

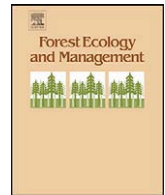


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Influence of wildfire severity on riparian plant community heterogeneity in an Idaho, USA wilderness

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ARTICLE INFO

Article history:

Received 17 July 2009

Received in revised form 19 September 2009

Accepted 21 September 2009

Keywords:

Fire
Stream
Riparian vegetation
Disturbance threshold
Wilderness
Idaho

ABSTRACT

Despite the increasing recognition of riparian zones as important ecotones that link terrestrial and aquatic ecosystems and of fire as a critical natural disturbance, much remains unknown regarding the influence of fire on stream-riparian ecosystems. To further this understanding, we evaluated the effects of mixed severity wildfire on riparian plant community structure and composition in headwater streams of the Big Creek Watershed of the Frank Church 'River of No Return' Wilderness of central Idaho. Five years after a large stand-replacing fire, we conducted riparian vegetation surveys at sixteen reaches across a range of burn types. Non-metric Multidimensional Scaling (NMS) and Multi-Response Permutation Procedure (MRPP) analyses showed an overall shift in community composition and structure between vegetation at unburned and severely burned reaches. Although total plant cover was significantly less at severely burned areas, recovery of the deciduous understory was apparent. Severely burned reaches were characterized by a marked increase in cheatgrass (*Bromus tectorum*). Reaches that were exposed to low-severity fire were indistinguishable from unburned reaches relative to vegetation community composition and structure, pointing to a possible disturbance threshold that may need to be crossed in order to alter riparian plant communities.

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1. Introduction

The importance of riparian habitats is well-documented (Bisson et al., 2003; Naiman et al., 2005). Riparian corridors are highly-dynamic ecotones linking terrestrial and aquatic environments that provide critical habitat and are vital in the transport of water, nutrients, and organisms across the landscape (Vannote et al., 1980; Junk et al., 1989; Dwire and Kauffman, 2003). Riparian vegetation strongly influences hill slope and bank stability, hydraulic fluxes, shade and microclimate (as a function of canopy cover), and aquatic habitat (Junk et al., 1989; Minshall et al., 1989; Gergory et al., 1991; Naiman and Decamps, 1997; Sullivan et al., 2004). Inputs from leaves of riparian trees and shrubs can be an important component of stream food webs (Vannote et al., 1980; Baxter et al., 2005). Riparian vegetation provides food and habitat for terrestrial invertebrates, which can provide substantial prey subsidies to aquatic consumers (Vannote et al., 1980; Baxter et al., 2005). In the arid and semi-arid West, riparian habitats are associated with a disproportionately high number of threatened and endangered species (Carrier and Czech, 1996).

Whereas fire has historically played an important role in structuring riparian plant community composition and structure (Everett et al., 2003; Skinner, 2003), the highly-linked structural and functional nature of riparian and stream ecosystems (Vannote et al., 1980; Junk et al., 1989; Baxter et al., 2005; Sullivan and Watzin, 2008) suggests the effects of fire on riparian zones have implications far beyond vegetation, affecting stream primary productivity, availability and quality of habitat for aquatic biota, and terrestrial to aquatic food subsidies for a variety of in-stream consumers. Longitudinal connectivity along the drainage network points to catchment-level implications of fire on riparian forests (Vannote et al., 1980; Junk et al., 1989; Pettit and Naiman, 2007a). Concurrently, fire frequency and severity have increased over the course of the last century both in riparian zones and in the western U.S. as a whole (Ellis, 2001).

Despite the importance of riparian areas to stream ecosystem health and hydrological processes in the American West and the recognition that fire may be an important source of disturbance, the role of fire in riparian zones is still not completely understood (Bisson et al., 2003; Dwire and Kauffman, 2003; Rieman et al., 2003). Additionally, although the effects of fire on stream-riparian ecosystems have been examined in the short-term (immediately following fire until the first spring runoff), the effects of fire in the midterm (from the first spring runoff following fire to sometime beyond the 10th year) have been neglected (Minshall et al., 2004).

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The lower portion of the Big Creek Watershed, located in the Frank Church 'River of No Return' Wilderness of central Idaho, provides a uniquely appropriate study region for investigating the influence of wildfire on riparian zones. The Frank Church is a 2 million acre wilderness area, whose landscape has been subjected to only limited anthropogenic activity. In 2000, the Diamond Point wildfire burned extensively, but with mixed severity in the lower portion of the Big Creek Watershed. Riparian-fire research in such a wilderness area is essential in providing counterpoints for related studies in regions more heavily impacted by anthropogenic activities (Leopold, 1941). The objective of this study, therefore, was to investigate the effects of low and high severity wildfire on species composition and structure of riparian vegetation communities in a wilderness watershed five years following fire.

2. Methods

2.1. Study area

The setting for this study was the Payette National Forest in Central Idaho, an ecoregion characterized by semi-arid mixed conifer forests dominated by Douglas fir (*Pseudotsuga menziesii*), and shrub-step dominated by mountain mahogany (*Cercocarpus montanus*). The Big Creek watershed drains a mixed conifer forest with an annual precipitation of approximately 40 cm; the majority falls as snow. Peak flows occur from late spring through mid-summer.

Historical fire regimes for *Pseudotsuga*-dominated mixed conifer forests in this area were highly variable in both severity and frequency (Agee, 1993). Historical fire return intervals for ponderosa pine-dominated forests in the region have been estimated to average thirteen years (Heyerdahl et al., 2008), but Pierce et al. (2004), looking at the fire record stored in alluvial sediments found that fire return intervals in the area over the last 8000 years have ranged from 33 to 80 years. It is unclear as to what extent fire suppression policy affected natural fire histories in this watershed, but given its remote location, it is likely that such activities had a relatively minimal impact on fire regimes (Agee, 1993, 2002; Pyne, 2001).

