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Controls on early post-fire woody plant colonization in riparian areas

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ABSTRACT

Fire in riparian areas has the potential to influence the functions riparian vegetation provides to streams and aquatic biota. However, there is little information on the effects of fire on riparian areas. The objectives of the present study were to: (*i*) determine how fire severity interacts with riparian topographic setting, micro-environmental conditions, and pre-fire community composition to control post-fire regeneration; (*ii*) determine how riparian regeneration patterns and controls change during early succession; and (iii) determine how critical riparian functions are influenced by and recover after fire. Study locations included the Biscuit Fire in southwestern Oregon and the B&B Complex Fire in the Cascade Mountain Range of west-central Oregon, USA. We measured post-fire woody species regeneration, and measured factors such as fire severity, pre-fire species composition, and stream size as potential factors associated with post-fire regeneration patterns. At a relatively coarse spatial scale, patterns in post-fire colonization were influenced by elevation. At finer spatial scales, both conifer- and hardwood-dominated riparian plant communities were self-replacing, suggesting that each community type tends to occur in specific ecological settings. Abundant post-fire regeneration in riparian areas and the self-replacement of hardwood- and conifer-dominated communities indicate high resilience of these disturbance-adapted plant communities.

1. Introduction

Riparian areas are among the most diverse, complex, and dynamic terrestrial habitats (Gregory et al., 1991; Naiman et al., 1993; Naiman and Decamps, 1997). Riparian areas provide key habitat to a diverse array of species and serve as a refuge for wildlife by providing a water source, forage, and escape from predators (Naiman and Decamps, 1997). Riparian areas also provide multiple ecological functions to stream systems. Root systems of riparian plants help to maintain soil structure and bank stability (Swanson et al., 1982; Minore and Weatherly, 1994; Johnson, 2004), and prevent erosion into streams (Naiman and Decamps, 1997). Shade provided by riparian tree canopies reduces stream temperatures, improving habitat for cold-water species such as salmonids (Swanson et al., 1982; Gregory et al., 1991; Minore and Weatherly, 1994; Johnson, 2004). Organic matter from riparian vegetation provides food resources for aquatic organisms (Swanson et al., 1982; Gregory et al., 1991; Naiman and Decamps, 1997). Riparian areas also act as a source of large woody debris for in-stream structure and habitat (Swanson et al., 1982; DeBano and Neary, 1996).

Many riparian areas are subject to frequent disturbance, including flood, avalanche, wind, fire, drought, plant disease, insect outbreaks and herbivory. Fire is a dominant disturbance process in many types of ecosystems, and although the effects of fire in upland systems are relatively well-studied, few studies have investigated riparian vegetation response to fire. Fire in riparian areas has the potential to influence the functions riparian vegetation provides to streams by changing plant community abundance, structure, and composition, and the regeneration of post-fire riparian vegetation likely dictates the magnitude and duration of fire effects on stream systems (Minshall, 2003). Determining management goals and associated management practices for these critical areas of the landscape requires an understanding of how disturbance processes affect them.

Riparian vegetation has potential for great resilience after fire due to a suite of adaptations that allow for rapid recovery (Dwire and Kauffman, 2003; Reeves et al., 2006; Richardson et al., 2007). For example, sprouting facilitates the survival of plants on site, while propagule dispersal by wind and water contribute to recolonization in post-disturbance environments (Dwire and Kauffman, 2003). Riparian areas are characterized by high soil moisture and high water tables, which can lead to faster vegetation recovery compared to uplands (Reeves et al., 2006). The network structure of riparian areas may also increase resilience to disturbance (Swanson et al., 1998). The linkages between the

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floodplain and channel (lateral linkages), upstream and downstream and upstream river sections (longitudinal linkages), and river bed and channel (vertical linkages) have been identified as critical elements that lend resilience to riverine systems (Sedell et al., 1990; Richardson et al., 2007). These linkages allow surviving species in areas with low disturbance severity (refugia) to recolonize areas with high disturbance severity (Sedell et al., 1990; Swanson et al., 1998).

Plant community successional processes and species composition are controlled by a long-recognized array of ecological factors, including environmental conditions, available resources, soil characteristics, and disturbance (Gleason, 1926; Pickett et al., 1987; Wimberly and Spies, 2001). Factors at both fine and coarse scales have been shown to control plant community composition in riparian areas (Baker, 1989; Bendix, 1994; Turner et al., 2004). However, the ecological role of fire in riparian plant community succession and species composition is uncertain, as is the relative role of fire versus other ecological controls on plant community composition.

The present study examined post-fire woody plant regeneration processes through observations of riparian plant communities 2 and 4 years post-fire. Specific objectives were to: (i) determine how fire severity interacts with topographic setting, microenvironmental conditions, and pre-fire community composition to control post-fire regeneration; (ii) determine how riparian regeneration patterns and controls change during early succession (from 2 to 4 years post-fire); and (iii) determine how critical riparian functions like shade and bank stability are influenced by and recover after fire.

In addition to expected patterns in species composition with elevation and plant association, we hypothesized that: (i) post-fire riparian deciduous hardwood regeneration is most abundant in areas where local topography is conducive to deciduous hardwood growth (along larger streams, in wider valleys, and in areas with more gentle stream gradient and slope) and with greater pre-fire deciduous hardwood composition; (ii) post-fire riparian conifer regeneration is most abundant where local topography is conducive to conifer growth (along smaller streams, in narrow valleys, and in areas with steeper slopes and stream gradients) and where there is greater live conifer abundance before and/or after the fire; and (iii) post-fire riparian regeneration is influenced by fire severity, and the importance of seed bank and dispersed seed strategies increases with fire severity, while sprouters are more abundant in areas with lower fire severity. We expected these patterns to become more apparent as early succession progressed from 2 to 4 years post-fire. In addition, because of adaptations that allow for rapid vegetation recovery in riparian areas, we expected effects of fire on riparian functions to be short-lived and less apparent with increasing time since fire.

