Journal of Ecology

British Ecological Society

Journal of Ecology 2009, **97**, 142–154 doi: 10.1111/j.1365-2745.2008.01456.x

Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest

Daniel C. Donato[1]*, Joseph B. Fontaine[2], W. Douglas Robinson[2], J. Boone Kauffman[3] and Beverly E. Law[1]

[1]Department of Forest Science and [2]Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA; and [3]Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, HI 96720, USA

Summary

1. Variations in disturbance regime strongly influence ecosystem structure and function. A prominent form of such variation is when multiple high-severity wildfires occur in rapid succession (i.e. short-interval (SI) severe fires, or 're-burns'). These events have been proposed as key mechanisms altering successional rates and pathways.

2. We utilized a natural experiment afforded by two overlapping wildfires occurring within a 15-year interval in forests of the Klamath–Siskiyou Mountains, Oregon (USA). We tested for unique effects of a SI fire (15-year interval before 2002 fire) by comparing vegetation communities 2 years post-fire to those following a long-interval (LI) fire (> 100-year interval before 2002 fire) and in mature/old-growth (M/OG) stands (no high-severity fire in > 100-year).

3. Nearly all species found in M/OG stands were present at similar relative abundance in both the LI and SI burns, indicating high community persistence through multiple high-severity fires. However, the SI burn had the highest species richness and total plant cover with additions of disturbance-associated forbs and low shrubs, likely due to a propagule bank of early seral species that developed between fires. Persistence of flora was driven by vegetative sprouting, on-site seed banks, and dispersal from off-site seed sources. Several broadly generalizable plant functional traits (e.g. rapid maturation, long-lived seed banks) were strongly associated with the SI burn.

4. Sprouting capacity of hardwoods and shrubs was unaltered by recurrent fire, but hardwood/shrub biomass was lower in the SI burn because individuals were smaller before the second fire. Conifer regeneration densities were high in both the SI and LI burns (range = 298–6086 and 406–2349 trees ha^{-1}, respectively), reflecting similar availability of seed source and germination substrates.

5. *Synthesis.* SI severe fires are typically expected to be deleterious to forest flora and development; however, these results indicate that in systems characterized by highly variable natural disturbances (e.g. mixed-severity fire regime), native biota possess functional traits lending resilience to recurrent severe fire. Compound disturbance resulted in a distinct early seral assemblage (i.e. interval-dependent fire effects), thus contributing to the landscape heterogeneity inherent to mixed-severity fire regimes. Process-oriented ecosystem management incorporating variable natural disturbances, including 'extreme' events such as SI severe fires, would likely perpetuate a diversity of habitats and successional pathways on the landscape.

Key-words: Biscuit Fire, compound disturbance, conifer regeneration, fire interval, functional traits, mixed-severity fire regime, plant diversity, reburn, Silver Fire, shrub sprouting

Introduction

Variations in disturbance frequency and severity strongly influence ecosystem structure and function (Bond & van Wilgen 1996; Agee 2005). For disturbances such as fire, frequency and severity are typically negatively correlated, such that frequent disturbances are of lower severity (Agee 1993 and references therein). However, in many ecosystems high-severity events occasionally occur in rapid succession, resulting in a compound disturbance (Paine *et al.* 1998), with

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*Correspondence author. E-mail: dan.donato@oregonstate.edu lasting influence on ecosystem pattern and process (e.g. Zedler *et al.* 1983; Johnstone & Chapin 2006).

In forests with mixed- and high-severity fire regimes, such as in the Pacific Northwest, USA, intervals between stand-replacing fires are typically several decades to several centuries (Agee 1993). Occasionally these fires are followed closely by recurrent fires during early succession (i.e. 're-burns' – Franklin & Hemstrom 1981; Agee 1991, 1993; Gray & Franklin 1997; Thompson *et al.* 2007). Retrospective (dendrochronological) studies in mature Pacific Northwest forests suggest these short-interval (SI) fires may exert large influence on successional rates and pathways (Franklin & Hemstrom 1981; Agee 1991; Gray & Franklin 1997). In the present study, we report vegetation responses immediately following recurrent high-severity fire to clarify the potential mechanisms underlying such influences.

A key tenet of many successional theories is how the interval length between disturbances influences outcomes of succession ('interval-dependent fire effects'; Bond & van Wilgen 1996). SI fires occur in early seral vegetation and may differ qualitatively from long-interval (LI) fires, which generally occur in mature forests. Young stands contain distinct fuel conditions (and thus potential fire behaviour) that are legacies of recent disturbance including low-stature continuous vegetation, open microclimates, and woody fuels derived from fire-killed trees (Agee & Huff 1987). SI fires also affect plant species at earlier life-history stages, potentially influencing post-fire reproduction capacity (Noble & Slatyer 1980; Bond & van Wilgen 1996). In boreal forests, for example, recruitment of serotinous conifers (*Pinus* and *Picea spp.*) was significantly reduced following SI fires since the fire interval was shorter than the time to reproductive maturity (Johnstone & Chapin 2006). However, interactions between fire interval and life history will vary widely among species depending on their method and timing of reproduction, dispersal, and growth – with some species favoured by short intervals. As such, SI fires may lead to distinct post-fire assemblages and alternative successional pathways (Noble & Slatyer 1980; Bond & van Wilgen 1996).

Ecosystem response to recurrent severe fire varies among regions, from declines in plant productivity or diversity (e.g. Isaac & Meagher 1936; Zedler *et al.* 1983; Delitti *et al.* 2005; Eugenio *et al.* 2006) to high resilience or even increases (e.g. Beck & Vogl 1972; Delitti *et al.* 2005; Wittenberg *et al.* 2007). Generalities across ecosystems, or mechanisms underlying differences, have remained elusive. However, one promising tool is the analysis of plant functional traits (or 'vital attributes') – autecological qualities with common response to the environment across taxa. Noble and Slatyer (1980) described a qualitative scheme for predicting shifts in plant communities subject to recurrent disturbance, using functional traits relating to regenerative strategy (e.g. seed longevity, dispersal capacity, sprouting ability) and competitive relations (e.g. growth rate, shade tolerance). By assessing logically determined interactions between functional groups and fire interval, this approach provides a broadly applicable framework for understanding the role of disturbance frequencies in the origin of different successional pathways (Noble & Slatyer 1980).

In this study, we examined the effects of recurrent high-severity disturbance in the Klamath–Siskiyou ecoregion, USA, utilizing two overlapping wildfires as a natural experiment on fire interval variation. The region provides an exceptional opportunity to study responses of vegetation, particularly functional traits, to SI fire. First, the region comprises the most diverse forest flora of western North America, both in terms of species and physiognomy (Whittaker 1960); thus a broad range of functional traits is represented. Secondly, a complex fire regime prevails, with frequent but variable fire intervals (*c.* 5–75 years) and mixed severity over time and space (Agee 1991, 1993; Taylor & Skinner 1998; Stuart & Salazar 2000). When stand-replacement occurs, rapid recovery of vegetation and fuel continuity, coupled with dry summers and frequent lightning, create the potential for recurrent high-severity fires over decadal time scales (Thompson *et al.* 2007). Thus, SI severe fires have likely been a component of the complex fire regime and a factor structuring vegetation in the region (Agee 1991, 1993).

