

Reintroducing fire into a ponderosa pine forest with and without cattle grazing: understory vegetation response

BECKY K. KERNS,[†] MICHELLE BUONOPANE, WALTER G. THIES, AND CHRISTINE NIWA

United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory,
3200 SW Jefferson Way, Corvallis, Oregon 97331 USA

Abstract. Reestablishing historical fire regimes is a high priority for North American coniferous forests, particularly ponderosa pine (*Pinus ponderosa*) ecosystems. These forests are also used extensively for cattle (*Bos* spp.) grazing. Prescribed fires are being applied on or planned for millions of hectares of these forests to reduce fuel loads, alter forest structure, and maintain and enhance the productivity of native plant communities. However, cattle grazing is ubiquitous in ponderosa pine forests and the consequences of post-fire cattle grazing on plant communities are not well understood. We evaluated cattle grazing effects (grazing, no grazing) on upland bunchgrass and *Carex geyeri* dominated ponderosa pine plant communities over five growing seasons after prescribed fires (spring reburn, fall reburn, no burn). Vegetation was measured prior to a 5-year interval reburn and the subsequent exclusion of cattle, and in the second and fifth growing seasons thereafter. We found no interactions between reburning and grazing for the understory response variables. For all reburn treatments, including unburned areas, five growing seasons of cattle grazing exclusion significantly increased: (1) total vegetative cover, (2) native perennial forb cover, (3) grass stature, (4) grass flowering stem density, and (5) the cover of some shrub species and functional groups. Grazing exclusion did not strongly affect plant compositional patterns, although differences were detected. Compared to unburned areas, neither spring nor fall reburning increased perennial native species cover or richness, and reburning reduced sedge cover. Fall reburning increased cover of native colonizers, and exotic species cover and richness (largely *Bromus tectorum* and *Cirsium vulgare*), although overall exotic cover remains low (<1%). We document several potentially chronic impacts of cattle grazing in both burned and unburned areas, and show that the understory release from a long history of cattle grazing caused a greater degree of change than the initial reintroduction of fire. If a goal of ecological restoration in these forests is increased cover of native perennial plants, and the potential for increased native perennial grass reproduction, then cattle grazing exclusion, or a change in cattle management, could provide critically important options in restoration plans.

Key words: cattle grazing; cheatgrass; fire effects; forest management; maintenance burning; Oregon; *Pinus ponderosa*; prescribed fire; season of burn; vegetation.

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[†] E-mail: bkerns@fs.fed.us

INTRODUCTION

Knowledge about the effects of fire on understory vegetation in coniferous forested ecosystems typically comes from single-burn prescribed

fire or wildfire studies that exclude domestic livestock grazing. Fewer studies have examined the interaction of fire and cattle grazing together. Yet livestock grazing occurs on approximately 91% of all federal lands in the 11 contiguous

Western States (Armour et al. 1991; a total of 95 million hectares in the U.S.; United States General Accounting Office 2005). Many of these lands are also the focus of extensive restoration efforts involving the reintroduction of fire. Exclusion of livestock allows a researcher to isolate fire or other treatment effects, but application of results from such studies to realistic management situations where livestock grazing is a factor may be misleading. Ungulates can exert important influences on ecosystem processes and have profound direct and indirect effects on vegetation development and species composition (Hobbs 1996, Weisburg and Bugmann 2003, Wisdom et al. 2006, Bakker and Moore 2007). Livestock consume and reduce the abundance of grasses and the herbaceous understory, and can shift dominance from palatable perennial bunchgrasses to more unpalatable grasses and herbaceous species, and aid shrub and tree encroachment (Madany and West 1983, Belsky and Blumenthal 1997, Augustine and McNaughton 1998, Jones 2000). In ecosystems that evolved with frequent fire regimes and where fire is being reintroduced, it is critical to understand how fire effects on the understory plant community differ with and without post-fire cattle grazing.

