
Tree-Growth and Understory Responses to Low-Severity Prescribed Burning in Thinned *Pinus ponderosa* Forests of Central Oregon

Matt D. Busse, Steven A. Simon, and Gregg M. Riegel

ABSTRACT. The growth of ponderosa pine and associated understory vegetation was evaluated for a 6 yr period following spring underburning of surface fuels. Underburn and control (unburned) plots were paired at 15 replicate sites in pole-sized ponderosa pine forests of central Oregon. The burns were generally low in severity, as noted by low O horizon mass reduction (24%) and tree mortality (6%). A small but significant decline in basal area and volume growth rates of surviving trees was found in the 6 yr following underburning. The reduction in tree growth was related to a combination of crown length reduction, O horizon reduction, and site productivity. More productive stands had the highest proportional reduction in growth due to burning. By comparison, site conditions including stand density, initial basal area, elevation, parent material, and soil fertility were not related to the observed growth reduction. Understory vegetation showed a mixed response to burning. Shrub cover, dominated by *Purshia tridentata*, declined significantly following burning and remained well below preburn levels for the length of the study, even though one-fourth of all burned *Purshia* plants successfully resprouted. Total herbaceous vegetation cover and production were unaffected by burning, while species diversity increased slightly. With the exception of the decline in *Purshia* cover, the results indicate that low-severity prescribed burning has a relatively minor impact on tree-growth and understory response in thinned ponderosa pine stands. *FOR. SCI.* 46(2):258–268.

Additional Key Words: Ponderosa pine, spring underburning, site productivity, crown scorch, root mortality, *Purshia tridentata*, plant diversity.

The ecological role of fire in central Oregon ponderosa pine forests was recognized as early as the 1940s (Weaver 1943). Wildfire exclusion, which began shortly after the turn of the century, had already contributed to excessive fuel accumulation, overstocked stands, and tree stagnation in forests which experienced low-intensity surface fires every 4 to 24 yr during the previous 2 centuries (Bork 1985, Miller and Rose 1999).

Reducing fire hazard, while potentially improving stand growth, was an argument for prescribed fire in ponderosa pine forests. Since the initial observation by Weaver, however, application of prescribed fire as a management tool has not been widespread. Public concern for air quality and wildlife habitat, budget considerations, and the availability of alternative silvicultural methods to reduce both fuel and stocking levels contributed to the

Matt D. Busse, USDA Forest Service, Pacific Southwest Research Station, 2400 Washington Ave., Redding, CA 96001—Phone: (530) 242-2456; Fax: (530) 242-2460; E-mail: mbusse@c-zone.net. Steven A. Simon, USDA Forest Service, 160 Zillicoa St., Asheville, NC 28801—Phone: (704) 257-4810; E-mail: ssimon/r8,nc@fs.fed.us. Gregg M. Riegel, USDA Forest Service, Area Ecology Program, 1645 Highway 20 E., Bend, OR 97701—Phone: (541) 383-5423; E-mail: riegel/r6pnw.deschutes@fs.fed.us.

Acknowledgments: We are grateful to the Fremont National Forest for their generous assistance in locating study sites, conducting the burns, and collecting fire-behavior data, and to Chuck Graham and Dick Johnson for their commitment in supporting this research. We thank Bill Johnson, Peter Sussman, Richard Stubbs, Paul Cooler, and Lew Nelson for their technical assistance. We also thank Robert F. Powers, Sara Lovtang, and four anonymous reviewers for their constructive suggestions, which led to considerable improvements to this manuscript.

Manuscript received January 26, 1999. Accepted September 15, 1999.

This article was written by U.S. Government employees and is therefore in the public domain.

limited use of prescribed fire. In addition, fuel moisture requirements for first-entry ignition and unpredictable seasonal weather often created logistical hurdles, restricting the window for safe surface fires.

Recent region-wide assessments have refocused attention on the role of prescribed fire to reduce fuel buildup and catastrophic fire hazard in western forests (Sierra Nevada Ecosystem Project 1996, USDA Forest Service 1997). van Wagendonk (1996) compared the relative effectiveness of several fuel treatments, including fuel breaks, prescribed burning, biomass removal, pile and burning, and cutting and scattering, on wildfire spread. Using a deterministic fire model, he found prescribed burning was the most effective method to reduce wildfire spread. Use of prescribed fire in combination with other silvicultural techniques such as partial cutting has also been recommended for forest restoration and maintenance (Weatherspoon 1996).

How ponderosa pine will respond to first-entry prescribed fire is difficult to predict. Conclusions from previous fire-effects studies have been conflicting, largely due to differences between studies in stand density and age, fire intensity and severity, season of burn, geographic location, and climate (Morris and Mowat 1958, Wyant et al. 1983, Grier 1989, Sutherland et al. 1991, Swezy and Agee, 1991, Landsberg 1992). Prescribed fire is credited with an array of effects, including reductions (Grier 1989, Landsberg 1992), increases (Van Sickle and Hickman 1959, Wyant et al. 1983), and minimal long-term change (Sutherland et al. 1991) of ponderosa pine growth. Variability in response to fire is also noted for many understory plants (Noste and Bushey 1987). *Purshia tridentata*, for example, a dominant understory species in central Oregon, is considered a fire intolerant shrub (Hormay 1943, Billings 1952) even though it evolved in a region where fire burned at frequent intervals historically. The low intensity and severity of historic fires, in combination with livestock grazing from 1880 through the early 1920s, which reduced competition from graminoid species, were crucial to the successful establishment of *Purshia*. Wildfire exclusion has since increased the dominance of *Purshia* in central Oregon (Sherman and Chilcote 1972). Whether *Purshia* responds successfully following prescribed fire, however, depends on its unpredictable ability to resprout at the basal crown (Driscoll 1963, Nord 1965, Martin 1983, Martin and Driver 1983) or to germinate from rodent seed caches (West 1968, Sherman and Chilcote 1972, Martin 1983, Vander Wall 1994).

Once used inconsistently, prescribed fire is now a primary tool to reduce hazardous fuel conditions in ponderosa pine forests in central Oregon. Our objectives were to determine the effects of first-entry prescribed fire on ponderosa pine and understory vegetation growth, and to identify site characteristics and burn conditions related to changes in vegetation production and composition. We intended to develop a unifying theme of vegetation response to low-severity burning in central Oregon ponderosa pine forests by utilizing a wide geographical range of burn sites and forest conditions.

Materials and Methods

Study Area

The study sites are located within the ponderosa pine forest type on the Fremont National Forest in southcentral Oregon (Figure 1). An aggressive fuels program began on the National Forest in 1985, and has since averaged 6,000 ha burned annually in the targeted area (unpublished data on file, Fremont National Forest). Fifteen replicate study sites, located in thinned, second-growth ponderosa pine stands, were selected to provide a wide geographical distribution and a range of plant community types and fuel conditions. Soils developed from two dominant parent materials: (1) pumice from the eruption of Mount Mazama about 7,700 calendar years B.P., and (2) residual basalt, rhyolite, or pyroclastics. The pumice soils are moderately deep (0.8 to 1.5 m) and the surface horizon textures are loamy sands. Surface horizon textures of the residual soils are sandy loams or loams. All sites are on flat or gently sloped (5-18 %) landscapes, and, consequently, no criteria or restrictions were made for aspect during site selection. The moisture regime is xeric, ranging from 38 to 89 cm of annual precipitation among sites, mainly as snow. Mean maximum temperature is 27.7°C in July and 4.4°C in January.

