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DYNAMIC RESPONSES OF A BRITISH COLUMBIAN FOREST-GRASSLAND INTERFACE TO PRESCRIBED BURNING

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ABSTRACT.—Ponderosa pine *Pinus ponderosa* and Douglas-fir *Pseudotsuga menziesii* forests in the Interior of British Columbia, Canada, are adjacent to grasslands. Forest ingrowth and tree encroachment, mainly due to fire suppression, represent threats to both forest and ranching industries in the region. The use of prescribed burning for ecological restoration is being practiced, but the associated ecosystem effects of restoration treatments have been little studied in the region. We used a randomized complete block design in a prescribed burning experiment. Tree survival and the responses of understory vegetation to burning were monitored for 3 years. The transect method along with crown projection areas (onto the ground) were used in comparisons between areas inside and outside of the burned area. Fire was effective in eliminating small ponderosa pine (dbh < 10 cm) and Douglas-fir (dbh < 20 cm) trees. Therefore, the objective of controlling the encroachment of trees was met by the prescribed burn. Species composition at both sites was modified by prescribed burning, but spatial variability was overridden by treatment and temporal effects. Immediate, short-term reduction of big sagebrush *Artemisia tridentata* ssp. *wyomingensis* was observed in grassland sites, while reduction in rabbitbrush *Chrysothamnus nauseosus* in the forest was observed. Data trends indicate that 3 years after burning, total biomass and forb biomass increased in grasslands, but graminoid biomass in forests was reduced and total understory biomass was not affected by burning. Burning also reduced the shrub component in these ecosystems. While aboveground biomass production may be enhanced by burning in grasslands, the impact of burning on forest understory was minimal and burning may result in reduction of graminoids. Therefore, burning can be used to control tree encroachment and forest ingrowth in this region. Management plans must incorporate topography, species diversity, and tree survival to target areas that are most susceptible to tree encroachment and to achieve desired results. Extended monitoring is necessary to determine the long-term effects of burning on species diversity in and productivity of these ecosystems.

Key words: forage production, forest, fuel reduction, grassland, ponderosa pine, prescribed burning, restoration, tree encroachment.

Grasslands in British Columbia, Canada, are located on lower valley slopes adjacent to dry forests at higher elevations dominated by ponderosa pine *Pinus ponderosa* Dougl. and Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco (McLean 1970, Wikeem et al. 1993). The spatial vegetation distribution pattern in the region is controlled by elevation and the topographic moisture gradient (Peet 2000). Frequent, low-intensity fires are historically the major natural disturbance in this region, a regime that encourages ecosystem structures of moderately open, uneven stands with a herbaceous understory free of trees and shrubs (Humphrey 1962). Within the Rocky Mountains, frequent fires created and maintained grasslands, shrublands, and conifer forest savannas (Barrett 1994). However, in the last 90–100 years, the forest management practice of fire suppression in British Columbia has resulted in forest ingrowth and tree encroachment into grassland. These conditions allow fuel accumulations and increase the risk of intense wildfires (Covington and Sackett 1984, Daigle 1996, Gayton 1996). Results of a spatial simulation model in a Rocky Mountain watershed also showed infiltration of conifer stands into sagebrush/grassland sites from the mid-1800s to the mid-1990s (Gallant et al. 2003). Throughout the Rocky Mountains, extensive conifer encroachment into grasslands has been well documented (Gruell 1983). Decreased rangeland area, reduced carrying capacity, altered ecosystem structure, deteriorated range condition, and loss of biodiversity are associated with forest ingrowth and tree encroachment (Bai et al. 2004). Forest ingrowth and tree encroachment also lead to a reduction in habitats for species relying on these sagebrugh/grassland ecosystems (Hansen and Rotella 2000).

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Prescribed burning has been used in forest management to reduce fuel load, to control forest ingrowth and tree encroachment, and to enhance understory productivity in these ecosystems (Covington et al. 1997, Allen et al. 2002, Kaye et al. 2005). Fire can act as a natural "thinning" agent within forest stands that in turn reduces competition among plants for resources (Humphrey 1962) such as light and nutrients (Gayton 1996). In addition, fires can remove accumulated conifer needles that can inhibit grass production (Weaver 1951). However, the effects of fire on ground cover of *Festuca*- and *Agropyron*-dominated grasslands include reduced moss and lichen cover, increased soil temperatures, and reduced near-surface soil water (Antos et al.1983). Several factors interact to determine the responses of vegetation to fire. These factors include climate, grazing, fire severity, ecosystem type, and plant morphology, vigor, and phenology (Feller 1996).

Goals of prescribed burning include improvement in the quality of forage and control of undesirable plant species, as well as alteration of the botanical composition of the plant community (Wright 1974, Wikeem and Strang 1983), enhancement of decomposition rates, nutrient cycling, and net primary productivity (Moore et al. 1999); reduction in fire hazard; facilitation of planting; and provision of the soil seedbed for establishment of plants (Lindeburgh 1990). In addition, prescribed burning can be used to reduce competition from shrubs and trees, to thin stands, to reduce diseases and insects, to improve aesthetics, to enhance browse or grazing potential, and to improve wildlife habitats (Lindeburgh 1990). Controlled burns usually cause more damage to shrubs and small trees than they do to perennial grasses and forbs (Humphrey 1962). Timing of prescribed burning can be a major determinant of fire effect. For example, burning tends to be more damaging to grasslands in autumn than in spring, especially in *Festuca* and *Stipa-Agropyron* grasslands (Redmann et al. 1993). Burning when plants are dormant will impact plants least (Wright 1974). Burning is being recommended to improve the structure and function of historically fire-adapted ponderosa pine forests (Moore et al. 1999, Fiedler et al. 2001, Allen et al. 2002), but the associated ecosystem effects of restoration treatments have been little studied over much of the distributional range of ponderosa pine (Dodson and Fiedler 2006).

The objectives of this research were to determine the short-term effects of burning on understory species diversity and biomass production in the ponderosa pine forests and bluebunch wheatgrass grasslands of Interior British Columbia. Burning is important for ecosystem restoration and it may increase forage production in grasslands and aid in maintaining long-term sustainability. We hypothesized that reducing tree canopy with burning would increase species diversity and standing crop of the understory vegetation in the forest-grassland interface of British Columbia.