In North American coniferous forests, reintroducing fire is a high priority for forest restoration and management, particularly in ponderosa pine (*Pinus ponderosa*) ecosystems. These forests are also used extensively to graze livestock. Existing policies and legislation (e.g., National Fire Plan, Healthy Forest Restoration Act) emphasize the widespread use of prescribed fire and mechanical thinning, driven by increasing concerns regarding undesirable changes in forest structure and function such as loss of biodiversity; risk of large, uncontrollable, severe and costly wildfires; insect and disease outbreaks; low tree vigor and drought-related tree mortality; and widespread ecosystem "collapse" (sensu Covington 2000). Ponderosa pine forests are a major forest type in western North America (Oliver and Ryker 1990) and their ecological history has served as a textbook example for the reintroduction of fire and the use of prescribed fire to restore forest structure and function (Moore et al. 1999, Allen et al. 2002, Hessburg and Agee 2003). The role and importance of fire as a disturbance process in forests (Agee 1993, Fulé et al. 1997, Hessburg and

Agee 2003) and disruption of fire regimes coinciding with Euro-American settlement and associated fire suppression and exclusion (Covington and Moore 1994, Swetnam et al. 1999, Hessburg et al. 2005) have been extensively presented and discussed. Ponderosa pine forests are targeted for restoration using prescribed fire because impacts of fire exclusion and suppression, land use, and climate are thought to be greatest and treatments most ecologically relevant in forests that historically experienced very frequent fires and periodic drought (Covington 2000, Brown et al. 2004, Hessburg et al. 2005). However, most of these forests are now subject to cattle grazing, which is considered a novel disturbance because there is no evolutionary history of a comparable grazing ungulate in the Great Basin and Intermountain West, such as is found in other ecosystems (e.g., bison [*Bison bison*] in the North American tallgrass prairie) (Mack and Thompson 1982, Harris 1991, Jones 2000, Adler et al. 2004, Bates et al. 2009, Davies et al. 2009).

Although knowledge about fire and grazing interactions in forested ecosystems is limited, this disturbance combination has been examined in many other ecosystems, particularly rangelands that evolved with fire and ungulate grazing such as the North American tallgrass prairie and African savannahs (Collins 1987, Hobbs et al. 1991, Van Langevelde et al. 2003, Fuhlendorf and Engle 2004, Collins and Smith 2006, Burns et al. 2009, Staver et al. 2009). Results from these studies suggest that (1) grazers preferentially select burned areas; (2) burning reduces plant diversity as common and abundant species increase; (3) grazing increases plant diversity, reducing dominant grass cover and increasing ruderal forb cover, even when burned, although effects differ by species and grazing animals; (4) fire and grazing interact through positive and negative feedbacks to cause a shifting mosaic; and (5) synergistic effects can result in woodland encroachment. Cingolani et al. (2005) concluded that ecosystems with a long history of grazing have evolved resilience mechanisms that allow for reversible changes associated with grazing intensity, but systems with short grazing histories often lack these mechanisms and may cross irreversible transitions.

There is also a body of literature documenting

the effects of wildfire and prescribed burning on understory abundance or diversity in the absence of cattle grazing (Covington et al. 1997, Gildar et al. 2004, Metlen and Fiedler 2006, Knapp et al. 2007, Laughlin and Fulé 2008, Webster and Halpern 2010). Evidence from these studies suggest that understory abundance or diversity can be enhanced by prescribed fire, although some report variable responses (Laughlin et al. 2004, Laughlin 2006, Moore et al. 2006). Other studies (Youngblood et al. 2006, Kuenzi et al. 2008, Schwilk et al. 2009) and a recent literature review (Bartuszevige and Kennedy 2009) concluded that fire generally increased understory species response but failed to note the presence or absence of livestock grazing. The one study we found that did note the presence of post-fire livestock grazing reported a decline in understory abundance after fire (Metlen et al. 2004), but the authors did not specifically attribute this decline to grazing.

We developed a study to evaluate an array of forest understory vegetation responses to repeated prescribed burning (5-yr interval: spring, fall, and no burning) and cattle grazing (grazing, no grazing) and the interaction of this disturbance combination in an eastern Oregon ponderosa pine forest. Five-year interval burning represents the approximate lower limit of historical fire-return intervals in eastern Oregon and Washington ponderosa pine forests (4–11 years; Bork 1984, Heyerdahl et al. 2001, 2008, Hessler et al. 2004). Spring and fall burning were tested because although most historical fires burned in the summer or fall, spring fire, weather, and fuel conditions allow fuel consumption and fire behavior to be more easily controlled. Managers are often concerned about potential deleterious effects owing to spring burning because it is outside the natural range of variability for these systems. We concentrate on the forest understory (shrubs, grasses, forbs, regenerating conifers) because the understory contributes virtually all plant biodiversity in western conifer forests; and helps regulate many processes such as conifer regeneration, soil retention, nutrient cycling, and watershed function; and underpins faunal diversity (Harrod 2001, Allen et al. 2002, Kerns and Ohmann 2004, Moore et al. 2006).