The study was initiated after two recent fires in Oregon, USA, the Biscuit Fire in the Klamath–Siskiyou ecoregion of southwestern Oregon and the B&B Complex Fire in the Cascade Mountains of west-central Oregon. In both regions, fire is an important, recurring disturbance agent (Agee, 1993). Thus, this study gives an indication of the present-day effects of fire in riparian areas of fire-prone forests.

2. Methods

2.1. Study area

2.1.1. Biscuit Fire

The 2002 Biscuit Fire occurred in the Siskiyou Mountains of southwestern Oregon. The fire covered an area of approximately 200 000 ha, with nearly equal areas of low severity (up to 25% canopy mortality), moderate severity (25–75% canopy mortality), and high severity (>75% canopy mortality) (assessment from satellite imagery; USDA Forest Service, 2004).

Climate in the study area is characterized by cool, wet winters and warm, dry summers. Mean annual precipitation in the study area ranges from 250 to 300 cm (PRISM Group, 2004), with higher precipitation levels on the western (coastal) side of the study area. Most precipitation falls between November and April. Mean temperature in January ranges from 2 to 5 °C, and mean temperature in July ranges from 18 to 20 °C.

Terrain in the Biscuit Fire region is highly dissected with steep slopes. Elevation of study sites ranged from 200 to 1200 m. Parent material in the study area is primarily schist-phyllite, metamorphic/volcanic, metasedimentary/conglomerate, and metasandstone/siltstone. Major soil subgroups include Typic Dystrochrepts and Typic Hapludults. Ultramafic soils are common in the study region but were not sampled.

Prior to the Biscuit Fire, riparian forest overstories were dominated by conifers such as Port-Orford-cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don). Red alder (*Alnus rubra* Bong.) was also a major component of the overstories, while vine maple (*Acer circinatum* Pursh), red alder, tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), and willow (*Salix* spp. L.) dominated the midstories.

2.1.2. B&B Complex Fire

The 2003 Bear Butte and Booth (B&B) Complex Fire occurred on the east slope of the Cascade Range in west-central Oregon. The fire burned over approximately 37 000 ha, with 38% unburned or low severity, 18% moderate severity, and 44% high severity (assessment from satellite imagery; USDA Forest Service, 2005).

Climate in the B&B Complex Fire area is moderate with cool, wet winters and warm, dry summers. Annual precipitation in the fire area ranges from 50 cm at the lower elevations to 140 cm at the upper elevations (USDA Forest Service, 2005). Most of the precipitation falls from November to March. Precipitation above 1000 m falls mainly as snow in the winter.

The B&B Complex fire area is characterized by gentle to moderately steep topography. Slope aspects within the fire area are generally easterly with north- and south-facing valley slopes. Elevation of sample areas ranged from 800 to 1500 m. The east slope of the Cascades where the B&B Complex Fire burned is a geologically young and complex volcanic region.

Prior to the B&B Complex Fire, riparian forest overstories were dominated by ponderosa pine (*Pinus ponderosa* P. & C. Lawson), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), grand fir and white fir hybrid (*Abies grandis* (Douglas ex D. Don) Lindl. × *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), and Douglas-fir. Understories were dominated by deciduous shrubs, such as thinleaf alder (*Alnus incana* (L.) Moench), Pacific ninebark (*Physocarpus capitatus* (Pursh) Kuntze), white spiraea (*Spiraea betulifolia* Pallas), boxwood (*Pachistima myrsinites* (Pursh) Raf.), and thimbleberry (*Rubus parviflorus* Nutt.).

In both fire areas, activities such as logging, mining, fire suppression, and cattle grazing likely took place in some study plots. Although we were not able to account for all past land management activities in our study plots, there was no detectable evidence of recent (<15 years ago) prior fire or logging.

2.2. Site selection

A stratified random sampling design was used to select points in each fire area that represented a range of plant associations/productivity, broad fire severity classes (low, moderate and high), pre-fire tree size classes (small, medium, and large), and stream sizes (stream classes 1–3). In the Biscuit Fire, watersheds were used as a proxy for plant association and productivity (the west watershed was characterized by relatively high productivity and the east watershed was characterized by relatively low productivity). In the B&B Complex Fire, sampling was conducted in the ponderosa pine, dry mixed conifer, and wet mixed conifer plant associations. The ponderosa pine sites represent the least productive sites in the study area, followed by dry mixed conifer, and then the wet mixed conifer. See Halofsky and Hibbs (2008) for further details on site selection.

We attempted to sample each combination of plant association/watershed, fire severity class, stream class, and tree size class in each fire. However, not all combinations were found on the landscape. Number of points sampled in the Biscuit Fire totaled 47 (of a possible 54), and number of points sampled in the B&B Complex Fire totaled 54 (out of a possible 81).

2.3. Sampling methods

Sampling was conducted 2 and 4 years after each fire event, in the summers of 2004 and 2006 in the Biscuit Fire, and in the summers of 2005 and 2007 in the B&B Complex Fire. To assess fire severity at each randomly selected point (2 years post-fire), a slope-corrected 10-m $\times$ 25-m plot was established in the riparian area. Half of the plot (5-m $\times$ 25-m) was on one side of the stream, and the other half of the plot (5-m $\times$ 25-m) was on the other side. The half-plots on each side of the stream were directly adjacent to and parallel with the stream. Within each 10-m $\times$ 25-m plot, fire severity was assessed based on measurements of percent exposed mineral soil and percent basal area mortality. Cover of exposed mineral soil was visually estimated to the nearest 5% in each plot. This assessment was conducted by the same two individuals throughout data collection, and an average of the two estimates was used. Basal area of all live and dead trees greater than 5 cm DBH was measured in each plot. Stream gradient (degrees slope) within the plots, percent slope to each of the upland plots, bank-full width, and valley floor width were also measured.

To estimate vegetation cover (shade) over streams (Biscuit Fire in 2006, and B&B Complex Fire in 2005 and 2007), six equally spaced transects were set up across the stream over the length of the plot. Percent of the stream width covered by deciduous and coniferous vegetation (including canopy cover) was determined for each transect.