METHODS

Site Description

Dew Drop (Tranquille Ecological Reserve) is located 20 km northwest of Kamloops, British Columbia (BC) (50°45′N 120°36′W), within the ponderosa pine and Interior Douglas-fir biogeoclimatic zones. The reserve covers 235 ha of forests and grasslands, ranging from 610 to 1160 m in elevation. Vegetation changes from open grasslands, with big sagebrush *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young and bluebunch wheatgrass *Agropyron spicatum* (Pursh) Scribn. & Smith as dominant species at low elevations, to ponderosa pine forests and eventually to Douglas-fir forests at high elevations. Soils are Dark Brown Chernozems with sandy loam texture (McLean and Tisdale 1972). Average precipitation in Kamloops was 264 mm in 1998, 268 mm in 1999, 277 mm in 2000, 254 mm in 2001, and 221 mm in 2002 (Environment Canada 2005). The area was fenced by the BC Ministry of Forests in 1993 to exclude livestock and to preserve a representative ponderosa pine / Douglas-fir ecosystem in a prominent valley (Morrow 1993). Historical fire-return intervals in the open grasslands average 7–10 years, while the fire-return interval for ponderosa pine stands averages 10–12 years (Morrow 1993). Until the late 1970s the BC Ministry of Environment had a burning program in the Dew Drop area that consisted of controlled burns to increase or maintain plant species diversity for wildlife habitats.

Experimental Design and Treatment Design

Five pairs of 40 × 50-m plots were established in open grassland and in forest in July

TABLE 1. Average basal diameter of ponderosa pine ($\bar{x} \pm s_{\bar{x}}$) selected for studying the effect of canopy on understory vegetation at Dew Drop, British Columbia, Canada.

Treatment	Basal diameter (cm)	Range (cm)
Control	26.7 ± 9.1	22.3–44.3
Burning	37.8 ± 1.5	30.9–43.3
P-value	0.256	

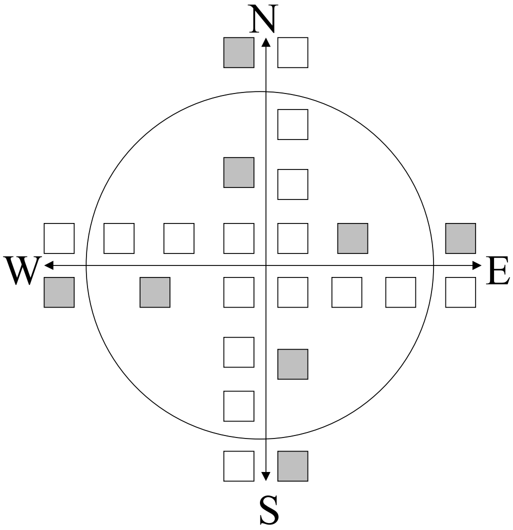

Fig. 1. Layout of transects and quadrats surrounding the bole stem under and outside the canopy projection area. Unfilled squares were quadrat locations for ground cover and species composition in the order of Q1, Q2, Q3, and Q4 from the center to the edge of canopy. Standing crop was determined in quadrats represented by filled squares.

1998 (total 10 pairs). Burning was conducted at Dew Drop between 13:20 and 17:20 on 1 April 1999 in conjunction with the BC Park Service and the BC Ministry of Forests. The air temperature was between 14 and 16 °C, with relative humidity between 36% and 38% and wind speed between 8 and 12 km · h^{-1}. The forest was burned in one large patch, and firebreaks were made before ignition to protect the control plots. This study was a randomized complete block design (RCBD) with 5 replicates. Preburning tree density averaged 43 stems · ha^{-1} for the grassland plots and 790 stems · ha^{-1} for the forest plots. Tree densities were similar in the burned and control plots (P = 0.256). Post-burning tree density in 2002 averaged 10 stems · ha^{-1} for the grassland plots and 370 stems · ha^{-1} for the forest plots.

EXPERIMENT 1: BURNING ON UNDERSTORY VEGETATION: TRANSECTS.—We established 2 transects, 20 m in length, at the center of each plot. The first transect was positioned to be representative of the plot, and the second transect was placed at the left side and 10 m apart from the first one. We subdivided the 20 × 20-m area within 5 m of both sides of transects into sixteen 5 × 5-m subplots. Diameter at breast height (dbh; for trees taller than 2 m) or height (for trees shorter than 2 m) was measured for each tree. The scorch heights on ponderosa pine and Douglas-fir trees within each plot were measured immediately after burning, and the survival of each tree was estimated 3 years after the burning.

EXPERIMENT 2: BURNING ON CANOPY PROJECTION AREAS.—We selected 4 ponderosa pine trees within each plot to study the effect of tree canopy and burning on understory vegetation. Selected trees had intermediate sizes among trees within each plot, relatively straight stems, and regular (round) and even (equal dimensions along all directions) canopies. We avoided selecting trees with partial canopy overlaps because they may have compromised the influence of individual trees. Sizes of selected trees were similar between the control and burning treatments as measured by basal diameter (Table 1). Four transects were established, one in each cardinal direction (N, E, S, and W) from the stem to the edge of the crown projection area of each tree (Fig. 1). Crown projection area was estimated by visually projecting the edges of the canopy down to the soil surface (Barbour et al. 1999).

Data Collection

EXPERIMENT 1: BURNING ON UNDERSTORY VEGETATION: TRANSECTS.—Ten 0.4 × 0.5-m quadrats, were placed 2 m apart on the right side of each 20-m transect. Within these quadrats, percent canopy cover (Barbour et al. 1999) of each vascular plant species, litter (barks, needles, and other dead plant materials), and bare soil were visually estimated to the closest 5% in June–July 1998 (before treatment), 1999, and 2002. The height of live vegetation and the depth of litter within each quadrat were also measured in 3 subsamples. All aboveground standing plant materials were clipped to ground level in late July 2002 on the left side of each 0.4 × 0.5-m quadrat, at 5 and 15 m along the transect. They were oven-dried at 60 °C for 12–24 hours and then weighed. Samples were then sorted into shrubs, forbs, live graminoids, and dead graminoids, and each portion was weighed separately.

