

Effects of fire exclusion on forest structure and composition in unlogged ponderosa pine/Douglas-fir forests

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Abstract

Research to date on effects of fire exclusion in ponderosa pine (*Pinus ponderosa*) forests has been limited by narrow geographical focus, by confounding effects due to prior logging at research sites, and by uncertainty from using reconstructions of past conditions to infer changes. For the work presented here, reference stands in unlogged ponderosa pine/Douglas-fir (*Pseudotsuga menziesii*) forests at seven sites across a broad region of Idaho and Montana were selected for study. Within each site, understory and overstory community structure and composition were surveyed in 2–4 stands exposed to different numbers of fires during the 20th century. Student's *t*-tests were used to test differences between the most fire-excluded (“unburned”) and the most frequently burned (“burned”) stands across the entire study. Multivariate analyses were used to characterize successional changes resulting from lack of fire. Understory community composition varied from site to site and was not related to fire exposure. However, species richness was higher in unburned stands. Overall tree densities and densities of shade-tolerant tree species increased with the absence of fire. There was a marginally significant association between xeric understories and ponderosa pine dominated overstories and mesic understories and Douglas-fir or grand fir dominated overstories. Our multivariate analysis suggests that while general trajectories of succession with absence of fire may be predictable, the structure and composition of ponderosa pine/Douglas-fir communities across complex landscapes may be difficult to relate to specific exposure to fire or time-since-fire. This study highlights the importance of natural variability and heterogeneity in ponderosa pine/Douglas-fir forests of the inland Northwest, and supports other recent research calling for cautious approaches to restoration in these forests.

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1. Introduction

Pure and mixed ponderosa pine (*Pinus ponderosa*) forests extend across western North America from northern Mexico to southern Canada (Oliver and Ryker, 1990). Fire is likely the most important natural disturbance agent in ponderosa pine forests throughout this region. Since 1900, fires have become much less frequent across the western United States as a result of fire exclusion policies (Agee, 1993; Arno et al., 1995a; Keane et al., 2002), and less indigenous burning (Barrett and Arno, 1982). The accumulation of fuels during the fire exclusion period is seen as a major cause of widespread and relatively severe forest fires in recent years. Largely in response

to forest structure changes attributed to fire exclusion, restoration efforts are underway in national forests to reduce stand densities by reintroducing fire, thinning stands mechanically, or by combination of both burning and thinning (Allen et al., 2002; White House, 2002; Arno, 1999).

Successful restoration of fire-excluded ponderosa pine forests may benefit from a clearer understanding of how changes in fire frequency affect natural forest communities. Fire exclusion is thought to increase stand densities, increase shade-tolerant species in the overstory, increase overall plant cover, decrease grasses, slow nutrient cycling, and decrease overall species diversity (Cooper, 1960; Merrill et al., 1980; Covington and Moore, 1994a,b; Arno et al., 1995b; Fulé et al., 1997; Keane et al., 2002; MacKenzie et al., 2004; DeLuca and Sala, 2006). However, it is increasingly recognized that fire effects in ponderosa pine forests can vary considerably in space and time (Brown et al., 1999; Schoennagel et al., 2004) and

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vegetation responses may reflect this variability. Recent research suggests that perspectives on fire exclusion and restoration in ponderosa pine forests must broaden to include substantial natural heterogeneity, highly dynamic ecosystems and persistent scientific uncertainty (Allen et al., 2002).

Ponderosa pine forests encompass different natural stand structures and fire regimes depending on geography and topography. Much of what is known about fire exclusion in ponderosa pine forests comes from research focused on dry, pure stands in low-elevation forests of the Southwest US (Schoennagel et al., 2004). In these forests, frequent, low-severity fires historically maintained open stands (Swetnam and Baisan, 1996). However, at mid-elevations and at more northern latitudes where ponderosa pine is seral to Douglas-fir (*Pseudotsuga menziesii*) or grand fir (*Abies grandis*), stand structure may be more variable. Mid-elevation and more northern ponderosa pine forests historically experienced a mixture of low severity and high severity fires, probably at less frequent intervals (Schoennagel et al., 2004). This mixed-severity fire regime creates a mosaic of fire effects with high spatial variability in forest structure at the landscape level (Arno, 1980; Schoennagel et al., 2004). Because mixed-severity fire regimes are inherently more complex than the low-severity fire regimes of the Southwest, restoration strategies adopted in the Southwest may not be applicable to ponderosa pine/Douglas-fir (PP/DF) forests of the inland Northwest. Greater insight into the range of natural variability in northwestern PP/DF forests is needed to guide future restoration strategies in these forests (Landres et al., 1999).

A limitation in our understanding of fire and fire exclusion in western forests is that much of the available data comes from forests that were logged some time in the past. In fact, it is difficult to find examples of forest conditions that are clearly a product of absence of fire alone. High stand densities commonly attributed to fire exclusion may be partially a result of previous removal of older, fire-resistant trees resulting in the incursion of dense stands of younger trees (Laudenslayer and Darr, 1990; Stephens, 2000; Kaufmann et al., 2000). In order to separate effects of fire exclusion from confounding effects of previous logging, there is a critical need for research in forests with no prior logging history.