Experimental Design

Two treatments (burn and control—no burn) were arranged as paired plots at each of 15 sites (Figure 1). Paired plots were selected with the objective of attaining similar stocking, fuel loads, and vegetation composition and cover. Stand conditions for each plot, measured prior to treatment, are listed in Table 1. Paired plots were separated by a 50 m buffer (minimum), and treatments were randomly assigned to the plots. Plot sizes ranged from 0.1 to 0.2 ha, depending on stocking level required to provide a pretreatment minimum of 30 trees per plot. All burns were completed in the spring under prescriptions that matched the standards of the Fremont NF natural fuels program of 25–33% reduction in fine fuel (0–2.5 cm diameter wood) and average flame lengths of 0.15 to 0.30 m. Five plots were underburned in 1988, nine plots in 1989, and one plot in 1990.

Fire Behavior and Fuel Measurement

Air temperature, relative humidity, wind speed, flame length, and rate of spread were measured during underburning. Moisture content of downed wood (2.5–7.6 cm diameter) was determined prior to ignition. Downed-wood mass was measured using the planar intersect method (Brown 1974) both at the end of the growing season prior to treatment and within 30 d following underburning. O horizon depth was measured at 2 m intervals along four, 20 m transects per plot in the fall prior to underburning and immediately following underburning to determine O horizon reduction. Bulk density (Mg m^{-3}) of the O horizon was determined using a composite of five, 0.25 m² samples from each plot in order to convert O horizon depth to a mass basis.

Tree Growth

Diameter at breast height (*D*) was measured prior to treatment on all trees > 5 cm *D* to determine initial basal area.

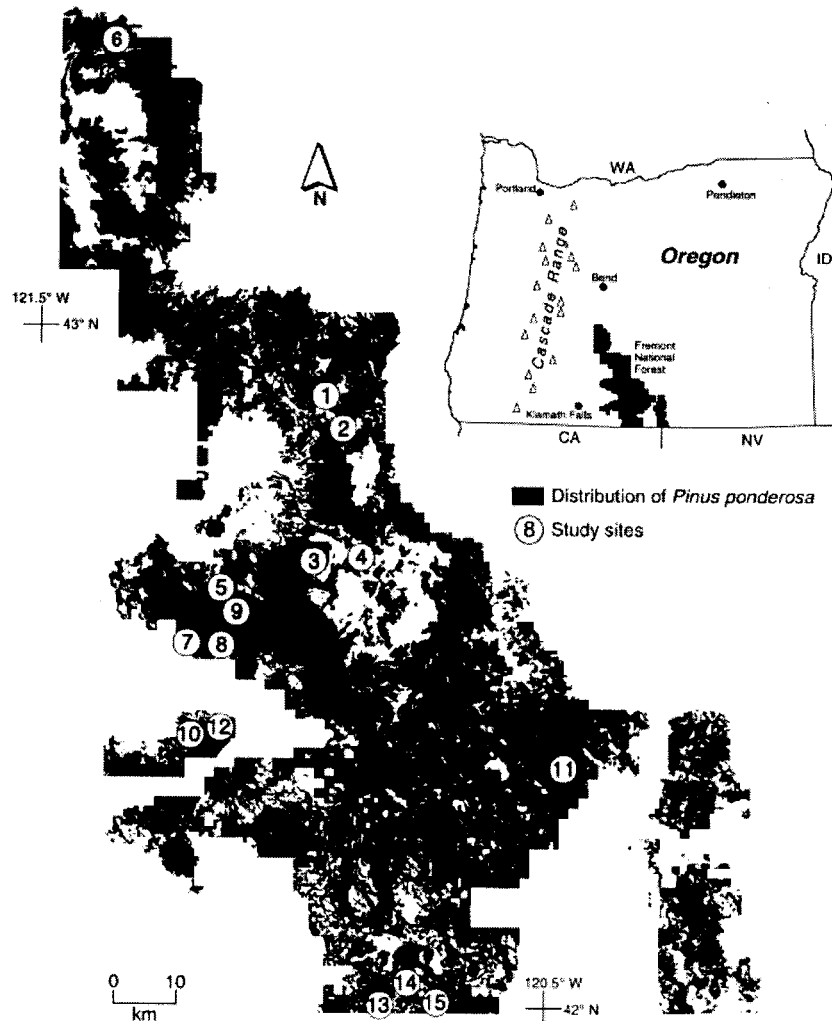


Figure 1. Distribution of ponderosa pine-associated forest types on the Fremont National Forest and location of study sites.

Table 1. Pretreatment stand characteristics and date of burn for paired plots located on soils developing from pumice or residual parent material. Site number corresponds to the location indicated in Figure 1.

Site	Dominant understory species ^a	Elevation (m)	Age (yr)	Site index ^b (m)	Density		Mean stem diameter		Basal area		Burn date
					Burn	Control	Burn	Control	Burn	Control	
				 (trees ha ⁻¹) (cm) (m ² ha ⁻¹)		
Pumice											
1	FEID, PUTR	1,713	81	24.4	465	612	28	30	32.5	48.8	4/88
2	FEID, PUTR	1,631	86	27.4	440	346	24	24	22.0	17.9	4/88
3	FEID, PUTR	1,695	57	18.3	427	427	18	18	13.0	12.8	4/89
4	FEID, PUTR	1,676	70	18.6	254	247	23	24	11.1	11.9	4/89
5	FEID, PUTR	1,689	75	30.4	415	474	27	29	26.3	36.0	4/90
6	CELE, FEID, PUTR	1,396	80	19.2	514	504	22	20	22.5	18.4	4/88
7	ARPA, FEID, PUTR	1,472	53	26.8	208	266	26	24	11.4	12.1	4/89
8	ARPA, FEID, PUTR	1,390	67	23.5	153	178	27	26	8.5	9.6	4/89
9	CEVE	1,579	64	25.9	198	163	24	24	10.2	7.6	6/89
Residual											
10	FEID, PUTR	1,477	53	19.2	435	504	22	21	17.6	19.3	4/88
11	FEID, PUTR	1,591	67	23.8	296	291	23	24	14.7	14.5	5/88
12	WYMO	1,336	76	26.2	267	346	33	31	23.6	29.0	4/89
13	WYMO	1,606	57	21.3	524	623	22	21	20.2	24.4	4/89
14	WYMO	1,643	80	22.3	316	504	28	27	20.8	30.2	5/89
15	WYMO	1,585	70	26.2	662	376	22	24	27.6	18.3	5/89

^a FEID = *Festuca idahoensis*; PUTR = *Pursia tridentata*; CELE = *Cercocarpus ledifolius*; ARPA = *Arctostaphylos patula*; CEVE = *Ceanothus velutinus*; WYMO = *Wyethia mollis*.

^b 100 yr basis (Barrett 1978).

In each plot, 11 to 15 trees were randomly selected to determine height (H) and age. Tree height was measured using an optical dendrometer. The relationship between H and D was determined by the equation,

$$\ln H = a + bD \quad (1)$$

where a and b are the regression coefficients determined for each plot. Cubic volume (V) for boles, including stump and tip, was then determined for those trees with measured heights using the equation,

$$V = 0.005454 * H * F * (D - B)^2 \quad (2)$$

where F is a cylindrical form factor determined by D and H (DeMars and Barrett 1987), and B is the double bark thickness defined as a function of D (DeMars and Barrett 1987). The relationship between D and V was then determined by the equation,

$$\ln V = c + d(\ln D) \quad (3)$$

where c and d are the regression coefficients determined for each plot based on 11 to 15 trees. Height and V of the remaining trees were then estimated by Equations (1) and (3). In October 1992, tree D was remeasured on all trees, and H was remeasured on the same 11 to 15 trees per plot that were measured prior to treatment. Periodic annual increment (PAI; growth divided by number of growing seasons) for basal area, height, and volume was determined using only those trees that were alive at the end of the growth period.