This study is part of a larger experiment in eastern Oregon designed to examine multiple

prescribed fire effects (Smith et al. 2004, Thies et al. 2005, 2006, Kerns et al. 2006, Hatten et al. 2008). Vegetation cover and richness and grass height and flowering density were measured prior to a 5-year interval reburn and the subsequent exclusion of cattle, and in the first, second, and fifth growing seasons thereafter. To better link our results to cattle grazing impacts rather than simply measuring utilization (plant material removed by cattle), vegetation on nearly all plots was measured each year prior to seasonal introduction of cattle and their utilization of vegetation. Our study is uncommon and robust in that (1) we have pre-grazing exclusion vegetation data, and (2) our grazing exclosures are replicated and were established in random locations within each prescribed fire treatment unit. We assess changes in understory plant abundance, richness, reproduction and species composition, considering broad functional groups of plants. We also explore plant community composition in relation to the type of disturbance, fire severity, forest structure, soil properties, and environmental heterogeneity using multivariate statistics.

METHODS

Study area

The study was conducted using four upland forested stands located at the southern end of the Blue Mountains, Emigrant Creek Ranger District, Malheur National Forest, Oregon (Fig. 1, Table 1). Stands ranged in size from 40–56 ha, with individual treatment units ranging from 4–18 ha. The stands were identified and delineated by US Forest Service district staff in 1995 and span a productivity gradient from the west (more productive) to the east (less productive), and are part of a larger, relatively continuous ponderosa pine and mixed-conifer forested landscape. Two stands (Driveways 14 and 26) are located in the southeastern part of the district at the edge of the forest zone adjacent to the Northern Great Basin (Fig. 1). The other two stands (Trout and Kidd Flat) are located 18 km to the west. Each stand received a thinning prescription in 1994 or 1995 (consistent within each stand), including areas later delineated in this study as controls. Stands were thinned from below and no trees greater than 53 cm diameter at breast height were

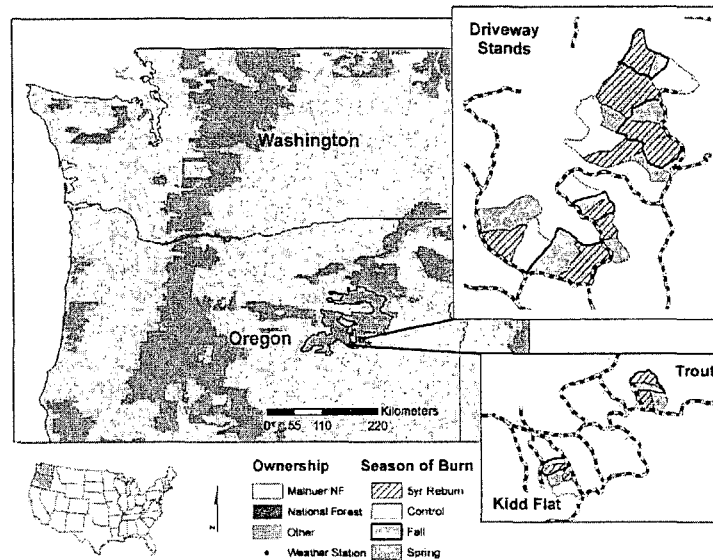


Fig. 1. The study area showing the location of the Malheur National Forest, the four study stands, and the layout of the burning and grazing treatments.

Table 1. Results comparing environmental, soil, and vegetation characteristics for the four study stands.