Tree species in the mixed-conifer forest include ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), and Douglas fir (*P. menziesii*). Riparian forests also include water birch (*Betula*

occidentalis), black cottonwood (*Populus trichocarpa*), quaking aspen (*Populus tremuloides*), and green alder (*Alnus viridis*). Common understory species include red-osier dogwood (*Cornus stolonifera*), rocky mountain maple (*Acer glabrum*), red raspberry (*Rubus idaeus*), thimbleberry (*Rubus parviflorus*), mallow ninebark (*Physocarpus malvaceus*), and snowberry (*Symphoricarpos albus*). Incidence of exotic species in this area is low. The most common exotic species is cheatgrass (*Bromus tectorum*) followed by reed canary grass (*Phalaris arundinacea*).

We selected tributaries of lower Big Creek as study streams; Big Creek flows into the Middle Fork of the Salmon River located within the Frank Church 'River of No Return' Wilderness. We conducted all field research out of the University of Idaho's Taylor Wilderness Research Station (Fig. 1). Due to its remote location, land cover in the lower Big Creek Watershed has been largely unaltered by humans.

We included riparian zones of all tributaries of lower Big Creek within a one-day hike from the Taylor Wilderness Research Station in the study. We selected three different fire classes based principally on the presence or absence of an intact conifer canopy: (1) high-severity burn—fire removed both the riparian understory and the conifer canopy. Riparian undergrowth has returned but conifer canopy remains absent. (2) Low-severity burn—fire removed the riparian understory, but canopy remains largely intact. Riparian undergrowth has recovered since fire. The only visible sign of fire at these reaches was the presence of fire scars on large trees. (3) Unburned—riparian vegetation at these tributaries was either unburned, or was burned greater than 50 years ago. Of the sixteen selected reaches, we classified eight as high-severity burn (Calf Creek [CA], Cow Creek [CW], Canyon Creek [CY], Rush Creek [RS], Pioneer Creek [PN], Cliff Creek [CL], Cave Creek [CV], and Cabin Creek [CB]), three as low-severity burn (Dunce Creek [DC], Goat Creek [GT], and Lower North Fork of Cabin Creek [LW]), and five as unburned (Burnt Creek [BT], Cougar Creek [CG], Upper North Fork of Cabin Creek [UP], West Fork of Rush Creek [WF], and the North Fork of the West Fork of Rush Creek [NF]) (Table 1 and Fig. 2).

Eight sites (hereafter 'reaches') represented independent tributary watersheds (CY, PN, CL, CV, DC, GT, BT, and CG). The remaining eight reaches were located within three nested drainages. All study reaches were approximately 100m in length.

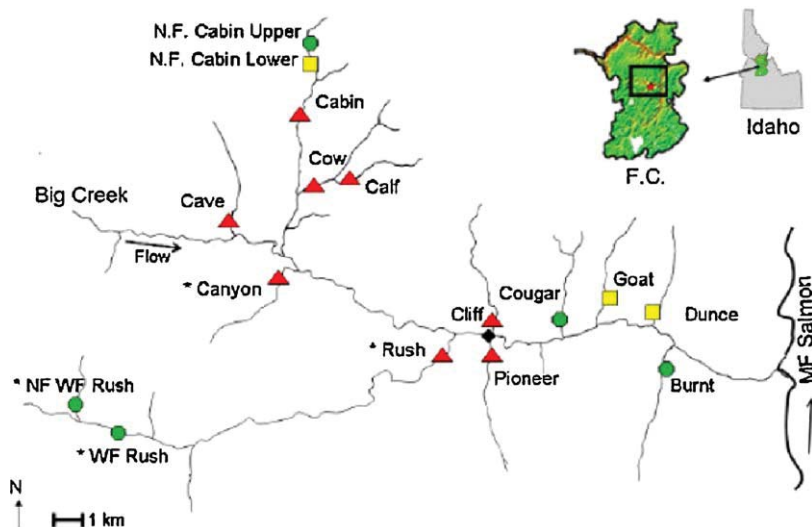


Fig. 1. Study reaches in the Big Creek Watershed, located in the Frank Church 'River of No Return' Wilderness Area in central Idaho. Reaches are all located on tributaries of Big Creek—a major tributary of the Middle Fork of the Salmon River. Twelve reaches were sampled in 2005, and four additional reaches were sampled during 2006 (marked with asterisks). Circles represent unburned reaches ($n = 5$), squares low severity burn reaches ($n = 3$), and triangles high severity burned reaches ($n = 8$). The diamond marks the location of Taylor Ranch Wilderness Field Station (Malison, 2008, in press).

Table 1

Physical and geomorphologic characteristics, along with dominant tree species, of all study reaches of the Big Creek watershed. Tree codes: PSME (*Pseudotsuga menziesii*), POTRI (*Populus trichocarpa*).