An additional and inherent difficulty in studying any long-term process in forests is the uncertainty in our knowledge of past conditions. Unlogged forest stands that might serve as references to past conditions are rare, and often located in remote wilderness areas, posing considerable logistical challenges to researchers. Many studies rely solely on historical accounts or reconstructions of pre fire exclusion era stand structure rather than seeking suitable reference stands in contemporary forests. Documentary records such as photographs or written descriptions, though valuable, are often incomplete or spatially biased toward areas close to early settlements (Kaufmann et al., 2000; Swetnam et al., 1999). Reconstructions of historical forest structure using dendrochronological techniques (Covington and Moore, 1994b; Arno et al., 1995b; Arno et al., 1997) or General Land Office survey data (Habeck, 1994) are also subject to bias (Wright and Agee,

2004). Dendrochronology can only make use of wood that has survived to present times and therefore will not detect trees that died and decayed before research is initiated (Stephenson, 1987; Fulé et al., 1997; Allen et al., 2002). Similarly, General Land Office surveys may have failed to record the presence of smaller size-classes and certain species (Manies et al., 2001; Whitney and DeCant, 2001; Wright and Agee, 2004). Natural reference stands in contemporary forests that have continued to experience the historical fire frequency can provide essential independent benchmarks of natural variability to verify historical data or reconstructions (Swetnam et al., 1999; Gildar et al., 2004; Laughlin et al., 2004).

Another benefit of using reference stands as opposed to reconstructions is that the understory community may be studied (Laughlin et al., 2004). Although historical understory composition in forests may be modeled or simulated (Covington and Moore, 1994b), dendrochronology cannot be used to reconstruct historical understories. Uncertainty persists about the long-term effects of frequent fire versus fire exclusion on understory plant communities. Because most ponderosa pine forests usually contain only a small number of overstory species, understory plants represent a far greater contribution to biodiversity than does the overstory in these ecosystems. Reestablishment of natural understory structure and species composition is seen as a vital part of restoration of natural ecosystem processes and fire dynamics in fire-excluded forests (Allen et al., 2002). Understory responses to fire and absence of fire therefore deserve careful study alongside overstory responses.

In the work presented here, we compare forest stands exposed to different numbers of fires during the 20th century within remote sites in unlogged PP/DF forests in Idaho and Montana. These sites were used to assess the influence of recurrent fire at roughly historical frequencies versus lower fire frequencies on community structure and composition. Our use of natural reference stands provides benchmarks of forest change independent of historical accounts or reconstructions and without the confounding influence of prior logging. A total of seven sites, ranging across a broad geographical area, but within a coherent forest type (PP/DF) were selected. We surveyed both the understory and overstory. In addition, soil characteristics, nutrient cycling and tree physiology were studied and are subjects of related forthcoming papers (see DeLuca and Sala, 2006).

2. Methods

2.1. Site selection

With the aid of a GIS database built from USFS fire maps (see Rollins et al., 2002), seven study sites were located in low- to mid-elevation ponderosa pine/Douglas-fir forests in western Montana and Idaho. Sites were chosen in areas with no previous logging history, either within or on the periphery of wilderness areas. Site locations, names, and abbreviations are shown in Fig. 1. Within each site, 2–4 stands were identified, each with 0, 1, 2, or 3+ recorded fires since 1880. Sites were selected where

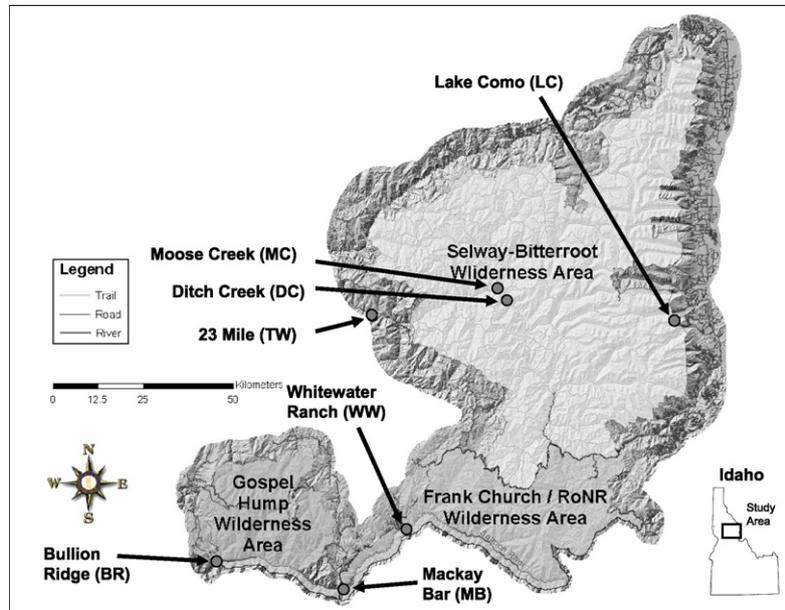


Fig. 1. Study area and site locations.

stands shared similar physiographic (elevation, aspect, slope) characteristics. Stands were chosen so that years of first, second and third burns were relatively consistent across the entire study. Consequently, all stands of the same burn number have experienced roughly the same fire-free time interval up to the present, and effects resulting from number of fires versus time since last fire are not separated. The most recent fire at any site was more than a decade before this study was conducted; therefore documented effects are not simply short-term responses to recent fire.

Due to restrictions prohibiting the use of chain saws in wilderness areas, detailed fire scar analyses could not be conducted at every site. Instead, published USFS fire histories in the GIS maps were verified by visual reconnaissance based on the presence of charcoal and fire-scarred trees. Increment cores from fire-scarred trees were further analyzed in the laboratory (Barrett and Arno, 1988). However, at two sites (TW and MB) a detailed fire-scar analysis was conducted in 2005, subsequent to our field surveys (E. Heyerdahl, J. Riser, Fire Sciences Laboratory, USFS; unpublished data). At MB, results of this study verified the 20th century fire history in the GIS. At TW, four stands (0-, 1-, 2-, and 3-burns) were sampled in 2003. However, the fire-scar analysis conducted in 2005 found that a majority of trees within 0-, 1-, and 2-burn stands had in fact experienced two 20th century fires. Data from these three stands were averaged and analyzed as a 2-burn stand. The USFS recorded fire history was used to demarcate stands at all other sites.