EXPERIMENT 2: BURNING ON CANOPY PROJECTION AREAS.—From the base of each ponderosa pine tree, a transect was laid along each of the 4 directions N, E, S, and W), and 4 quadrats were placed along each transect: (1) tree bole (Q1); (2) halfway between the tree bole and edge of the crown projection area (Q2); (3) 30 cm inside the edge of the crown projection area (Q3); and (4) 60 cm outside the edge of the crown projection area (Q4) (Fig. 1). Quadrat 3 (Q3) was not measured when the crown projection area was too small to separate Q2 from Q3. A 0.3 × 0.3-cm quadrat was used for Q1–Q4 to determine percent ground cover and canopy cover of understory species in June 2001 and 2002. Understory standing crop was determined in 0.3 × 0.3-m quadrats by hand clipping plants to ground level. Quadrats for standing crop were placed at the left side of each transect, within and outside the tree canopy (at the same location as Q2 and Q4). Plant materials were pooled for Q2 and for Q4, respectively, in all 4 directions. The plant materials were oven-dried at 60 °C for 12–24 hours and weighed. Samples were then sorted into shrubs, forbs, live graminoids, and dead graminoids, and each portion was weighed separately.

Data Analysis

EXPERIMENT 1: BURNING ON UNDERSTORY VEGETATION: TRANSECTS.—Species cover from quadrats along the two 20-m transects were pooled for each plot. Species richness (R), species evenness (E), and the Shannon-Weiner diversity index (H') (Barbour et al. 1999) were calculated for each plot within each year using PC-ORD (McGarigal et al. 2000). Data were then analyzed separately within each year using ANOVA (SAS Institute, Inc. 1995) to determine the effect of burning treatment on species composition. Data from 1998, 1999, and 2002 were combined for ordination with rare species (species that occurred in ≤2 plots or ≤10% of total plots) being removed (McGarigal et al. 2000). Cover data were relativized by the species maximum prior to detrended correspondence analysis (DCA). Scores of the first 3 axes of DCA were calculated and analyzed with ANOVA to determine the effect of year and treatment on plot separation along the 3 axes. The 1st axis represents the maximum amount of variation explained by a single dimension. The 2nd axis is constrained by orthogonality and maximization of the remaining variance. Therefore, the 2nd axis is statistically independent of the 1st axis and explains the maximum remaining variation not explained by the 1st axis (McGarigal et al. 2000).

Ground cover (including rocks, logs, bare soil, litter, and lichens), the cover of functional groups (including forbs, graminoids, shrubs and total cover), litter depth, and vegetation height were analyzed within years using ANOVA to determine the effects of burning (Snedecor and Cochran 1980). Graminoids include grasses, sedges, and rushes. The shrub category also included small trees (<0.5 m tall), but excluded pasture sage (*Artemisia frigida* Willd.), which was treated as a forb. Standing crop of forbs, live graminoids, dead graminoids, shrubs, and total understory standing crop were analyzed using ANOVA. Means were separated using the least significant difference test (LSD; Snedecor and Cochran 1980). P-values <0.05 were considered statistically significant.

EXPERIMENT 2: BURNING ON CANOPY PROJECTION AREAS.—Species composition data along the 4 cardinal directions from each tree bole were pooled according to quadrat positions (Q1, Q2, Q3, or Q4). Data were combined from trees within each plot (subsamples) and then pooled according to quadrat locations. All 3 quadrats under the canopy (Q1, Q2, and Q3) were averaged for ground cover and are collectively referred to as "under the canopy." For each plot and year, we used PC-ORD software to calculate R, E, and H' for under the canopy (using Q2 only) and outside the canopy (Q4), and we analyzed within each year (2001 and 2002) using the general linear model (GLM; SAS Institute, Inc. 1995). Each combination of canopy cover type (under the canopy or outside the canopy) was treated as a "plot" in ordination after removal of rare species (McGarigal et al. 2000). Data were relativized by the species maximum and then subjected to DCA separately for each year. Scores of the first 3 axes of DCA were calculated and analyzed with GLM to determine whether the effect of treatment and canopy cover type on species composition can be separated along the 3 axes.

