *Populus*; *Salix*; California.

INTRODUCTION

Riparian plant communities are a vital element of the dry landscapes of the western United States,

both for the floristic diversity they provide (Holstein 1984) and for their role as critical habitat for a wide range of organisms (Baltz and Moyle 1984; Erman 1984; Szaro and Jakle 1985). Both the composition and the structure of the vegetation may be relevant to fauna using riparian habitat (Powell and Steidl 2000). Consequently, the processes affecting these plant communities are highly significant to the availability of habitat (Franzreb 1990; Scott and others 2003). The response of

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riparian vegetation to disturbance has been the topic of many studies (Bendix 1998; Cowell and Dyer 2002; Stromberg 2006). Most such studies focus on flood impacts, however, (Bendix and Hupp 2000) and there has been relatively little attention to the role of fire (Dwire and Kauffman 2003; Pettit and Naiman 2007a). The reasons for the emphasis on flooding are perhaps obvious, as floods are intrinsic to riparian habitats. Yet Bendix (1998) has suggested that sites experiencing frequent floods may not be substantially affected by any given flood event because the existing vegetation will be flood-adapted, allowing for a quasi-equilibrium vegetation composition unlikely to change due to flood disturbance. By this reasoning, it is the cumulative effect of repeated floods, rather than the individual disturbance that controls composition over decadal and greater timescales. Fire, by contrast, is relatively rare in riparian settings, so that vegetation is less likely to be equilibrated to it. Hence when fires do burn riparian habitat, there may be a greater likelihood of compositional change than is the case with floods (Pettit and Naiman 2007b). Because some riparian plant communities are subject to at least occasional fire (Ellis 2001; Dwire and Kauffman 2003; Charon and Johnson 2006), their response to such events is important for a complete understanding of riparian disturbance regimes in fire-susceptible environments. Here we provide an example of the impact of fire on riparian habitat within a chaparral matrix in southern California.

Chaparral landscapes represent an environment in which fire is particularly likely to affect riparian vegetation because of the frequent occurrence of severe wildfires, and particularly because the meteorological conditions in which such fires occur tend to overcome local variations in fuel (Keeley and others 1999), so that the higher fuel moistures typical of riparian vegetation do not prevent burning. Although a few studies have documented that fire does affect riparian plant communities in the area (Davis and others 1989; Bendix 1994), few details are available about the specific impacts of fire, or the variability of those impacts. The impact of fire in riparian plant communities depends on total mortality of stems, on differential mortality among species, and on whether the recruitment of new stems by resprouting or germination mimics the composition of the stems that were lost. Variation in impacts may be due to differences in species' vulnerability, but also to varied spatial locations. Because of the potential role of both sheltered position and moisture in reducing fire severity (Pettit and Naiman 2007a), it is possible

that a given species might show different fire responses depending on whether individuals are located at the channel margin or up on floodplain terraces (Kobziar and McBride 2006). In this study, we examine these aspects of fire impact by addressing four specific questions about woody riparian vegetation burned in a chaparral wildfire: (1) what was the community composition before the fire, and the population size structure of the dominant species (the latter as an indicator of their likely quasi-equilibrium status)?; (2) was there differential survivorship among species?; (3) did the dominant species resprout after the fire, and were there differences in resprouting among species that imply compositional change?; and (4) did fire-related mortality rates differ with distance from the channel or landform position?

METHODS

Study Area

We report here on data collected following the 2002 Wolf Fire, in the Los Padres National Forest. The Wolf Fire, ignited by target shooters in the main stem of Sespe Creek on June 3, 2002, burned eastward over the ensuing 8 days, burning approximately 8760 ha. We sampled along two streams, Potrero John Creek and Piedra Blanca Creek (Figure 1), whose valley bottoms had burned in the first 3 days of the fire (Wolf BAER Team 2002). The steep hillslopes surrounding these streams had a dense cover of chaparral, principally chamise (*Adenostoma fasciculatum*) and manzanita (*Arctostaphylos* sp.). Common valley bottom species included white alder (*Alnus rhombifolia*), Fremont cottonwood (*Populus fremontii*), coast live oak (*Quercus agrifolia*), scrub oak (*Quercus dumosa*), and willows (*Salix* spp.). The fire had extensively burned the valley floor vegetation along all of the reaches we sampled. Both valleys are alluvial, with floodplains occupied by compound channels in which flow is generally limited to a single main channel, but rises to occupy braided subchannels on the floodplain during high flows (Bendix and Cowell, forthcoming). The dry summers of the Mediterranean-type climate, and the occasional occurrence of desiccating foehn winds in the study area are, as in much of southern California, conducive to severe summer and fall wildfires.