For purposes of analysis, the lowest fire frequency stand at each site is referred to as “unburned” and the highest fire-frequency stand is referred to as “burned” (Table 1). At one site (MB), the unburned stand experienced one fire early in the 20th century (in 1919). At all other stands, unburned stands had not experienced fire since 1880. One site (TW) lacked an unburned stand and was not included in analyses where burned and

unburned stands were compared. “Burned” stands burned two–four times during the 20th century. Although some physiographic differences between stands existed, on average there were no systematic physiographic differences between unburned and burned stands from each site across the entire study. While we cannot determine whether fires may have been actively suppressed even in these remote areas, the fire return intervals in our burned stands are within the historical range, which can be more than 25 years for mixed ponderosa pine forests in the northwest region (Arno and Allison-Bunnell, 2002; Arno, 1980).

2.2. Data collection

Data collection was completed during June and July of 2003. In each stand, three 400 m² plots were established at random perpendicular distances from three stratified points along an access route. Plots were located within the boundaries demarcating that stand. Each plot was defined by two 20 m transects running at right angles through a plot center. At every plot center, GPS coordinates, elevation, slope, and aspect were recorded. Table 1 lists the environmental and fire history data associated with all stands at every site.

At points every 20 cm along each transect, vegetation intersecting the transect was identified and recorded in three vertical strata: <0.5 m, 0.5–3 m, and >3 m. Species recorded in the lower two strata were considered “understory” while species recorded in the high strata were considered “overstory”. Plants not identified to the species level were lumped at the generic level. Plants not positively identified but recognized across a site were recorded as unknowns and counted for plant functional group and species richness measures only. In addition, all trees in each plot were counted and diameters at breast height (dbh) were measured for all trees with dbh greater than 5 cm. Trees with dbh less than 5 cm were counted and recorded as seedlings.

Table 1
Physiographic data and fire histories for all stands within seven sites

Site	No. of burns since 1880 ^a	Mean aspect (°)	Mean elevation (m)	Mean slope (°)	Year first burn	Year second burn	Year third burn	Year fourth burn
23 mile (TW)	2	113.1	827	35.9	1910	1934		
	3	134.7	869	33.3	1910	1934	1992	
MacKay Bar (MB)	1 [*]	236.0	1813	27.3	1919			
	3 [†]	250.7	1536	32.7	1919	1960	1987	
Whitewater Ranch (WW)	0 [*]	220.0	1285	30.0				
	1	206.7	1027	25.0	1919			
	3 [†]	93.3	949	35.0	1919	1933	1988	
Lake Como (LC)	0 [*]	304.7	1552	21.0				
	2 [†]	273.3	1577	35.0	1924	1988		
Bullion Ridge (BR)	0 [*]	61.3	1665	37.3				
	3 [†]	49.3	1464	29.3	1914	1944	1992	
Moose Creek (MC)	0 [*]	270.0	957	33.3				
	1	116.7	1278	25.0	1910			
	4 [†]	258.0	915	42.3	1910	1934	1981	1987
Ditch Creek (DC)	0 [*]	166.0	805	17.3				
	1	124.0	832	28.3	1919			
	2 [†]	202.7	844	23.3	1919	1979		

^a Marked stands were used for testing differences between “unburned” stands (*) and “burned” stands (†) across all sites.

2.3. Data analysis—understory

Cover values were calculated by counting the number of times vegetation of a given species intersected a transect point and dividing by the total number of transect points per plot. Because more than one plant could be counted at a single point, cover values can exceed 100% for a given plot. Species richness was calculated by counting the total number of unique species recorded across all plots within a stand. Plants were categorized into one of the following functional groups: grass, forb, deciduous shrub, evergreen shrub (non-ericaceous), ericaceous shrub, and tree. In addition, plant status as exotic or N-fixer was tabulated. Species richness and mean cover values for all functional groups, exotics and N-fixers were calculated for each stand. Variables which did not meet the normal distribution and homogeneity of variance assumptions for student's *t*-test were transformed using a square-root function. To test differences across the entire study, only the lowest burn frequency stand (“unburned”) and highest burn frequency stand (“burned”) were used from each site (see Table 1). *T*-tests were used to test for differences in plant functional groups and species diversity between burned and unburned stands across the entire study.

A multivariate approach was used to compare community structure based on species data. The goal of this approach was to determine whether plant community similarity was greater between stands grouped by fire history versus stands grouped by site. In addition to these two *a priori* grouping schemes (by fire history or by site), multivariate techniques were used to find a non-*a priori* grouping scheme that grouped stands by the highest degree of community similarity. The non-*a priori* grouping scheme (hereafter referred to as “community groups”) could then be used to determine whether factors other than site or fire strongly affect the plant community.

In order to separate stands into community groups based on similarity, mean cover values for individual understory species were calculated for each stand, and these values were arranged in a multivariate data matrix (stand × species) for processing using the software program PC-ORD (McCune and Grace, 2002). Understory percent cover values were not relativized or transformed. Potential grouping schemes were generated using either hierarchical cluster analysis or two-way indicator species analysis (TWINSPAN). Cluster analysis uses distance measures to generate a dendrogram that displays subgroups with high similarity nested within larger groups of decreasing similarity. A grouping scheme is then selected by choosing cut-off points along branches of the dendrogram. TWINSPAN uses “differential species” to divide the sample plots into progressively smaller groups until a final grouping scheme is produced.