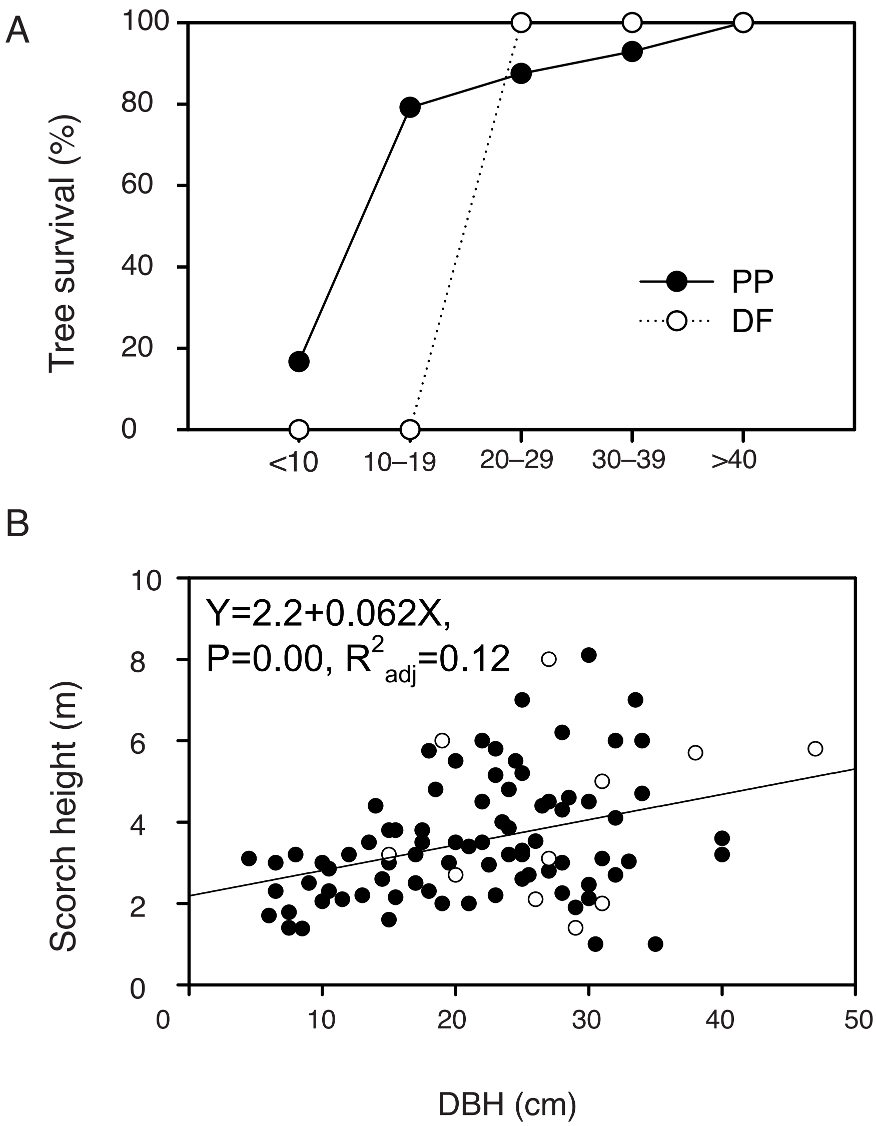

Fig. 2. A, Survival of ponderosa pine and Douglas-fir in relation to diameter at breast height (dbh) classes at Dew

Ground cover, canopy cover of functional groups, litter depth, and vegetation height were pooled, respectively, according to quadrat location within each plot. We analyzed these variables within each year, using GLM to determine the effects of canopy and quadrat location. Data from the 3 quadrats under the tree canopy were then combined and analyzed using GLM. Standing crop of forbs, live graminoids, dead graminoids, shrubs, and total understory standing crop were also analyzed with GLM as described above. We separated means using LSD procedures (Snedecor and Cochran 1980). P-values <0.05 were considered statistically significant.

RESULTS

Burning Effects on Tree Survival and Understory Plant Species Composition

EXPERIMENT 1: BURNING ON UNDERSTORY VEGETATION: TRANSECTS.—Scorch height was positively correlated with tree size ($P < 0.01$; Fig. 2). Tree survival after burning increased with increasing tree size for both species. The survival of ponderosa pine trees increased by

TABLE 2. Burning effects on species richness (R), species evenness (E), Shannon-Weiner diversity index (H'), and the canopy cover of functional groups ($\bar{x} \pm s_{\bar{x}}$) at Dew Drop, British Columbia, Canada (the transect study). Prescribed burning was conducted in April 1999. Means with different lowercase letters within a column, site, and year are significantly different at $P \leq 0.05$.

					Cover (%)		
Site, year	Treatment	R	E	H'	Forb	Shrub	Graminoid
Grassland							
1998	Control	14.0 ± 0.8	0.70 ± 0.02	1.84 ± 0.08	4 ± 0.9	9 ± 1.6	15 ± 1.1 b
	Burning	16.0 ± 2.1	0.62 ± 0.02	1.69 ± 0.05	3 ± 0.5	8 ± 2.4	20 ± 2.2 a
	P-value	0.389	0.060	0.225	0.785	0.795	0.038
1999	Control	18.4 ± 1.6	0.69 ± 0.02	2.00 ± 0.08	5 ± 0.9	8 ± 1.3 a	19 ± 3.1
	Burning	17.8 ± 0.6	0.71 ± 0.03	2.05 ± 0.09	3 ± 0.9	1 ± 0.4 b	12 ± 0.9
	P-value	0.722	0.689	0.705	0.364	0.005	0.164
2002	Control	14.4 ± 0.7	0.71 ± 0.03	1.87 ± 0.06	4 ± 0.5	2 ± 0.8	17 ± 0.7
	Burning	17.2 ± 1.0	0.70 ± 0.01	1.98 ± 0.03	5 ± 0.8	<1 ± 0.2	20 ± 1.0
	P-value	0.094	0.789	0.228	0.490	0.191	0.102
Forest							
1998	Control	8.8 ± 1.8	0.56 ± 0.11	1.25 ± 0.29	1 ± 0.7	2 ± 1.5	8 ± 1.6
	Burning	7.0 ± 0.9	0.53 ± 0.06	0.97 ± 0.06	<1 ± 0.1	2 ± 0.7	5 ± 0.6
	P-value	0.405	0.743	0.334	0.265	0.896	0.299
1999	Control	9.0 ± 2.2	0.51 ± 0.07	1.09 ± 0.24	1 ± 0.4	<1 ± 0.4	7 ± 1.1 a
	Burning	5.8 ± 0.6	0.45 ± 0.09	0.80 ± 0.21	<1 ± 0.1	0 ± 0.0	2 ± 0.3 b
	P-value	0.199	0.464	0.293	0.066	0.374	0.014
2002	Control	11.0 ± 1.9	0.80 ± 0.03 a	1.86 ± 0.17 a	2 ± 0.7	<1 ± 0.3	3 ± 0.7
	Burning	6.8 ± 0.5	0.70 ± 0.05 b	1.35 ± 0.13 b	1 ± 0.1	0.0 ± 0.0	3 ± 1.0
	P-value	0.863	0.014	0.038	0.240	0.374 x	0.568

TABLE 3. Burning effects on canopy cover (%) and relative rankings (in parentheses) of the dominant species at Dew Drop, British Columbia, Canada, in 1998, 1999 and 2002 (the transect study). Prescribed burning was conducted in April 1999.