Characteristic	Eastern study area		Western study area	
	Driveway 14	Driveway 26	Trout	Kidd Flat
Stand size (ha)	56	44	40	35
Environment				
Elevation (m)	1570–1740	1645–1725	1640–1670	1680–1730
Slope (%)	14–49	5–22	3–14	4–32
Aspect	S–SW	SE–SW	various	N–NE
Soils†				
Soil texture, <2 mm	sandy clay loam, sandy loam, clay	sandy loam, sandy clay loam, clay	sandy clay loam, sandy loam	sandy clay loam, loam, sandy loam
pH (2:1 H ₂ O/soil)	6.3 (6.1–6.6)	6.2 (5.8–7.1)	6.2 (5.8–6.6)	6.2 (5.7–6.6)
Total carbon (%)	2.7 (1.9–3.5)	3.7 (2.6–4.5)	2.5 (1.6–3.9)	6.4 (2.3–11.1)
Total nitrogen (%)	0.2 (0.1–0.2)	0.2 (0.1–0.3)	0.1 (0.1–0.2)	0.3 (0.1–0.5)
C:N	18 (15–20)	18 (16–19)	26 (26–30)	20 (18–22)
Understory vegetation (% cover)‡				
Total plant cover	19 (8–47)	15 (6–22)	22 (8–38)	65 (29–95)
Exotics	0.3 (0–1.5)	0.1 (0–0.2)	0	0.1 (0–0.2)
Annual forbs	0.3 (0–1.1)	1.2 (0.2–4.9)	0.2 (0–0.4)	0.2 (0–0.9)
Perennial forbs	2.8 (0.8–7.4)	3.1 (1.2–4.8)	5.9 (0.3–19.1)	11.4 (1–28.4)
Perennial grasses	12.8 (2.2–41.9)	7.0 (1.1–9.5)	2.0 (0.6–4.8)	4.8 (0.8–11.3)
Sedges	2.5 (0–4.6)	2.1 (0–7.8)	7.4 (1.6–13.1)	44.4 (14.9–60.9)
Shrubs	<0.10 (0–0.3)	0.9 (0–3.3)	2.1 (0.4–6.8)	3.8 (1.6–5.4)
Tree structure§				
DBH (cm)¶	24.7 (17.1–33.6)	29.7 (23.3–37.6)	27.3 (21.5–33.3)	25.4 (19.6–37.7)
Density (ha ⁻¹)	383 (237–840)	266 (148–445)	202 (158–252)	253 (119–410)
Tree basal area (m ² /ha)	19.6 (14.9–26.8)	20.0 (15.1–24.8)	17.2 (11.4–27.6)	15.8 (10.2–25.9)
Canopy cover (%)	28 (16–40)	34 (8–49)	39 (29–56)	35 (11–61)

Note: Soil and vegetation data are means and ranges.

† Data are based on the <2 mm mineral fraction, 0–15 cm depth and were collected in 2007.

‡ Data are from untreated control plots sampled in 2002.

§ Data are from preexisting subplots (0.20 ha) established by others (Thies et al. 2005) and sampled in 1998.

¶ DBH = diameter at breast height, 1.37 m.

removed.

Estimated mean annual cumulative precipitation was 610 mm per year (1982–2008), falling mostly as snow between October and April (all climate data based on the Rock Springs SNOTEL Site, elevation 1612 m, 20 km northwest of the study sites, USDA-NRCS 2009) (Fig. 1). Mean water year annual precipitation (MWYAP, October 1–September 30) was 452 mm, and the mean growing season (1989–2008) was 162 days. Snowmelt typically occurs late May–mid-June and then spring ephemeral annual and biennial plants emerge. Perennial grasses and forbs are in a period of rapid growth and expansion and begin to flower by mid-June. Peak flowering is usually in July, and most plants are dormant by mid to late August. In 2002, water year annual precipitation (WYAP) was 88% of MWYAP, and the growing season length was 93% of the historic average. In 2004, WYAP was 102% of MWYAP, and the growing season was about average (164 days). In 2007, WYAP was 75% of normal, and the growing season length was 124% of the historic average.

Parent materials consisted of basalt, andesite, rhyolite, tuffaceous interflow, altered tuffs, and breccia (Carlson 1974). The soils received ash from pre-historical eruptions of ancient Mount Mazama and other volcanoes in the Cascade Mountains to the west (Powers and Wilcox 1964). Mount Mazama ash occurred on north-facing slopes, especially at Kidd Flat, which may partially explain the higher plant cover and tree productivity at this stand (C. Johnson, *personal communication*). Soils were generally dominated by Mollisols, but Inceptisols and Alfisols were also present (Carlson 1974, Hatten et al. 2008). Soil texture and pH among the stands were quite similar, but Kidd Flat had higher total carbon (C) and nitrogen (N) concentrations (Table 1).