Grouping schemes were evaluated using Indicator Species Analysis (Dufrêne and Legendre, 1997). Indicator values are calculated by multiplying relative abundance (proportion of a given species found in a specific group) by relative frequency (proportion of sample units that contain that species within a specific group). High indicator values reflect high faithfulness and even membership to stands within a group. By this method, species can be associated with specific community groups. The Monte-Carlo test compares the indicator value for species in the tested grouping scheme to maximum indicator values for 1000 randomly generated grouping schemes and reports a significance value for each indicator species assigned to a tested group. A high number of significantly associated indicator species ($p \leq .05$) reasonably distributed among groups was used as the criterion for judging the various grouping schemes generated (McCune and Grace, 2002).

A multivariate indirect ordination scatter plot was generated using Nonmetric Multidimensional Scaling (NMS) in the PC-ORD software package (McCune and Grace, 2002). Sorenson distance was used with PC-ORD's autopilot mode to select the optimal solution. Autopilot uses 40 runs with real data and 50 runs with randomized data, and chooses the highest dimensionality that yields a final stress that has stabilized and is lower than 95% of the random runs. Potential groups were overlaid with the ordination for possible further refinement of groups. Any new groups emerging from the ordination were evaluated again using Indicator Species Analysis and results were compared until optimal groups were selected. Ancillary information from the US Forest Service Plant database (<http://www.fs.fed.us/database/feis/plants>) was used to tabulate descriptions of ecological characteristics of all indicator species and these descriptions were used to characterize each group.

Multi-response permutation procedures (MRPP) in PC-ORD were used to evaluate differences in community composition between final community groups compared to differences when stands were grouped either by site or by fire history. MRPP generates an agreement statistic, *A*, that describes within-group homogeneity compared to random chance, and a significance value. As with NMS, our MRPP analyses used the Sorenson distance measure.

In order to identify potential drivers of the understory community structure, the NMS ordination axes were correlated with relevant environmental data treated as independent variables. Independent variables for each stand included elevation, heat index (a transformation of aspect and slope outlined in Stage (1976), time-since-fire, species richness, % cover >3 m (a surrogate for shade), and 14 soil variables (see DeLuca and Sala, 2006).

2.4. Data analysis—overstory

Counts of tree species were converted to trees per hectare and diameter measures were converted to basal area per hectare for all tree species. For each stand, mean densities and basal areas of the three most commonly occurring overstory species (ponderosa pine, Douglas-fir, and grand fir) were calculated. As with the understory, variables were tested for normal distribution and homogeneity of variance assumptions and transformed using a square-root function if necessary. A *t*-test was used to test differences in dominant overstory species density and basal area between unburned and burned stands across the entire study.

For the multivariate analysis of the overstory, counts of ponderosa pine, Douglas-fir, and grand fir for each plot were separated into eight size classes and mean count values of each species in each size-class per hectare were calculated for every stand. Data were arranged in a multivariate data matrix (stand × spp. in each size class) and log-transformed and relativized by column maximum in order to eliminate skew toward size-classes with much higher counts (i.e. seedlings). The community grouping procedure was exactly as for understory species (see above) except that overstory community groups

were distinguished by indicator species in particular size-classes, rather than species alone. Size-class distributions (plotted as bar charts) of each stand were also used to evaluate the final grouping scheme and as a more precise method for comparing differences between stands.

2.5. Data analysis—overstory/understory relationships

To examine the association of overstory and understory, an NMS ordination scatter plot for all stands was produced from the tree species/size-class matrix and both overstory and understory groups were overlaid. Overstory-understory associations were tested using a χ^2 -test.

3. Results

3.1. Understory

Eighty-nine understory plant species were positively identified across all sites. On average, seven additional unidentified species per site were also recorded. There was no consistent understory plant functional group response to number of burns (data not shown). However, species richness was significantly higher ($p \leq .05$) in the unburned stands (Fig. 2).

Multi-response permutation procedures results show that grouping stands by site produced higher understory within-group homogeneity than grouping by fire history (Table 2a). An optimal community grouping scheme was produced by cluster analysis (flexible beta linkage method, Sorenson distance measure). Table 3 lists the indicator species in the understory groups generated and the associated *p*-values from the Monte-Carlo test for each species. Three groups and a total of 21 species with *p*-values below 0.05 were found. The three groups were characterized as (1) moist, shade adapted species (mesic), (2) dry, open canopy adapted species (xeric), and (3) high elevation adapted species (high). Although this grouping scheme produced the highest number of indicator species, it

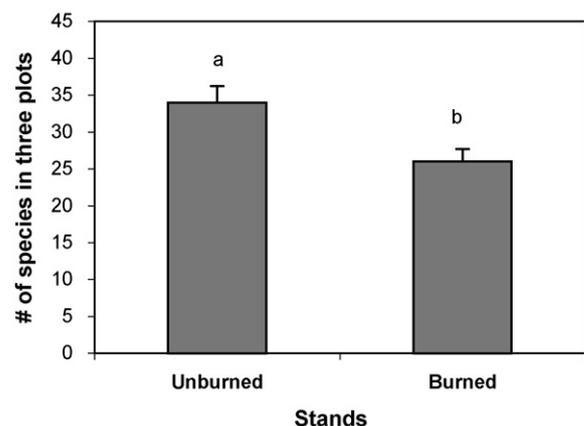


Fig. 2. Mean species richness from lowest fire frequency stands ("unburned") versus highest fire frequency stands ("burned") ($n = 6$). Error bars are standard errors. Bars with different letters denote significant differences between unburned and burned stands.