	Control			Burning		
Site, species	1998	1999	2002	1998	1999	2002
Grassland						
Agropyron spicatum	2.0 (4)	2.1 (4)	1.4 (3)	2.9 (5)	1.9 (4)	1.7 (3)
Antennaria microphylla	0.6 (6)	1.2 (6)	1.4 (3)	0.6 (7)	0.6 (7)	0.6 (7)
Artemisia frigida	1.0 (5)	0.7 (7)	0.5 (7)	1.1 (6)	0.3 (8)	0.9 (6)
Artemisia tridentata	5.4 (2)	6.7 (1)	1.2 (6)	8.1 (2)	1.1 (5)	0.0 (8)
Koeleria macrantha	3.4 (3)	4.2 (3)	7.2 (1)	4.1 (3)	2.8 (2)	6.3 (2)
Poa pratensis	0.0 (7)	0.0 (8)	0.0 (8)	3.7(4)	2.0 (3)	1.0 (5)
Poa sandbergii	0.0 (7)	1.3 (5)	1.4 (3)	0.0 (8)	0.7 (6)	1.3 (4)
Stipa comata	7.7 (1)	6.5 (2)	5.9 (2)	8.8 (1)	7.2 (1)	8.6 (1)
Forest						
Achillea millefolium	0.1 (7)	0.2 (4)	0.2 (7)	0.1 (5)	0.1 (2)	0.2 (4)
Agropyron spicatum	5.0 (1)	5.1 (1)	1.6 (1)	4.2 (1)	1.7 (1)	1.8 (1)
Chrysothamnus nauseosus	0.9 (3)	0.0 (7)	0.3 (3)	2.0 (2)	0.0 (3)	0.0 (6)
Festuca campestris	0.7 (4)	0.0 (7)	0.3 (3)	0.6 (3)	0.0 (3)	0.3 (2)
Juniperus scopulorum	1.0 (2)	1.0 (2)	0.0 (8)	0.0 (7)	0.0 (3)	0.0 (6)
Koeleria macrantha	0.2 (6)	0.2 (4)	0.3 (3)	0.2 (4)	0.0 (3)	0.2 (4)
Oxytropis campestris	0.5 (5)	0.2 (4)	0.4 (2)	0.1 (5)	0.0 (3)	0.3 (2)
Poa sandbergii	0.0 (8)	0.3 (3)	0.3 (3)	0.0 (7)	0.0 (3)	0.0 (6)

60% when dbh increased from <10 cm to a range of 10 to 19 cm. Survival increased to 100% in Douglas-fir when dbh was at least 20–29 cm. Species richness (R), species evenness (E) and the Shannon-Weiner diversity index (H') were similar between the control and treatment plots before burning in both grassland and forest plots (Table 2). Burning had no significant effect on R, E, and H' in the year immediately after burning in grassland and forest plots or 3 years after burning in grasslands. For the forest plots, E was 13%

TABLE 4. Canopy cover (%) with relative ranking (in parentheses) of the dominant species under and outside the canopy of ponderosa pine at Dew Drop, British Columbia, Canada, in 2001 and 2002 after burning. Prescribed burning was conducted in April 1999.

	Control		Burning	
Year, species	Under	Outside	Under	Outside
2001				
Achillea millefolium	0.1 (6)	0.3 (5)	0.3 (2)	0.2 (5)
Agropyron spicatum	2.3 (1)	3.2 (1)	1.7 (1)	3.9 (1)
Chrysothamnus nauseosus	2.0 (2)	1.6 (2)	0.0 (7)	0.0 (8)
Erigeron spp.	0.1 (6)	0.4 (4)	0.1 (6)	0.2 (5)
Koeleria macrantha	0.2 (4)	1.0 (3)	0.2 (4)	0.6 (2)
Oxytropis campestris	0.3 (3)	0.0 (7)	0.2 (4)	0.2 (5)
Stipa comata	0.0 (8)	0.0 (7)	0.0 (7)	0.3 (3)
Stipa curtiseta	0.2 (4)	0.1 (6)	0.3 (2)	0.3 (3)
2002				
Achillea millefolium	0.4 (3)	0.4 (3)	0.3 (2)	0.3 (5)
Agropyron spicatum	1.6 (1)	2.0 (1)	2.2 (1)	3.3 (1)
Antennaria microphylla	0.2 (6)	0.4 (3)	0.1 (6)	0.1 (7)
Chrysothamnus nauseosus	1.0 (2)	0.1 (7)	0.0 (8)	0.0 (8)
Erigeron spp.	0.1 (7)	0.2 (6)	0.1 (6)	0.2 (6)
Koeleria macrantha	0.4 (3)	0.9 (2)	0.3 (2)	0.7 (2)
Oxytropis campestris	0.3 (5)	0.0 (8)	0.2 (4)	0.6 (3)
Stipa comata	0.1 (7)	0.3 (5)	0.2 (4)	0.4 (4)

lower ($P = 0.014$) and H' was 27% lower ($P = 0.038$) in the burned plots than in the control plots 3 years after burning (2002).

Forb cover in grasslands and forest understory was not affected by burning (Table 2). Shrub cover in grasslands was reduced from 8% to 1% ($P = 0.005$) immediately after burning (1999), but the difference in shrub cover between the control and burned plots was not significant in 2002 ($P = 0.191$). Shrub canopy cover in forest understory was small and not different between the control and burning plots ($P = 0.374$ in 1999 and 2002). Graminoid cover in grasslands was greater in treatment plots (20%) than in control plots (15%) before the burning in 1998 ($P = 0.038$), but it was not significantly different between the control and burned plots in subsequent years ($P = 0.164$ in 1999, $P = 0.102$ in 2002), indicating a relative reduction in graminoid cover by burning. Within the forested plots, graminoid cover was lower in burned plots (2%) than in control plots (7%) in 1999 ($P = 0.014$), but it reached 3% for both burned and control plots by 2002 ($P = 0.568$). The most abundant grass species in the grassland was needle and thread *Stipa comata* Trin. & Rupr. (Table 3). No dramatic changes in the relative ranking of species were noted within grasslands, except that burning reduced big sagebrush. Bluebunch wheatgrass was the most abundant species in forest understory, and its cover was reduced by burning. Spatial variability in species composition among blocks was greater than that caused by burning or year as revealed by DCA (data not shown); therefore, burned plots cannot be separated from the control plots based on understory plant species composition.