To assess post-fire riparian regeneration, one slope-corrected 4-m $\times$ 25-m plot was established within the larger 10-m $\times$ 25-m fire severity plot at each randomly selected point; only the first 2 m from the stream (on each side) were sampled for regeneration. Within established plots, stem count of all regenerating trees and shrubs was recorded by species. It was noted whether regeneration was by seed or sprout. If a single dead stem had multiple basal sprouts, all sprouting stems were counted individually. Percent shrub cover was visually assessed by species. Signs of flooding (watermarks on trees, drift lines, and new log jams) and evidence for ungulate browsing (browsed vegetation) were noted for each plot during sampling 4 years post-fire.

2.4. Statistical data analyses

Nonmetric multidimensional scaling (NMS) (Kruskal, 1964; Mather, 1976) was used to examine patterns in species abundance and composition of regenerating plant communities in riparian areas of both the Biscuit and B&B Complex Fires 2 years post-fire and 4 years post-fire (fires and years analyzed separately). NMS was chosen because it avoids the assumption of linear relationships among variables and is appropriate for non-normal community data (McCune and Grace, 2002). NMS also allows quantification of the correlation between ordination axes and environmental variables, thus allowing determination of the relationships between patterns in the ordination of plant community species composition and abundance and environmental variables (Objectives 1 and 2). In analyses for the present study, variables included in the environmental matrices to explain patterns in the ordinations included local topography variables (stream class, bank-full width, valley floor width, stream gradient, and slope to uplands), pre- and post-fire community composition variables (pre-fire live hardwood basal area or percent hardwood stems, pre-fire live conifer basal area, post-fire live conifer basal area, and post-fire live hardwood basal area), fire severity variables (exposed mineral soil and basal area mortality), elevation, and watershed/plant association.

Stem count data of all regenerating species was used in NMS analyses for both the Biscuit and B&B Complex Fires. A square root transformation was used to decrease skewness, and data were relativized by species column total to ensure that the ordination was not structured by only a few abundant species. Species that occurred in less than five percent of the plots were omitted from the analysis in order to filter out noise in the data and to aid recognition of structure in the data (McCune and Grace, 2002). NMS analyses were run with PC-ORD v5.0 (McCune and Mefford, MjM Software Design, Gleneden Beach, OR, USA) using the Sørensen distance measure.

To further investigate relationships between post-fire riparian plant community composition and abundance and environmental variables (Objective 1), multi-response permutation procedure (MRPP) was used to test for differences in regenerating plant communities among plots along different stream classes, and in different watersheds or plant associations. MRPP is a nonparametric method used to test for differences between groups. All MRPP analyses were run in PC-ORD v5.0 with the Sørensen distance measure.

Successional vectors (McCune, 1992; McCune and Grace, 2002) were created in PC-ORD v5.0 to examine direction and rate of change in species composition and abundance within a study plot between 2 and 4 years post-fire (Objective 2); a successional vector represents observed changes in species composition and abundance in a plot between two times in multidimensional species space (McCune, 1992). MRPP was used to compare direction of vectors for plots along different stream classes and in different fire severity classes and watersheds/plant associations. ANOVA was used to compare average length of successional vectors for plots along different stream classes and in different fire severity classes and watersheds/plant associations. ANOVA was also used to compare fire severity levels (basal area mortality and exposed mineral soil) for plots along different stream classes and in different plant associations. For both ANOVA analyses, PROC MIXED in SAS v9.1 (SAS Institute, Cary, NC, USA) was used to fit a mixed effects model to the data (successional vector length and fire severity data). The MIXED procedure was used over PROC GLM because the mixed procedure can better accommodate unbalanced data, which we had in these cases. Assumptions of normality and constant variance were checked prior to interpreting results of the analyses. LSMEANS with a Bonferroni adjustment was used for multiple comparisons of means.

3. Results

3.1. Post-fire mortality and regeneration levels

Mean basal area mortality in riparian areas 2 years post-fire was approximately 50% in both fires (range 0–100%), while mean exposed mineral soil was 33% in the Biscuit Fire and 59% in the B&B Complex Fire. Both basal area mortality and exposed mineral soil

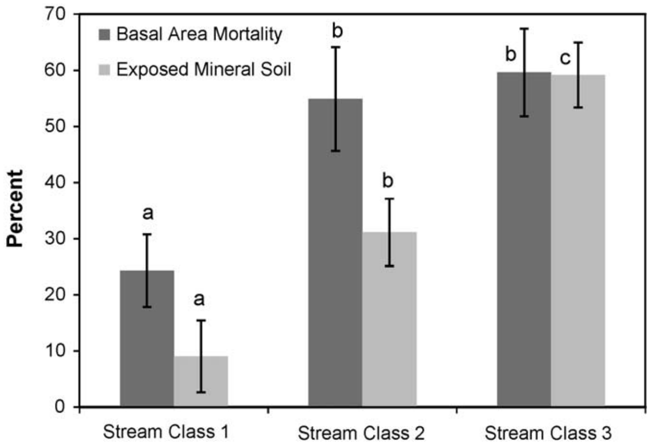

Fig. 1. Mean riparian basal area mortality and exposed mineral soil levels by stream class in the Biscuit Fire. Class 1 streams are fish-bearing streams with a steady flow. Class 2 streams are also fish-bearing with moderate flow, and class 3 streams have few fish and low flow. Standard errors are shown for each mean value. For a given fire severity measure, significant difference between stream classes ($p < 0.05$) is indicated with a difference in letters between stream classes.