Live crown lengths were measured with a clinometer on all trees in the fall prior to underburning and at the end of the first growing season after treatment. Percent crown length reduction was determined from the weighted average (by height) of all trees on a plot. The weighted average was used because of the range of tree heights within a plot, and was calculated by dividing the preburn crown length of an individual tree by the preburn crown length for the tree of average height.

Understory Vegetation Measurements

Percent cover of individual shrub, graminoid, and forb species were determined ocularly in 1987, 1988, 1990, and 1993 using 20 microplots (1.0 × 1.0 m), systematically located along two transects between the diagonal corners of each plot. Species richness (number of species present) and diversity (Shannon Diversity Index; Magurran 1988) were calculated for herbaceous plants found within the microplots. Species nomenclature follows Hitchcock and Cronquist (1973). Herbaceous plants were clipped to the top of the litter surface in July 1993 to determine total aboveground biomass. Biomass samples were collected from 10 systematically located microplots (0.6 × 0.6 m) and dried for 72 hr at 60°C prior to weight determination. Fire-induced sprouting of *Purshia* plants was quantified within five subplots (6.4 × 6.4 m) per plot at a maximum of 50 days after burning. Plants were aged by destructive sampling at the surface of the mineral soil and counting of annual growth rings. Sprouting success was remeasured at the end of the fifth growing season on all remaining plants.

Mineral Soil Analyses

Composite samples (four random subsamples per plot) were collected from 0–10 cm depth. Collection dates included (1) within 7 days prior to underburning, (2) at the end of the first growing season after underburning, and (3) in fall 1992. All samples were sieved, air-dried, and analyzed for total C (Walkley-Black); total N (Kjeldahl); P (Bray); mineralizable N (anaerobic incubation); pH; cation exchange capacity CEC; and extractable K, Ca, Mg, and Na by Oregon State University Soil Testing Laboratory, Corvallis, OR.

Statistical Analyses

Differences between treatment means in basal area PAI, height PAI, and volume PAI were tested with analysis of covariance (SAS Institute Inc. 1988), using pretreatment basal area and stand density as covariates. Identification of site characteristics and underburn conditions associated with tree growth response following burning was made using Pearson's correlation coefficient test. Characteristics with significant correlation coefficients ($P < 0.10$) were then used as independent variables in multiple linear regression analysis to determine the overall correlation with tree growth. A variance inflation factor of 4.0 was used to test for multicollinearity and ensure that the independent variables were not highly correlated or redundant.

Herbaceous cover and soil nutrient responses to underburning were tested using repeated measures analysis (SAS Institute Inc. 1988), and were considered significant if (1) no pretreatment differences between paired plots were found using the least significant difference test, and (2) a time × treatment interaction was found. The response of aboveground biomass of herbaceous plants to underburning was tested using one-way analysis of variance. All data for statistical comparisons were found normally distributed, and differences between treatments were considered significant at $P < 0.10$.

Results

Fire Behavior and Intensity

Flame length, fire-line intensity, and fuel reduction were quantified on 14 out of 15 plots (data from site 5 was missing). Average flame length was 0.26 m, with a range from 0.15 to 0.46 m. Corresponding fire-line intensities averaged 13.9 kW m⁻¹, with a range from 4.2 to 48.0 kW m⁻¹. Combined woody fuel and O horizon mass was reduced an average of 23.4 Mg ha⁻¹ by underburning (Table 2), with more than two-thirds of the mass loss accounted for by consumption of wood > 7.6 cm diameter. Reduction in O horizon mass was low (< 30% of preburn level) at all sites with the exception of two (sites 9 and 11), which both had > 60% reduction in O horizon mass. Exposed mineral soil increased significantly from 12 ± 2.4% (SE) at preburn to 19 ± 3.6% immediately following underburning ($P = 0.029$).

Crown Reduction and Tree Mortality

Underburning resulted in an average crown length reduction of 13.7 ± 2.7%, with a range from 2.5 to 37.1% for

Table 2. Preburn and postburn fuel mass and percent reduction by fuel type. The values are means (standard error) of 14 sites.

	O horizon	Wood diameter (cm)			Total
		0–2.5	2.5–7.6	>7.6	
Preburn (Mg ha ⁻¹)	21.7 (2.9)	3.1 (0.6)	6.4 (0.8)	26.4 (4.4)	57.7 (8.4)
Postburn (Mg ha ⁻¹)	16.6 (2.7)	1.7 (0.2)	5.2 (0.7)	10.9 (1.2)	34.3 (3.8)
Reduction (%)	24	47	19	59	41

individual sites. Tree mortality was relatively minor between 1987 and 1992. Forty-six out of 709 trees (> 5.1 cm D) were killed by underburning at the 15 sites. Stands declined from an average of 371 trees ha⁻¹ in 1987 to 346 trees ha⁻¹ on underburn plots compared to a reduction from 413 to 405 trees ha⁻¹ on control plots. Trees killed by fire had a smaller mean diameter than surviving trees (16.0 vs. 23.9 cm, respectively). The resulting mortality based on pretreatment basal area of living trees was 3.0% for underburn plots compared to 1.4% for control plots.

Tree Growth

For surviving trees, basal area PAI was reduced 13% and volume PAI was reduced 24% by underburning in comparison with control plots (Table 3). The growth reduction was found unrelated to pretreatment differences in basal area ($P = 0.533$) or stand density ($P = 0.878$) between burn and control plots. Three independent variables had a weak, yet significant correlation to tree growth reduction: crown length reduction, O horizon reduction, and site growth potential (Table 4). Correlation coefficients were negative for each variable, indicating that plots with greater average crown length reduction, O horizon reduction, and site potential showed the poorest tree-growth response following fire. When combined in multiple linear regression, the three variables explained 61% of the variance in tree growth ($P = 0.004$; adjusted multiple $r^2 = 0.61$; $n = 15$) and were not highly correlated to each other (variance inflation factors < 2.9).

Soil Nutrients and O Horizon Accumulation

Mineral soil N, P, S, pH, mineralizable N, and CEC were not statistically different between treatment plots prior to burning. Changes in soil chemical properties following underburning were limited to an increase in SO₄-S, a decrease in P, and a small increase in pH and mineralizable N (Table 5). Differences in SO₄-S and P were no longer significant by the fall of 1992. This transient effect resulted in significant time × underburning interactions in repeated measures analysis.

Remeasurement of the O horizon in 1993 showed a slow rate of accumulation following underburning. Pretreatment depths were reached after 5 to 6 yr of litter accumulation (Table 6). No significant differences were found between underburn and control treatments in the annual rate of litter accumulation.

Table 3. Effect of low-severity underburning on basal area, height, and volume periodic annual increment of surviving ponderosa pine. The values are means (standard error) of 15 sites.

Annual growth rate	Burn	Control	<i>P</i> value
Basal area (m ² ha ⁻¹ yr ⁻¹)	0.40 (0.03)	0.46 (0.04)	0.097
Height (m yr ⁻¹)	0.18 (0.01)	0.19 (0.01)	0.393
Volume (m ³ ha ⁻¹ yr ⁻¹)	3.24 (0.70)	4.28 (0.70)	0.078

Understory Vegetation

Total cover of understory vegetation averaged 22 ± 4% prior to underburning, with no significant differences between burn and control plots in either total, graminoid, forb, or shrub cover. The primary effect of burning was a sharp reduction in shrub cover (Figure 2). Shrub cover was reduced more than 50% by burning, whereas control plots showed no change. This response resulted in a significant time × underburn interaction in repeated measures analysis. In contrast, there were no significant effects of burning on either forb or graminoid cover.