Response to SI stand-replacing fire can be evaluated against LI fire responses within a framework of three alternative models, based on previous studies: [1] cyclical dynamics, whereby post-fire regeneration is similar regardless of fire interval (Wittenberg *et al.* 2007). Under this model, response to a SI fire event would be no different than to a LI fire. [2] interval-dependent dynamics with abrupt, potentially long-lasting differences in the SI burn due to declines in vegetation abundance/diversity, soil productivity, or tree establishment (Isaac & Meagher 1936; Zedler *et al.* 1983; Eugenio *et al.* 2006). Expectations of this model often underlie post-fire management actions aimed at avoiding re-burns (e.g. USDA 1988). [3] interval-dependent dynamics in which the SI fire retains most/all species as part of the post-fire assemblage, but leads to reduced dominance of woody forest components, generating gaps in which ruderal species may persist (Delitti *et al.* 2005). Under this model, repeated SI fires would maintain distinct seral communities, but given a sufficiently long fire-free interval, succession would trend toward mature forest condition. We explored this framework with the following specific questions:

(1) How does vegetation response following a SI fire compare to that following a LI fire in terms of initial vegetation cover, diversity, and species composition? We hypothesized an interval-dependent response, with an increase in disturbance-associated components, but a decrease in overall diversity and cover due to the effects of two severe fires on fire-sensitive/late-seral associated components, soil propagule banks and productivity.

(2) Is regeneration of major structural components – hardwoods, shrubs, and conifers – reduced in the SI burn relative to the LI burn? For sprouting hardwoods and shrubs, a brief fire interval may be shorter than the recovery time of below-ground carbohydrate reserves (Bond & van Wilgen 1996). Also, combustion of woody fuel accumulations derived from trees killed in the first fire may result in higher soil heat flux and mortality of below-ground meristematic tissues. Based on these expectations and results of previous works (Bond & van Wilgen 1996; Delitti *et al.* 2005), we hypothesized that repeated fires reduce sprouting probability and biomass. For conifers, retrospective studies in Pacific Northwest forests have pointed to sparse or altered regeneration following SI fires (e.g. Agee 1991; Gray & Franklin 1997), but the mechanisms behind this pattern have not been identified (i.e. seed source limitations, unfavourable germination substrates, or subsequent survival). In this study we quantified early conifer establishment to test whether initial establishment conditions (seed source, substrate) limited regeneration in the SI burn.

(3) To elucidate mechanisms and improve predictive capability across ecosystems, we explored the question: What plant functional traits are associated with the different fire histories (SI fire, LI fire, mature/old-growth (M/OG) stands with no recent fire)? We focused on broadly applicable traits (related to those in Noble & Slatyer 1980) including regenerative strategy, life form, and dispersal strategy. We hypothesized that disturbance-associated traits (e.g. rapid growth to reproduction, highly dispersive propagules, and *in situ* seedbanks) would be positively associated with SI fire, while traits typical of late-seral associated components (e.g. fire-sensitivity, shade tolerance, slow maturation) would be negatively associated with SI fire.

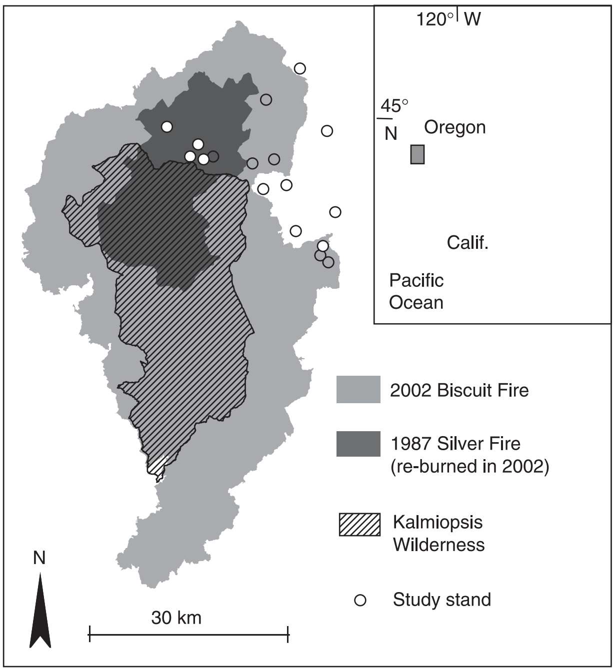

Fig. 1. Map of the study area. The area of the 1987 Silver Fire was re-burned by the 2002 Biscuit Fire; both fires were mixed-severity. In this study of repeated severe disturbance, sampling of both burns was restricted to stand-replacement patches only. We sampled all large, unmanaged twice-burned forest stands we could find ($n = 6$), plus an equivalent number of once-burned and unburned stands well-matched in terms of abiotic and biotic site characteristics (see text).

Methods

STUDY AREA AND RECENT FIRE HISTORY

The study was conducted in the Illinois River drainage of the Klamath–Siskiyou Mountains, a Pacific coastal range in southwestern Oregon, USA (Fig. 1). A mixed-severity fire regime, complex geology, and steep topographic and climatic gradients support a diverse mosaic of plant communities in the region (Whittaker 1960). Climate regime is wet Mediterranean-type with warm, dry summers and cool, moist winters. Annual precipitation ranges from 1500–3000 mm over the study area (Daly *et al.* 2002, www.prismclimate.org), with < 15% falling from May–September. Soils were derived from metasedimentary, metavolcanic, and coarse-grained igneous parent materials. Ultramafic (serpentine) substrates (Whittaker 1960) were avoided in this study.

Study sites were in the upper mixed-evergreen zone, where it begins to intergrade with white fir (*Abies concolor*) (Franklin & Dyrness 1973). All sites supported – currently or before recent fires – Douglas-fir (*Pseudotsuga menziesii*) dominated mature or old-growth forest (> 100-year old; see Bingham & Sawyer 1991; Agee 1993 for developmental/structural descriptions). Mature/old-growth (M/OG) stands are typically dominated by conifers Douglas-fir, white fir, sugar pine (*Pinus lambertiana*), and incense cedar (*Calocedrus decurrens*); evergreen hardwoods tanoak (*Lithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), Pacific madrone (*Arbutus menziesii*), and chinquapin (*Chrysolepis chrysophylla*); and woody shrubs greenleaf manzanita (*Arctostaphylos patula*), snowbrush (*Ceanothus velutinus*), and Sadler oak (*Q. sadleriana*). (Nomenclature followed Hickman (1993); see Appendix S1 in Supporting Information for species list.)

In 1987, the Silver Fire burned with mixed severity over an area of 38 000 ha, including patches of stand replacement with subsequent establishment of early seral stands. Fifteen years later, in 2002, the 200 000-ha Biscuit Fire re-burned the entire Silver Fire area, with most early seral stands again experiencing stand replacement (Thompson *et al.* 2007). In the interim, post-fire logging occurred over much of the high-severity portions of the Silver Fire; unlogged stands were left primarily due to remoteness or socio-political factors during the planning effort (USDA 1988) rather than any systematic ecological differences. (Note that the Kalmiopsis Wilderness interior [Fig. 1] was excluded from the study due to inaccessible terrain with generally steeper slopes, thinner soils and differing forest structure.) In this study of the effects of repeated severe disturbance, sampling of both burns was restricted to high-severity patches only (defined here as ≥ 90% overstorey mortality, top-kill of all understorey and surface layer vegetation, and combustion of most ground layer organic matter). Thus, sampled disturbance histories were: 2 × stand-replacement fire, 1 × stand-replacement fire, and unburned (no recent fire).

Our approach was to sample all the unmanaged twice-burned stands we could find that met the above criteria for stand type/age present before the first fire (M/OG conifer-dominated forest), plus an equal number of once-burned and unburned stands well-matched in terms of stand type/age, plant association (Atzet *et al.* 1996), and topoedaphic character. No stands had experienced prior timber harvest. All study areas were assessed for similar ca. 1986 overstorey and understorey composition/structure via detailed stem surveys, agency data layers, and aerial photographs. The abiotic/biotic character of all study sites was thus defined by the available twice-burned stands, which had biophysical characteristics common to the area. Study sites were on 35–80% slopes on westerly, northerly and easterly aspects; mid- to upper slope positions; and elevations of

700–1150 m. High-severity burn patches were > 100 hectares in size. Patch edges (< 80 m) were avoided; distances to adjacent intact forest were < 400 m due to complex patch shapes.