Data Collection

We sampled 11 transects across valley cross-sections of the two streams (Figure 1), at elevations between 950 and 1400 m. The transects extended

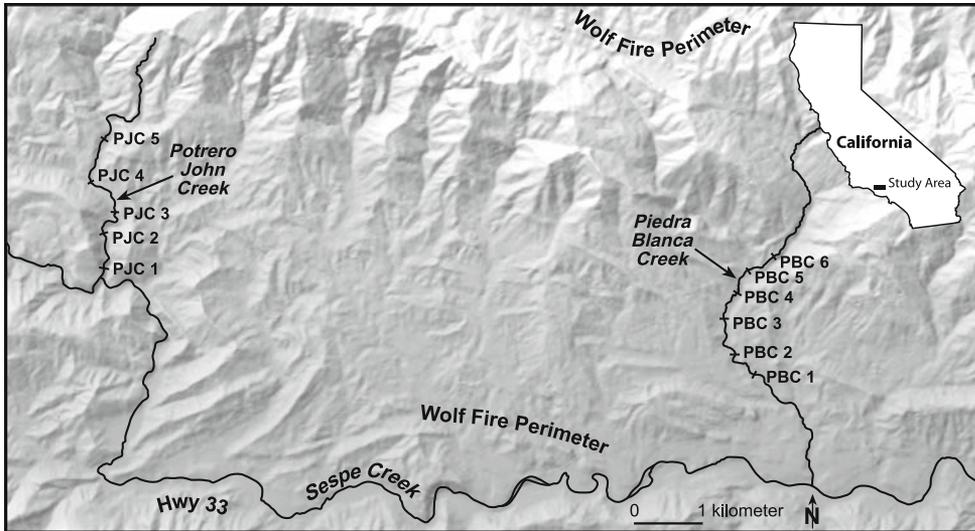


Figure 1. Location of Wolf Fire and sampling transects.

to the slope break at the valley wall on each side, encompassing the channel(s), floodplain, and low alluvial terraces. Six 5×10 m quadrats were spaced evenly along each transect. The distance between quadrats varied from 0 to 4 m, depending on valley width. The valley floor at one site (PBC6) was too narrow to accommodate more than five quadrats, so the total sample comprised 65 quadrats. Eleven of these (primarily mid-channel quadrats) had no trees; the analyses reported here are based on the remaining 54.

Within each quadrat, we recorded species and diameter at breast height (DBH) of all living and dead stems greater than 3 cm DBH. Because our data include the stems that had been killed by the fire, this provides a record of the vegetation that was present before the fire, as well as of what was growing 1 year after it. Because few if any stems this large were completely consumed by the fire, the result is a clear picture of the major overstory species that were present before the fire. Skeletal remains of dead stems were identified by form, branching pattern, bark, and the grain revealed where bark had been burned off (see Keeley and others 2005 for a similar methodology). *Salix* spp. are treated collectively here, because with the foliage burned individual species could not be distinguished. In this setting, however, willows of this size are likely to have been red willow (*Salix laevigata*). For each stem, we recorded whether it had been burned, and if so whether there were signs of sprouting from stem or crown; burned trees without such sprouts were classified as top-killed (Bond and van Wilgen 1996; Ellis 2001). We also recorded the presence or absence of basal or root-crown sprouts. All references to “mortality” in this article

refer to the fate of individual stems rather than entire organisms, due to the ability of some top-killed trees to generate such sprouts. These data were initially collected in July 2003, when, based on our observations, even stems that had been killed by the fire were still standing. Each quadrat was reexamined in July 2005, allowing ample time for post-fire sprouting to occur. We surveyed the valley cross-section at each transect with level and rod, and classified the geomorphic location of each quadrat as “channel,” “floodplain,” or “terrace.” If a quadrat overlapped two landforms, we classified it as falling within the landform comprising the majority of its area.