Reaches by burn type	Elevation (m)	Aspect	Stream order	Bankfull width (m)	Bankfull depth (m)	Width/depth ratio	Entrenchment ratio	Incision ratio	Stream gradient (%)	Dominant tree species (dominance)
Unburned										
Burnt	1300	N	1	4.50	0.55	8.26	9.00	0.33	**	PSME (100)
Cougar	1180	S	1	4.50	0.68	6.67	10.00	0.60	12	PSME (89)
NF Cabin Upper	1601	S	1	2.50	0.34	7.46	9.00	0.50	18	PSME (94)
NFWF Rush	1642	S	1	1.25	0.34	3.73	7.55	0.72	8	PSME (100)
WF Rush	1623	E	2	3.00	0.29	10.53	10.50	0.00	5	PSME (100)
Low-severity										
Dunce	1165	S	1	1.75	0.46	3.85	7.75	0.43	26	PSME (96)
Goat	1328	S	1	1.75	0.47	3.72	15.00	0.00	7	PSME(68)
NF Cabin Lower	1584	S	1	2.50	0.51	4.90	7.00	0.57	14	PSME (100)
High severity										
Cabin	1406	S	2	6.50	0.89	7.30	24.43	0.48	5	PSME (61)
Calf	1394	SW	1	3.00	0.37	8.11	26.00	0.24	14	PSME (100)
Canyon	1267	N	1	3.50	0.49	7.14	9.50	1.23	9	PSME (100)
Cave	1238	S	2	7.00	0.67	10.45	26.50	0.60	6	PSME (100)
Cliff	1213	S	1	3.50	0.97	3.61	14.33	0.53	13	PSME (67)
Cow	1373	SW	1	5.00	0.72	6.99	9.50	1.70	13	POTRI (85)
Pioneer	1248	N	1	3.00	0.38	7.89	5.50	0.00	10	PSME (100)
Rush	1182	N	3	15.00	1.65	9.12	27.85	0.48	2	PSME and POTRI (50)

** Data unavailable.

We used hierarchical reach classification to identify comparable and representative reach types based on channel bankfull width and depth, floodplain width, reach gradient, substrate type, and valley segment type (Montgomery and Buffington, 1997; Davis et al., 2001). The mean elevation for all reaches was 1360 m. Mid-elevation streams are generally highly constrained and are geomorphically distinct from lowland streams (Schumm, 1977). Due to the large spatial extent of the study, and the limited access of the reaches, an unbalanced study design was unavoidable.

2.2. Sampling

We sampled during the summers in 2005 and 2006, five to six years following fire. We distinguished riparian areas from the

upland by the distinct shifts in vegetation. In general, riparian zones were quite narrow (~8–12 m). Once identified and delineated, we surveyed riparian and adjacent upland vegetation at all sixteen reaches on both sides of the channel at three locations per reach (i.e. upper, middle and lower sections). Most of the sixteen tributaries had a north-south aspect (Table 1). We did not expect a marked difference between vegetation characteristics on each side of the channel due to similar light regimes on opposing banks. At those streams that exhibited a slight east-west aspect, we sampled riparian vegetation at four locations within the reach to account for any potential differences in riparian vegetation between channel sides.

To measure riparian plant species composition and community structure, we used point-line intercept methods (25 m linear

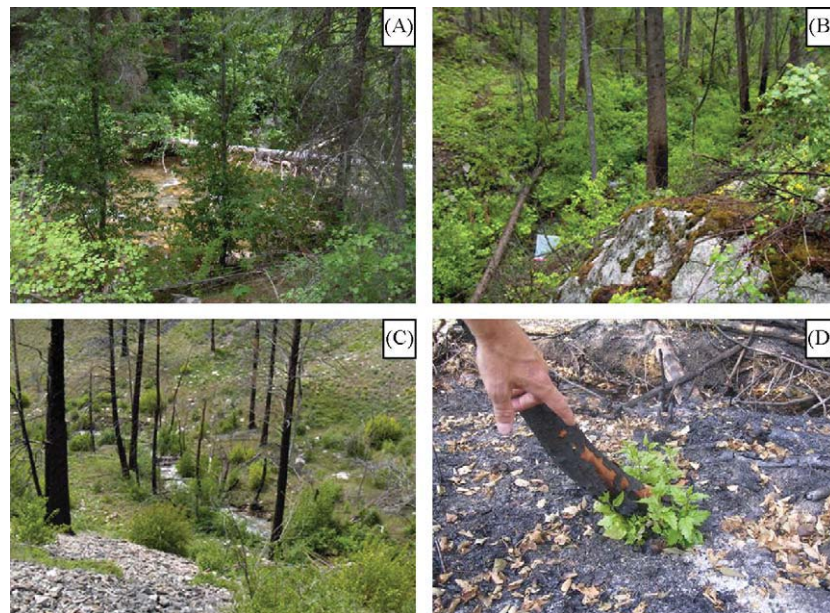


Fig. 2. Pictures of the three fire classes based upon the appearance of post-fire vegetation in 2005: (a) unburned, within the last 50 years; (b) low-severity burn, where fire burned riparian vegetation (as evidenced by circled fire scar), but canopy remained intact; (c) high-severity burn, with both canopy and riparian understory removed by wildfire; and (d) stump sprouting by *Betula occidentalis* ten days following a re-burn through one of the study reaches. Photos A, B, and C courtesy of Rachel Malison (Malison, 2008).

transects parallel to the stream channel; $n = 3, 4$ per reach) following Muller-Dombois and Ellensburg (1974). Transects were relatively homogeneous and representative of the vegetation characteristics of the reach. We recorded the intercept of the transect line by tree and shrub species to the nearest 5 cm and 1 cm, respectively. We recorded point intercepts of herbaceous species at 1 m intervals along each transect line.

We established nested tree, shrub, and herb plots in the upland plant communities adjacent to each riparian vegetation transect. Herb plots were 1 m × 1 m, shrub plots were 2 m × 4 m, and tree plots were 5 m × 10 m (long side parallel to the stream). Within each nested plot, we visually estimated percent cover for all plant species (grasses, forbs, and woody plants). We used a spherical densiometer to determine canopy cover over the stream. We took measurements in the center of the stream channel every 25 m starting at the bottom of the reach for a total of five measurements per reach.