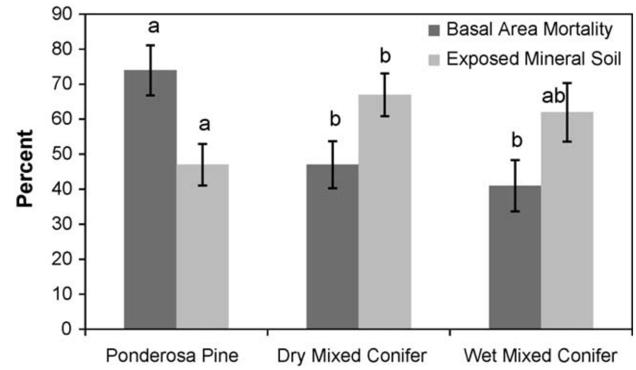

Fig. 2. Mean riparian basal area mortality and exposed mineral soil levels by plant association in the B&B Complex Fire. Riparian plots were sampled in the ponderosa pine, dry mixed conifer, and wet mixed conifer plant associations. Standard errors are shown for each mean value. For a given fire severity measure, significant difference between plant associations ($p < 0.05$) is indicated with a difference in letters.

varied by stream class in the Biscuit Fire, with significantly lower fire severity along larger class 1 streams than smaller streams (Fig. 1). In the B&B Complex Fire, basal area mortality and exposed mineral soil varied by plant association more than stream size; basal area mortality was significantly higher in the ponderosa pine plant association than in the dry and wet mixed conifer plant associations, but exposed mineral soil was significantly lower in the ponderosa pine plant association than in the other plant associations (Fig. 2). See Halofsky and Hibbs (2008) for further details on patterns and drivers of riparian fire severity in the Biscuit and B&B Complex Fires.

There was further mortality between the second and fourth year post-fire in approximately half of the plots in both fires; in these plots, mean percent basal area mortality between 2 and 4 years post-fire was 20% in the Biscuit Fire and 30% in the B&B Complex Fire. In addition, further disturbance occurred in riparian plots of both fires between the second and fourth year post-fire. Approximately 15% of sampled riparian plots in the Biscuit Fire showed signs of flooding 4 years post-fire. As most streams in the B&B Complex Fire are spring-fed, there was little evidence of flooding. However, 65% of sampled riparian plots had signs of ungulate browsing in the B&B Complex Fire 4 years after fire. There was little evidence for other disturbance, such as ungulate browsing, in Biscuit Fire riparian areas.

Mean shrub cover was 11% in the Biscuit Fire both 2 and 4 years post-fire, and there was an insignificant decrease in mean shrub cover between the second and fourth year post-fire in the B&B Complex Fire (Table 1). In the Biscuit Fire, mean percent deciduous (tree, shrub and herb) cover over streams was 38%, and mean percent coniferous tree cover was 23% (Table 1). Despite further mortality in some plots in the B&B Complex Fire, mean cover over streams increased between the second and fourth year after fire (Table 1). Mean seedling density increased between the second and fourth year post-fire in both the Biscuit and B&B Complex Fires (Table 1). Sprout density was higher than seedling density in both fires, and mean sprout density increased between the second and fourth year after both fires (Table 1).

3.2. Post-fire patterns in species composition and abundance

3.2.1. Biscuit Fire

Three dimensions, or gradients, best represented the structure of the Biscuit Fire woody plant regeneration data (final stress = 18.12, and final instability = 0.00). Almost 29% of the variance in the data was represented by the first axis, 19.3% of the variance was explained by the second axis, and 15.8% of the variance was explained by the third axis (cumulative $R^2 = 0.64$).

Axis 1 was strongly negatively associated with percent exposed mineral soil, a measure of fire severity, and elevation (Table 2; Fig. 3). Axis 1 was positively correlated with bank-full width and slope to uplands (Table 2; Fig. 3). Regeneration of upland-associated species, such as dwarf Oregon-grape (*Mahonia nervosa* (Pursh) Nutt.), Pacific rhododendron (*Rhododendron macrophyllum* D. Don ex G. Don), and tanoak, was strongly negatively correlated with axis 1 (Table 2; Fig. 3), suggesting that regeneration of upland-associated species is greater at higher elevations, along smaller streams, and in riparian areas with greater exposed mineral soil. Regeneration of riparian-associated species, such as red alder, willow, and Pacific serviceberry (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roemer) was strongly positively correlated to axis 1 (Table 2; Fig. 3), indicating that regeneration of riparian-associated species is greater along larger streams and in more incised valleys. MRPP also showed significant differences in regenerating woody plant communities among stream classes

Table 1
Mean riparian regeneration levels (and range) 2 and 4 years post-fire in the Biscuit and B&B Complex Fires.

	Biscuit Fire		B&B Complex Fire	
	2 years post-fire	4 years post-fire	2 years post-fire	4 years post-fire
Deciduous stream cover (%)	NA	38 (0–100)	42 (0–92)	56 (6–100)
Coniferous stream cover (%)	NA	23 (0–94)	11 (0–62)	15 (0–71)
Shrub cover (%)	11 (1–33)	11 (1–33)	16 (3–55)	13 (0–39)
Seedling density (per ha)	863 (0–4320)	1652 (0–15,480)	4989 (0–23,440)	11,211 (0–181,480)
Sprout density (per ha)	5897 (80–21,880)	8272 (40–31,040)	5801 (0–17,520)	8543 (40–257,60)

Table 2
Correlations (r^2) and direction of correlation between nonmetric multidimensional scaling ordination axes and environmental variables and species for the Biscuit and B&B Complex Fires.