Data Analyses

For our first question, regarding the pre-fire dominant species, we calculated relative basal area, relative density, relative frequency, and importance value (IV) of all species sampled. IV was calculated as the mean of the other values, so has a maximum value of 100 (this would thus be termed “importance percentage” by some; Mueller-Dombois and Ellenberg 1974). We also plotted diameter class distributions of common tree species, to determine whether they were recruiting sufficient new stems that their dominance would likely have continued had the fire not intervened. For our second question, we used paired *t*-tests to compare densities and basal area of common species between the overall data set (pre-fire vegetation) and the subset of stems that were not top-killed (post-fire vegetation), so that a significant *t*-value would represent a significant change in a species’ abundance or dominance. The unit of analysis for this

and the subsequent analyses was the quadrat. To assess differences in resprouting among species, we calculated the percentage of burned stems of each of the common species in each quadrat that had basal or root-crown sprouts. For the question regarding distance from the channel, we calculated the mean vertical height of each quadrat above the thalweg (deepest point) of the channel. Vertical distance was used here because it was more closely related to moisture conditions than horizontal distance from the channel. We used regression analysis to test the relationship between the relative change in total density and this distance measure. We used one-way ANOVA to test for an influence of landform position on the same dependent variable.

RESULTS

Pre-Fire Vegetation

There were 362 stems in our sample; five species dominated the pre-fire riparian vegetation (Table 1). By all measures, *Alnus rhombifolia* was the most important; no other species combined abundance and size to a comparable degree. *Salix* and *Quercus dumosa* stems were common, but small. *Quercus agrifolia* was rare, but large; *Populus fremontii* was similarly modest in numbers, but with large enough stems to rank third in relative basal area. Diameter class distributions varied considerably for these five species (Figure 2). *Salix* and *Q. dumosa* both had negative exponential “inverse-J” distributions indicative of active pre-fire recruitment. The demographic status of *A. rhombifolia* and *P. fremontii* was less clear, as the limited number of stems in the smallest size class suggests at least the possibility of declining recruitment with an even-

tual overall decrease in density (Whipple and Dix 1979). *Quercus agrifolia* showed only scattered pulses of establishment.

Species' Survivorship

Fire-related mortality rates were very high, with 338 (93.4%) of the stems in the sample top-killed. Of the five most important species, *A. rhombifolia*, *Salix*, and *Q. dumosa* all experienced significant decreases in mean density; they also, along with *P. fremontii* had significant decreases in basal area (Table 2). Only *Q. agrifolia* was relatively immune, losing less than half of its density and basal area. Most dramatic was the loss of *A. rhombifolia*, as the formerly dominant species was reduced to a few scattered stems (Tables 1 and 2; Figure 2). Also notable was the complete loss of *Q. dumosa*, along with three species that had been rare even before the fire: *Cercocarpus betuloides*, *Rhamnus californica*, and *Amorpha californica*.

Resprouting

Because individual species were quite variable in their frequency of occurrence in the quadrats before the fire (Table 1), the data are not amenable to statistical comparison (that is, ANOVA would be inappropriate). They do, however, allow for a straightforward qualitative comparison (Figure 3). *Salix* and *Q. dumosa*, both species that had experienced high mortality (top-kill) rates (Table 2), resprouted at a very high rate, averaging more than 80%. *Quercus agrifolia* and *P. fremontii* both averaged over 50% resprouting. In contrast, *A. rhombifolia* was a poor resprouter, averaging less than 20%.

Table 1. Relative Basal Area, Relative Density, Relative Frequency and Importance Value of Sampled Species Before and After Fire, Arranged by Pre-Fire Importance Value