We identified all plants using Hitchcock and Cronquist (1973) as a guide. We designated common species as those that occurred in one or more transects within a study reach. We did not classify *Salix* species below genus due to the high level of hybridization among species. We recorded additional observational data related to vegetation structure, extent, and composition (e.g., new burns and resprouting) in a field journal.

We measured a suite of common stream channel geomorphologic measurements at each reach following Sullivan et al. (2004). For each stream reach, we recorded one cross-sectional transect at a representative riffle or run. Along this transect, we measured bankfull width, bankfull depth, and floodplain width. We also recorded slope for each reach.

2.3. Numerical and statistical analysis

From geomorphic field measurements, we calculated width to depth, entrenchment, and incision ratios (Rosgen, 1996; Sullivan and Watzin, 2008) using the following formulae:

$$\text{width to depth ratio} = \frac{\text{bankfull width}}{\text{mean bankfull depth}} \quad (1)$$

$$\text{entrenchment ratio} = \frac{\text{floodprone width}}{\text{bankfull width}} \quad (2)$$

$$\text{incision ratio} = \frac{\text{low-bank height}}{\text{maximum bankfull depth}} \quad (3)$$

Width to depth ratio is a key measure in assessing the available energy within the channel and the degree to which the channel may be widening. Stream entrenchment is a common measurement relating to the degree to which a channel is inset in its valley. Incision ratios are used as a supplemental measure of bed degradation, often indicating incipient downcutting.

To identify potential differences in riparian and upland plant community composition among burn types, we used Non-metric Multidimensional Scaling (NMS) and Multi-Response Permutation Procedure (MRPP) ordinations (Kruskal, 1964) using PC-ORD 5 (McCune and Mefford, 1999). We converted field estimates of percent cover to an octave scale and used the midpoints of each octave class to minimize sampling errors while preserving fine-scale differences (Muller-Dombois and Ellensburg, 1974; Moore and Chapman, 1986). The octave classes we used were: 1 (trace), 2 (0–1%), 3 (1–2%), 4 (2–5%), 5 (5–10%), 6 (10–25%), 7 (25–50%), 8 (50–75%), 9 (75–95%), 10 (>95%). For riparian trees and shrubs and for upland vegetation, we obtained an importance value from the mean of relative frequency and relative cover estimates and used for ordination. We used relative frequency for the riparian herb

community ordination. We excluded rare species with an importance value less than 0.5% from the analysis.

We selected NMS ordination because of its suitability for analysis of plant community data (McCune et al., 2002). Additionally, it does not make assumptions relative to the structure of the data and it preserves the distance between communities in ordination space better than other ordination techniques (Legendre and Legendre, 1988; McCune et al., 2002). We performed each NMS using Sorenson (Bray Curtis) distance. For each, we used an initial ordination with a step down from six dimensions, and a randomized starting configuration to determine the appropriate number of dimensions. We ran the final ordination with the final starting configuration from the previous ordination. We conducted both initial and final ordinations with 50 runs of real data and a Monte-Carlo test with 250 runs of randomized data. We obtained Pearson's r rank coefficients for riparian vegetation and physical and geomorphologic parameters.

We followed NMS ordination of each community with MRPP to test for differences in plant community composition and structure among burn types. MRPP is a multivariate non-parametric procedure used broadly in ecological applications (see Mielke, 1984; Meilke and Berry, 2001 as cited in McCune et al., 2002) where testing for potential differences among pre-defined groups (e.g., high-severity burn, low-severity burn, unburned) is warranted. MRPP provides an A -statistic and p -value based on 250 Monte-Carlo simulations. We applied a Bonferroni correction to account for multiple comparisons (Miller, 1981). We used Sorenson (Bray-Curtis) distances for this procedure as well. We used PC-ORD software for both NMS and MRPP analyses (McCune et al., 2002).

3. Results

Mean canopy cover was greatest at unburned ((89.1% ± 14.9 (SD)) and low-severity (92.74% ± 1.9 (SD)) burned sites: Cougar Creek (98.0%), Upper North Fork of Cabin Creek (97.6%), Burnt Creek (96.8%), Dunce Creek (94.9%), Lower North Fork of Cabin Creek (91.9%). Not surprisingly mean canopy cover was lowest at high-severity burn sites (60.0% ± 23.6 (SD)): Rush Creek (20.1%), Canyon Creek (25.5%), Cave Creek (42.4%) and Cliff Creek (53.8%).

Species richness for woody vegetation was relatively consistent among reaches with a mean of 27.5 ± 6.2 (SD). There did not appear to be a strong relationship between burn severity and species richness of woody vegetation. Species richness was highest at Cabin Creek (high-severity, 39 species) followed by the Upper North Fork of Cabin (unburned, 36) and Rush Creek (high-severity, 34). Reaches exhibiting low species richness included Dunce Creek (low-severity, 17), Cougar Creek (unburned, 19), Cow Creek (high-severity, 22), and Cliff Creek (high-severity, 22).

We detected a total of seventy-eight riparian species (Table 4). The most common riparian plant species we observed, in descending order, were red osier dogwood (*C. stolonifera*), rocky mountain maple (*A. glabrum*), thimbleberry (*R. parviflorus*), elderberry (*Sambucus cerulea*), gooseberry (*Ribes lacustre*), birch-leaved spiraea (*Spiraea betulifolia*), Oregon-grape (*Berberis repens*), water birch (*B. occidentalis*), mock orange (*Philadelphus lewisii*), and red raspberry (*R. idaeus*). Mean total canopy cover was 71.8 ± 25.3% (SD).