This study took advantage of an existing arrangement of two superimposed wildfires (i.e., a natural experiment). Like most natural experiments, detailed pre-fire data were unavailable, and interspersion of sample groups was not possible (see Fulé *et al.* 2004; Johnstone 2006). Comparability of sites experiencing different burn histories was maximized to the extent possible (for example with respect to abiotic characteristics, plant associations, and pre-fire stand type/age) but some pre-existing differences likely existed. Also, because the arrangement of fires was pre-existing and not implemented randomly, statistical inference from our results is limited to our study area. We interpret our results in this context. For brevity, sites of differing recent fire history are referred to as 'treatments' in this article.

FIELD MEASUREMENTS

Field data were collected from late June–August 2004, two growing seasons after the Biscuit Fire. A 1-ha plot was randomly placed in each of 18 stands: six twice-burned (Silver-Biscuit, SI fire), six once-burned (Biscuit only, LI fire), and six unburned (immediately outside the Biscuit Fire perimeter, M/OG with no recent fire). Cover (%) of all hardwoods, shrubs, forbs, and low (suffrutescent) shrubs was quantified, by species, in each hectare plot in four non-overlapping, regularly spaced circular subplots (35 m apart; see USDA 2003 for layout) with a minimum area of 20 m^2. To ensure adequate sampling when shrubs occurred at low density, subplots were increased in size to capture *c.* 70 hardwood/shrub individuals across the hectare plot, up to 79 m^2 (one low-density stand had subplots of 314 m^2 – no results were significantly changed by excluding this plot so we retained it in analyses). Variable radius was accounted for in all analyses where relevant. We also recorded substrate in each subplot as percent cover of mineral soil, rock > 1 cm diameter, moss/lichen, woody detritus > 1 cm diameter, and litter.

Individual hardwood trees and shrubs were also measured for height, width and breadth of live crown; basal diameter of live stems; number of dead stems tallied by 2-cm diameter classes; and categorized as re-sprout/seedling/dead. We calculated live biomass of hardwoods and shrubs by entering basal diameter and crown dimensions into species-specific allometric equations (see Appendix S2). For top-killed portions of hardwoods and shrubs, dead stem basal area was computed based upon stem counts by diameter class. Conifer seedlings were sampled in four 75 × 0.5 m subplots radiating from plot centre in subcardinal directions. Long narrow subplots were chosen for small seedlings to more effectively capture variability in heterogeneous microsites across each sampled stand, and to obtain more precise estimates of stand-level density than that afforded by circular subplots (Elzinga *et al.* 1998). Species, rooting substrate, and plot quadrant were recorded for each seedling.

Environmental parameters recorded for each plot included elevation, slope, aspect, soil parent material (USDA 1995), plant association group (Atzet *et al.* 1996), and estimated mean annual precipitation (Daly *et al.* 2002). Aspect was mathematically folded about the SW-NE axis so that SW slopes were assigned the highest (warmest) value and NE slopes the lowest (coolest) value, then combined with slope measurements to create one continuous variable estimating potential annual solar heat load in each stand (McCune & Keon 2002). Because slopes were similarly steep throughout the study area (mean ± SD: 59% ± 15%), heat load primarily reflected aspect influence and encompassed most of the topographical variation aside from elevation.

DATA ANALYSIS

We used a combination of univariate and multivariate analytical techniques to compare vegetation among treatments (SI burn, LI burn, M/OG). For univariate responses, we computed 95% confidence intervals (CIs) obtained by a t-multiplier and standard errors (Ramsey & Schafer 2002). Lack of overlap of CIs with means of other groups was interpreted as strong evidence for differences. Conifer regeneration was analysed separately from broadleaf vegetation due to quantification by density rather than cover (density being a more meaningful and commonly used metric for conifer seedlings; e.g. Shatford *et al.* 2007).

Community composition

To test the hypothesis of no compositional difference between treatments, we used the nonparametric multi-response permutation procedure (MRPP) using relative Sørensen distance (McCune & Grace 2002). An A-statistic from MRPP provides an estimate of within-group homogeneity in species composition relative to that expected by randomly partitioning the data; a P-value estimates the probability of the A-statistic due to chance.

To identify which species drove any community differences among treatments, we conducted Indicator Species Analysis (ISA; Dufrene & Legendre 1997) using PC-ORD software version 5.04 (McCune & Mefford 2006). ISA combines relative frequency and abundance information to assign an indicator value for strength of association between each species and *a priori* groups (treatment) (range 0–100, 0 = no association, 100 = complete association; see Table 1). An accompanying Monte Carlo randomization with 1000 runs provides a P-value for whether the indicator value is stronger than that expected by chance.

Vegetation abundance and diversity

Differences in vegetation cover and diversity among treatments were assessed by comparing 95% CIs. For abundance metrics, hardwood and woody shrub data were grouped together due to similar early growth forms (primarily coppiced sprouts). Diversity metrics included alpha diversity (mean number of species detected at the hectare-plot scale), gamma diversity (total number of species detected in each treatment), and Shannon evenness (index of even species proportions vs. dominance by a few species; range 0–1, 1 = perfectly even; Magurran 1988). These metrics are influenced by area sampled and vegetation abundance (Gotelli & Colwell 2001). Abundance effects were accounted for in part by defining subplot size in accordance with shrub density, which normalizes the number of individuals sampled across plots and reduces the need for rarefaction-based analysis (Gotelli & Colwell 2001), though this does not necessarily account for forb/low-shrub abundance that can also influence richness. Area effects were minimal in this study since total area sampled was roughly equivalent for each treatment, and since little relationship between subplot size and richness was found for the scale sampled (Donato 2008).

Hardwood, shrub and conifer responses

For top-killed hardwoods and shrubs, sprout biomass is known to increase with size of the pre-fire individual (Harrington & Tappeiner 1997). We tested for unique effects of a short-interval fire within the context of this known relationship: if two closely-spaced fires reduce sprouting biomass for shrubs of a given size, then the intercept of

Table 1. Indicator values, diversity statistics, and mean abundance for eight of the most common hardwoods/shrubs, low shrubs, and forbs by recent burn history