Species	Pre-fire				Post-fire surviving stems			
	Rel. BA (%)	Rel. dens. (%)	Rel. freq. (%)	I.V.	Rel. BA (%)	Rel. dens. (%)	Rel. freq. (%)	I.V.
<i>Alnus rhombifolia</i>	56.5	29.4	29.9	38.6	0.2	4.4	10.0	4.8
<i>Salix</i> spp.	9.0	26.0	26.4	20.5	0.3	8.7	20.0	9.7
<i>Quercus dumosa</i>	3.3	15.2	12.6	10.4	0.0	0.0	0.0	0.0
<i>Quercus agrifolia</i>	18.2	3.0	5.7	9.0	91.2	26.1	30.0	49.1
<i>Populus fremontii</i>	9.3	7.5	9.2	8.7	7.5	39.1	30.0	25.5
<i>Arctostaphylos glauca</i>	3.2	10.5	4.6	6.1	0.8	21.7	10.0	10.9
<i>Cercocarpus betuloides</i>	0.3	5.0	5.7	3.7	0.0	0.0	0.0	0.0
<i>Rhamnus californica</i>	0.1	2.2	2.3	1.5	0.0	0.0	0.0	0.0
<i>Amorpha californica</i>	0.1	1.1	3.4	1.5	0.0	0.0	0.0	0.0

Data collected in 2003, confirmed in 2005 (see text).