Table 2

Within-group homogeneity from multi-response permutation procedures (MRPP) for understory (a) and overstory (b) grouping schemes with associated *p*-values from Monte-Carlo test^a

(a) Understory			(b) Overstory		
Grouping scheme	Within-group homogeneity (A)	Monte-Carlo test <i>p</i> -value	Grouping scheme	Within-group homogeneity (A)	Monte-Carlo test <i>p</i> -value
Four fire groups	-.028	.895	Four fire groups	.017	.267
Seven site groups	.227	.000	Seven site groups	.000	.489
Three community groups	.120	.000	Four community groups	.166	.000

^a MRPP used the Sorenson distance measure to evaluate within-group homogeneity (A) for three grouping schemes (fire, site, community). (A) Monte-Carlo test generated *p*-values for tested groups compared to 1000 randomly generated groups.

Table 3

Indicator species for understory community groups and associated Monte-Carlo test *p*-values^a

Community group	Scientific name	Common name	Monte-Carlo test <i>p</i> -value
Mesic	<i>Adenocaulon bicolor</i>	Pathfinder	.001
	<i>Angelica</i> spp.	Angelica	.009
	<i>Bromus</i> spp.	Bromus	.018
	<i>Calochortus</i> spp.	Mariposa Lily	.051
	<i>Ceanothus velutinus</i>	Ceanothus (evergreen)	.024
	<i>Moehringia lateriflora</i>	Blunt-leaved Sandwort	.034
	<i>Osmorhiza berteroi</i>	Mountain Sweet-Cicely	.001
	<i>Physocarpus malvaceus</i>	Mallow Ninebark	.005
	<i>Rubus parviflorus</i>	Thimbleberry	.004
	<i>Symphoricarpos albus</i>	Common Snowberry	.003
	<i>Vicia</i> spp.	Vetch	.046
Xeric	<i>Apocynum androsaemifolium</i>	Spreading Dogbane	.014
	<i>Balsamorhiza sagittata</i>	Arrow-leaved Balsamroot	.001
	<i>Centaurea maculosa</i>	Spotted Knapweed	.032
	<i>Ceanothus sanguineus</i>	Red-stemmed Buckbrush	.038
	<i>Festuca idahoensis</i>	Idaho Fescue	.049
	<i>Lupine</i> spp.	Lupine	.039
High-elevation	<i>Arctostaphylos uva-ursi</i>	Kinnikinnick	.040
	<i>Calamagrostis rubescens</i>	Pinegrass	.006
	<i>Shepherdia canadensis</i>	Canada Buffaloberry	.040
	<i>Vaccinium globulare</i>	Mountain Huckleberry	.009

^a See Section 2 for analysis details.

failed to produce larger within-group agreement than grouping by site (Table 2a). With the exception of two sites, MB and MC, all stands within a site were classified in the same understory group. Correlations of environmental variables with the NMS ordination plot (not shown) indicated that the high elevation community group was indeed correlated with higher elevations and the mesic community group was associated with higher NH_4^+ and higher species richness than the xeric community group. There was no significant correlation with time-since-fire.

3.2. Overstory

When averaged across all sites, unburned stands had significantly higher ($p \leq .05$) total tree densities and Douglas-fir densities than burned stands (Fig. 3). Total basal area and Douglas-fir basal area was also higher in unburned stands, but differences were not statistically significant (Fig. 4). Grand fir was abundant in unburned stands at two sites (LC and BR)

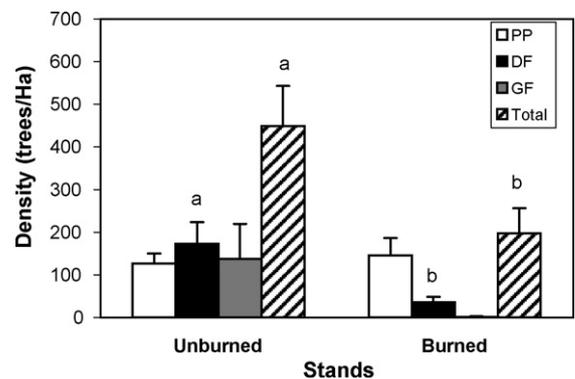


Fig. 3. Mean tree densities for ponderosa pine (PP), Douglas-fir (DF), grand fir (GF) and total tree density (total) in the lowest fire frequency stands ("unburned") versus highest fire frequency stands ("burned") ($n = 6$). Error bars are standard errors. Bars with different letters denote significant differences between unburned and burned stands within a category.

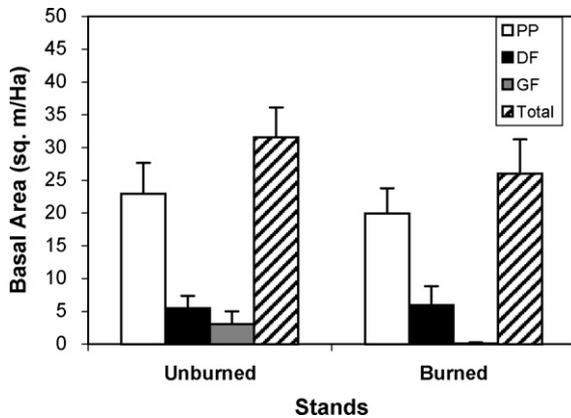


Fig. 4. Mean basal areas for ponderosa pine (PP), Douglas-fir (DF), grand fir (GF) and total tree density (total) in the lowest fire frequency stands (“unburned”) versus highest fire frequency stands (“burned”) ($n = 6$). Error bars are standard errors. There were no significant differences between unburned and burned stands within a category.

but when averaged across all sites, differences were not statistically significant.