Prior to burning, there were no significant differences between treatment plots in percent cover of the dominant understory species (Table 7). Following underburning, both *Purshia* and *Festuca idahoensis* declined significantly and remained below preburn levels for the 5–6 year measurement period. *Purshia* cover declined 79% following underburning, with only a 14% decline for the control treatment by 1993. *Festuca* cover was 44% below its preburn level by the second growing season and 29% below preburn level in the sixth growing season. A 9% increase in *Festuca* was found on control plots during the same period.

At the four sites which had greater than 10% cover of *Purshia* prior to treatment (sites 3, 4, 7, 8), underburning reduced cover from 17% at pretreatment to 3.6% by the fifth growing season after burning. Control plots averaged 21.7% cover at pretreatment and 15.6% cover in the fifth season after treatment. Resprouting of burned plants was moderate: 39% (1297 out of 3348 plants ha⁻¹) had resprouted within two months after burning. By the fifth growing season, 25% of burned plants remained alive. The greatest resprouting success was found for plants younger than 20 yr (51% resprouting). By comparison, only 5% of plants older than 30 yr resprouted.

Total aboveground biomass averaged 120.7 ± 27.1 kg ha⁻¹ for underburn plots and 99.4 ± 26.7 kg ha⁻¹ for control

Table 4. Correlation between reduced stand growth (basal area P.A.I.) following underburning and selected plot characteristics.

Plot characteristic	<i>r</i>	<i>P</i> value
Site factors		
Stand density	-0.048	0.754
Dominant understory vegetation	-0.280	0.311
Growth rate of control plot	-0.562	0.029
Parent material	0.130	0.801
Soil N	-0.212	0.453
Elevation	-0.255	0.359
Underburn characteristics		
Fuel moisture content	-0.142	0.506
Flame length	-0.044	0.875
Year of burn	-0.032	0.913
O horizon reduction	-0.527	0.044
Crown length reduction	-0.566	0.027

Table 5. Selected chemical properties of mineral soil (0–10 cm depth) sampled in the fall prior to spring underburning (preburn), fall immediately following underburning (postburn, year 1), and fall 1992 (postburn, year 4–5).^a

Sampling date	pH	N (g kg ⁻¹)	Min. N	P	S	CEC (cmol. kg ⁻¹)
		(mg kg ⁻¹).....			
Preburn						
Burn	6.3a	1.2a	47a	46a	2.5a	23a
Control	6.3a	1.5a	40a	51a	2.4a	23a
Postburn, year 1						
Burn	6.5a	1.4a	56a	43a	4.9a	23a
Control	6.3a	1.2a	42a	53b	2.4b	21a
Postburn, year 4–5						
Burn	6.4a	1.1a	35a	48a	2.0a	24a
Control	6.3a	1.2a	40a	44a	2.9a	24a
Repeated measures analysis (<i>P</i> value)						
Treatment × sampling date	0.131	0.893	0.216	0.031	0.006	0.971

^a Paired treatment means for each sampling date followed by the same letter do not differ significantly at *P* = 0.10.

plots at peak standing crop in 1993 (Table 8). Graminoid biomass was 33% greater on underburn plots, primarily due to the response of *Sitanion hystrix* and *Carex rossii*. The increase in graminoid production was not significant (*P* = 0.192) due to variation between sites (CV = 48.8%).

Species diversity and richness both increased in the 2 yr period following underburning, while no change was found for control plots (Table 9). The most common species found after burning that were not present in the control plots were *Lupinus caudatus*, *Lathyrus lanszwertii*, *Lomatium triternatum*, *Potentilla glandulosa*, *Paeonia brownii*, and *Epilobium angustifolium*.

Discussion

Tree Growth

The results of our study provide evidence that low-severity prescribed burning slightly reduces growth of thinned, pole-sized ponderosa pine stands in central Oregon. Mean periodic annual increment for basal area and volume both declined as a result of spring underburning. The 15 sites compared in this study were well distributed geographically, and represented a range of stand densities and ages, fuel concentrations, and understory composition common in the ponderosa pine region. All burns were also comparable to the Fremont NF practices of light to moderate fire intensity and severity. Low flame lengths, tree mortality, consumption of organic material, and minimal changes in soil chemical properties confirm the low-severity of these burns. Small, yet measurable growth declines immediately following underburning, therefore, should be anticipated for much of the region.

Previous studies have also documented growth declines in thinned ponderosa pine stands due to single-entry prescribed

Table 6. Depth of O horizon in the fall prior to underburning (preburn), immediately following underburning (year 1), and in fall 1993 (year 5–6). The values are means (standard error) of 14 sites.

Treatment	Preburn	Postburn		Annual increase (cm yr ⁻¹)
		Year 1	Year 5–6	
	(cm).....		
Burn	3.9 (0.4)	2.7 (0.3)	3.8 (0.4)	0.2 (0.1)
Control	4.1 (0.7)	—	5.1 (0.5)	0.2 (0.1)

burning (Grier 1989, Landsberg 1992). Comparison of our results with these studies is tenuous, however, due to differences in burn severity and intensity. For example, Grier (1989) reported reduced wood biomass production following moderate-severity (70% woody fuel reduction) and heavy-severity (93% woody fuel reduction) fires in northcentral Washington. Woody fuel reduction was considerably lower in our study, averaging 50% for all sites. Landsberg (1992) found basal area growth was significantly reduced following burning at four sites in central Oregon. Average flame length and fire-line intensity were 1.5 to 5 times greater in her study than ours, however. Even though no direct comparisons can be made between studies, reduction in growth immediately following initial-entry fire, regardless of burn severity or intensity, is a common theme. Declines in ponderosa pine growth have also been observed following repeated pre-

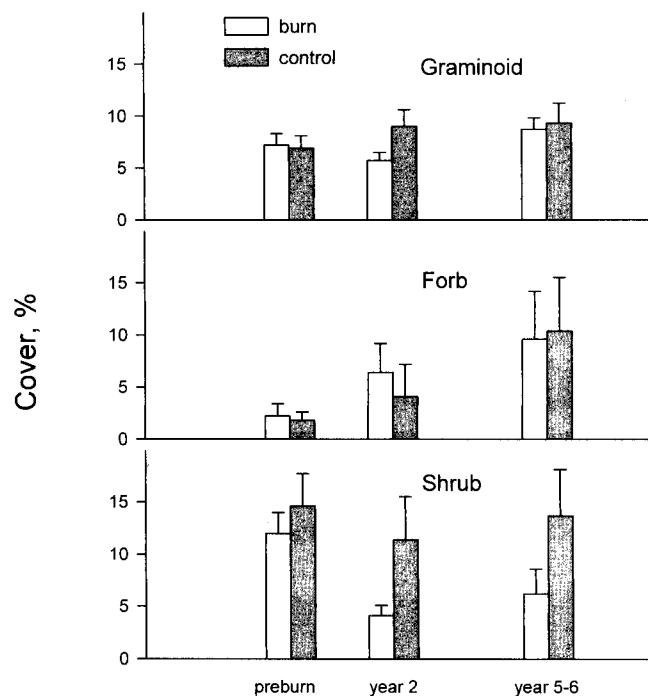


Figure 2. Response of understory vegetation lifeforms to low-severity underburning. Error bars represent one standard error from the mean (*n* = 15).