		Mature/old-growth [M/OG]		Long-interval fire [LI]		Short-interval fire [SI]	
Species	Indicator value* – group	Percent cover (SE)	Percent frequency	Percent cover × (SE)	Percent frequency	Percent cover × (SE)	Percent frequency
Forbs							
Chimaphila menziesii	**85.7 – M/OG**	0.5 (0.2)	100	0.0 (0.0)	0	0.1 (0.1)	17
Goodyera oblongifolia	**66.7 – M/OG**	0.3 (0.2)	67	0.0 (0.0)	0	0.0 (0.0)	0
Achlys triphylla	44.7 – SI	1.1 (0.7)	50	0.3 (0.1)	67	2.7 (1.4)	67
Graminoid species	**88.2 – SI**	0.1 (0.1)	17	0.0 (0.0)	0	0.6 (0.3)	100
Lotus crassifolius	64.7 – SI	0.0 (0.0)	0	0.3 (0.3)	17	9.5 (6.7)	67
Pteridium aquilinum	**95.4 – SI**	0.0 (0.0)	17	0.9 (0.6)	50	18.7 (9.8)	100
Trientalis latifolia	**93.3 – SI**	0.0 (0.0)	0	0.2 (0.1)	67	2.0 (1.0)	100
Vancouveria hexandra	**66.3 – SI**	0.0 (0.0)	0	0.0 (0.0)	17	4.3 (2.3)	67
Low shrubs							
Polystichum munitum	21.0 – M/OG	0.7 (0.6)	33	0.0 (0.0)	17	0.4 (0.2)	50
Berberis nervosa	44.1 – SI	4.2 (1.5)	100	3.6 (1.1)	100	6.1 (2.0)	100
Rosa gymnocarpa	55.9 – SI	0.7 (0.3)	67	1.2 (0.4)	83	2.3 (0.5)	100
Rubus ursinus	**97.5 – SI**	0.0 (0.0)	17	0.5 (0.3)	50	19.0 (7.8)	100
Rubus leucodermis	**65.0 – SI**	0.0 (0.0)	0	0.0 (0.0)	17	0.8 (0.4)	67
Symphoricarpus mollis	**94.4 – SI**	0.1 (0.1)	17	0.1 (0.0)	33	3.2 (1.2)	100
Whipplea modesta	20.0 – SI	0.5 (0.2)	50	0.4 (0.2)	67	1.3 (1.1)	33
Xerophyllum tenax	36.2 – SI	1.9 (1.9)	50	0.4 (0.4)	17	2.7 (1.1)	67
Hardwoods and woody shrubs							
Lithocarpus densiflorus	39.6 – M/OG	13.6 (4.4)	83	8.4 (2.1)	100	6.6 (2.5)	100
Quercus chrysolepis	34.3 – M/OG	11.0 (4.2)	67	6.9 (2.0)	100	3.5 (3.1)	50
Quercus sadleriana	25.4 – M/OG	9.1 (8.6)	33	2.8 (2.2)	33	0.0 (0.0)	0
Arbutus menziesii	**75.3 – LI**	0.2 (0.2)	17	4.7 (1.3)	83	0.3 (0.2)	33
Ceanothus velutinus	12.5 – LI	0.0 (0.0)	0	0.4 (0.2)	50	1.1 (1.1)	17
Garrya species	18.5 – LI	1.7 (1.7)	17	2.4 (2.3)	33	0.2 (0.2)	33
Arctostaphylos patula	46.8 – SI	1.8 (1.3)	33	0.7 (0.6)	50	5.8 (3.1)	67
Chrysolepis chrysophylla	23.5 – SI	0.8 (0.8)	17	1.3 (1.3)	17	1.9 (1.4)	50
Mean number of species detected in ha plot (95% CI)		14.0 (9.1–18.9)		19.2 (11.5–26.8)		31.2 (26.5–35.8)	
Total number of species detected in sample		39		42		59	
Number of significant indicator species		2		1		7	

Notes: $n = 6$ per group.

*Metric combining relative abundance and frequency for most strongly associated group (burn history) (Dufrene & Legendre 1997). Range 0–100, 100 = always and only occurs in given group. Values in bold indicate strong (≥ 65) affinities, which have $P \leq 0.01$ by randomization test.

this relationship should shift downward. To test for differences in sprouting probability for the 745 individuals present in the plots at the time of the 2002 fire, we used a mixed effects logistic regression model (GLME) for the binary sprouting response as a function of pre-fire size (basal area), a plot random effect, and treatment as the predictor of interest. To test for differences in sprout mass for the 554 individuals that sprouted, we used a hierarchical linear model (HLM) of above-ground biomass as a function of pre-fire size, a plot random effect, and treatment as the predictor of interest. Regressions were performed using S-Plus 7.0 software www.insightful.com with $\log_e$-transformed data where necessary to better meet model assumptions of linearity/constant variance (Ramsey & Schafer 2002); model fits were assessed with residual-vs.-fit plots. Proportion of seeding, sprouting, and killed individuals was compared among treatments via 95% CIs.

Differences in conifer density among treatments were assessed by comparing 95% CIs. Densities were $\log_e$-transformed to reduce positive skewness and disproportionate influence of extremely high values (Ramsey & Schafer 2002). To evaluate substrate preference of conifers, abundance was also separated by proportion of seedlings on the various substrates and compared to available substrate proportions by treatment. Available substrate proportions were compared between treatments using multivariate analysis of variance (MANOVA; Ramsey & Schafer 2002).

Trait analyses

To quantify associations between plant functional traits and recent fire history, we conducted ISA and nonmetric multidimensional scaling (NMS) ordination on the abundance of traits in each plot (McCune & Grace 2002). We computed trait abundance by multiplying the species abundance matrix by a binary matrix of traits for each species. Selection of traits for analysis was guided by the US Fire Effects Information System www.fs.fed.us/database/feis, which summarizes functional traits relevant to post-fire regeneration and development for each species. These traits overlap broadly with the vital attributes described by Noble and Slatyer (1980). Categories of traits included fire regenerative strategy, seed dispersal vector, general life form, Raunkiær life form, structural/functional attributes, and successional/community association (Table 2). Trait NMS and ISA were conducted using PC-ORD 5.04 (McCune & Mefford 2006) following data preparation and ordination procedures outlined by McCune and Grace (2002). For NMS, relative Sørensen distance was used as the dissimilarity metric to relativize abundances

Table 2. Results of indicator analysis of plant traits by recent burn history

Trait	Description	Indicator value*	Group† of maximum association
General life form			
Forb	Little or no wood above-ground; above-ground parts of < 1-year duration	**88.9**	**SI**
Graminoid	Monocotyledonous plant of the family Poaceae	**95.7**	**SI**
Low shrub	Low-stature shrubs, generally with little secondary growth	**66.7**	**SI**
Hardwood/shrub	Broadleaf woody spp., often multi-stemmed, hardwoods can be trees	43.8	M/OG
Raunkiær life form			
Phanerophyte	Perennating tissue > 25 cm above soil surface (trees, lg. woody shrubs)	40.7	M/OG
Chamaephyte	Perennating tissue within *c.* 25 cm of soil surface (typically low shrubs)	60.3	SI
Hemicryptophyte	Perennating tissue at the soil surface (forbs and trailing shrubs)	**88.0**	**SI**
Therophyte	Perennating tissue contained in seed (annual forbs)	**87.0**	**SI**
Geophyte	Perennating tissue below the soil surface (rhizomatous perennials)	61.6	SI
Fire regenerative strategy			
Avoider	Fire-sensitive; usually shade-tolerant, late-successional	**77.4**	**M/OG**
Invader	Highly dispersive, pioneering fugitives with short-lived disseminules	**78.9**	**SI**
Evader	Long-lived propagules stored in soil/canopy that germinate after fire	**90.3**	**SI**
Endurer	Sprouts from above- or below-ground structures when top-killed	52.7	SI
General structure and function			
Rhizomes	Having underground, often elongate, more or less horizontal stems	**71.7**	**SI**
Fibrous root	Root system composed of many roots similar in length and thickness	45.9	LI
Tap root	Main, tapered root that generally grows straight down into soil	36.6	SI
Obligate Seeder	Incapable of sprouting after top-kill; relies on regeneration by seed	**92.0**	**SI**
Sprout-root crown	Sprouting occurs primarily from root crown (surface)	54.0	SI
Sprout-root deep	Sprouting occurs primarily from central below-ground burl/lignotuber	34.6	SI
Sprout-diffuse	Sprouting occurs from > 1 location, generally from spreading rhizomes	**69.8**	**SI**
Nitrogen fixer	Association with microbes that fix atmospheric N to usable forms	**96.3**	**SI**
Deciduous	Leaves not persistent > 1 year	**81.4**	**SI**
Evergreen	Leaves persistent > 1 year	41.6	M/OG
Annual	Completing life cycle within 1 year or growing season	**87.0**	**SI**
Perennial	Living more than 2 years or growing seasons	54.9	SI
Seed dispersal vector			
Wind dispersed	Seeds primarily dispersed by wind	**83.8**	**SI**
Animal dispersed	Seeds primarily dispersed by animals	45.4	SI
Successional/community association			
Late seral associated	Most associated with closed late seral forest (not exclusively); shade tolerant	64.3	SI
Early seral associated	Most associated with open early seral forest (not exclusively); shade intolerant	**92.4**	**SI**
All seral associated	Typically found in both early and late seral forests	40.6	M/OG
Non-native	Not native to Pacific Northwest region	45.8	SI
Ruderal	Prefers disturbed sites, usually rapid maturity/death, little community assoc.	**96.0**	**SI**

Notes: Sources for trait definition/assignment were Raunkiær (1934), Rowe (1983), Agee (1993), Hickman (1993), www.plants.usda.gov, fs.fed.us/database/feis. Conifer seedlings were analysed separately due to quantification by density rather than cover.