The four stands were dominated by mixed-aged ponderosa pine, but *Juniperus occidentalis* and *Cercocarpus ledifolius* also occurred. Ponderosa pine trees in the study area were approximately 80–100 years old with infrequent individuals of about 200 years old (Emigrant Creek Ranger District, *unpublished data*). Differences in understory floristic composition among the stands were apparent. The lower site productivity eastern area stands had more xeric vegetation than the two western stands (Table 1),

and were dominated by bunchgrasses (*Elymus elymoides*, *Achnatherum occidentale*, *Poa wheeleri*, *P. secunda*, *Bromus carinatus*), *Carex rossii*, and *Chrysothamnus* spp. *Pinus ponderosa*/*Agropyron spicatum* was the major plant association. Exotic species (mostly *Bromus tectorum* and *Cirsium vulgare*) were common but only abundant in localized patches (Table 1). The western stands were dominated by *Carex geyeri*, and forbs such as *Arnica cordifolia* and *Kelloggia galioides*. *Pinus ponderosa*/*Carex geyeri* was the major plant association. Exotics were much less common in the western than in the eastern stands. Shrubs were a much larger component of the flora and included *Berberis repens*, *Purshia tridentata*, *Symphoricarpos albus* and *S. oreophilus*, and both *Prunus virginiana* var. *melanocarpa* and *P. emarginata*. Kidd Flat had the highest mean total cover, with relatively low total cover at the other sites (Table 1).

From 2002–2007, each stand was grazed by cattle from late June/early July through early to mid-August (except in the no grazing exclosures), when the cool-season grasses that characterize the area are at the peak flowering stage. A grazing record exists for the study area from 1946 to the present (Table 2). This history revealed that the area had been grazed almost continuously since 1946, although data are missing for some years. Staff indicated that the areas were grazed by cattle prior to 1946, and prior to the formation of the National Forest Reserves in the late 1880s. Both the eastern and western stands (each included in a single grazing area) were more heavily grazed from the 1940s until the mid-1990s (Table 2). Not only were more cattle in each area during this period, but the grazing season extended longer into the fall. For the past 10 plus years (mid-1990s on), cattle numbers were reduced significantly, and the season of use was cut approximately in half.

Experimental design

This study is part of a larger experiment that was established in 1997 as described by Thies et al. (2005). Our study was established in 2002 and is a split-plot randomized complete block with two factors: reburning and grazing (Fig. 2). Blocking was based on stand ($n = 4$, Table 1). Reburning was the whole plot treatment with three factor levels that appear one time in each block: control, spring 5-yr reburn, and fall 5-yr

Table 2. Grazing history for the four study stands, with specific details for the experimental sampling period.

Period	Ragged Rock Area		North Idlewild Area		
	No. animals	Season	No. animals	No. yearlings	Season
Historical					
1946–1996	160–605	6/1–10/15	60–520		6/1–10/15
1997–2001	270–296	6/26–8/20	345–348		7/1–8/7
Experimental					
2002	285	6/29–8/10	345	33	7/1–8/5
2003	285	7/1–8/1	345	33	7/1–8/5
2004	184	7/1–8/15	348	33	7/1–8/6
2005	184	7/1–8/15	348	30	7/1–8/6
2006	285	7/1–8/15	348	30	7/1–8/6
2007	184	6/24–8/15	348	30	7/1–8/6

Note: Summarized from brief grazing histories provided by the Emigrant Creek Ranger District. Both Driveway stands are in the Ragged Rock Area. Trout and Kidd Flat are in the North Idlewild Area. No yearlings were noted for the Ragged Rock Pasture in the grazing history.