Table 7. Effect of low-severity underburning on percent cover of dominant understory species.

Species	No. of sites	Cover ^a						P value ^b
		Preburn		Year 2		Year 5-6		
		Burn	Control	Burn	Control	Burn	Control	
<i>Purshia tridentata</i>	8	9.0a	10.9a	1.9b	9.9a	1.9b	9.4a	0.006
<i>Festuca idahoensis</i>	10	5.5a	5.9a	3.1b	6.4a	3.9b	6.4a	0.082
<i>Stipa occidentalis</i>	13	0.3a	0.1a	0.2a	0.1a	0.8a	0.9a	0.666
<i>Sitanion hystrix</i>	14	1.7a	1.6a	1.6a	1.7a	2.5a	1.5a	0.713
<i>Carex rossii</i>	14	1.0a	0.8a	1.3a	0.8a	2.5a	1.6a	0.307

^a Paired treatment means within a row for each sampling date followed by the same letter do not differ significantly at $P = 0.10$.

^b Treatment x sampling date interaction in repeated measures analysis.

scribed burning (Peterson et al. 1994). Their study, conducted in densely stocked ponderosa pine stands in northern Arizona, also identified the confounding effect of fire-return interval on tree response. For example, annual basal area increment declined with 1, 2, 8, and 10 yr return intervals, yet increased unexplainably for 4 and 6 yr return intervals.

Three factors were identified that explained 61% of the variation in tree growth after burning: crown length reduction, O horizon reduction, and site growth potential. The correlation was negative for each factor; sites with more crown scorch, O horizon reduction, and greater site potential yielded the lowest growth rates in comparison to adjacent unburned plots. Of equal interest are several site factors that were found unrelated to tree growth following burning. For example, stand density and dominant understory species both showed a poor relationship to the reduction in tree growth, indicating that the response to fire was consistent for the range of stand densities (153– 662 trees ha⁻¹) and for the major ponderosa pine plant communities found in central Oregon. Clearly, the response of ponderosa pine growth to fire is complex (Peterson et al. 1994). We suspect that additional, unquantified factors such as fire-induced cambial injury and postfire microclimate changes associated with removal of understory vegetation and surface organic matter may also have contributed to the growth decline.

The negative correlation between crown length reduction and tree growth was presumably due to a loss of photosynthetic capacity. This observation is surprising, however, given that crown scorch was low at most sites. Crown length reduction did not exceed 40% at any site, and averaged less than 15% for all sites. In contrast, Wyant et al. (1983) suggest that loss of the lower tree crown during prescribed fire should mimic the effect of pruning by removing the least photosynthetically efficient foliage, with a minimal impact on net growth. Pruning up to 25%

of the total live crown has been shown to have little effect on ponderosa pine growth in central Oregon (Dahms 1954). Our results are contrary and suggest that crown scorch, even from low intensity fires, can reduce tree growth. Crown scorch explained only 32% of the variation in tree growth, however. Alone, crown scorch is a weak predictor of tree growth response after low-severity fire.

We hypothesize that the negative correlation between O horizon reduction and tree growth was a function of fine-root mortality. Increases in O horizon consumption are indicative of higher burn severity and greater heat penetration in the soil profile. Temperatures in the organic and upper mineral soil often surpass the critical range (above 60°C) for root mortality during prescribed fire (Grier 1989, Swezy and Agee 1991, Shea 1993). Shea (1993) observed temperatures between 15 and 100°C in the surface mineral soil during spring prescribed burns at three ponderosa pine sites in central Oregon. Interestingly, Grier (1989) suggested that fine-root mortality was the primary factor responsible for reduced tree growth in an unreplicated, prescribed fire study in northcentral Washington. This conclusion could only be supported by his data for a heavy-severity fire, however, because soil temperatures did not reach 60°C, and there were no obvious differences in fine-root biomass between burned and unburned plots for a moderate-severity fire. Swezy and Agee (1991) found more than 50% mortality of fine roots following a prescribed burn in old-growth ponderosa pine. The fire severity was considerably higher in their study, however, as noted by 37% mortality of overstory pine. Our hypothesis of a direct link between O horizon consumption, root mortality, and, ultimately, tree growth was not tested and requires further attention.

Stands with greater growth, defined by the periodic annual growth of the control plot, were more affected by burning in comparison with less productive sites. This observation contradicts the results of Sutherland et al. (1991) who found that the best growing trees before prescribed fire also performed best after fire. Of the two sites in their study, one was burned in the fall, while records were unavailable for the other. Differences between our studies suggest that the season of year may play an important role in how ponderosa pine stands respond to fire. Root activity is generally greater near the surface in the spring compared to the fall (Grulke et al. 1998). The potential for fine-root mortality and reduced tree growth is greater for spring burns, and may have contributed to the discrepancies between studies.

Table 8. Aboveground biomass production of dominant herbaceous species and lifeforms in 1993, 5 to 6 yr following low-severity underburning.

Species or lifeform	No. of sites	Biomass		P value
		Burn	Control	
<i>Stipa occidentalis</i>	13	5.4	3.2	0.566
<i>Sitanion hystrix</i>	14	20.3	9.3	0.191
<i>Carex rossii</i>	14	11.9	7.2	0.015
<i>Festuca idahoensis</i>	10	71.6	74.7	0.875
Graminoid	14	74.7	56.0	0.186
Forb	14	48.1	51.3	0.845

Table 9. Preburn and postburn herbaceous species diversity and richness indices.

Sampling date	Shannon Diversity Index			Species richness		
	Burn	Control	<i>P</i> value	Burn	Control	<i>P</i> value
Preburn	1.49	1.53	0.697	6.2	7.0	0.275
Postburn (year 2)	1.90	1.57	0.045	10.1	7.1	0.024

We had expected that the reduction in understory vegetation following fire would benefit tree growth by reducing competition for water and nutrients. In fact, Sutherland et al. (1991) included water and nutrient status as independent variables in a general model of post-fire tree growth. There was no apparent benefit from reducing competing vegetation in our study, however. This was likely due to a combination of factors, including the depauperate nature of the understory vegetation and the failure of the burns to produce substantial increases in nutrient availability. Understory vegetation cover averaged only 22% before burning, well below the critical level of 30% cover reported to severely reduce ponderosa pine growth (Oliver 1984).

Prescribed fire has been shown repeatedly to modify soil chemical and biological properties (see Raison 1979 for review). Increases in inorganic and mineralizable N (White 1986, Covington and Sackett 1992, Knoepp and Swank 1993), sulfate concentrations in soil solution (Chorover et al. 1994), along with decreases in microbial activity and biomass (Fritze et al. 1993, Peitkainen and Fritze 1993) are among numerous, well-documented responses. By comparison, the low-severity burns in our study resulted in nominal changes in soil chemical properties, and failed to provide a "flush" of available nutrients for tree growth. Although short-term benefits to plant nutrient availability are expected with higher severity burns, concurrent site nutrient losses due to volatilization can be substantial, particularly for nitrogen (Raison et al. 1985, Monleon et al. 1997). This fact led Jurgensen et al. (1997) to conclude that detrimental losses of site organic matter and nutrients should be avoided by restricting or eliminating the use of high severity prescribed fires in inland Northwest forests.