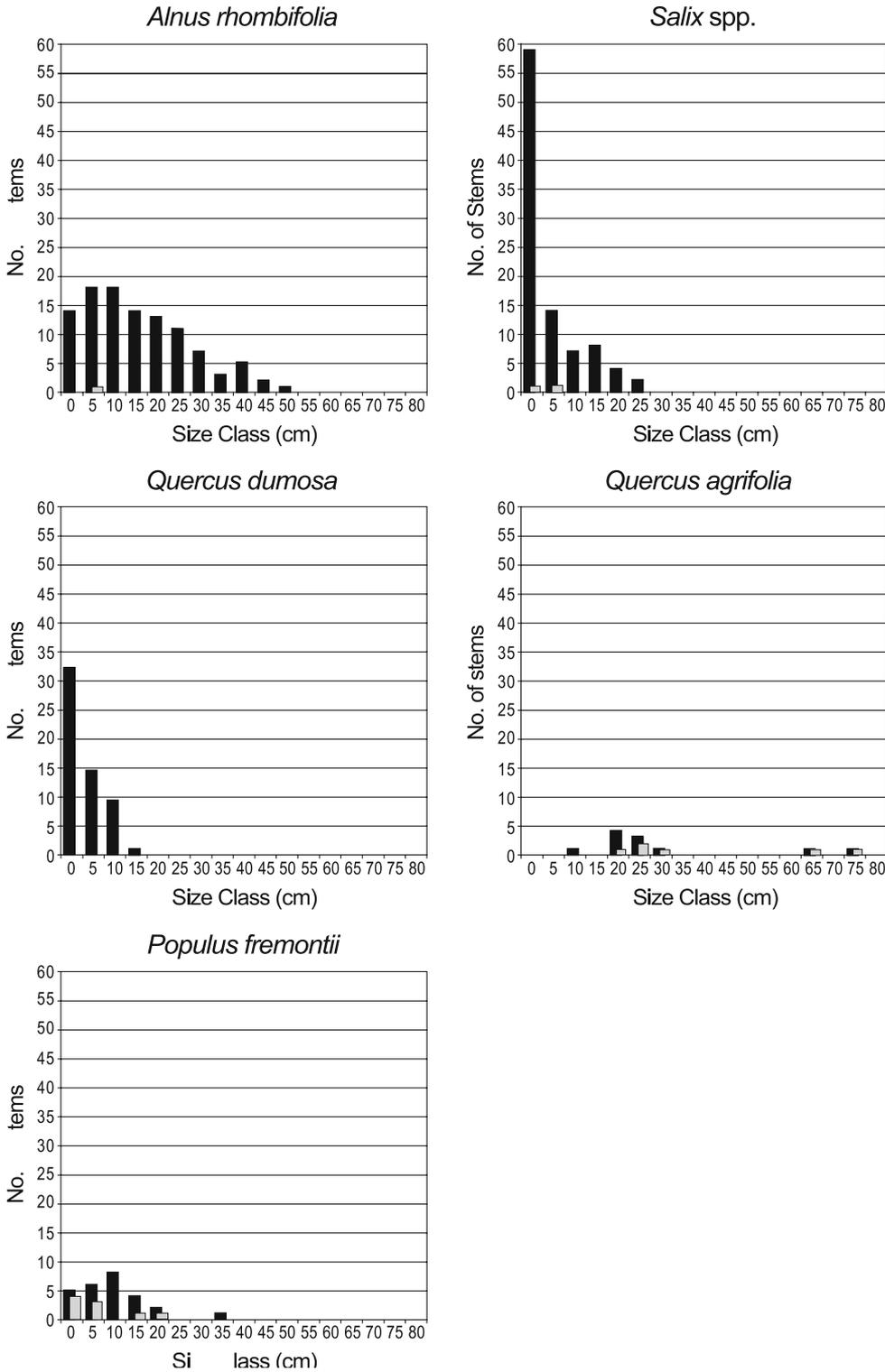


Figure 2. Size class distributions of the five most important (as indicated by IV) tree species in the sample. Black bars denote trees that were present before the fire, gray bars represent stems that were still alive after the fire. Note that the smallest size class includes only stems 3.0 cm or greater DBH.

Location and Fire Impacts

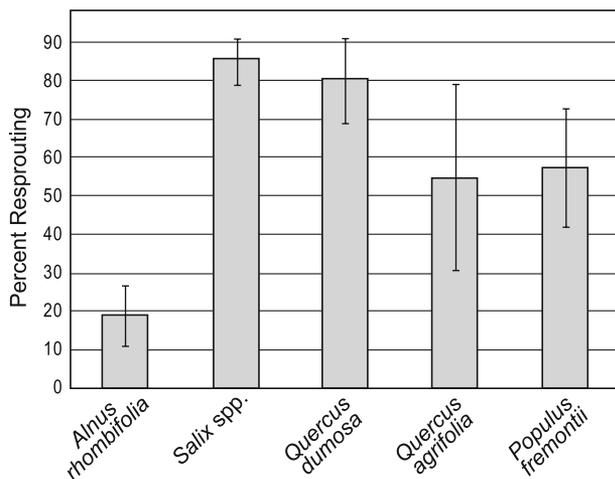
Quadrat heights ranged from 0.1 to 5.4 m above the stream. They were evenly distributed across landforms, with 18 in the channel, 20 on the floodplain, and 16 on terraces. The mortality rates

of stems within quadrats were unrelated to distance above the thalweg ($R^2 = 0.03$, $P > 0.05$). This result reflects the high overall mortality—with so few living stems, there was little variance to explain. Similarly, there was no significant difference in

Table 2. Means for Density and Basal Area of Pre- and Post-Fire Stems Within Quadrats, with Paired *t*-Test Results

Species	Density (stems ha ⁻¹)				Basal area (m ² ha ⁻¹)			
	Pre-fire mean	Post-fire mean	<i>t</i>	<i>P</i>	Pre-fire mean	Post-fire mean	<i>t</i>	<i>P</i>
<i>Alnus rhombifolia</i>	392.6	3.7	-5.55	<0.0001	14.60	0.01	-4.12	<0.0001
<i>Salix</i> spp.	348.1	7.4	-3.97	0.0001	2.33	0.01	-2.54	<0.01
<i>Quercus dumosa</i>	203.7	0.00	-3.32	<0.001	0.85	0.00	-2.47	<0.01
<i>Quercus agrifolia</i>	40.7	22.2	-1.22	>0.05	4.70	4.00	-1.07	>0.05
<i>Populus fremontii</i>	100.0	33.3	-1.60	>0.05	2.40	0.33	-1.97	<0.05

n = 54.

**Figure 3.** Mean percent by species of burned stems that had basal or root crown sprouts by 2005. Error bars show \pm SE.

stem mortality among landforms, with mean mortality rates above 90% for each landform type ($F = 0.18$, $df = 53$, $P > 0.5$).

DISCUSSION

The pre-fire gallery forest lining Piedra Blanca and Potrero John Creeks was a mix of riparian species, clearly dominated by *A. rhombifolia*. The abundance of the smallest size class for *Salix* and *Q. dumosa* suggest successful recruitment that would have kept them prominent indefinitely. *Quercus agrifolia* was the one major species with no recent reproduction. Such limited regeneration is common, although not universal, among the large California oak species (Tyler and others 2006). This arguably stable assemblage was dramatically realigned by the Wolf Fire. Clear differences in fire survivorship emerged, as *A. rhombifolia*, the pre-fire dominant was largely lost, and *P. fremontii* and *Q. agrifolia*

replaced it as dominants among the surviving stems. High mortality rates of *Salix* and *Q. dumosa* were also notable. Those taxa, however, are likely to recover prominence through time, given their high resprouting rates, whereas *A. rhombifolia* combined high mortality with the lowest resprouting rate. Thus, on both immediate and longer timescales, the species that dominated before the fire has been largely removed.