*Metric combining relative abundance and frequency for most strongly associated group (treatment) by Indicator Species Analysis (Dufrene & Legendre 1997). Range 0–100, 100 = always and only occurs in given group. Values in bold indicate strong (≥ 65) affinities, which have significance level $P \leq 0.01$ by randomization test.

†M/OG = unburned mature/old-growth, LI = long-interval fire (single burn), SI = short-interval fire (re-burn); $n = 6$ per group.

by sample unit totals, account for variable subplot radius, and allocate proportional influence to small and large distances (McCune & Grace 2002). We used PC-ORD's autopilot mode with random starting configurations and 250 runs of real data, obtaining a two-dimensional solution with final instability < 0.0001.

Results

VEGETATION ABUNDANCE, DIVERSITY AND COMPOSITION

Total vegetation cover 2 years after fire was markedly higher in the SI burn (mean 117%, range 55–176%) than in the LI burn (mean 39%, range 27–60%). The higher cover in SI burn stands was composed largely of forbs and low shrubs (Fig. 2a,b). 95% CIs for differences indicated that, compared to LI burn stands, SI burn stands had higher forb cover by 26–80% and higher cover of low shrubs by 9–54%. Hardwood/shrub cover showed the opposite trend, decreasing with number of recent burns, although confidence intervals overlapped substantially among treatments (Fig. 2c). There were no strong differences in forb, low shrub, or hardwood/shrub cover between the LI burn and M/OG stands (Fig. 2a–c). Comparisons between the SI burn and M/OG stands were thus similar to comparisons between the SI and LI burns (Fig. 2).

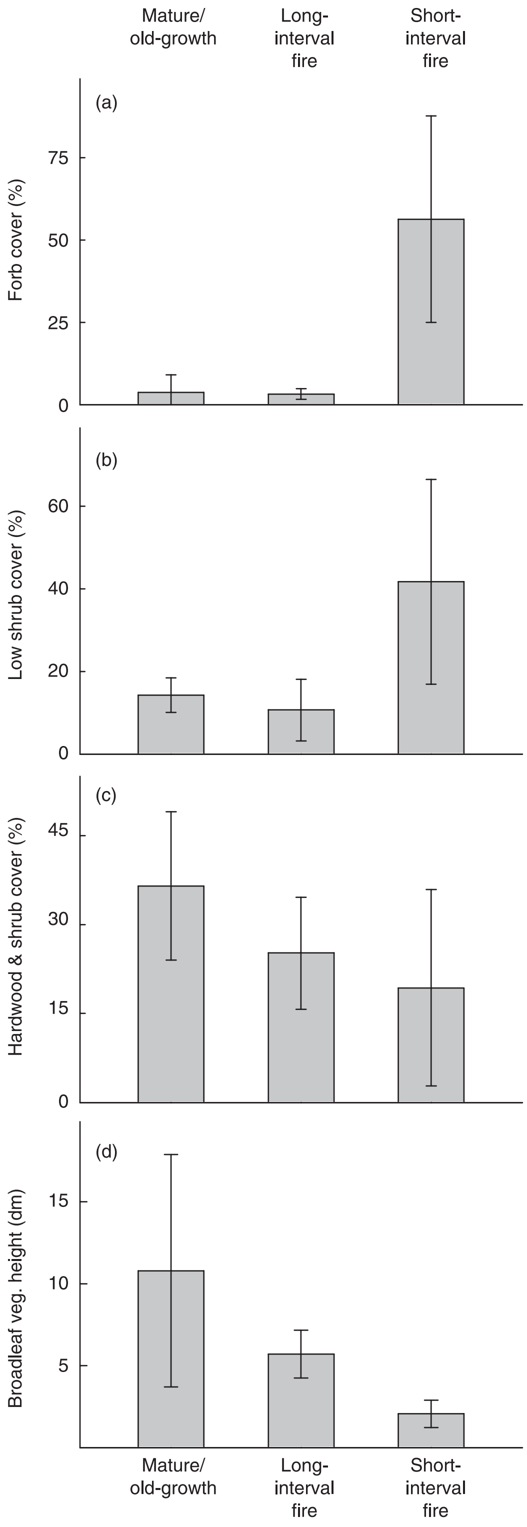

Fig. 2. Mean (± 95% CI): (a) forb cover, (b) low shrub cover, (c) hardwood/shrub cover, and (d) broadleaf vegetation height, for mature/old growth stands, long-interval burn stands, and short-interval burn stands (0, 1 and 2 recent burns, respectively). Heights were calculated as a weighted average based on cover × height of each species.

Species richness increased with the number of recent fires and was highest in the SI burn (Table 1). This trend was similar when assessed at either the sample-wide (gamma) or plot (alpha) level. Fifty-nine species were detected in the SI burn sample compared to 42 in the LI burn sample. The SI burn had 4.2–19.8 (95% CI) more species per plot than the LI burn. Some portion of the richness in the SI burn was likely associated with comparatively high forb/low-shrub abundance. There were no strong differences in species richness between the LI burn and M/OG stands (Table 1). The higher richness in the SI burn was not dominated by a few species; Shannon evenness was fairly high (0.75, 95% CI 0.67–0.83) and not different from the LI burn (0.73, 95% CI 0.66–0.79).

Species composition differed little between the LI burn and M/OG stands (MRPP: $A = 0.0095$, $P = 0.33$), but was strongly different in the SI burn compared to both the LI burn ($A = 0.13$, $P = 0.001$) and M/OG stands ($A = 0.12$, $P = 0.002$). Consistent with the patterns of increased abundance and diversity, the difference was due primarily to additions or increases in the abundance/frequency of several species in the SI burn, rather than species loss (Table 1). Most of the increases were of forb and low stature shrub species. Composition of hardwoods and shrubs showed a decreasing trend with number of recent burns in mean cover of *L. densiflorus* and *Q. chrysolepis*, the dominant hardwoods of these plant associations (Table 1). *Arbutus menziesii* and *Q. sadleriana* were mostly absent in the SI burn (Table 1). In contrast, *A. patula* occurred in greatest abundance in the SI burn (Table 1). The increase in low vegetation components, coupled with reduced cover of major hardwood species, resulted in overall lower-stature communities in the SI burn (Fig. 2d).

ISA results were also consistent with an additive effect of the SI fire (Table 1). Only two species, the fire-sensitive forbs *Goodyera oblongifolia* and *Chimaphila menziesii*, were uniquely associated with M/OG conditions and only one species, *A. menziesii*, was strongly associated with the LI fire. In contrast, seven species were strongly associated with the SI fire (Table 1). Thus, overall, most species found in M/OG forests occurred with similar abundance/frequency when subject to one or even two high-severity fires, with increases/additions of several disturbance-associated species in the SI burn.