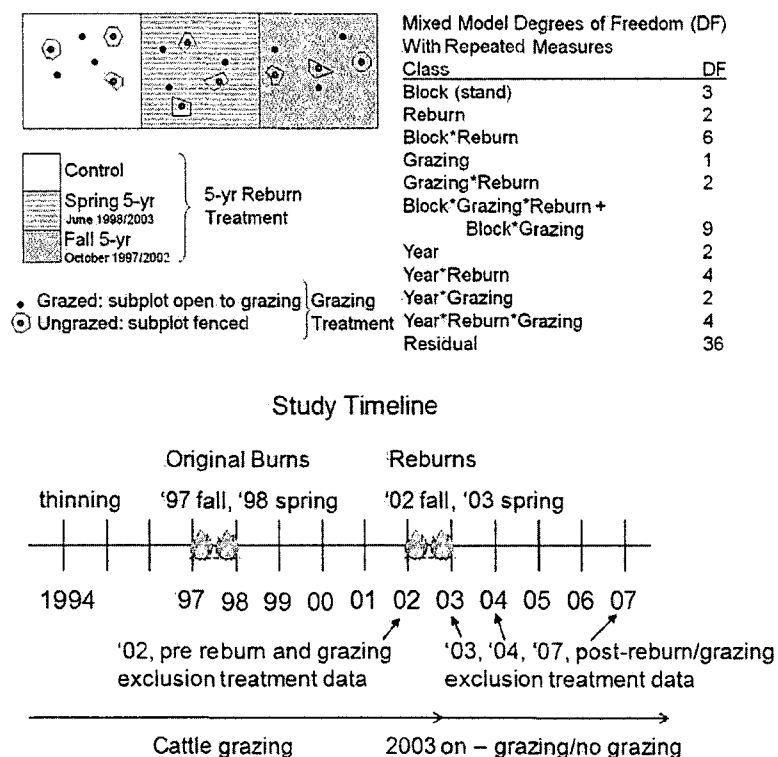


Fig. 2. Top left: schematic of a single block (stand) showing the study design. This design was replicated using four blocks ($n = 4$), and measurements were taken for most variables in 2002, 2004, and 2007. The table on the top right shows the degrees of freedom for the repeated measures mixed model ANOVA. The bottom schematic shows the study timeline.

reburn. Prior to burning, each stand was divided into three units with boundaries established along roads and topographic features to control prescribed burns. Treatments were then randomly assigned. The fall burn was applied in October

1997/2002, and the spring burn in June 1998/2003. Fires were ignited by hand-carried drip torches using a multiple-strip head-fire pattern. Crews attempted to maintain flame lengths at approximately 60 cm during the burns. Temperature,

humidity, and wind speed and direction were similar during the application of all burns.

For the grazing treatment, we established three 10-m radius vegetation subplots open to grazing and three subplots that were not open to grazing within each burn treatment (Fig. 2), for a total of 72 observations. For subplots open to grazing, we used the preexisting systematically designed subplots set up in 1997 (Thies et al. 2005). We then built three fenced exclosures and located a single 10-m radius subplot within each exclosure. Exclosures were located along a random bearing a minimum distance of 50 m from the preexisting subplots using a compass and tape. This distance provided a minimum 36-m buffer between cover quadrats. However, the actual average distance between exclosures and grazed subplots was often greater, although highly variable (mean = 100 ± 65 m, using GPS/GIS). Seven subplots were only 38–50 meters apart. Three of these subplots were in one small control treatment (Trout) that was established after the original control was accidentally burned in 1997. Sizes of the exclosures differed slightly because trees were opportunistically used for posts; but all measurements (unless noted, e.g., tree canopy cover, see *Methods: Vegetation*) were done within the 10-m radius subplots. Because the original subplots were established to examine black stain root disease and mortality in ponderosa pine, subplot locations for exclosures were rejected if they fell in areas with few or no ponderosa pine trees (Thies et al. 2005), or if they fell in areas not representative of the open grazing subplot. Thus our results are only applicable to upland forested areas.

Cattle grazing use was operational in nature and we made no attempt to manage grazing for consistent use across our plots. Therefore some plots were more heavily grazed than others simply based on preference. Grazing season of use and number of animals for each area during the experimental period is shown in Table 2. The fenced exclosures we built only excluded cattle. Native ungulates (deer, elk, and antelope) and other herbivores could easily enter by jumping over or going under the barbed wire, and we documented that native ungulates were accessing the exclosures by observing fresh dung and utilization. In addition, we only closed the fences when cattle were present in the area.