This is in keeping with Davis and others (1989) who also found low resprouting rates, and concluded that severe fire might eliminate *A. rhombifolia* for decades, as well as with Bendix's (1994) finding that *Alnus* was concentrated at the riparian sites that had experienced the longest fire-free periods. Although *Alnus* is a prolific seeder, the high interfluvies between valleys in this rugged terrain make dispersal into a given catchment difficult if the population is removed as a seed source. Moreover, the window of opportunity for seedling establishment after fire was brief, as the abundant resprouting by other species left little unoccupied space for colonization. The only seedlings observed at our sites were scattered *Salix* seedlings noted in 2003 so low on the channel margin of Piedra Blanca Creek that they had been removed by floods when we revisited in 2005. Hence the persistence or recolonization of the species depends not only on life history traits relative to disturbance frequency (Lytle and Poff 2004), but on the complex interplay between life history traits, disturbance history, and dispersal capability (Cattellino and others 1979).

More generally, the relative prominence of species after the fire can be seen as reflecting the balance between variable mortality rates and variable resprouting rates (Figure 4). In settings where post-fire seedling establishment is successful (Dwire and Kauffman 2003), the vertical axis of Figure 4 could also include germination rates. Such settings may be rare, however, as seedling colonization requires not

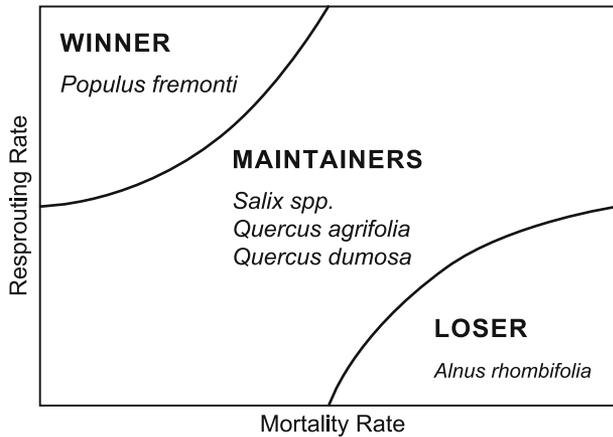


Figure 4. Compositional impacts of survivorship rate and resprouting rate on prominent riparian tree species following fire.

only survival of mature stems to serve as seed sources but also coincidence of the colonization opportunity with appropriate climatological and hydrological conditions (Stella and others 2006), a coincidence that mitigates against germination's importance relative to resprouting, at least in the many riparian environments that include potential resprouters in their species mix (Pettit and Naiman 2007a).

Beyond this compositional change, vegetation structure was altered from what had been a gallery of overstory cover along the creeks to low thickets of sprouts (Figure 5). This is a near inevitability where there is high mortality of mature stems, and is in keeping with the observed reduction of canopy cover in burned plots on the Upper San Pedro River in Arizona (Stromberg and others 2009). But because fire recovery is often couched in terms of compositional and diversity measures, it is worth noting that forest structural change is ecologically important independent of composition. Given the disproportionate importance of riparian habitat (Knopf and others 1988), this structural change could affect numerous avifauna and other vertebrate species, particularly those that require habitat with mature overstory (Olson and Gray 1989).