EXPERIMENT 2: BURNING ON CANOPY PROJECTION AREAS.—No significant effects of burning or quadrat location were found for R, E, and H' ($P > 0.05$). In 2001, R, E, and H' were 7.0, 0.66, and 1.29, respectively, and in 2002, R, E, and H' were 10.0, 0.70, and 1.62, respectively. Forb cover in forest understory was low (averaging 1%) and was not affected by treatment or quadrat location ($P > 0.05$; data not shown). Burning reduced shrub cover from 2% to <1% beneath the canopy in 2001 ($P = 0.016$), but graminoid cover remained unaffected by burning ($P = 0.354$). Graminoid cover was greater outside the tree canopy than under the canopy in 2001 and 2002 ($P = 0.007$ and $P = 0.032$, respectively). Overall average shrub cover was <1%, grass cover was 3%, and total understory vegetation cover was 5% (data not shown). Bluebunch wheatgrass was most abundant both under and outside the tree canopy (Table 4), which was similar to results from experiment 1. Outside of the canopy, the cover of rabbitbrush *Chrysothamnus nauseosus* (Pall.) Britt. decreased, while that of needle and thread increased, in 2001 and 2002 after burning.

TABLE 5. Effects of burning on of bare soil cover, litter cover, litter depth, vegetation height, and total vegetation cover ($\bar{x} \pm s_{\bar{x}}$) at Dew Drop, British Columbia, Canada (the transect study). Prescribed burning was conducted in April 1999. Means with different lowercase letters within a column, site, and year are significantly different at $P \leq 0.05$.

Site, year	Treatment	Bare soil (%)	Litter cover (%)	Litter depth (cm)	Vegetation height (cm)	Vegetation cover (%)
Grassland						
1998	Control	67 ± 4.6 a	32 ± 4.8 b	0.5 ± 0.0	41.6 ± 2.3	27 ± 1.9
	Burning	47 ± 4.6 b	52 ± 4.5 a	0.5 ± 0.0	47.5 ± 4.6	31 ± 2.7
	P-value	0.043	0.044	0.376	0.178	0.426
1999	Control	42 ± 5.2	57 ± 5.9	0.8 ± 0.2 a	43.0 ± 2.2 a	32 ± 2.7 a
	Burning	47 ± 6.7	52 ± 6.4	0.3 ± 0.1 b	32.5 ± 0.8 b	16 ± 1.3 b
	P-value	0.337	0.370	0.035	0.002	0.009
2002	Control	13 ± 3.2	61 ± 4.4	2.9 ± 0.2	32.3 ± 2.5	23 ± 0.7
	Burning	14 ± 4.3	64 ± 4.3	3.1 ± 0.2	28.9 ± 1.7	25 ± 1.3
	P-value	0.823	0.588	0.526	0.153	0.291
Forest						
1998	Control	7 ± 2.0	87 ± 4.6	2.9 ± 0.5	29.4 ± 6.2	11 ± 3.2
	Burning	3 ± 0.9	96 ± 0.9	3.2 ± 0.2	27.9 ± 1.6	8 ± 0.9
	P-value	0.123	0.142	0.673	0.773	0.364
1999	Control	5 ± 1.6	93 ± 2.8	2.7 ± 0.7 a	25.6 ± 4.0	9 ± 1.8 a
	Burning	11 ± 4.3	84 ± 5.2	0.5 ± 0.1 b	11.1 ± 2.0	2 ± 0.3 b
	P-value	0.236	0.207	0.037	0.053	0.024
2002	Control	2 ± 1.1	87 ± 2.8	4.6 ± 0.6	30.2 ± 2.9 a	5 ± 1.1
	Burning	2 ± 0.5	91 ± 2.6	3.3 ± 0.1	18.8 ± 2.4 b	4 ± 1.0
	P-value	0.855	0.425	0.076	0.044	0.270

TABLE 6. Burning effects on litter cover, litter depth, and lichen cover ($\bar{x} \pm s_{\bar{x}}$) under and outside the canopy of ponderosa pine trees at Dew Drop, British Columbia, Canada. Prescribed burning was conducted in April 1999. Means with different lowercase letters within a column, year, and quadrat location are significantly different at $P \leq 0.05$. Means with different capital letters within a column and year are significantly different at $P \leq 0.05$.

Year, location	Treatment	Litter (%)	Litter depth (cm)	Lichen (%)
2001				
Under canopy	Control	90 ± 2.1 a	3.8 ± 0.3 a	5 ± 1.4 a
	Burning	74 ± 3.6 b	1.7 ± 0.1 b	0 ± 0.0 b
	Mean	82.2	2.7	2.4 B
Outside canopy	Control	82 ± 2.3	2.5 ± 0.4	11 ± 3.3 a
	Burning	76 ± 4.7	1.6 ± 0.2	1 ± 0.5 b
	Mean	79.0	2.0	5.7 A
2002				
Under canopy	Control	90 ± 2.7 a	3.9 ± 0.4 a	34 ± 1.2 a
	Burn	78 ± 3.5 b	1.9 ± 0.1 b	<1 ± 0.2 b
	Mean	84.0	2.9	1.9 A
Outside canopy	Control	87 ± 1.9	2.7 ± 0.4	7 ± 1.7 a
	Burn	81 ± 4.2	1.8 ± 0.1	1 ± 0.3 b
	Mean	83.4	2.3	3.8 A

Tree Canopy and Burning Effects on Ground Cover

EXPERIMENT 1: BURNING ON UNDERSTORY VEGETATION: TRANSECTS.—Before burning, the cover of bare soil was lower ($P = 0.043$) and litter cover was greater ($P = 0.044$) in the control than in burned plots in grasslands, while neither was significantly different between the burned and the control plots in forest understory (Table 5). Litter depth ($P = 0.035$ in grassland and $P = 0.037$ in forest), and total vegetation cover ($P = 0.009$ in grassland and $P = 0.024$ in forest) were reduced by burning for both grassland and forest sites in 1999, but recovered by 2002. Vegetation height was reduced in grasslands in 1999 but had recovered by 2002 ($P = 0.002$). In the forested sites, vegetation height was reduced by burning in 2002 ($P = 0.044$).

TABLE 7. Aboveground biomass in the understory ($\bar{x} \pm s_{\bar{x}}$; g · m^{-2}) at Dew Drop, British Columbia, Canada, in 2002 (the transect study). Prescribed burning was conducted in April 1999. Means with different lowercase letters within a column and site are significantly different at $P \leq 0.05$.