Fire	Axis	Environmental variable or species	Correlation with axis (r^2)	Positive (+) or negative (−) correlation
Biscuit Fire	1	Percent exposed mineral soil	0.51	−
Biscuit Fire	1	Elevation	0.41	−
Biscuit Fire	1	Dwarf Oregon-grape	0.37	−
Biscuit Fire	1	Pacific rhododendron	0.32	−
Biscuit Fire	1	Tanoak	0.25	−
Biscuit Fire	1	Bank-full width	0.47	+
Biscuit Fire	1	Slope to uplands	0.29	+
Biscuit Fire	1	Willow species	0.32	+
Biscuit Fire	1	Red alder	0.25	+
Biscuit Fire	1	Pacific serviceberry	0.20	+
Biscuit Fire	2	Pre-fire hardwood basal area	0.20	−
Biscuit Fire	2	Post-fire hardwood basal area	0.14	−
Biscuit Fire	2	Whitebark raspberry	0.23	−
Biscuit Fire	2	Stink currant	0.19	−
Biscuit Fire	2	Western azalea	0.31	+
Biscuit Fire	2	Twinflower	0.18	+
B&B Fire	1	Pre-fire percent hardwoods	0.28	−
B&B Fire	1	Red osier dogwood	0.22	−
B&B Fire	1	Pacific ninebark	0.20	−
B&B Fire	1	Twinberry	0.19	−
B&B Fire	1	Pre-fire conifer basal area	0.37	+
B&B Fire	1	Douglas-fir	0.58	+
B&B Fire	1	Engelmann spruce	0.44	+
B&B Fire	1	Grand fir and white fir hybrid	0.30	+
B&B Fire	1	Western hemlock	0.23	+
B&B Fire	2	White spiraea	0.40	−
B&B Fire	2	Thinleaf alder	0.20	−
B&B Fire	2	Vine maple	0.38	+
B&B Fire	2	Western hemlock	0.17	+
B&B Fire	2	Douglas-fir	0.16	+
B&B Fire	3	Slope to uplands	0.41	−
B&B Fire	3	Percent exposed mineral soil	0.39	−
B&B Fire	3	Pacific ninebark	0.24	−
B&B Fire	3	Elevation	0.57	+
B&B Fire	3	Snowbrush	0.50	+
B&B Fire	3	Sticky currant	0.47	+
B&B Fire	3	Thimbleberry	0.38	+

($p < 0.05$ and $A = 0.06$, where A is a chance-corrected estimate of within-group agreement).

Axis 2 was negatively correlated with pre-fire deciduous hardwood basal area and post-fire live deciduous hardwood basal area (Table 2; Fig. 3). Regeneration of species abundant in poorly drained, wetter environments, such as whitebark raspberry (*Rubus leucodermis* Dougl. ex Torr. & Gray) and stink currant (*Ribes bracteosum* Dougl. ex Hook.), was negatively correlated with axis 2 (Table 2; Fig. 3), suggesting that regeneration of species that are abundant in wetter environments was higher in locations with higher pre- and post-fire deciduous hardwood basal area. In contrast, regeneration of species common in well-drained areas, such as western azalea (*Rhododendron occidentale* (Torr. & Gray ex Torr.) Gray), and twinflower (*Linnaea borealis* L.), was positively associated with axis 2 (Table 2; Fig. 3), suggesting that regeneration of well-drained soil species is higher in locations with lower pre- and post-fire deciduous hardwood basal area. Thus, axis 2 could represent the distinction between deciduous hardwood-dominated plant communities and plant community types associated with well-drained soils.

There was weak evidence for differences in regenerating riparian woody plant communities between watersheds in the Biscuit Fire (MRPP yielded $p < 0.05$ and $A = 0.02$). Watersheds separated somewhat on axis 3; plots in the same watershed were more similar in species composition and abundance (grouped together in ordination space) than plots between watersheds.

Four year post-fire ordination results were almost identical with the second year so are not presented; the same environmental factors and species structured post-fire riparian woody plant communities in both years. However, further analyses were conducted examining successional patterns in plots between 2 and 4 years post-fire. These analyses indicated that there were no differences in the amount or direction of successional change among plots in different fire severity classes or watersheds in the Biscuit Fire ($p > 0.05$). Directions and lengths of successional vectors generally showed complex and indistinguishable patterns. However, there was evidence for differences in the amount of successional change in riparian plant communities along different-sized streams. On average, there was significantly greater change in plant community composition and abundance between 2 and 4 years post-fire in plots along the largest (class 1) streams than in plots along the smallest (class 3) streams ($p < 0.05$). Significant difference in vector length between large and small streams was found in the ordination space of axes 1 versus 2 and axes 2 versus 3. This suggests that successional change was in relation to axis 2, which was associated mainly with hardwood composition and abundance. Though there were no directional changes in hardwood composition in these plots as a group (increasing or decreasing hardwood composition with time), the relationship between amount of successional change and stream size/species composition in the Biscuit Fire suggests that differences in species composition may be driving these differences in amount of successional change.

3.2.2. B&B Complex Fire

Three dimensions best represented the structure of the B&B Complex Fire woody plant regeneration data (final stress = 15.97, and final instability = 0.00). Almost 22% of the variance in the data