HARDWOOD, SHRUB AND CONIFER RESPONSES

Sprouting was the dominant mode of regeneration for hardwoods and woody shrubs in both the SI and LI burn (Fig. 3). On average, a greater proportion of pre-fire individuals were killed (did not sprout) in the SI fire, but responses were highly variable (Fig. 3). At the individual level, sprouting probability was strongly positively associated with pre-fire size (GLME: $F_{1,732} = 24.9$, $P < 0.0001$), and there was no strong shift in this relationship between the SI and LI burns ($F_{1,10} = 1.78$, $P = 0.21$). Similarly, for individuals that sprouted, sprout biomass was strongly positively associated with pre-fire size (HLM: $F_{1,540} = 338.2$, $P < 0.0001$), and there was also no strong shift in this relationship between the SI and LI burns ($F_{1,10} = 1.12$, $P = 0.32$). However, relative to the LI burn, individuals in the SI burn were smaller at the time of the second fire (mean pre-fire basal area = 15.3 cm^2 shrub^{-1} in SI burn, 52.2 cm^2 shrub^{-1} in LI burn), which was associated with

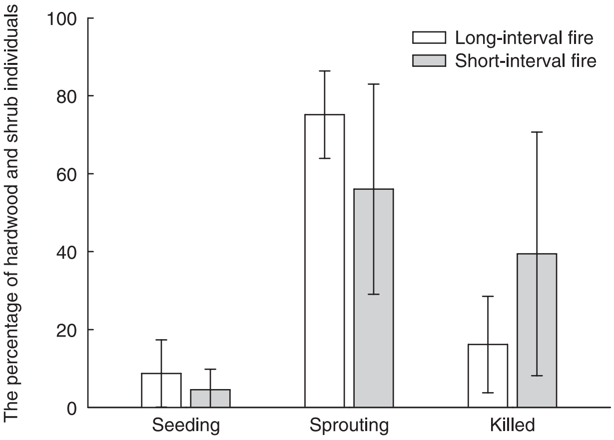

Fig. 3. Hardwood and shrub reproductive modes by percent of individuals in each plot (mean ± 95% CI). No strong shift in dominant regenerative mode in the SI burn was apparent; sprouting dominated over seeding in both treatments. There is suggestive evidence of higher mortality of pre-fire individuals in SI burn plots; however, variability was high. See Appendix S3 for species composition of seeding and sprouting individuals.

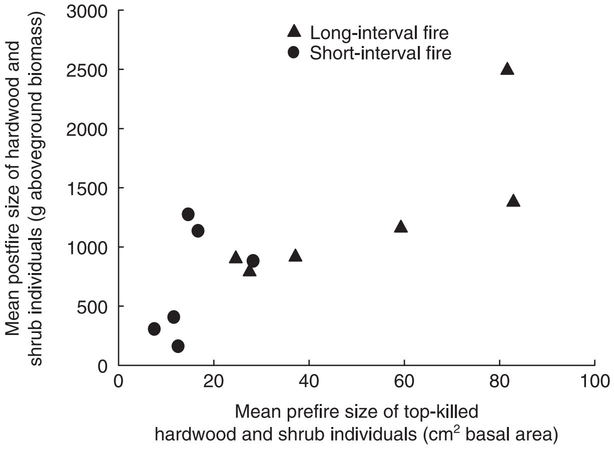

Fig. 4. Mean post-fire biomass of hardwoods and shrubs as a function of mean pre-fire size of hardwoods and shrubs. Data are shown aggregated by plot for clearer visual display of trend; regression analysis was performed on 554 individual shrubs, with plot as a random effect. There was no strong evidence for differences between burn histories in the relationship between pre- and post-fire size (HLM: $F_{1,10} = 1.12$, $P = 0.32$), but individuals were smaller before the short-interval fire which was associated with smaller post-fire size (HLM: $F_{1,540} = 338.2$, $P < 0.0001$).

smaller post-fire size (mean sprout mass = 690.7 g shrub^{-1} in SI burn, 1271.8 g shrub^{-1} in LI burn) (Fig. 4). This trend was driven largely by *Q. chrysolepis*, followed by *Chrysolepis chrysophylla*, *A. menziesii*, and *A. patula* (but notably not by *L. densiflorus*, which had similar pre-fire basal area between treatments). Thus, individuals of a given size had the same sprouting probability and biomass in both treatments, but plot-averaged biomass was lower in the SI burn since individuals were smaller before the second fire (Fig. 4).

Conifer establishment roughly spanned an order of magnitude in both burn areas, ranging from 298–6086 ha^{-1} (median 1495 ha^{-1}) in the SI burn and 406–2349 ha^{-1} (median 1002 ha^{-1}) in the LI burn. There was no significant difference in conifer regeneration density between the SI and LI burns (95% CI for SI : LI ratio = 0.4–5.8). Conifer seedling composition in SI burn plots was 99% *P. menziesii* with incidental amounts of *P. attenuata* and *P. lambertiana*, whereas LI burn plots contained 66% *P. menziesii*, 20% *P. attenuata* and 11% *P. lambertiana*. Nearly all seedlings became established in 2004, 2 years post-fire, except for knobcone pine (primarily 2003). Seedlings occupied most plot quadrants in both the SI and LI burn (mean of 80% and 93% occupancy, respectively). We detected no strong difference in available substrate proportions between the SI and LI burn (MANOVA $F_{5,6} = 1.45$, $P = 0.33$), with mean values of 24–32% mineral soil, 47–56% rock, 10–15% litter, 5–10% wood, and < 1% moss/lichen. Substrates utilized by conifer seedlings largely reflected the pattern of availability in both the SI and LI fires.

TRAIT ANALYSIS

Trait analysis showed little difference between communities in M/OG stands and the LI burn, while the SI burn differed markedly from the other two treatments (Fig. 5a). The ordination of plant functional traits had an R^2 with the original trait distance matrix of 0.98; ranks of scores along ordination Axis 1 (burn axis) show increasing associations of functional traits with the SI burn (Fig. 5b). Similar to species patterns, the difference of the SI burn was primarily due to increases in the abundance/frequency of several disturbance-associated traits, rather than reductions in late-seral type traits (Table 2). The SI burn was associated with increases in ruderal, small-stature, high turnover community components including native annual forbs, low shrubs and deciduous species (Fig. 5, Table 2). Obligate seeders, especially species with soil seed banks (evader strategy) or wind-dispersed seeds (invader strategy), responded positively to the SI burn. Sprouters (endurer strategy) exhibited a gradient in response, with those that sprout diffusely from rhizomes better represented in the SI burn than those that sprout from root crowns/burls, which include evergreen hardwoods and shrubs. Fire-sensitive species (avoiders) were strongly negatively associated with number of recent burns. Nitrogen (N) fixers were most abundant in the SI burn, primarily due to forbs of the Fabacae family (e.g. *Lotus crassifolius*, *Lupinus spp*., *Thermopsis macrophyllum*). Species typically associated with late seral forests were located in the middle of the burn axis, reflecting their general presence across all treatments.

Within the trait ordination, number of recent burns had a stronger Pearson correlation coefficient ($r = 0.87$ with Axis 1) than any of the environmental parameters ($0.14 < |r| < 0.36$) (Fig. 5) regardless of axis rotation, suggesting that disturbance drove much of the community gradient within this range of environmental conditions. Correlations were generally low between environmental variables and both ordination axes. Categorical variables for plant association and soil type (not