Sampling

Fire severity and fuels.—A fire severity classification based on the percentage of the subplot that was burned, burn patchiness, and the post-fire appearance of litter and soil was developed to relate fire severity to ecosystem response, using broadly defined discrete classes that ranged from low to medium to high fire severity (modified from DeBano et al. 1998). Because we were measuring fire severity on reburned plots, some typical measurements (bole scorch, crown scorch) were problematic and could not be used. Woody fuels were measured in 2002 to collect pre-burn treatment information, and in 2003 after the burning, except controls were only measured in 2002 (for fuels only). Each treatment contained a total of fourteen 20.12 m long transects. Two transects were established at the center of each of the three subplots using a random azimuth and corresponding back azimuth (six transects). An additional eight transects were set up 40.23 m from an established subplot center at a random azimuth between established subplots. For control units, the six established subplots were used to establish 12 transects as described above, then two additional random transects were established (as above), for a total of 14 transects. Along each transect litter and duff (not differentiated) accumulation was measured and woody debris was tallied according to Brown (1974).

Vegetation.—Measurements were designed to assess plant community responses without destructive sampling, as well as some aspects of rangeland health (Pellant et al. 2000, Pyke et al. 2002). The drier eastern sites are sampled before the mesic western stands, which allows each stand to be sampled at near peak biomass and minimizes sampling effects due to phenology. We strived to sample vegetation prior to cattle utilization of vegetation, although sometimes cattle were released onto the area while we were sampling. However, the vast majority of plots were not grazed prior to sampling. We used a series of nested plots as described below prior to the 5-year interval reburns in 2002, and again in the first (2003), second (2004), and fifth (2007) growing season thereafter. Within each 10-m radius subplot, current year's understory plant canopy cover was visually estimated and recorded by species to the nearest percentage point on eight 1-m² quadrats using a marked (0.10 m)

PVC square. Quadrats were arranged 5 and 6 m from the subplot center in each cardinal direction. Ground cover (e.g., bare soil, rock, litter, woody debris >10 cm diameter) data were also recorded. To increase consistency in ocular estimates of plant cover, standardization exercises were performed periodically throughout each field season, and crew continuity was maintained all season and year-to-year when possible. We also recorded the maximum grass leaf height, maximum flower stem height, and number of flowering stems for each grass species on each quadrat in 2007. Presence of all species was recorded on the entire 10-m radius subplot. In 2007, shrub cover was recorded by species on the whole subplot. Conifer regeneration (trees <1.37 m in height) was tallied within the whole 10-m radius subplot by species for all sampling years. We measured overstory tree canopy cover using a moosehorn densiometer at the subplot center, and 5 and 15 m from the center in each cardinal direction (total of nine points for each subplot).

Forest floor and soils.—To directly couple data to our vegetation plots, we measured O horizon (litter plus duff) depth 7 m from the subplot center in each cardinal direction. Mineral soil samples were collected in each 10-m radius subplot in 2007. A single sample (0–15 cm) was removed 6 m from the subplot center along a random bearing (0–359°, sampling without replacement). Understory vegetation quadrats were avoided. In the laboratory, soils were air dried for 48 hours, large visible organic matter was removed, and then the soil was passed through a 2-mm sieve. Samples were then sent to the Analytical Service Center, College of Forest Resources, University of Washington, and analyzed for texture, total C, N, and pH (H₂O/soil, 2:1). Texture was determined by the hydrometer method for silt (Gee and Bauder 1986), and wet sieving (50 µm) for sand. Clay concentration was then determined mathematically (100 – (sand + silt) = clay %). Total C and N concentrations were calculated on ground soil using a Perkin Elmer ELMER 2400 CHN analyzer (Nelson and Sommers 1996).

Data analysis

Because of the number of species (~217 taxa) and large floristic differences among the stands, species-specific analyses were generally not

practical. Instead, we examined species functional group categories for several general understory response variables, including plant abundance (cover, density, and height), richness, and reproductive capability (flowering stem height and density). Functional groups were based on species life history traits (Table 3). Life history and functional traits are a useful way to develop a general understanding of plant community responses to disturbance characteristics (Connell and Slatyer 1977, Halpern 1989, McIntyre et al. 1999, Pausas et al. 2004). Our grass group was composed of native perennial cool season grasses. There were no warm season grasses in the study area and there were no native annual grasses. Sedges were not included with graminoids because they are functionally different as they flower and senesce later in the season and are important fall forage for wildlife. For the exotics group, we were unable to statistically analyze the two dominant species separately (*Bromus tectorum* and *Cirsium vulgare*), thus they were combined. Forbs were broken into annuals and perennials. Dominate annual forbs were early successional species that emerged, flowered, and reached peak biomass very early in the growing season. Dominate perennial forbs were persistent in the flora, and tended to flower and senesce much later than the annual forbs. For shrubs, only four species occurred frequently enough at all four stands to analyze individually: *Amelanchier alnifolia*, *Berberis repens*, *Cercocarpus ledifolius*, and *Ceanothus velutinus*. Three other shrub functional groups, excluding these four species, were developed based on resprouting ability and known response to fire using information from the Fire Effects Information System (United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Science Laboratory 2009) and the USDA Plants database (USDA-NRCS 2010) (Table 3).