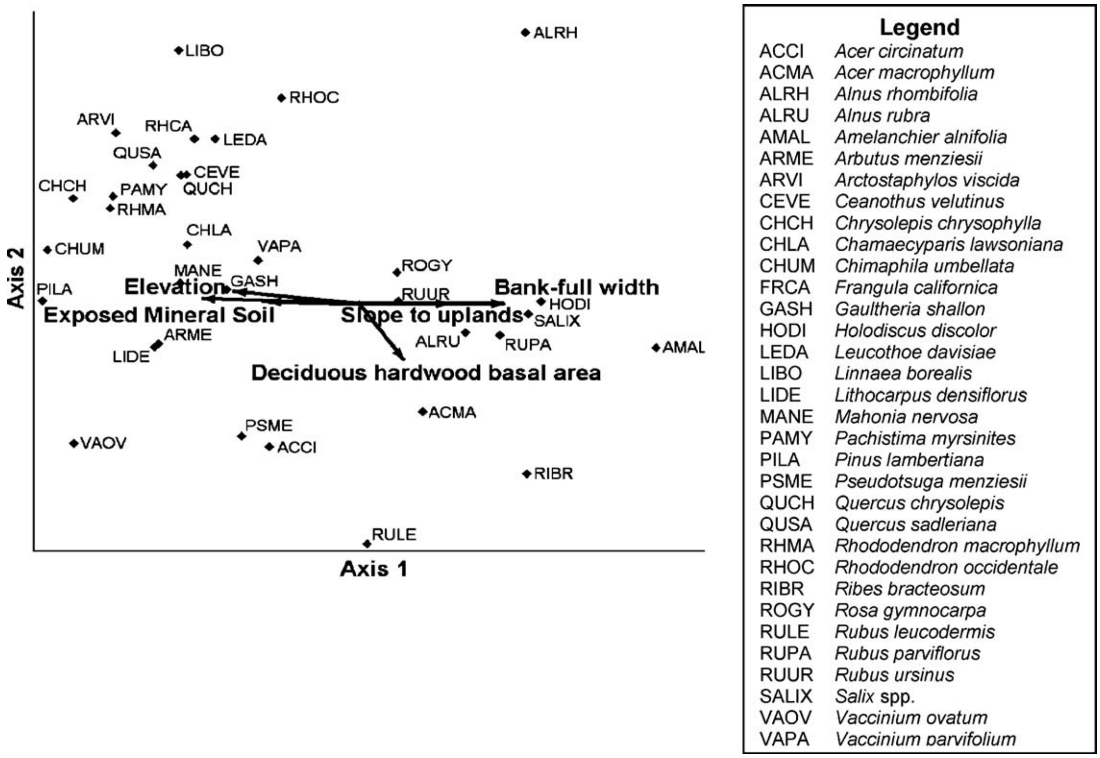

Fig. 3. Joint plot of NMS ordination results for regenerating species in plot space for the Biscuit Fire. Angles and length of lines represent the direction and strength of relationships between variables and ordination scores. Almost 29% of the variance in the data was represented by the first axis, and 19.3% of the variance was explained by the second axis (cumulative R^2 for 3-dimensional solution = 0.64).

was represented by the first axis, 22.9% of the variance was explained by the second axis, and 29.3% of the variance was explained by the third axis (cumulative R^2 = 0.74).

Pre-fire conifer basal area had the highest (positive) correlation with the first axis (Table 2; Fig. 4), and regeneration of conifer species, such as Douglas-fir, Engelmann spruce, grand fir and white fir hybrid, and western hemlock, was strongly positively associated with axis 1 (Table 2; Fig. 4). This indicates that conifer regeneration was greater in riparian areas with higher pre-fire conifer basal area. Conversely, regeneration of riparian-associated hardwood species was greater in areas with lower pre-fire conifer basal area and higher pre-fire percent hardwood composition; pre-fire percent hardwood composition had a relatively high (negative) correlation with axis 1, and regeneration of riparian-associated hardwood species, such as red osier dogwood (*Cornus sericea* L.), Pacific ninebark, and twinberry (*Lonicera involucrata* (Richards.) Banks ex Spreng.), was strongly negatively related to axis 1 (Table 2; Fig. 4). Overall, axis 1 seems to represent the distinction between conifer-dominated sites and hardwood-dominated sites, and pre-fire species composition is reflected in the post-fire regeneration patterns.

There was evidence for differences in regenerating woody plant communities among plant associations in the B&B Complex Fire (MRPP yielded $p < 0.05$ and $A = 0.07$). Plant associations separated somewhat on axis 2 (not shown). In particular, ponderosa pine plots separated from those in the dry and wet mixed conifer plant associations. Regeneration of hardwood species associated with the low elevation ponderosa pine plant association, such as white spiraea and thinleaf alder, was strongly negatively associated with axis 2, while regeneration of species associated with the higher elevation dry and wet mixed conifer plant associations, such as vine maple, Douglas-fir, and western hemlock, as well as several other conifer species, was strongly positively associated with axis 2 (Table 2).

Elevation had the highest (positive) correlation with axis 3 (Table 2; Fig. 4). Regeneration of species associated with higher elevations, such as snowbrush (*Ceanothus velutinus* Dougl. ex Hook.), sticky currant (*Ribes viscosissimum* Pursh), and thimbleberry, was positively associated with axis 3, while regeneration of species associated with lower elevations, such as Pacific ninebark, was negatively associated with axis 3 (Table 2; Fig. 4). Slope to uplands and exposed mineral soil also had high positive correlations with axis 3 (Table 2; Fig. 4).

There was weak evidence for differences in regenerating woody plant communities among stream classes in the B&B Complex Fire (MRPP yielded $p < 0.05$ and $A = 0.02$). However, other factors seem to have greater influence on regenerating communities in riparian areas of the B&B Complex Fire.

For the B&B Complex Fire, only results from 2 years post-fire are presented (above) because 4 year post-fire ordination results were almost identical to those from 2 years post-fire; the same environmental factors and species structured post-fire riparian woody plant communities in both years. Further analyses of successional change between 2 and 4 years post-fire indicated that the amount and direction of successional change did not vary significantly by stream class, fire severity class, or plant association.

4. Discussion

4.1. Controls on post-fire riparian regeneration

Riparian vegetation is controlled by factors at multiple spatial scales, from local disturbance processes to coarse-scale gradients in climate and geology (Baker, 1989; Bendix, 1994; Minore and Weatherly, 1994; Pabst and Spies, 1998; Wimberly and Spies, 2001; Dixon et al., 2002; Sarr and Hibbs, 2007). We found controls on post-fire riparian regeneration patterns to be consistent with these general multi-scale controls.