Site, treatment	Forb	Shrub	Standing live graminoid	Standing dead graminoid	Total aboveground
Grassland					
Control	14.7 ± 4.9 b	19.0 ± 8.2	76.8 ± 7.9	110.6 ± 9.5	211.0 ± 11.3
Burning	40.1 ± 13.3 a	6.2 ± 5.6	98.8 ± 14.5	170.0 ± 30.6	315.1 ± 41.8
P-value	0.064	0.231	0.146	0.131	0.057
Forest					
Control	0.8 ± 0.6	0.5 ± 0.5	31.8 ± 5.7 a	31.8 ± 6.5 a	64.9 ± 12.3
Burning	7.1 ± 2.8	0.2 ± 0.2	16.8 ± 2.9 b	15.4 ± 4.6 b	39.2 ± 8.7
P-value	0.104	0.704	0.049	0.097	0.148

TABLE 8. Effects of burning on understory biomass ($\bar{x} \pm s_{\bar{x}}$; g · m^{-2}) under and outside the canopy of ponderosa pine trees at Dew Drop, British Columbia, Canada, in 2002. Prescribed burning was conducted in April 1999.

Location, treatment	Forb	Shrub	Standing live graminoid	Standing dead graminoid	Total aboveground
Under canopy					
Control	1.0 ± 0.4	1.3 ± 0.8	6.0 ± 1.0	5.5 ± 0.9	13.7 ± 1.2
Burning	0.7 ± 0.1	0.0 ± 0.0	10.8 ± 4.3	11.2 ± 5.2	22.7 ± 9.7
Outside canopy					
Control	2.3 ± 1.1	0.2 ± 0.2	9.4 ± 3.3	12.9 ± 4.5	24.8 ± 9.0
Burning	2.0 ± 0.5	0.0 ± 0.0	14.2 ± 2.1	20.5 ± 4.1	36.7 ± 6.3
P-value	0.177	0.087	0.230	0.055	0.102

EXPERIMENT 2: BURNING ON CANOPY PROJECTION AREAS.—One year after burning (2001), log cover was reduced from 4% to 2% under the canopy and from 7% to 2% outside the canopy ($P = 0.005$), while the cover of bare soil increased from 3% to 10% under the canopy and from 3% to 5% outside the canopy in the burned plots ($P = 0.010$; Table 6). Litter cover was similar between quadrat locations within the control ($P = 0.078$) and within burned plots ($P = 0.484$). Burning did not affect litter cover outside the canopy ($P = 0.149$), but litter cover was reduced by burning under the canopy ($P = 0.037$). Litter depth was not different between treatments outside the canopy ($P = 0.123$), but it was reduced by burning under the canopy ($P = 0.009$). Burning reduced lichen cover both outside ($P = 0.045$) and under the canopy ($P = 0.044$); lichen cover was greater outside the canopy than under the canopy ($P = 0.032$).

Three years following burning (2002), litter cover, litter depth, and lichen cover were lower in the burned plots than in the control plots ($P = 0.005$, 0.010, and 0.016, respectively). Only outside the canopy was lichen cover reduced by burning ($P = 0.013$). Understory vegetation height was not affected by burning ($P = 0.649$) or quadrat location ($P = 0.679$).

Understory Biomass Production

EXPERIMENT 1: BURNING ON UNDERSTORY VEGETATION: TRANSECTS.—Although results were nonsignificant ($P > 0.05$), there was a trend that burning increased forb biomass by 173% ($P = 0.064$) and total understory biomass by 50% ($P = 0.057$) in the grassland in 2002 (Table 7). Graminoid biomass in forest understory was reduced 47% by burning ($P = 0.049$).

EXPERIMENT 2: BURNING ON CANOPY PROJECTION AREAS.—Aboveground biomass of forbs, shrubs, graminoids, and total vegetation was not affected by burning in 2001, but graminoid biomass was greater outside the canopy than under the canopy (data not shown). In the control under the canopy, biomass (g · m^{-2}) was 2.5 for forbs, 0.0 for shrubs, 10.4 for live graminoids, and 19.5 for dead graminoids, and total standing crop was 32.4 g · m^{-2}. Biomass (g · m^{-2}) in the burned plots under the canopy was 1.4 for forbs, 0.0 for shrubs, 22.3 for live graminoids, 20.2 for dead graminoids, and 43.9 for total aboveground vegetation. Biomass (g · m^{-2}) in the control outside thecanopy was 5.5 for forbs, 0.0 for shrubs, 8.3 for live graminoids, 16.3 for dead graminoids, and 30.1 for total aboveground vegetation. Biomass (g · m^{-2}) in the burned plots outside the tree canopy was 1.8 for forbs, 0.0 for shrubs, 18.4 for live graminoids, 20.4 for dead graminoids, and 40.6 for total aboveground vegetation. Aboveground biomass of forbs and graminoids was not affected by burning or quadrat location in 2002 (P = 0.177 and P = 0.230, respectively; Table 8). There was a trend that burning reduced shrub biomass under tree canopy, but total understory biomass was not affected by burning or quadrat location (P = 0.087 and P = 0.102, respectively).

Discussion

Crown scorch height, a measure of fire severity, can be a predictor of tree mortality (van Mantgem and Schwartz 2004). In this study, even though the positive correlation between scorch height and tree size was weak (R^2_{adj} = 0.12), fire was effective in eliminating small ponderosa pine (dbh < 10 cm) and Douglas-fir (dbh < 20 cm) trees. Therefore, this prescribed burning experiment was a successful example of ecological restoration aiming at the recovery of historical forest structure (Covington et al. 1997, Allen et al. 2002). Increased survival for larger trees is attributed to the increasing bark thickness, the principal factor affecting cambium temperature during burning (Costa et al. 1991). Ponderosa pine trees tend to have fire-resistant bark and to dominate the canopy in fire-maintained forests (Gayton 1996). In contrast, Douglas-fir trees are relatively thin-barked and are the primary tree that in-grows in stands where fire is excluded in the forests of Interior British Columbia (Gayton 1996). Tree species, tree size, fuel consumption, and season of burn affect fire resistance (Stephens and Finney 2002).