3.1. Riparian woody vegetation

Out of 29 woody species and 49 herbaceous species detected; 24 and 29, respectively, had an importance value greater than 0.5% and were included in NMS and MRPP analyses. MRPP showed that riparian woody plant community composition differed significantly ($p = 0.040$) among the three burn types (High-Severity Burn, Low-Severity Burn, and Unburned) (Table 4). Based on multiple

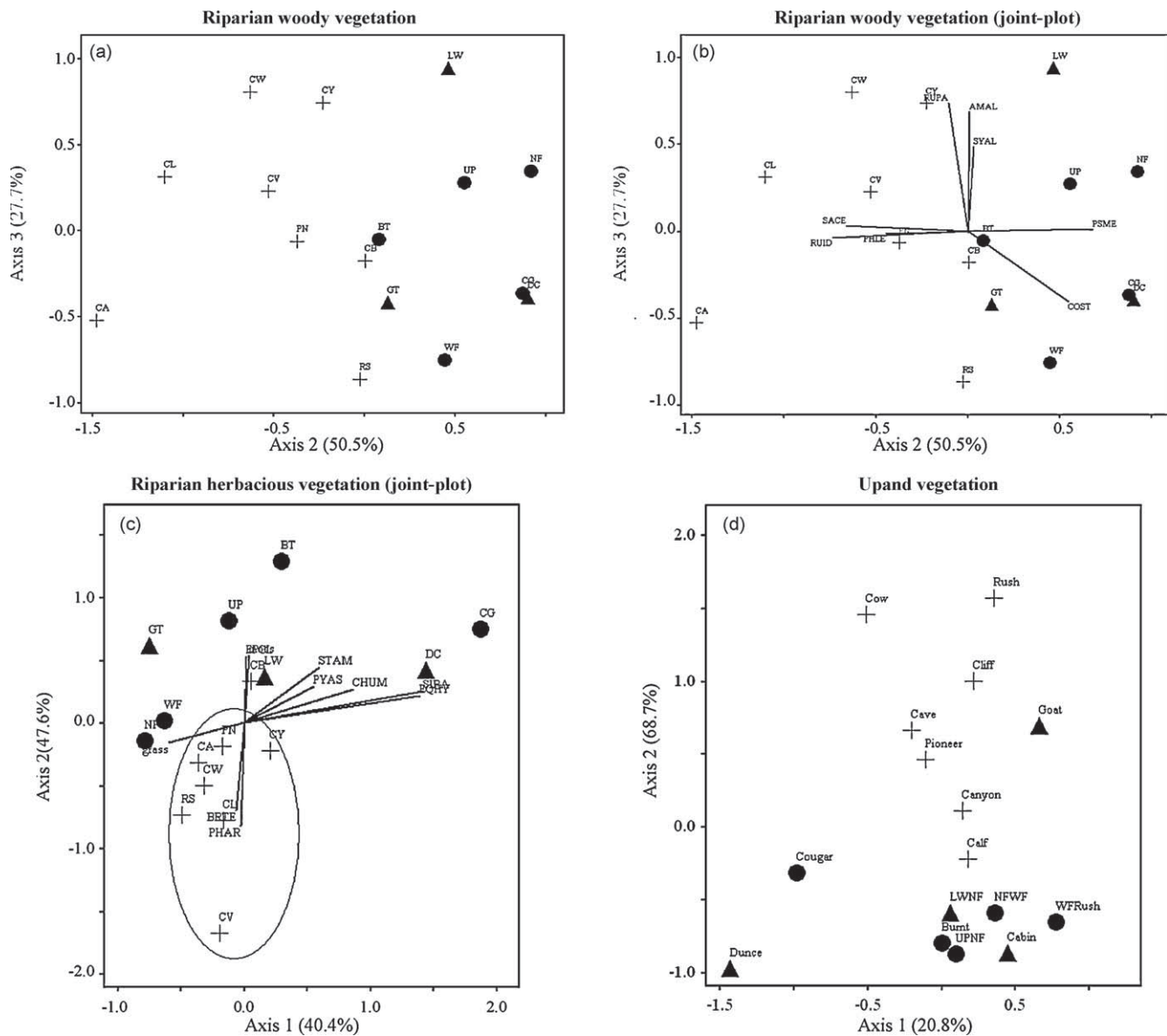


Fig. 3. NMS ordination of (a, b) riparian woody vegetation, (c) riparian herbaceous vegetation and (d) upland vegetation. Unburned reaches are represented by circles, low-severity reaches by triangles, and high-severity reaches by crosses. The amount of variation represented by each axis is indicated in parentheses. Joint plots have been included in (b) and (c) to show correlations (Pearson's $r > 0.5$) between specific plant species and grouping of reaches according to burn severity. The oval in (c) indicates the clustering of high-severity burn reaches and highlights the correlation between exotic species *Bromus tectorum* (BRTE) and *Phalaris arundinacea* (PHAR) with Axis 2 in the direction of high-severity burn reaches.

MRPP comparisons, the greatest differences in riparian community composition resulted from differences between unburned reaches and high-severity burn reaches. Differences between low-severity and high-severity burn reaches also contributed to the overall significance of the model. NMS ordination echoed these results. The three-axis NMS solution (stress = 10.1, $p = 0.02$) represents 85.1% of the total variation; 6.9% on axis 1, 50.5% on axis 2, and 27.7% on axis 3 (Fig. 3a).

Sun-loving generalists such as *R. idaeus* were positively correlated (Pearson's Rank Coefficient) with axis 2 ($r = 0.72$). The dominant tree species, *P. menziesii*, and species preferring moist sites such as *C. stolonifera* were negatively correlated with axis 2 ($r = -0.72$ and -0.70 , respectively). Entrenchment ratio was also positively correlated with axis 2 ($r = 0.61$), whereas incision ratio was negatively correlated ($r = -0.61$) with this axis. *C. stolonifera* and *B. occidentalis*, both species preferring moist sites, were positively correlated with axis 3 ($r = 0.70$ and 0.79 , respectively). *S.*

albus, an upland species preferring well-drained sites was negatively correlated with axis 3 ($r = -0.79$) (Table 3 and Fig. 3b).