Finally, we found no evidence to suggest that prescribed fire will have a long-term impact on stand productivity. Changes in both nutrient capital and exposed mineral soil were kept to a minimum, while factors showing the strongest correlation to tree-growth reduction (crown scorch and potential root damage) can be considered ephemeral in nature. Prescribed fire has been shown to produce transient, short-term reductions in tree growth in northern Arizona (Sutherland et al. 1991) and northcentral Washington (Grier 1989) ponderosa pine stands. Indirect evidence from central Oregon, in contrast, suggests that low- to moderate-severity surface fires may have a sustained and negative impact on stand growth: fire exclusion for nearly a century has resulted in increased radial-increment growth of naturally regenerated ponderosa pine stands (Cochran and Hopkins 1991). In addition, Landsberg (1992) found that ponderosa pine growth was reduced for the length of her study (12 yr) following single-entry, prescribed burning in central Oregon. Collectively, these studies underscore regional and local differences in the effects of prescribed fire on ponderosa pine growth, and also highlight our limited knowledge of the long-term impact of prescribed fire.

Small losses in site productivity might be considered an acceptable tradeoff by many forest managers in order to reduce fuel concentrations and wildfire danger. As an alternative, the use of complementary silvicultural techniques, such as thinning, can help avoid a strict reliance on prescribed burning to reduce fuel buildup. Combining the two methods has been suggested as a means to (1) accelerate forests toward a desired structure and composition, (2) reduce undesired fire effects, and (3) lower the risk of losing fire containment (Fiedler 1996, Weatherspoon 1996). Reducing stand density prior to burning also yields a lower rate of fuel buildup and delays the need for retreatment. Reducing the frequency of burning to the upper end of its historic range (every 24 yr in central Oregon, for example) would then encourage the natural decay of organic matter by soil organisms and provide a longer period of recovery for fire-intolerant species such as *Purshia*.

Purshia tridentata

How *Purshia* responds to fire is of concern to forest managers in central Oregon because of its high value as a wildlife browse species (Guenther et al. 1993). *Purshia* is the major constituent of the winter diet of mule deer (*Odocoileus hemionus*), accounting for about 85% of their total annual diet in southcentral Oregon (Gay 1998). In addition, *Purshia* contributes to granivore food source (VanderWall 1994) and soil N accretion (Busse 2000). We found a mixed response by *Purshia* to low-severity burning. Shrub cover declined dramatically following burning and showed little increase in the subsequent 5 to 6 yr. Resprouting from the basal crown was moderately successful, however, suggesting that *Purshia* will recover slowly if browsing and fire disturbance are not excessive. Use of a mosaic prescribed burning pattern, as suggested by Simon (1990), would further benefit *Purshia* recovery by maintaining scattered, unburned plants as a seed source for regeneration, developing a greater range of shrub age classes, and reducing the risk of catastrophic wildfire.

The literature on *Purshia*'s ability to sprout from the basal crown following fire is extensive and often contradictory. Several studies have identified populations capable of sprouting following burning (Blaisdell 1950, Blaisdell and Muggler 1956, Clark et al. 1982, Cook et al. 1994), while studies from the pumice soils of central Oregon and northeastern California have reported infrequent sprouting following fire (Driscoll 1963, Nord 1965, Martin 1983, Martin and Driver 1983). Our results are contrary to the studies in the pumice region as we found 25% of the population sprouted and survived through the fifth growing season after burning. This discrepancy is not surprising given the extreme genotypic and phenotypic variability of the shrub (Winward and Findley 1983), and it emphasizes the site-specific response of *Purshia* to fire.

Additional factors that likely contributed to successful basal crown sprouting in our study include soil moisture

content and plant phenology at the time of burning, low fire intensity and severity, and plant age. Nearly all of our *Purshia* sites (7 out of 8) were burned in early spring when soil moisture conditions were near optimum to limit heat flux to the basal crown and to allow for sufficient growth of sprouts. Phenologically, burning early in the growing season provides greater recovery time for plants with sufficient carbohydrate reserves to sprout and resume photosynthesis (Agee 1993). The low intensity and severity of these burns also implies a reduced level of heat flux to the basal crown. Earlier studies have shown an inverse relationship between fire intensity and severity and the sprouting success of *Purshia* (Blaisdell 1950, Driscoll 1964). Finally, we found plant age influenced the sprouting success of *Purshia*, which agrees with previous findings that plants between 5 to 20–40 yr are most successful at sprouting (Martin and Driver 1983, Simon 1990).

Recovery of *Purshia* following fire also relies on the recruitment of seedlings from rodent seed caching (West 1968, Sherman and Chilcote 1972, Martin 1983, Vander Wall 1994). Successful caches are made in the spaces between shrubs where the litter layer is sparse. While we presume that prescribed fire resulted in increased seed caching by reducing the thickness of the litter layer, our study did not test this. Proof of this hypothesis would be difficult because seedling recruitment is confounded by requirements of sufficient rodent populations and availability of viable seed. Only a 30% reduction to an already thin litter layer (4 cm average) resulted from the low intensity fires, which suggests minimal improvement of conditions for seed caching at our study sites.

Efforts to stimulate *Purshia* stands in central Oregon forests will benefit from optimizing the frequency of prescribed fire. *Purshia* cover and seed production decline as a direct consequence of fire, and have been suggested to take a minimum of 10 yr to reach preburn levels (Riegel, unpublished data), depending on annual precipitation, burn intensity, and residual vegetation. In contrast, fire return intervals greater than 40 yr reduce successful resprouting of burned plants. Thus, a recommended fire return interval between 10 and 40 yr would yield the highest seed production and potential seedling recruitment while still maintaining sprouting capability of the basal crown.

Herbaceous Vegetation

The primary response of herbaceous plants was a slight increase in diversity and a change in the relative dominance of graminoid species, *Sitanion*, *Carex*, and *Festuca*. *Sitanion* and *Carex* both increased in biomass and cover, while *Festuca* cover declined. These trends are consistent with the known response of the three plants to fire (Agee 1993). Fire stimulates *Sitanion* root and shoot biomass of surviving plants and increases seedling recruitment (Young and Miller 1985, Vose and White 1991). *Carex* has shallow rhizomes and is capable of responding rapidly to disturbance. In comparison, *Festuca*, a tufted bunchgrass, varies from moderate to severe susceptibility to fire, depending on the amount of detritus in the basal tufts that cause fire to linger and kill the perennating buds (Johnson 1998).

With the exception of the changes in relative species abundance, the herbaceous plant community was unresponsive to the low-severity burns. Neither total forb nor graminoid cover increased significantly as a result of burning during the 6 yr period. Mean aboveground biomass of graminoids was greater on burn plots than controls in 1993; however, the difference was not significant due to variation among sites. Our results are counter to the findings of other studies that low to moderate fire stimulates herbaceous production by reducing competition for soil resources, reducing litter, and increasing nutrient availability (Saveland and Bunting 1988). Studies in northern Arizona have also found an inconsistent response of herbaceous plants to fire in ponderosa pine stands with similar tree diameters and densities to our study sites (Harris and Covington 1983, Andariese and Covington 1986, Vose and White 1991). Oswald and Covington (1984), in fact, found a decrease in forage production following fire.