In the multivariate analyses, grouping by site produced slightly higher within group homogeneity than grouping by fire history, but neither grouping scheme was statistically significant (Table 2b). An optimal community grouping scheme was generated by TWINSPAN. Table 4 lists indicator species/size-classes in the overstory groups generated and the associated p -values from the Monte-Carlo test for each species/size-class. Four groups with a total of 10 indicator species/size classes with p -values under 0.05 were found. The four groups were characterized as (1) ponderosa pine-small, (2) ponderosa pine-large, (3) mixed (ponderosa pine/Douglas-fir), and (4) grand fir. General descriptions of these groups are included in Table 4. Table 2b shows this community grouping scheme produced larger within group agreement than grouping by site or fire history.

Table 4
Indicator species/size classes for overstory community groups and associated Monte-Carlo test p -values^a

Group	Group description	Species	Size class (cm)	Monte-Carlo test p -value
Ponderosa pine-small (PIPO-sm)	Stand is dominated by ponderosa pine in practically all size classes. More pine in smaller size classes than in larger	Ponderosa pine	10	.004
		Ponderosa pine	20	.008
		Ponderosa pine	30	.004
		Ponderosa pine	40	.015
Ponderosa pine-large (PIPO-lg)	Stand is dominated by ponderosa pine in practically all size classes. More pine in large size classes than in smaller	Ponderosa pine	>60	.029
Mixture of pine and fir (PSME)	Mixed dominance in large size classes, Douglas-fir dominant in smaller size classes.	Douglas-fir	10	.025
Grand fir (ABGR)	Grand fir dominant in small and medium size classes. Ponderosa pine or grand fir dominant in large size classes	Grand fir	<5	.004
		Grand fir	10	.013
		Grand fir	20	.013
		Grand fir	30	.021
		Grand fir	40	.001

^a See Section 2 for analysis details.

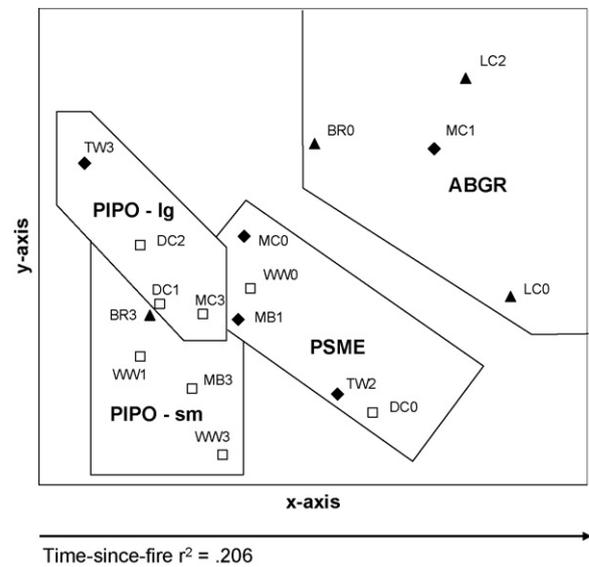


Fig. 5. Non-metric dimensional scaling (NMS) ordination of stands based on overstory structure data (species in size-classes) with overstory groups overlaid in boxes (labeled) and understory groups overlaid with symbols ((♦) mesic; (□) xeric; (▲) high elevation). Ordination explained 71.4% of variance in original data and was rotated so that time-since-fire correlated with x -axis. Sorenson distance measures were used. Understory and overstory groups are described in Tables 3 and 4.

The NMS ordination for the overstory is shown in Fig. 5 with the overstory groups overlaid with boxes and the understory groups overlaid as symbols. This ordination explained 71.4% of the variation in the original overstory data. The ordination was rotated such that the x -axis correlated positively with time-since-fire ($r^2 = .206$), and thus could be used to roughly locate stands on a gradient from early to late succession. The four overstory groups show a gradual transition from stands dominated by early succession species (ponderosa pine) to stands dominated by later succession species (Douglas-fir, grand fir), with some overlap between groups. Forest floor total

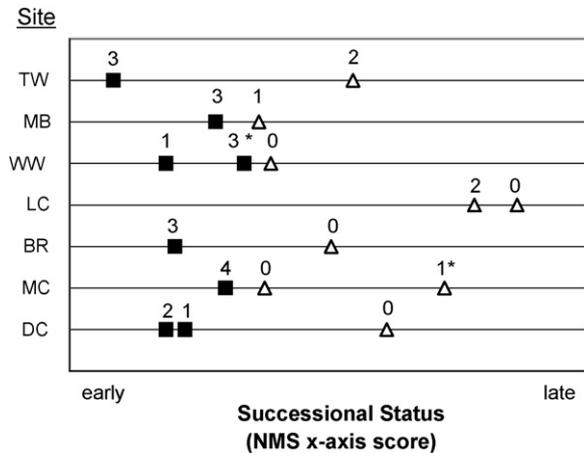


Fig. 6. Successional status (early to late) of stands within sites inferred from NMS x -axis scores based on overstory species/size class data. Numbers above symbols refer to # of burns associated with that stand. (■) are stands classified into one of two early succession overstory groups (PIPO-sm, PIPO-lg). (△) are stands classified into one of two late succession overstory groups (PSME, ABGR). See Table 4 for further description of overstory groups. Stands with elevation and/or aspect greatly different from other stands at the same site are flagged with an asterisk.

N also correlated positively with the x -axis ($r^2 = .319$). There were no strong y -axis correlations with any environmental or soil variable.