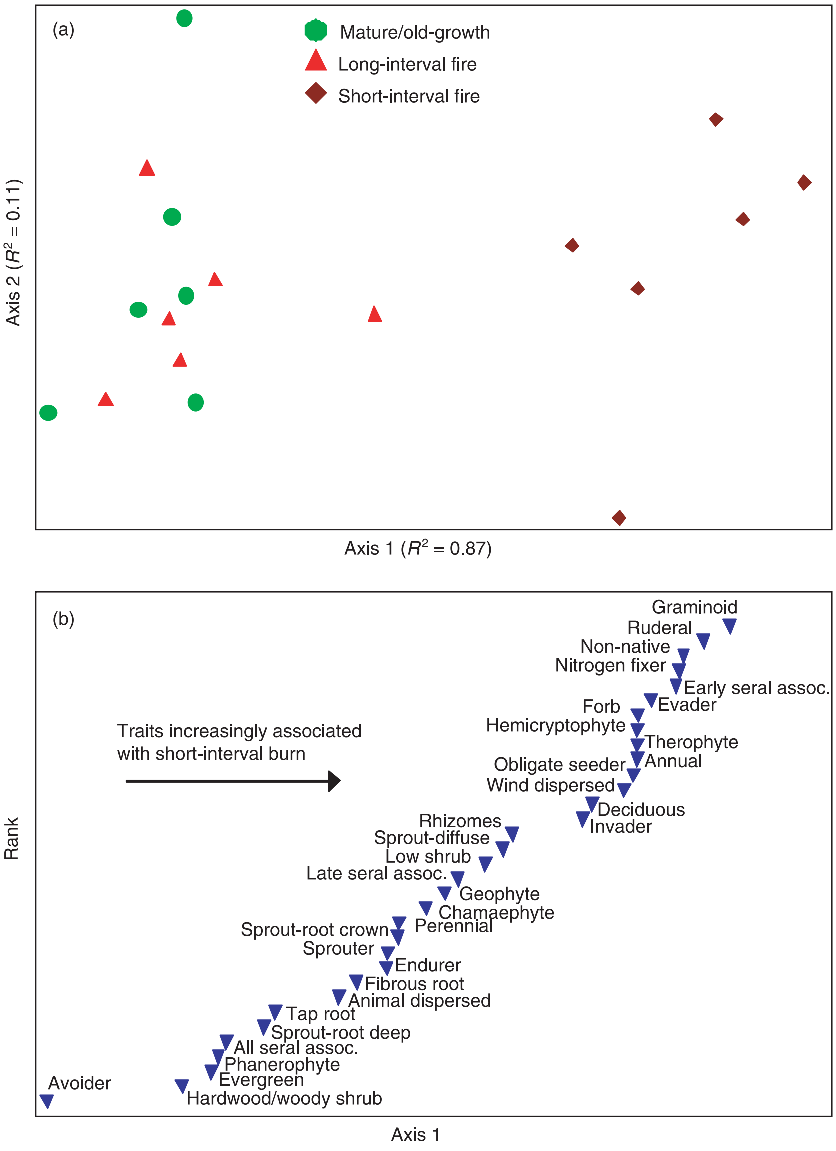

Fig. 5. (a) Ordination of plots in plant functional trait space. Larger distances between points represent larger differences in abundance of traits; SI burn plots are separated strongly from other treatments. R^2 values signify portion of original variance explained by each axis. Pearson's *r* correlations with environmental variables were (Axis 1, Axis 2, respectively): # burns (0.86, 0.04), elevation (0.22, 0.20), annual precipitation (–0.19, –0.14), annual solar heat load [aspect proxy] (–0.36, –0.35). (b) Ranks of plant functional traits along Axis 1. Attributes to the right are increasingly associated with (but not exclusive to) the SI burn, and vice versa. The 'Non-native' data point is due to minor occurrences of *Cirsium* spp. or *Senecio sylvaticus*.

shown) were well-distributed across axes, suggesting these factors were not major drivers of compositional gradients relative to disturbance history.

Discussion

The early post-fire data were most consistent with model 3: interval-dependent dynamics with no decline in diversity or abundance after SI fire (or 're-burn'). The SI fire resulted in unique post-fire communities containing nearly all species found in M/OG stands and in the LI burn, plus additions or increases in several disturbance-associated species (Table 1). This shift to higher richness and abundance, coupled with lower dominance by woody broadleaf components (Fig. 2), lends comparatively little support for model 1 (cyclical dynamics independent of fire interval) or model 2 (interval-dependent dynamics with major reductions in diversity/abundance). Regeneration of major structural species (e.g. conifers, hardwoods) in the SI burn suggested that, in the absence of repeated severe fires, these stands retained the potential to develop toward mature forest condition.

VEGETATION ABUNDANCE, DIVERSITY AND COMPOSITION

The consistent presence of a core assemblage including nearly all species found in mature forests suggests high community resilience following one and even two stand-replacing fires. The increase in species richness in the SI burn was unanticipated and mainly due to additions of ruderal or disturbance-associated flora such as *Rubus spp.* and bracken fern (*Pteridium aquilinum*), the latter also noted by Isaac (1940) following recurrent burning of cutover areas in the Douglas-fir region. The pattern we observed – SI fire leading to lesser dominance by woody broadleaf components, generating gaps in which additions of ruderal/low-stature species lead to higher species richness and cover – is similar to that observed by Delitti *et al.* (2005) in a Spanish Mediterranean ecosystem.

The mechanisms for increases in early seral species and total richness in the SI burn could be abiotic, such as changes to soil properties that favour such species, or biotic, as in the development of a propagule bank for early seral species during the 15 years between fires (Noble & Slatyer 1980). Based on the abundance in the SI burn of short-lived, rapidly maturing species (ruderal, annual), and those with long-lived seed banks (evaders) (Table 2, Fig. 5), we infer that increases in early seral species were driven primarily by the biotic mechanism of propagule availability. This mechanism represents a positive feedback legacy effect, whereby small compositional changes following a single fire (minor increases in early seral species and associated seed banks) lead to greater modifications following a second fire (major increases in these species).

Pre-existing variability among treatments could explain the differences we observed, particularly because of the lack of spatial interspersion of treatments. However, a nearly identical core set of species was found in all three treatments which provides supporting evidence that the sample groups were comparable before recent disturbance. Moreover, the primary difference observed in the SI burn – addition of disturbance-associated components – is logically consistent with a fire response.

HARDWOOD, SHRUB AND CONIFER RESPONSES

Hardwood and shrub regeneration

Hardwood and shrub individuals of a given size had similar sprouting probability and biomass in the SI and LI burns. A 15-year interval between fires appears sufficient for below-ground carbohydrate reserves to support sprouting following top-kill for the species examined in this study. Similarity of sprouting between treatments also suggests there was no difference in heat-related damage to below-ground tissues; thus fire severity was apparently similar across treatments in this respect. Nevertheless, it is possible that a shorter interval fire, or further repeated fires, could reduce the sprouting response relative to what we observed (Delitti *et al.* 2005).

Because the relationship between post-fire sprouting biomass and pre-fire size was the same across treatments, the lower post-fire hardwood/shrub cover and biomass in the SI treatment may be due to the smaller size of individuals at the time of the second fire (Fig. 4). This may be associated with: (i) the conversion by the first fire of large hardwood trees to smaller, multi-stemmed sprouts with lower leaf/basal area (see Bond & van Wilgen 1996); (ii) a compositional shift toward smaller species that colonized the site over time following the first burn (e.g. *A. patula*) (Table 1); or (iii) pre-existing differences in hardwood/shrub sizes. The conversion by the first fire of tree forms to sprout-shrub forms, and its feedback to re-burn response (smaller subsequent sprouts), is a possible mechanism by which recurrent burning could reduce dominance by hardwoods and shrubs during early succession, creating growing space for other vegetation (model 3, see Fig. 2).

Conifer establishment

Initial post-fire conditions were apparently not limiting to total conifer establishment in the Silver-Biscuit SI burn. Thus, if differences emerge later between conifer regeneration in the SI vs. LI burns (*sensu* Gray & Franklin 1997), it could be inferred that latent differences (e.g. competition, herbivory, soil properties) drove the difference. Dense early conifer establishment in the SI burn suggests that the availability of seed sources and suitable germination substrate was similar to that in the LI burn. Distance to contiguous seed source ranged from 85–300 m for SI burn plots compared to 80–370 m for LI burn plots, a range applicable to 70–90% of the stand-replacement portions of the Biscuit Fire excluding serpentine areas (based on US Forest Service GIS data; see Donato 2008). (Note that precipitation during post-fire growing seasons, an important factor for regeneration and one that may vary widely among years, likely did not contribute abnormally to regeneration, as it was generally within one S.D. of 30-year mean, and if anything was generally below average [Donato 2008]).

A mixed-severity fire typically produces complex patterns of tree mortality on the landscape (Agee 1993, 2005). These patterns result in much of a burned area being close to live-tree seed sources, even in large fires with substantial stand replacement (Turner *et al.* 1994). In the Silver-Biscuit SI burn, areas that burned with low severity in the initial fire tended to re-burn with low severity (Thompson *et al.* 2007), such that the mosaic of available seed sources largely persisted through the second fire. The persistence of the mosaic over certain time scales may result in well-dispersed seed sources following repeated mixed-severity fires. This dynamic differs from observations of sparse regeneration following SI fires in ecosystems reliant on *in situ* re-seeding from serotinous conifers (fire interval < reproductive age) (Eugenio *et al.* 2006; Johnstone & Chapin 2006) or on off-site seed sources as in this system, but with seed sources reduced by the second fire (Isaac & Meagher 1936). Our inference of off-site source in this study is based on nearly all seedlings establishing 2 years post-fire, too late for a dead-tree canopy seed bank source.