3.2. Riparian herbaceous vegetation

MRPP analysis revealed significant ($p = 0.063$) differences in riparian herbaceous plant communities among burn types (Table 2). We observed the greatest variation in community composition in differences between unburned and high-severity burn reaches. NMS ordination resulted in a two-axis solution (stress = 10.9, $p = 0.004$) representing 88.0% of the total variation, with 40.4% on axis 1 and 47.6% on axis 2 (Fig. 3c). The two most common exotic species, *P. arundinacea* and *Bromus tectorum*, were both positively correlated with axis 2 ($r = 0.67$ and 0.63 respectively). Three shade-preferring herbaceous species, *Equisetum hyemale*, *Smilacina racemosa*, and *Chimaphila umbellata* were positively correlated with axis 1 ($r = 0.89$, 0.89 , and 0.69 ; respectively). None

Table 2

Results from MRPP analysis of (a) riparian woody vegetation (based on relative importance data); (b) riparian herbaceous vegetation (based on relative frequency data); and (c) upland vegetation (based on relative percent cover data).

Source	Riparian woody vegetation		Riparian herbaceous vegetation		Upland vegetation	
	A	p-value	A	p-value	A	p-value
Burn type	0.128	0.040*	0.083	0.063	0.208	0.005*
Unburned vs. low-severity	-0.125	0.923	-0.066	0.749	0.024	0.267
Unburned vs. high-severity	0.140	0.014***	0.070	0.044*	0.267	0.003***
Low-severity vs. high-severity	0.135	0.039*	0.111	0.019*	0.103	0.045*

Significance is indicated as * $p < 0.05$, *** $p < 0.017$ after Bonferroni correction for multiple comparisons.

of the physical or geomorphological parameters were strongly correlated with either axis (Table 3 and Fig. 3c).

In 2006, the Big Creek Watershed experienced another wildfire that affected many of the reaches in this study. Less than one week following the fire, we observed stump sprouting and re-growth from rhizomes in riparian areas, sometimes exceeding 10 cm (Fig. 1).

Table 3

Correlations (Pearson's r) of physical and geomorphologic parameters and individual plant species variables with Axis resulting from NMS ordinations of riparian woody plant communities, riparian herbaceous plant communities, and upland plant communities.

Parameters	Pearson's r		
	Axis 1	Axis 2	Axis 3
Riparian Woody Plant Community			
Physical parameters			
Elevation	-0.44	-0.25	-0.27
Width/depth	-0.41	-0.40	0.05
Entrenchment	-0.27	0.61	0.41
Incision	-0.33	-0.61	0.18
Slope	0.22	-0.29	-0.08
Species ($r > 0.50$)			
<i>Sambucus cerulea</i>		0.76	
<i>Rubus idaeus</i>		0.72	
<i>Pseudotsuga menziesii</i>		-0.72	
<i>Cornus stolonifera</i>		-0.70	0.70
<i>Betula occidentalis</i>			0.79
<i>Symphoricarpos albus</i>			-0.79
Riparian Herbaceous Plant Community			
Physical parameters			
Elevation	-0.51	-0.18	
Width/depth ratio	-0.28	0.33	
Entrenchment ratio	-0.23	0.52	
Incision ratio	0.13	0.25	
Slope	0.46	-0.14	
Species ($r > 0.50$)			
<i>Equisetum hymale</i>	0.89		
<i>Similacina racemosa</i>	0.89		
<i>Chimaphila umbellata</i>	0.69		
<i>Phalaris arundinacea</i> [†]		0.67	
<i>Bromus tectorum</i> [†]		0.63	
Upland Plant Community			
Physical parameters			
Elevation	0.50	-0.46	
Width/depth ratio	0.26	0.03	
Entrenchment ratio	0.29	0.34	
Incision ratio	-0.31	0.30	
Slope	-0.64	-0.24	
Species ($r > 0.50$)			
<i>Bromus tectorum</i> [†]		0.90	
<i>Pseudotsuga menziesii</i>		-0.64	
<i>Rosa acicularis</i>		0.53	
<i>Cornus stolonifera</i>	-0.69		
<i>Betula occidentalis</i>	-0.76		
<i>Streptopus amplexifolius</i>	-0.67		
Native grasses	-0.60		

[†] Non-native species.

3.3. Adjacent upland vegetation

For the upland plant communities, MRPP analysis mirrored results for the riparian community (Table 2). We detected a significant ($p = 0.005$) difference among the three burn types with most of the variation in community composition observed between unburned and high-severity burn types. NMS ordination revealed a two-axis solution (stress = 10.8, $p = 0.01$) representing 90% of the overall variation: 21% on axis 1 and 69% on axis 2 (Fig. 3d).

B. tectorum, which we observed to be prolific in burned upland plots and adjacent hillsides, was highly correlated with axis 2 ($r = 0.90$), while *Pseudotsuga menziesii* was negatively correlated with the same axis ($r = -0.64$). Shade-loving plants preferring moist soils such as *C. stolonifera*, *B. occidentalis*, *Streptopus amplexifolius*, and native grasses, were negatively correlated with axis 1 ($r = -0.69$, -0.76 , -0.67 , and -0.60 respectively). None of the physical or geomorphologic parameters were patently correlated with either axis (Table 3 and Fig. 3d).