Fig. 6 plots overstory NMS x -axis scores for all stands at every site. The NMS x -axis alone explained 51.5% of the variation in the original overstory data. Time-since-fire correlated with the NMS x -axis, and overstory community groups separated along this axis. Therefore, Fig. 6 can be used to compare successional status between stands within sites, much the way successional vectors would be used in an ordination plot. Locations and relative distances along the axis in Fig. 6 relate to degree of difference between stands in overstory structure with early succession characteristics (ponderosa pine) low on the axis, grading into late succession characteristics (Douglas fir, grand fir) higher on the axis. Numbers above symbols in Fig. 6 refer to the number of burns associated with that stand. Filled squares are stands that were classified by TWINSpan and Indicator Species Analysis into one of two early succession groups, while open triangles are stands classified into one of two late succession groups (see Table 4). Two stands marked with an asterisk (WW3 and MC1) are stands that differed significantly in both aspect and elevation from the other stands in their respective sites (see Table 1).

3.3. Overstory/understory relationships

Fig. 5 allows examination of the relationship between overstory and understory groups. Six out of the eight stands where the understory was classified as xeric (open squares in Fig. 5) were classified into one of the two early succession overstory groups. Similarly, four out of five stands where the understory was classified as mesic (closed diamonds in Fig. 5) were classified into one of the two later succession overstory

groups. A χ^2 -test revealed these understory-overstory associations to be marginally significant ($p = .057$).

4. Discussion

In this study, we collected data over a broad geographical area in forests representative of the complex, mixed-severity fire regime in the inland Northwest where current knowledge is limited (Schoennagel et al., 2004). Our study focused on effects due to absence of fire, ruling out effects related to prior logging, and avoiding uncertainties associated with using reconstructions of past conditions as a basis for inferring changes. We have addressed a critical need for study of long-term effects resulting from recurrent natural wildfire versus no fire, rather than short-term responses to experimental fire (Van Mantgem et al., 2001).

Consistent understory community or plant functional group responses related to fire exposure were not apparent in our results. NMS ordination results for the understory (not shown) and the MRPP results (Table 2a), suggest that site-influences in general, and elevation in particular (based on NMS correlations and the understory community grouping scheme), were more powerful drivers of plant community composition than fire exposure. Significant short-term understory responses directly following fire have been documented in other ponderosa pine forests, but effects appear to be very site-specific and without a general pattern (Merrill et al., 1980; Armour, 1984; Bock and Bock, 1984; Covington and Moore, 1994a,b; Metlen et al., 2004; Wienk et al., 2004; Laughlin et al., 2004). Studies of long-term effects of fire exclusion on the understory are rare (but see MacKenzie et al., 2004), however there is evidence that at greater time and spatial scales, environmental factors and spatial variability are stronger forces than fire in shaping the understory community (Gildar et al., 2004). At the scale of our study, it appears that site-to-site variation in understory community composition masked any consistent fire-related responses.

On the other hand, overall species richness was higher in unburned stands than in burned stands (Fig. 2). This finding contradicts the general view that plant diversity decreases with advancing succession during periods of fire exclusion (Keane et al., 2002; Covington and Moore, 1994b). However, reported decreases in diversity related to lack of fire were comparisons with short-term responses to single fires (Wienk et al., 2004). In the Southwest, measuring longer term trends in reference stands, Laughlin et al. (2004) found lower species richness in an unburned stand, but this effect was not duplicated at another nearby unburned stand (Gildar et al., 2004). Our results indicate that over long time periods the presumed general effect of increasing understory species richness with frequent fire (Covington and Moore, 1994b; Keane et al., 2002) may not hold.

Higher species richness in unburned stands may be related to differences in plant available N. We found higher rates of nitrification in frequently burned stands (DeLuca and Sala, 2006). In addition, the mesic understory community group was associated with higher NH_4^+ , higher species richness, and late

succession overstory. It is possible that more uniform availability of mobile NO_3^- is driving species richness down in frequently burned stands. Likewise, patchy availability of relatively immobile NH_4^+ coupled with plant specialization for uptake of NH_4^+ and organic nitrogen may drive richness up in unburned stands (Gundale et al., 2005).

Note that very few studies have looked at understory diversity responses to fire in unlogged stands. It is possible that the disturbance of prior management may interact with the disturbance of fire to produce higher species richness by favoring colonizer plant species in managed forests that have burned. In unlogged forests, this interaction would be absent and other factors associated with lack of fire (patchy N or light availability in the understory) may increase richness by creating new niches for different species in unburned stands. Our results clearly point to the need for further study of understory plant community responses to long-term fire regime change in natural forest settings, and suggest that generalizations from short-term studies or studies in managed forests may not apply to natural forests.

There was a general pattern of xeric understory communities associated with ponderosa pine dominated overstory, and mesic understory communities associated with mixed, Douglas-fir, or grand fir dominated stands (Fig. 5). These associations may be simply correlated responses in both the overstory and understory to local environmental conditions. However, none of the environmental or soil chemistry variables measured in this study can clearly explain the association. Changes in the overstory related to absence of fire may indirectly affect the understory by increasing shade, altering soil moisture, or altering forest floor litter quality and composition (MacKenzie et al., 2004). These effects may not have been strong enough to be detected as direct understory responses related to number of burns. Although understory responses were not dramatic, the species richness response (Fig. 2) and the weak association between overstory and understory (Fig. 5) suggest that long-term fire frequency effects on the understory may not be entirely absent.