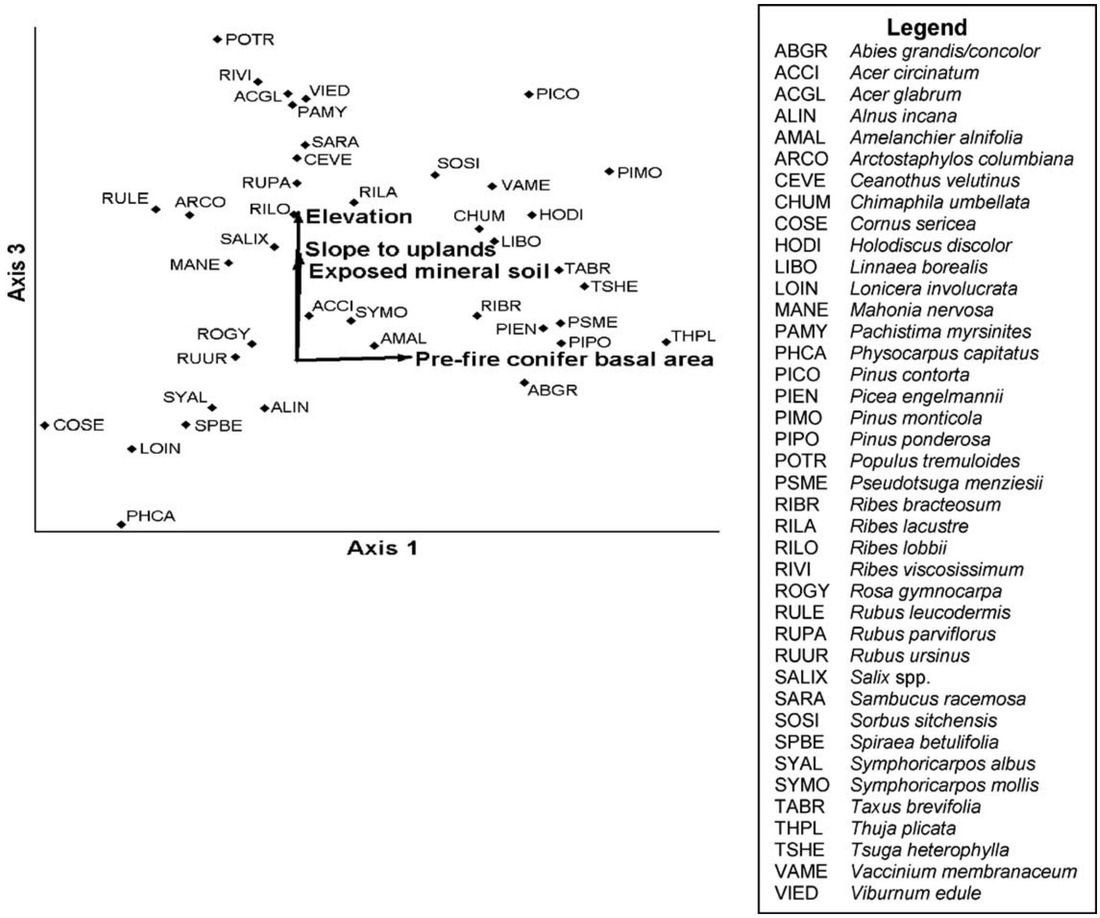

Fig. 4. Joint plot of NMS ordination results for regenerating species in plot space in the B&B Complex Fire. Angles and length of lines represent the direction and strength of relationships between variables and ordination scores. Almost 22% of the variance in the data was represented by the first axis, and 29.3% of the variance was explained by the third axis (cumulative R^2 for 3-dimensional solution = 0.74).

4.1.1. Coarse-scale controls

At a coarse spatial scale (thousands of ha), species composition and abundance of post-fire riparian regeneration in the Biscuit and B&B Complex Fires was influenced by factors associated with elevation, consistent with other studies of controls on riparian plant community patterns (Baker, 1989; Bendix, 1994; Minore and Weatherly, 1994; Reilly et al., 2006). In the steep topography of the Biscuit Fire area, post-fire riparian regeneration was influenced primarily by elevation and position of a stream within a watershed (headwater streams versus main stem stream channels). A number of topographic and physical attributes of streams and the adjacent riparian area vary predictably with elevation and position in a stream continuum (Vannote et al., 1980). Species composition and abundance in regenerating plant communities varied with these factors in the Biscuit Fire. Riparian plant communities along smaller headwater streams (at higher elevations) more closely resembled upland communities before the fire, with higher conifer basal area and a smaller hardwood component. These areas generally experienced greater fire severity (Halofsky and Hibbs, 2008) and were characterized by greater regeneration of upland-associated species, including conifers, than riparian areas along larger streams. In contrast, riparian plant communities along larger, main stem stream channels (at lower elevations) had greater hardwood composition before the fire, generally experienced lower fire severity (Halofsky and Hibbs, 2008) and were characterized by greater regeneration of riparian-associated hardwoods, such as red alder and willow, than riparian areas along smaller streams.

In the more gentle topography of the B&B Complex Fire, variations in moisture and topography with elevation were the primary coarse-scale controls on post-fire riparian regeneration patterns. Patterns in vegetation and topography varied little with stream size in the B&B Complex Fire area. Rather, plant community attributes and topography varied with elevation-distributed plant associations in the B&B Complex Fire area, where ponderosa pine communities occupy areas with gentle topography at lower elevations, and dry and wet mixed conifer plant associations occur in locations with gentle to moderately steep topography at higher elevations. Riparian plant communities in the ponderosa pine plant association were characterized by relatively high basal area mortality (Halofsky and Hibbs, 2008), a large deciduous hardwood component before the fire, and a high density of deciduous hardwoods post-fire. Riparian plant communities in the dry and wet mixed conifer plant associations were characterized by higher exposed mineral soil (Halofsky and Hibbs, 2008), high conifer basal area before the fire, and greater post-fire conifer seedling regeneration.

4.1.2. Fine-scale controls

At finer spatial scales in both fires (tens to hundreds of ha), riparian regeneration was influenced by differences in local site and pre-fire vegetation factors between hardwood- and conifer-dominated plant communities. As hypothesized, in both fire areas conifer regeneration was greater in areas with greater pre-fire conifer basal area, mostly higher elevation plots with steeper topography and well-drained soils. Other studies have found greater conifer seedling numbers in riparian areas with greater conifer basal area and lower hardwood basal area (Minore and Weatherly, 1994; Pabst and Spies, 1999; Hibbs and Bower, 2001). Greater conifer basal area increases conifer seed availability in riparian areas. In addition, communities dominated by conifer species are associated with a suite of environmental conditions that favor conifer species. For example, in the Biscuit Fire, conifers are dominant along smaller streams at higher elevations with higher stream gradients and well-drained soils.

Similarly, as hypothesized, higher pre-fire deciduous hardwood composition was associated with greater regeneration of deciduous hardwood species in both the Biscuit and B&B Complex Fires. Like conifer-dominated communities, communities dominated by deciduous hardwood species are associated with environmental conditions that favor hardwoods, mainly high soil moisture. Deciduous hardwood species serve as microsite indicators in the Biscuit and B&B Complex Fire areas in that their presence indicates generally mesic conditions. Hardwood abundance was also associated with more gentle topography in both fires. Hardwood species, such as red alder, have reproductive and physiological adaptations that allow them to thrive in mesic valley bottoms and lower slope settings with more gentle topography (Pabst and Spies, 1998). Thus, greater regeneration of species associated with wetter environments and more gentle topography would be expected in areas with a greater deciduous hardwood component. In addition, sprouting automatically ensures the continued presence of pre-fire individuals in the post-fire community.