We believe there were two primary factors that contributed to poor aboveground response of herbaceous plants to fire. First, the low-severity burns had little or no effect on tree mortality and stand density. Competition for soil water and nutrients between overstory and herbaceous plants was therefore unaltered. The decline in *Purshia* cover (from 9 to 2%) conceivably provided a competitive advantage to herbaceous plants, yet *Purshia* is a slow growing shrub with a low demand for soil nitrogen (Busse 2000) and a rooting pattern that is distinct from competing herbaceous plants. The second factor is the low productivity and diversity of the herbaceous understory in central Oregon. Herbaceous production in central Oregon is more than six-fold lower than production levels found in northeastern Oregon ponderosa pine stands (Riegel et al. 1991, Riegel et al. 1992), and may be considered marginal for supporting either wild or domestic grazing (Simon 1990). Wildfire exclusion in central Oregon forests has resulted in an understory that is shrub dominated, to the detriment of the seed bank of fire-adapted herbaceous plants. Moisture limitations further restrict the potential for response by herbaceous plants. We conclude that herbaceous plants do not respond strongly to single-entry, prescribed fire in these ecosystems when burns are low in severity and do not impact plant competition for soil resources.

Conclusions

Fire exclusion has resulted in increased stand density, shrub cover, and accumulation of downed wood and litter in ponderosa pine forests of central Oregon. Without treatment, natural fuels will continue to accumulate, adding to the risk of stand-replacement fire. Prescribed fire provides a viable means to reduce fuel buildup and wildfire danger. Our study demonstrated that low-severity prescribed fire following a prolonged period of wildfire exclusion produces a significant, yet slight reduction in tree growth in thinned ponderosa pine stands. Basal area growth reduction was proportional to the level of crown scorch and O horizon reduction during burning. Prescriptions for burning that limit crown scorch and O horizon reduction are recommended, therefore, for forests in which ponderosa pine production is a priority. Our results also confirm that reductions in cover of important

wildlife browse species such as *Purshia* and *Festuca* are likely following low-severity fire. Long-term recovery of *Purshia* will be aided by the ability of plants younger than 40 yr to resprout following fire.

Relatively minor reductions in stand productivity should be expected when using prescribed fire to reduce the risk of stand-replacement wildfire. Whether this tradeoff is acceptable will depend on the management considerations for a given landscape and the feasibility of using alternative or complementary practices such as mechanical thinning to reduce natural fuels. Of note, we found no evidence to suggest that prescribed fire will have a long-term impact on stand productivity. Specifically, soil resources, including nutrient content and exposed mineral soil, were unaffected by fire.

Literature Cited

- AGEE, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.
- ANDARIESE, S.W., AND W.W. COVINGTON. 1986. Changes in understory production for three prescribed burns of different ages in ponderosa pine. *For. Ecol. Manage.* 14:193–203.
- BARRETT, J.W. 1978. Height growth and site index curves for managed, even-aged stands of ponderosa pine in the Pacific Northwest. USDA For. Serv. Res. Pap. PNW-232.
- BILLINGS, W.D. 1952. The environmental complex in relation to plant growth and distribution. *Quart. Rev. Biol.* 27:251–265.
- BLASIDELL, J.P. 1950. Effects of controlled burning on bitterbrush on the Upper Snake River Plains. USDA For. Serv. Intermountain For. Range Exp. Sta. Res. Pap. 20.
- BLAISDELL, J.P., AND W. MUEGGLER. 1956. Sprouting of bitterbrush (*Purshia tridentata*) following burning or top removal. *Ecol.* 37:365–370.
- BORK, J.L. 1985. Fire history in three vegetation types on the east side of the Oregon Cascades. Ph.D. Thesis, Oregon State Univ., Corvallis.
- BROWN, J.K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Gen. Tech. Rep. INT-16.
- BUSSE, M.D. 2000. Ecological significance of nitrogen fixation by actinorhizal shrubs in interior forests of California and Oregon. In *Forest soil organisms*. Powers, R.F., D. Hauxwell, and G. Nakamura (eds.). USDA For. Serv. Gen. Tech. Rep. PSW. In press.
- CHOROVER, J., P.M. VITOUSEK, A. EVERSON, M. ESPERANZA, AND D. TURNER. 1994. Solution chemistry profiles of mixed-conifer forests before and after fire. *Biogeochem.* 26:115–144.
- CLARK, R.G., C.M. BRITTON, AND F.A. SNEVA. 1982. Mortality of bitterbrush after burning and clipping in eastern Oregon. *J. Range Manage.* 35:711–714.
- COCHRAN, P.H., AND W.E. HOPKINS. 1991. Does fire exclusion increase productivity of ponderosa pine? P. 224–228 in *Proc: Management and productivity of western montane forest soils*. Harvey, A.E., and L.F. Neuenschwander (comps.). USDA For. Serv. Gen. Tech. Rep. INT-280.
- COOK, J.G., T.J. HERSHEY, AND L.L. IRWIN. 1994. Vegetative response to burning on Wyoming mountain-shrub big game ranges. *J. Range Manage.* 47:296–302.
- COVINGTON, W.W., AND S.S. SACKETT. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Manage.* 54:175–191.
- DEMARS, D.J., AND J.W. BARRETT. 1987. Ponderosa pine managed-yield simulator: PP/SIM users guide. USDA For. Serv. Gen. Tech. Rep. PNW-203.
- DAHMS, W.G. 1954. Growth of pruned ponderosa pine. *J. For.* 52:444–445.
- DRISCOLL, R.S. 1963. Sprouting bitterbrush in central Oregon. *Ecology* 44:820–821.
- DRISCOLL, R.S. 1964. A relic area in the central Oregon juniper zone. *Ecology* 45:345–353.
- FIEDLER, C.E. 1996. Silvicultural applications: restoring ecological structure and process in ponderosa pine forests. P. 39–40 in *The use of fire in forest restoration*. Hardy, C.C., and S.F. Arno (eds.). USDA For. Serv. Gen. Tech. Rep. INT-GTR-341.
- FRITZE, H., T. PENNANEN, AND J. PIETIKAINEN. 1993. Recovery of soil microbial biomass and activity from prescribed burning. *Can. J. For. Res.* 23:1286–1290.
- GAY, D. 1998. A test of the southcentral Oregon mule deer habitat suitability index. M.S. thesis, Univ. of Idaho, Moscow, Idaho.
- GRIER, C.C. 1989. Effects of prescribed springtime underburning on production and nutrient status of a young ponderosa pine stand. P. 71–76 in *Multiresource management of ponderosa pine forests*. Teale, A., W.W. Covington, and R.H. Hamre (eds.). USDA For. Serv. Gen. Tech. Rep. RM-185.
- GRULKE, N.E., C.P. ANDERSON, M.E. FENN, AND P.R. MILLER. 1998. Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California. *Environ. Pollut.* 103:63–73.
- GUENTHER, G.E., C.L. WAMBOLT, AND M.R. FRISINA. 1993. Characteristics of bitterbrush habitats that influence canopy cover and mule deer browsing. *J. Environ. Manage.* 36:175–181.
- HARRIS, G.R., AND W.W. COVINGTON. 1983. The effect of a prescribed fire on nutrient concentration and standing crop of understory vegetation in ponderosa pine. *Can. J. For. Res.* 13:501–507.
- HITCHCOCK, C.L., AND A. CRONQUIST. 1973. *Flora of the Pacific Northwest*. Univ. of Washington Press, Seattle, WA.
- HORMAY, A.L. 1943. Bitterbrush in California. USDA For. Serv., Calif. For. Range Exp. Sta. Res. Note 34.
- JOHNSON, C.G., JR. 1998. Vegetation responses after wildfire in national forests of Northeastern Oregon. USDA For. Serv. Pac. Northwest Reg., R6-NR-ECOL-TP-06-98.
- JURGENSEN, M.F., ET AL. 1997. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of inland northwest forests. *For. Sci.* 43:234–251.
- KNOEPP, J.D., AND W.T. SWANK. 1993. Site preparation burning to improve southern Appalachian pine-hardwood stands: nitrogen responses in soil, soil water, and streams. *Can. J. For. Res.* 23:2263–2270.
- LANDSBERG, J.D. 1992. Response of ponderosa pine forests in central Oregon to prescribed underburning. Ph.D. Thesis, Oregon State Univ., Corvallis, OR.
- MAGURRAN, A. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ.
- MARTIN, R.E. 1983. Antelope bitterbrush seedling establishment following prescribed burning in the pumice zone of the southern Cascade Mountains. P. 82–90 in *Research and management of bitterbrush and cliffrose in western North America*. Tiedemann, A.R., and D.L. Johnson (comps.). USDA For. Serv. Gen. Tech. Rep. INT-152.
- MARTIN, R.E., AND C.H. DRIVER. 1983. Factors affecting antelope bitterbrush reestablishment following fire. P. 266–279 in *Research and management of bitterbrush and cliffrose in western North America*. Tiedemann, A.R., and D.L. Johnson (comps.). USDA For. Serv. Gen. Tech. Rep. INT-152.
- MILLER, R.F., AND J.A. ROSE. 1999. Fire history and western juniper encroachment in sagebrush steppe. *J. Range Manage.* 52:550–559.
- MONLEON, V.J., K. CROMACK, JR., AND J.D. LANDSBERG. 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Can. J. For. Res.* 27:369–378.
- MORRIS, W.G., AND E.L. MOWAT. 1958. Some effects of thinning a ponderosa pine thicket with a prescribed fire. *J. For.* 56:203–209.
- NORD, E.C. 1965. Autecology of bitterbrush in California. *Ecol. Monogr.* 35:307–334.