Litter was low in cover and depth at both grassland and forest sites in this study, which restricted the fire severity. Fire was also uneven due to the spatially uneven distribution of litter, and fuel reduction by prescribed burning was temporary. Therefore, these results suggest that the reduction of fuel on the ground in these ecosystems is not critical for preventing catastrophic fires. Thus, thinning, when applicable, may also serve the purpose of restoring historical forest structure. Burning reduced lichen cover; and after burning, areas outside the tree canopy had less lichen cover than areas beneath the canopy. Lichen colonies can be killed or severely damaged by fire in sand prairie (Schulten 1985) and in *Festuca* and *Agropyron* grasslands (Antos et al. 1983). In our study, lichen cover was significantly reduced by burning, and lichen recovery after fire was slow. Lichens have important ecosystem functions related to succession (McCune and Geiser 1997). In the dry forests of the Pacific Northwest of the United States, lichen biomass increased with increasing stand complexity and moisture (Lehmkuhl 2004). Changes in species richness, species evenness, and species diversity in grasslands after burning were not significant. However, species evenness and the diversity index were both reduced by burning in the forest 3 years after the treatment. The different responses in species diversity between grasslands and forests may be due to the higher fire severity associated with more fuel in the latter. Increases in species diversity are desirable, especially in grassland communities, because they may increase the ability of the ecosystem to withstand and recover from disturbances such as drought (Tilman and Downing 1994). Our result of reduction in species evenness and diversity of forests because of fire contradicts results of Busse et al. (2000) in which species richness and diversity increased for 2 years following underburning in thinned ponderosa pine stands. Species composition of both grasslands and forests in our study was modified by prescribed burning, but spatial variability was overridden by treatment and temporal effects. Immediate but short-term reduction in big sagebrush was observed at grassland sites and in rabbitbrush at forest sites.

Understory species cover was low at forest sites. Graminoid cover was higher outside the canopy than inside the canopy, and fire enhanced needle-and-thread cover. A low-severity prescribed burn in the spring in thinned ponderosa pine forests of central Oregon reduced shrub cover by more than 50%, but burning had little effect on forb or graminoid cover (Busse et al. 2000). Similar responses were observed in Montana 8 years following burning; bitterbrush and mountain big sagebrush cover was reduced in burned plots (Fraas et al. 1991). Minimal response of shrubs to canopy reduction by burning was observed in a ponderosa pine forest, possibly due to the inability of shrubs to respond to the additional light as quickly as graminoids or forbs (Riegel et al. 1995). No alien species invasion was observed in our study area, possibly due to the low level of disturbance and small sampling scale compared to conditions in other studies (e.g., Dodson and Fieldler 2006).

Changes in species composition are related to both direct and indirect modification of ecosystems by fire. The presence and structure of the overstory canopy directly influence light reaching the understory; understory vegetation productivity and structure are the result of competition for light (Dodd et al. 1972, Peltzer et al. 1998, Harrington and Edwards 1999, Aubin et al. 2000). Ideally, the removal of tree canopy will increase the amount of light reaching understory vegetation, but its effect on understory plant cover and species richness are species specific (Thomas et al. 1999, Rankin and Tramer 2002, Fornwalt et al. 2003). Burning can alter environmental attributes in grasslands and forests, such as light, air temperature, and soil temperature (Riegel et al. 1995, Hart et al. 2005).

Data trends from the present study indicate that 3 years after burning, total biomass, and forb biomass increased in grasslands, which agrees with previous reports that burning favors forbs over grasses (Daubenmire 1968, Antos et al. 1983). Fires are often used in grasslands to stimulate forage production and to control weedy and woody species (Wright 1974). Burning and subsequently increased grazing pressure promoted forb production and changed the plant community from grass-dominated to forb-dominated (Vermeire et al. 2004). Increases in biomass production do not necessarily equate with an increase in palatable forage species, and changes in species composition after burning must be interpreted with caution because these changes may be induced by greater grazing and browsing (Oswald and Covington 1984). For example, burning in a *Festuca-Stipa* grassland increased forbs such as three-flowered avens *Geum triflorum* (Pursh), milkvetch *Astragalus striatus* (Nutt.), yarrow *Achillea millefolium* L., and pussytoes *Antennaria spp.* Gaertn. (Bailey and Anderson 1978). Biomass production increased 3 years following burning in southwestern ponderosa pine forests, but the amount of palatable forage was reduced (Oswald and Covington 1984). Within forested sites of our study, burning reduced aboveground biomass production of graminoids but had no effect on forbs or total understory biomass. Changes in graminoid abundance may be attributed to changes in light and structural conditions in the forest (Naumburg and DeWald 1999). It should be noted that Busse et al. (2000) found no evidence that prescribed burning would have long-term impacts on stand productivity in ponderosa pine forests, possibly due to the adaptation of these ecosystems to frequent fires.

The dry forests of Interior British Columbia, Canada, are adjacent to grasslands, and the expansion of forests to grasslands caused the reduction of rangelands at a rate of 10% per decade between the 1960s and the 1990s (Bai et al. 2004). Because of low fuel on the soil surface, using prescribed burning to reduce surface fuel load in order to avoid catastrophic fires may not be critical. Burning, however, can be used to control tree encroachment and forest ingrowth of ponderosa pine and Douglas-fir forests in this region. While aboveground biomass production may be enhanced by burning in grasslands, its impact on forest understory was minimal, and burning may result in a reduction of graminoids. Using fire to control encroaching trees and forest ingrowth is complicated because each fire is a unique event, differing in fuel, topography, and weather conditions. Our previous research has shown that landscape dynamics play critical roles in forest ingrowth and tree encroachment in Interior British Columbia (Bai et al. 2004). Thus, it is difficult to predict the effects of prescribed burning on species composition, biomass production and range management (Wikeem and Strang 1983). Management plans must incorporate topography, species diversity, and tree survival initiatives in order to target areas that are most susceptible to tree encroachment and achieve desired results. Extended monitoring is necessary to determine the long-term effects of burning on species diversity and productivity in these ecosystems. We caution the reader, however, that even though these ecosystems historically had short fire-return intervals, repeated burning at short intervals may not be beneficial to ponderosa pine forests because fine root biomass and mycorrhizal root biomass, as well as below-ground nutrient pools, can be reduced (Hart et al 2005). Also, we should note that the recent outbreak of mountain pine beetles in British Columbia and in other parts of the Pacific Northwest has caused massive mortality of ponderosa pine trees. Thus, using prescribed burning to control tree encroachment and ingrowth in the region may not be a major management concern in the foreseeable future.

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