4. Discussion

Fire in riparian zones of this wilderness watershed significantly affected riparian vegetation, with marked differences in community composition and structure between unburned and severely burned reaches remaining five years post-fire. Heterogeneity in vegetation communities suggest that fire is a critical source of disturbance in stream-riparian ecosystems and that there may exist a disturbance threshold relating to fire severity that must be crossed to trigger new, alternate community states (Dale et al., 2005).

Both the presence of riparian vegetation five years following fire in both high-severity and low-severity burned reaches and the rhizomal stump-sprouting and regrowth following a 2006 wildfire throughout the study area (Fig. 2) represent observations consistent with disturbance-related adaptations of riparian plants that may contribute to recovery of streamside ecosystems following fire (Dwire and Kauffman, 2003). For example, clonal regeneration of quaking aspen (*P. tremuloides*) and cottonwoods (*Populus* spp.) is promoted by light-to moderate-severity fire (Jones and DeByle, 1985; Romme et al., 1995; Bartos and Campbell, 1998; Gom and Rood, 1999). *Populus* spp. and *Salix* spp. also exhibit clonal regeneration following browsing by beaver, suggesting they may respond in a similar way to fire disturbance (Dwire and Kauffman, 2003). Riparian shrubs such as alder (*Alnus* spp.), birch (*Betula* spp.), currant (*Ribes* spp.), rose (*Rosa* spp.), and snowberry (*Symphoricarpos* spp.) sprout from stumps, root crowns, and belowground stems following fire (Adams et al., 1982; Stickney, 1986; Miller, 2000). Thick bark may protect riparian tree species such as ponderosa pine from low-severity fire.

Adaptations of riparian plants to flow regimes (see Johansson and Nilsson, 2002; Naiman et al., 2005) may be particularly important by predisposing many plant species to disturbance and enabling recovery from fire. Riparian shrubs also likely have high survival rates in fire due to high soil moisture and reduced

combustion of soil organic matter and belowground tissues in riparian areas (Dwire and Kauffman, 2003). Conversely, many riparian woody species are uniquely dependent on the magnitude, timing, and frequency of flood events (e.g., willows and cottonwoods) for seed dispersal and regeneration (Dwire and Kauffman, 2003), so a combination of severe fire and unfavorable fluvial conditions may hinder riparian forest succession. The interplay between fluvial dynamics and other sources of disturbance such as fire encourage a complex mosaic of community composition and structure (Ward et al., 2002).

The heterogeneity resulting from a combination of fire- and fluvial-induced disturbances has been suggested to increase ecosystem resilience by providing greater options for system

response to subsequent disturbances (Dale et al., 2005; Pettit and Naiman, 2007b). Our study reaches were for the most part characterized by constrained streams lacking developed floodplains. Rush Creek was the largest of the streams (Table 1) and was the only study reach that supported an active floodplain. Although it was a high-severity burn site, it grouped with low-severity and unburned sites in relation to woody vegetation (Fig. 3a and b). This observation offers support of an increase in ecosystem resilience where the interaction of both fluvial and fire disturbances take place.

Despite the overall recovery of riparian vegetation five years following fire, species composition and structure were altered in severely burned riparian and adjacent upland plots. Of particular importance, the appearance of *B. tectorum* in burned plots is of

Table 4

Common herbaceous and woody species and their occurrence (X = presence, blank space = absence) at each study reach.

Species	Reaches															
	High-severity								Low-severity			Unburned				
	CA	CB	CL	CV	CW	CY	PN	RS	DC	GT	LW	BT	CG	NF	UP	WF
Woody species																
<i>Acer glabrum douglasii</i>	X	X	X		X	X	X	X	X	X	X	X	X	X	X	
<i>Alnus viridis</i>		X		X		X	X	X		X		X	X		X	X
<i>Amelanchier alnifolia</i>		X		X	X	X	X	X		X	X	X	X	X	X	X
<i>Berberis repens</i>		X	X		X	X	X	X	X	X	X	X	X	X	X	
<i>Betula occidentalis</i>		X	X		X	X	X	X	X	X	X	X	X	X	X	
<i>Cornus stolonifera</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Lonicera involucrata</i>				X												X
<i>Philadelphus lewisii</i>	X	X	X	X	X	X	X	X		X	X	X	X			
<i>Physocarpus malvaceus</i>		X			X		X	X	X	X	X		X	X	X	
<i>Pinus ponderosa</i>		X														
<i>Populus tremuloides</i>			X		X						X				X	
<i>Populus trichocarpa</i>	X	X		X	X											
<i>Prunus virginiana</i>			X					X	X	X		X				
<i>Pseudotsuga menziesii</i>		X							X	X	X	X	X	X	X	X
<i>Ribes hudsonianum petiolare</i>												X	X	X	X	X
<i>Ribes lacustre</i>	X	X	X	X		X	X	X	X	X		X	X	X	X	X
<i>Ribes viscosissimum</i>									X	X	X					X
<i>Rosa acicularis</i>	X	X		X	X		X	X	X	X	X	X		X	X	X
<i>Rubus idaeus</i>	X	X	X	X	X	X	X	X		X	X					X
<i>Rubus parviflorus</i>		X	X	X	X	X	X	X		X	X	X	X		X	X
<i>Salix scouleriana</i>								X	X	X	X					X
<i>Sambucus cerulea</i>	X	X	X	X	X	X	X	X	X	X	X	X			X	
<i>Spiraea betulifolia</i>	X	X	X		X	X	X			X	X	X	X	X	X	X
<i>Symphoricarpos albus</i>	X	X		X	X	X	X	X		X	X	X	X	X	X	X
Forbs																
<i>Achillea millefolium*</i>	X			X		X					X			X		X
<i>Actaea rubra</i>									X							
<i>Aquilegia coerulea</i>		X												X		X
<i>Asarum caudatum</i>												X				X
<i>Bromus tectorum*</i>	X		X	X	X	X	X	X					X			
<i>Chimaphila umbellata</i>												X	X			
<i>Cicuta douglasii</i>		X	X				X	X		X						X
<i>Clematis ligusticifolia</i>						X		X					X	X		
<i>Disporum trachycarpum</i>		X	X	X	X	X	X		X	X	X	X	X	X		
<i>Epilobium angustifolium</i>	X	X	X	X	X	X	X	X		X	X			X	X	X
<i>Epilobium glandulosum</i>		X				X					X			X	X	X
<i>Equisetum fluviatile</i>								X								X
<i>Equisetum hymale</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X
<i>Fragaria virginiana</i>															X	
<i>Galium triflorum</i>	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X
<i>Iliamna rivularis</i>	X	X				X			X			X				
<i>Mimulus guttatus</i>					X											X
<i>Osmorhiza berteroi</i>	X	X				X			X	X	X		X	X		X
<i>Phalaris arundinacea*</i>				X	X			X								
<i>Pyrola asarifolia</i>													X		X	
<i>Ranunculus acris</i>		X													X	
<i>Similacina racemosa</i>							X				X	X				
<i>Streptopus amplexifolius</i>	X	X	X				X			X	X	X	X	X	X	X
<i>Taraxacum ceratophorum</i>	X	X		X			X								X	
<i>Thalictrum occidentale</i>		X									X					
<i>Vaccinium membranaceum</i>												X				
<i>Viola orbiculata</i>	X	X									X	X			X	X