The high mortality rates at all heights and landforms, down to and including the channel, contrasts with other examples in which the moist, near-channel conditions may confer some protection against fire (Pettit and Naiman 2007a). In the northern Sierra Nevada, for instance, Kobziar and McBride (2006) found that the impacts of a fire backing slowly into the riparian zone were spatially segregated by landform and moisture. Consequently, much of their riparian vegetation was unburned or experienced low to moderate severity

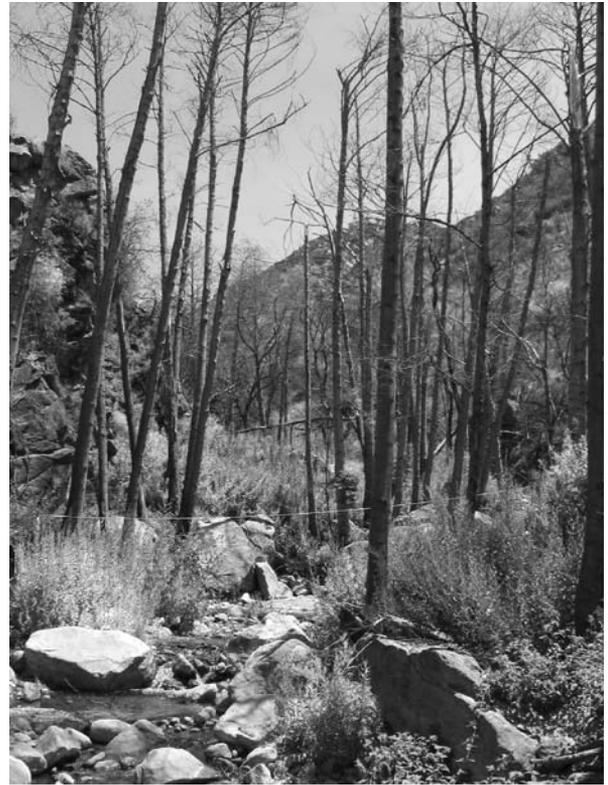


Figure 5. Dead stems of *Alnus rhombifolia* and *Salix* in the channel and floodplain of Piedra Blanca Creek.

fire. That contrasts sharply with our sample, in which all of our transects experienced high severity fire. The importance of the geographic variability of disturbance regimes is illustrated here, as our study area, some 600 km from that of Kobziar and McBride, exemplifies an environment in which fire-favoring meteorological conditions can overcome variations in fuel conditions (compare Keeley and others 1999; Keeley and Fotheringham 2001), thereby imposing a homogeneous impact across a landscape that might have shown topographically moderated mortality patterns in a less severe fire.

Pettit and Naiman (2007a) noted the need for assessments of the role of fire in a variety of ecosystems. In our study area, the role of fire is striking, and is strikingly different from disturbance by floods. Whereas flood disturbance tends to be variable across the valley floor (Bendix 1999), and may actually help to maintain compositional stability (Bendix 1998), disturbance by a severe fire had more uniform impacts across the riparian zone, and resulted in major changes to both composition and structure. The contrasting imprint of these disturbance types on riparian forest likely reflects differences in their frequency, predictability and mechanisms (Lytle and Poff 2004). Flooding is by

definition a recurring disturbance agent in the riparian zone, and in this steep, high energy environment, even floods with a sub-decadal recurrence interval may have significant severity and favor species able to withstand it (Bendix 1998). Fire is comparatively infrequent; an earlier study based on fire perimeters (Bendix 1994) found a median fire interval of 60 years for nearby riparian sites.

The lower frequency of disturbance by fire implies a greater likelihood that species vulnerable to it may become established during fire-free intervals, but, in turn, be lost when it does occur. Regeneration by sprouting appears to be a key mechanism distinguishing between the impacts of fire and flooding, with species such as *A. rhombifolia* able to resprout following floods, but not after fire. Whether viewed through the evolutionary perspective of life-history adaptations (Lytle and Poff 2004), or as a determinant of landscape equilibrium (Turner and others 1993), differences in the frequency and spatial scale of disturbance agents yield very different ecological results. With regard to size class structure, increased size reduces the likelihood of flood mortality (Bendix 1999), so that large stems are likely to endure. Against severe fire, by contrast, size conferred no advantage. Consequently most of the mature stems were killed (Figure 2). As with species composition, the different disturbance mechanism yielded a different result: conversion from a disturbance-maintained uneven size structure to a disturbance-induced structure of largely even-aged small stems. Taken together, the fire-induced changes in composition and in structure, and the spatial homogeneity of disturbance, are very distinct from those typical of flooding in southern California's riparian forests. Because severe fire is less frequent than flooding, when it does occur its disequilibrating effects are, at least on timescales of decades to centuries, profound.

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