TRAIT ANALYSIS

Analysis of plant functional traits showed several strong associations with recent fire history, providing support for the use of functional traits in predicting vegetation response to short-interval severe fires (Table 2, Fig. 5). Some associations were intuitive while others were unanticipated. As we hypothesized, several disturbance-associated traits and functional types were highly associated with the SI burn. Broadly applicable examples included invader and evader regenerative strategies, ruderal/early seral associates, and wind-dispersed seeds.

Several different regenerative mechanisms were important in the SI burn, including vegetative sprouting, *in situ* seed banks, and dispersal from *ex situ* seed sources. Assessing Noble and Slatyer's (1980) vital attributes against the 15-year fire interval, forbs and low shrubs were 'G' types (rapid maturation time and stored soil seed banks), hardwoods and shrubs were 'S' and/or 'V' types (vegetative sprouting ability and/or long-lived soil seed banks), and conifers were 'D' types (well-dispersed propagules from surrounding live tree sources). This diversity of available mechanisms likely in part underlies the robust vegetation response to SI fire.

Rapid time to reproduction was a major factor in species that increased following SI fire. Ruderal and low-stature community components including many low shrubs and forbs (mainly hemicryptophytes and therophytes) – particularly those with rapid maturation and shorter-lived tissues such as annuals and deciduous species – responded positively to the SI fire (Table 2). Delitti *et al.* (2005) also observed increases in low shrubs and forbs, especially hemicryptophytes, following recurrent fires in a Spanish Mediterranean ecosystem. For broadleaf evergreen woody vegetation, however, there was little association with any fire history, although these tended to have lower mass/cover in the SI burn – also similar to Delitti *et al.* (2005). Thus, species investing more resources in early reproduction, and less in long-lived leaves and secondary tissues (wood), may be expected to be relatively dominant immediately following recurrent stand-replacing fires (Table 2; Noble & Slatyer 1980).

Consistent with observations made by Lloret *et al.* (2005) in a Spanish Mediterranean ecosystem, seeder species were associated with recurrent fires while sprouter species (particularly those that sprout from central root crowns or burls) did not show strong associations with recent fire history (Table 2). The exception in our study was that species sprouting from diffuse rhizomatous structures responded positively to the SI fire. Diffuse sprouters may have increased due to a legacy effect associated with the establishment of these species after the first fire, or due to increased lateral growth associated with repeated top (apical) kill (Riba 1998).

Surprisingly, very few traits were strongly negatively associated with the SI burn (Table 2). Avoiders were the primary negative responders, but the community we studied only included four such species – the forbs and low shrubs *G. oblongifolia*, *C. menziesii*, *C. umbellata*, and *Pachystima myrcinites*. However, most species typically associated with late seral conditions (e.g. in the FEIS data base) were present with similar relative abundance/frequency in M/OG, LI burn, and SI burn stands. This response, coupled with the low number of species classified as avoiders, likely reflects a flora well-suited to the variable fire regime of the Klamath–Siskiyou region.

The functional trait patterns we quantified may provide insight into differing responses to recurrent fires among ecosystems. Regions in which negative overall responses have been reported (e.g. Kutiel 1997; Diaz-Delgado *et al.* 2002) may be drier and/or less productive than the Klamath–Siskiyou region, with greater proportional representation of sprouting woody species with slower maturation, and fewer low-stature herbaceous components (e.g. hemicryptophytes, therophytes), ruderal species, or species with invader/evader regenerative strategies. Also, interactions with recent management history are important (Paine *et al.* 1998) and vary widely by region; our study areas were relatively uninfluenced by recent forest management activities such as timber harvest. Perhaps most importantly, the Silver-Biscuit SI fire occurred in a mixed-severity fire regime context, in which wide variations in fire interval and severity have likely occurred for millennia.

SI FIRE, SUCCESSION AND MIXED-SEVERITY FIRE REGIMES

Post-fire succession can be divided into two phases (Noble & Slatyer 1980): the first, immediately post-fire, when competition for resources is low and species abundance is driven primarily by regenerative processes (the focus of this study); and the second, after this initial pulse, when resource competition becomes progressively important. Variations in the first phase may strongly influence the second. The results of this study suggest that SI fires produce unique post-fire communities relative to a single LI fire, but the degree to which this affects long-term trajectories remains an interesting hypothesis to test. Moreover, it remains possible that elements of models 1 and 2 could manifest themselves as these stands develop. For example, the presence in the SI burn of regenerating conifers and hardwoods (the major structural species of these forest types) suggests that in the absence of continued stand-replacing fires, succession may converge with that following a LI fire, trending toward mature forest condition (i.e. elements of model 1). Alternatively, if, for example, soil chemistry is dramatically altered by two fires (beyond the scope of this study), tree growth and thus canopy development may eventually differ in the SI burn (i.e. model 2).

The abundance, character and landscape distribution of SI fires have likely varied widely over time. Important factors in this variability may include long-term climatic variability (Whitlock *et al.* 2003) as well as recent fire exclusion which may have influenced pre-fire vegetation conditions (Agee 1991; Taylor & Skinner 1998). Also, stand-scale variation in fire interval may be important since feedbacks between multiple fires may exhibit threshold behaviour, with increased probability of high-severity re-burning over short-time scales (Thompson *et al.* 2007), but decreased probability over longer time scales that allow for canopy closure and large stature trees (Odion *et al.* 2004). Where positive feedbacks exist, continual SI fires could lead to further shifts and altered successional trajectories. Lastly, differences in fire severity among short-interval events would likely produce very different outcomes to what we observed.

Post-fire management activities are often focused, in part, on reducing anticipated adverse effects of repeat high-severity fires (expectation of model 2; USDA 1988). For certain objectives, such as the rapid attainment of late-successional condition, recurrent stand-replacement fires are clearly counterproductive in the short term. However, these events may be consistent with objectives for maintaining characteristic disturbance processes and regional vascular plant diversity (see Landres *et al.* 1999). These results indicate that much of the native biota is resilient to 'extreme' events such as recurrent severe fire. Given the Klamath–Siskiyou region's characteristic patterns of fire severity, productivity, and ignition source, there is good reason to believe that short-interval severe fires have historically been a component of the fire regime. These events contribute to the landscape heterogeneity inherent to mixed-severity fire regimes, in which variability in fire frequency, severity, and pattern can be more important than central tendencies (Agee 2005). Where consistent with land-use objectives, process-based disturbance management could include this variation, perpetuating a diversity of conditions across the landscape.

Acknowledgments

Authors thank B. McCune, C. Eisenberg, D. Hibbs, D. Peterson, G. Meigs, G. Riegel, J. Campbell, J. Halofsky, J. Jones, J. Tappeiner, J. Thompson, L. Kayes and T. Atzet for helpful reviews and/or discussions. Two anonymous referees greatly improved the article. M. Huso and A. Gitelman provided statistical assistance and reviews. A. Pfleeger, D. Clay, J. Boerner, L. Reidlinger, R. Linden and S. Hamilton braved brush and poison oak with us to collect these data. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of the US Government. Mention of trade names or commercial products does not constitute their endorsement by the US Government. This work was facilitated by the Siskiyou National Forest and Medford BLM. Funding was provided by the US Joint Fire Science Program and Department of Energy (DF-FG02104ER63917).

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Received 13 May 2008; accepted 2 October 2008
Handling Editor: Hans Cornelissen

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Complete species list.

Appendix S2 Hardwood and shrub mass allometry.

Appendix S3 Species composition of hardwoods and shrubs by seedling vs. sprouting forms.