In general, conifer- and hardwood-dominated riparian areas were found to occur in identifiable ecological locations, or particular positions in time and space. Other studies have found that riparian vegetation communities tend to occupy particular positions in time and space (Timoney et al., 1997). In both fires, conifers were dominant at higher elevations and in steeper topography, and thus in well-drained locations, while hardwoods were dominant at lower elevations and in more gentle topography, and thus in wetter areas. These patterns were similar to those found in other studies of riparian vegetation distribution (Minore and Weatherly, 1994; Pabst and Spies, 1998, 1999).

In addition, from one fire cycle to the next, conifer- and hardwood-dominated riparian communities were self-replacing through sprouting and congeneric seedling establishment. This self-replacement suggests that environmental conditions and biological legacies on a site influence post-fire successional processes, resulting in the maintenance of pre-fire patterns in species composition (Reilly et al., 2006; Xavier et al., 2007). These results also suggest that vegetation types in the Biscuit and B&B Complex Fire areas are resilient in space and time.

A measure of understory fire severity, exposed mineral soil, was also associated with patterns in riparian regeneration in riparian areas of both the Biscuit and B&B Complex Fires. As hypothesized, sprouting riparian hardwoods were more abundant in areas with lower exposed mineral soil, while seeders (mainly conifers) and seed bankers (such as snowbrush and manzanita) were more abundant in areas with higher exposed mineral soil. These patterns suggest that fire severity affects post-fire abundance by favoring sprouting species in areas of relatively low fire severity and seeding and seed banking species in areas of relatively high fire severity. Alternatively, these patterns could reflect pre-fire species composition and related local environmental factors that control riparian fire severity (Halofsky and Hibbs, 2008).

4.2. Controls on early post-fire successional patterns in riparian areas

As expected, similar gradients structured community composition and abundance both 2 and 4 years post-fire in the Biscuit and B&B Complex Fires, suggesting that these gradients, mainly elevation, topography/drainage, and pre-fire species composition, are the primary controllers of early post-fire succession in riparian areas. Successional patterns over time within a plot (between 2 and 4 years post-fire) were also explained by location along a stream continuum in the Biscuit Fire; vegetation change was greater for plots along larger streams. This change was associated with species composition, mainly hardwood abundance, suggesting that differences in species composition between larger and smaller streams may be driving differences in species composition and abundance over time. The flood regime in riparian areas is also known to influence plant colonization and abundance patterns (Walker et al., 1986; Bendix and Hupp, 2000). Greater flooding frequency along larger streams may lead to altered post-fire successional patterns, suggesting interaction effects of fire and flooding along larger streams (Pettit and Naiman, 2007a, 2007b; Minshall et al., 1989). Factors associated with position along a stream continuum seem to be stronger than fire severity in controlling early post-fire successional patterns; fire severity explained little variation in species composition and abundance within a plot over time.

4.3. Influence of fire on riparian vegetation functions

Post-fire mortality in riparian areas of both the Biscuit and B&B Complex Fires resulted in reduced canopy cover over streams, thus leading to higher stream temperatures (USDA Forest Service, 2004, 2005). This elevation in stream temperature can impact aquatic organisms in the short-term. However, increases in vegetative cover over streams between the second and fourth year after the B&B Complex Fire suggest that stream shade is recovering, thus ameliorating impacts of fire on aquatic organisms. Increases in seedling and sprout density also indicate that stream bank stabilization is being provided by recovering riparian vegetation.

Sprouting was the dominant post-fire mode of regeneration in sampled riparian areas, particularly in the Biscuit Fire. Studies of post-fire riparian regeneration in other regions also found that a high proportion of riparian plants observed in the first several years after fire regenerated primarily by sprouting (Davis et al., 1989; Gom and Rood, 1999; Ellis, 2001; Kobziar and McBride, 2006). Abundant sprouting helps minimize impacts of fire on aquatic systems by providing stream bank stabilization, preventing erosion, and providing shade over streams. The abundant sprouting of nitrogen-fixing alder species may further contribute to post-fire regeneration in riparian areas of both fires by replenishing nitrogen supplies in riparian soils (Binkley et al., 1994). In these ways, regeneration by sprouting plays a key role in the post-fire recovery of both riparian forests and adjacent aquatic systems.

Overall, there was rapid vegetation regeneration in most sampled riparian areas of the Biscuit and B&B Complex Fires. Abundant regeneration in riparian areas, along with the self-replacement of hardwood and conifer-dominated communities, indicates high resilience in these disturbance-adapted plant communities. This observed resilience supports theory that purports high stream system and riparian resilience conferred by plant species adaptations, high water availability, and the multiple linkages between disturbance refugia and areas affected by disturbance (Sedell et al., 1990; Swanson et al., 1998; Dwire and Kauffman, 2003; Reeves et al., 2006; Richardson et al., 2007).

Rapid post-fire riparian regeneration ensures that riparian vegetation will continue to provide ecological functions to adjacent streams; shrub cover and hardwood sprouts quickly provide stream bank stability and shade to adjacent streams, and tree regeneration will ensure these and other functions, such as organic matter and large woody debris input, are provided over the long term. Results of this study suggest that maintenance of riparian function can be expected after fire in other fire-prone regions. The resilience of these riparian plant communities suggests that, unless there is extensive pre-fire degradation of riparian forests, little post-fire riparian rehabilitation is necessary to ensure the continued functioning of riparian forests after fire. Furthermore, although conifers are important in the functioning of riparian systems, the integral role that hardwoods play, and the unique niche that hardwoods occupy in riparian systems, should be considered in the planning of any rehabilitation or management in riparian areas.

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