In the overstory, our results show increases in overall tree density and density of shade-tolerant, late succession tree species in unburned stands compared to burned stands (Fig. 3). A shift in forest structure and composition to higher densities of shade-tolerant, late succession tree species is perhaps the most extensively documented effect of fire exclusion in fire-adapted forests (Keane et al., 2002). Previous studies in northwestern PP/DF forests have found densities of shade-tolerant species to increase three- to five-fold with fire exclusion (Habeck, 1994 and Arno et al., 1995b as cited in Keane et al., 2002). Gildar et al. (2004) reported a roughly three-fold increase in overall tree density with fire exclusion in a study using reference stands in the Southwest. Averaged across our entire study, densities of combined shade-tolerant overstory species (Douglas-fir and grand fir) were considerably higher in unburned stands versus burned stands (Fig. 3). However, looking at individual sites and using the three- to five-fold increase as a standard of comparison, four sites in our study had higher inferred increases in shade-tolerant overstory species, two sites had

lower increases, and one site was within the range (data not shown). Our results confirm the general shift to higher densities of shade-tolerant tree species with absence of fire. However, the magnitude of this shift may be more variable across landscapes than what has been reported in other studies. Basal areas for total tree and shade-tolerant tree species were only moderately higher in unburned stands and differences were not statistically significant (Fig. 4). The magnitudes of inferred basal area increases for total trees and for shade-tolerant species were similar to increases reported by Arno et al. (1995b, 1997) in unlogged stands using reconstructed stand structure.

While increases in densities of shade-tolerant tree species may be a predictable trajectory of succession following exclusion of fire, Fig. 6 shows that sites exposed to the same number of fires had different overstory structure, and that rates of change due to lack of fire varied from site to site. These results suggest that forest structure and composition at a given moment in time may be difficult to relate to any specific fire frequency or time-since-fire. Outlier stands at two sites (WW3 and MC1) point to the possibility that differences in aspect or elevation may be responsible for site-specific successional responses to fire. However, topographic variables in the overstory NMS ordination did not correlate with community structure along the axis relevant to succession, suggesting no consistent effect of topography on forest structure. Preexisting differences in forest structure and composition between sites, coupled with differences in the severities of 20th century fires (see Keane et al., 2002), are likely factors in site-to-site variation in successional changes.

The study of recurrent wildfire versus fire exclusion presents notable statistical challenges (Van Mantgem et al., 2001). Because treatments are natural wildfires rather than experimental fires, randomization and independence of plots within treatments, and replication of treatments across sites is not possible. This would normally prevent generalization of results beyond a given site. This limitation was anticipated and addressed by selecting a relatively high number of sites (7) across a broad geographical area. However, this remedy had its own costs. Namely, conducting a study of this scale at remote sites in rugged terrain necessarily precluded extensive sampling at each site. For this reason, findings of no difference in understory species composition between stands should be viewed as suggestive rather than conclusive.

The use of reference stands as chronosequences requires addressing the possibility that measured differences between stands, and variability in general may be due to inherent environmental differences between stands. Rollins et al. (2002) found that fires in the Selway-Bitterroot Wilderness were more likely to occur on dry, western and southwestern aspects between elevations of 1000 and 1700 m elevation. This pattern raises the possibility that physiographic conditions drive fire frequency patterns across the landscape, and that these environmental differences between stands may confound plant community structure and composition differences otherwise attributable to fire. However, across our study, there were no systematic significant differences between burned and unburned stands in any physiographic variable (elevation,

aspect, slope, heat-index). Therefore, measured differences in stand structure and species richness are more likely a result of lack of fire than site environmental characteristics.

Because fire history before 1880 was not available for these sites at the time of our study, we cannot be certain that disturbance history prior to 1880 was similar for all stands within a site. Older fire histories would clarify whether 20th century fire frequency differences between stands is a recent phenomenon, akin to a “treatment”, rather than a persistent historical characteristic of the site. At one site (MB) where a detailed fire-scar analysis was conducted in 2005 (E. Heyerdahl, J. Riser, Fire Sciences Laboratory, USFS; unpublished data) results showed that the unburned stand experienced much higher fire frequencies prior to the 20th century. This evidence, plus the lack of any consistent physiographic differences between stands that would create intrinsically determined fire behavior, leads us to believe that fire frequency differences during the 20th century, and not pre-1880 fire histories, are responsible for the conditions at these sites. Further investigation is needed to clarify the relationship between prior fire history and contemporary fire behavior in PP/DF forests.

This study points to the need for continued research and cautious approaches to management of northwestern ponderosa pine forests. Our findings suggest that even within the relatively coherent PP/DF forest type, fire and absence of fire produce variable effects in the understory and different rates of successional change in the overstory across varied landscapes. Our study supports other recent research that cautions against specific targets for forest structure in restoration treatments (Allen et al., 2002), and underscores the importance of natural variability and heterogeneity in ponderosa pine forests (Schoenagel et al., 2004), especially in the complex, mixed fire-regime forests of the Northwest (Arno, 1980). Where possible, management approaches should be site-specific (Gildar et al., 2004). However, because of the difficulty in obtaining historical information at all locations, management may need to emphasize restoration of natural ecological processes, especially fire, rather than specific stand conditions. (Allen et al., 2002). Although some managed stands may require structural manipulation before fire can be reintroduced, restoration treatments should be guided by studies that separate fire exclusion from other anthropocentric impacts such as logging and grazing, and should take into account inherent spatial variability, even in forests with a long history of intensive management.

In addition to providing results reported here, research sites established in this study could be important for future research. Reference stands can provide before-disturbance data useful for studying later disturbance effects (Van Mantgem et al., 2001; Laughlin et al., 2004). The establishment of natural reference stands should prove valuable as benchmarks for future research as fire, fire exclusion, and global change continue to alter natural forest communities.

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