- NOSTE, N.V., AND C.L. BUSHEY. 1987. Fire response of shrubs of dry forest habitat types in Montana and Idaho. USDA For. Serv. Gen. Tech. Rep. INT-239.
- OLIVER, W.W. 1984. Brush reduces growth of thinned ponderosa pine in northern California. USDA For. Serv. Res. Pap. PSW-172.
- OSWALD, B.P., AND W.W. COVINGTON. 1984. Effect of a prescribed fire on herbage production in southwestern ponderosa pine on sedimentary soils. For. Sci. 30:22-25.
- PETERSON, D.L., S.S. SACKETT, L.J. ROBINSON, AND S.M. HAASE. 1994. The effects of repeated prescribed burning on *Pinus ponderosa* growth. J. Wildland Fire 4:239-247.
- PIETIKAINEN, J., AND H. FRITZE. 1993. Microbial biomass and activity in the humus layer following burning: short-term effects of two different fires. Can. J. For. Res. 23:1275-1285.
- RAISON, R.J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant Soil 51:73-108.
- RAISON, R.J., P.K. KHANNA, AND P.V. WOODS. 1985. Mechanisms of element transfer to the atmosphere during vegetation fires. Can. J. For. Res. 15:132-140.
- RIEDEL, G.M., R.F. MILLER, AND W.C. KRUEGER. 1991. Understory vegetation response to increasing water and nitrogen levels in a *Pinus ponderosa* forest in northeastern Oregon. Northwest Sci. 65:10-15.
- RIEDEL, G.M., R.F. MILLER, AND W.C. KRUEGER. 1992. Competition for resources between understory vegetation and overstory *Pinus ponderosa* in northeastern Oregon. Ecol. Applic. 2:71-85.
- SAS INSTITUTE INC. 1988. SAS/STAT users guide. Version 6, 3rd. ed. SAS Institute Inc., Cary, N.C.
- SAVELAND, J.M., AND S.C. BUNTING. 1988. Fire effects in ponderosa pine forests. P. 125-131 in *Ponderosa pine. The species and its management*, Baumgartner, D.M., and J.E. Lotan (eds.). Washington State Univ., Coop. Ext., Pullman, WA.
- SHEA, R.W. 1993. Effects of prescribed fire and silvicultural activities on fuel mass and nitrogen redistribution in *Pinus ponderosa* ecosystems of central Oregon. M.S. Thesis, Oregon State Univ., Corvallis, OR.
- SHERMAN, R.J., AND W.W. CHILCOTE. 1972. Spatial and chronological patterns of *Pushia tridentata* as influenced by *Pinus ponderosa*. Ecology 53:294-298.
- SIERRA NEVADA ECOSYSTEM PROJECT. 1996. Final report to Congress, Vol. I, assessment summaries and management strategies. Centers for Water and Wildland Resources, Univ. of California, Davis.
- SIMON, S.A. 1990. Fire effects from prescribed underburning in central Oregon ponderosa pine plant communities: first and second growing season after burning. Unpublished report on file, Fremont National Forest, Lakeview, OR.
- SUTHERLAND, E.K., W.W. COVINGTON, AND S. ANDARIESE. 1991. A model of ponderosa pine growth response to prescribed burning. For. Ecol. Manage. 44:161-173.
- SWEZY D.M., AND J.K. AGEE. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Can. J. For. Res. 21:626-634.
- USDA FOREST SERVICE. 1997. An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins. Quigley, T.M., and S.J. Arbelbide (eds.). USDA For. Serv. Gen. Tech. Rep. PNW-405.
- VANDER WALL, S.B. 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. Ecology 75:1911-1926.
- VAN SICKLE, F.S., AND R.D. HICKMAN. 1959. The effect of understory competition on the growth rate of ponderosa pine in north central Oregon. J. For. 57:852-853.
- VAN WAGTENDONK, J.W. 1996. Use of a deterministic fire growth model to test fuel treatments. P. 1155-1165 in *Sierra Nevada Ecosystem Project: Final report to Congress, Vol. II, Chap. 43*. Centers for Water and Wildland Resour., Univ. of California, Davis.
- VOSE, J.M., AND A.S. WHITE. 1991. Biomass response mechanisms of understory species the first year after prescribed burning in an Arizona ponderosa-pine community. For. Ecol. Manage. 40:175-187.
- WEATHERSPOON, C.P. 1996. Fire-silviculture relationships in Sierra forests. P. 1167-1176 in *Sierra Nevada Ecosystem Project: Final report to Congress, Vol. II, Chap. 44*. Centers for Water and Wildl. Resour., Univ. of California, Davis.
- WEAVER, H. 1943. Fire as an ecological and silvicultural factor in the ponderosa pine region of the Pacific slope. J. For. 41:7-14.
- WEST, N.E. 1968. Rodent-influenced establishment of ponderosa pine and bitterbrush seedlings in central Oregon. Ecology 49:1009-1011.
- WHITE, C.S. 1986. Effects of prescribed fire on rates of decomposition and nitrogen mineralization in a ponderosa pine ecosystem. Biol. Fertil. Soils 2:87-95.
- WINWARD, A.H., AND J.A. FINDLEY. 1983. Taxonomic variations of bitterbrush (*Purshia tridentata*) in Oregon. P. 25-31 in *Research and management of bitterbrush and cliffrose in western North America*, Tiedemann, A.R., and D.L. Johnson (comps.). USDA For. Serv. Gen. Tech. Rep. INT-152.
- WYANT, J.G., R.D. LAVEN, AND P.N. OMI. 1983. Fire effects on shoot growth characteristics of ponderosa pine in Colorado. Can. J. For. Res. 13:620-625.
- YOUNG, R.P., AND R.F. MILLER. 1985. Response of *Sitanion hystrix* (Nutt.) J. G. to prescribed burning. Am. Midl. Natur. 113:182-187.