* Non-native species.

special concern. *B. tectorum* is an invasive species that has been shown to have the capacity to alter disturbance regimes beyond the range of variation to which native species are adapted, resulting in ecosystem-level changes (Brooks et al., 2004). For example, *B. tectorum* has been shown to dramatically increase fire frequency, extent, and intensity in semi-arid forests and rangelands of the Western U.S. (Mack and D'Antonio, 1998; Harrod and Reichard, 2001; Brooks et al., 2004).

In spite of abundant research on the effects of *B. tectorum* (Stewart and Hull, 1949; D'Antonio and Vitousek, 1992; Billings, 1994; Brooks et al., 2004), the majority has focused in upland systems and, as yet, there is an incomplete understanding of the effects of *B. tectorum* on riparian zones. In the present study, *B. tectorum* was correlated with the NMS axes associated with high-severity burned reaches for riparian plots and highly correlated for upland plots (Fig. 3c and d). Personal observations supported this result. Although the presence of *B. tectorum* was obvious in severely burned reaches in general, severely burned riparian areas appeared to support lower densities of the grass than adjacent upland plots. This may be related to the ability of riparian plant communities to recover more quickly than upland species following disturbance (Dwire and Kauffman, 2003). Further inquiry into the relationship between fire and *B. tectorum* in riparian systems is clearly needed.

Although we expected to observe marked differences in vegetation community composition and structure between low-severity and unburned reaches, MRPP and NMS analyses showed limited differences between these burn types in both the upland and riparian zones. Beche et al. (2005) report similar results, observing that prescribed fires of low- to moderate-severity had limited effects on riparian plant communities. Given the lack of distinction observed in vegetation communities between low- and moderate-severity fires, combined with the significant difference in vegetation communities between severely burned reaches and both of the other fire classes (Table 4 and Fig. 3), it is possible that a fire-driven disturbance threshold exists that must be crossed in order to significantly alter plant communities in stream-riparian ecosystems in semi-arid regions. Thresholds – conditions beyond which an abrupt change in a quality, property, or function of an ecosystem is precipitated – are tightly connected to ecosystem condition (Turner, 2002) and likely affect the capacity of a nonlinear system to remain within a stable domain (Ludwig et al., 1997). If high-severity fire is required to push riparian vegetation beyond a stable state, then low-severity fire may be inadequate to alter the successional trajectory of the vegetation community (Holling and Gunderson, 2002; Ward et al., 2002) and contribute to a riparian equivalent of a shifting habitat mosaic [*sensu* (Stanford et al., 2005)] along the longitudinal extent of the drainage.

Our results provide evidence that high severity fires may be a source of critical disturbance in riparian vegetation communities. This result has important implications for management as many prescribed fires are low-severity. Further inquiry into the capacity of low-severity fires to affect riparian ecosystems is needed. Additionally the importance of scale should be carefully considered. Whereas it is vitally important both for ecological and management considerations to understand the relationships between fire and stream-riparian ecosystems, we also must recognize that the relationships observed at the reach scale may or may not play out in a similar way at broader or finer spatial scales. Focusing on long-term ecological goals such as land-use policies that retain or reestablish natural disturbance regimes at a landscape scale may be more effective in maintaining diversity and productivity of stream-riparian ecosystems rather than directing attention to the effects of a given fire on stream segments (Beschta et al., 2004). Finally, human-coupled systems beyond the wild-

erness setting will require a more comprehensive understanding of the potential interactions of fire and other anthropogenic effects including changes in land use and climate.

Acknowledgements

We dedicate this work to the memory and legacy of Dr. Jeffrey Braatne, whose support and mentorship were invaluable. Funding for this research was largely provided by the DeVlieg Foundation. This research was also supported in part by the Environmental Science Program, Office of Research, and Department of Fish and Wildlife Resources at the University of Idaho as well as by the Payette National Forest. Jim and Holly Akenson, managers of the Taylor Ranch Wilderness Research Station (University of Idaho), provided critical field support. Dr. G.W. Minshall, Dr. Colden Baxter, and Rachel Malison were collaborators in this research.

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