Subplot-level means for understory cover variables (e.g., cover, grass height) were generated using quadrat data. Understory conifers and shrub abundance (cover) were generated from subplot-level tallies and cover. Richness variables (total number of species) were generated from subplot-level species lists. We focused our analysis on simple metrics of species abundance and richness, rather than diversity indices, because these metrics are straightforward, readily under-

Table 3. The most common species from the study area for each of the plant functional groups analyzed (no more than five species are listed).

Group	Species
Grasses	<i>Elymus elymoides</i> , <i>Poa wheeleri</i> , <i>Achnatherum occidentale</i> ,† <i>Calamagrostis rubescens</i> , <i>Festuca idahoensis</i>
Sedges	<i>Carex geyeri</i> , <i>C. rossii</i> , <i>C. hoodii</i>
Perennial forbs	<i>Arnica cordifolia</i> , <i>Kelloggia galioides</i> , <i>Achillea millefolium</i> , <i>Thalictrum fendleri</i> , <i>Lupinus</i> <i>caudatus</i>
Annual forbs	<i>Onagraceae</i> spp.,‡ <i>Montia perfoliata</i> , <i>Collomia grandiflora</i> , <i>Cryptantha torreyana</i> , <i>Polygonum douglasii</i>
Exotics	<i>Bromus tectorum</i> , <i>Cirsium vulgare</i> , <i>Lactuca serriola</i> , <i>Verbascum thapsus</i>
Shrubs	
Resprouters, fire increasers	<i>Chrysothamnus nauseosus</i> , <i>C. viscidiflorus</i> , <i>Haplopappus bloomeri</i> , <i>Prunus emarginata</i> , <i>P.</i> <i>virginiana</i>
Resprouters, fire sensitive	<i>Rosa</i> spp., <i>Symphoricarpos albus</i> , <i>S. oreophilus</i>
Nonresprouters	<i>Ribes cereum</i> , <i>Artemisia tridentata</i> , <i>Purshia tridentata</i>
Understory conifers (<1.4 m)	<i>Pinus ponderosa</i> , <i>Juniperus occidentalis</i>

Notes: Data are based on cover using all plots and all years sampled. Species groups are native and perennial unless otherwise noted. Nomenclature of grasses based on Barkworth et al. (2007) and for all other groups on Hitchcock and Cronquist (1973).

† Includes a small component of *A. lemmonii*.

‡ Includes *Epilobium minutum* and *Gayophytum heterozygum*.

stood, and easy to communicate to managers and policymakers (McCune and Grace 2002).

Except for fuels and multivariate tests, data were analyzed as a randomized block, split-plot ANOVA design using Proc Mixed in SAS 9.1 (SAS Institute Inc. 2008). Main treatment effects (reburning, grazing) were fixed and block (stand) was random. When analyzing responses from multiple years (2002, 2004, and 2007), repeated measures analysis was used. Repeated measures analysis is distinct because of the covariance structure of observed data and the user must specify the nature of this covariance. We specified an unstructured covariance to allow heterogeneous variance and covariance among years, based on recommendations provided by Littell et al. (2006). The degrees of freedom associated with the repeated measures model are shown in Fig. 2. Because we are primarily interested in differences among the treatments, and because of the high number of statistical tests involved, we only present significant results for differences among treatments within each year that we sampled. Because fuels were not measured within the split-plot grazing treatment, a randomized complete block as described in Thies et al. (2005) was appropriate for analysis of these data.

Many variables were transformed to improve skewed distributions and heteroscedasticity based on an assessment of residuals. For presen-

tation of results throughout this text, including tables and figures, means or back transformed means associated with transformed data are presented, along with 95% confidence limits (CL) for data in association with statistical hypothesis testing, unless such a presentation interferes with graphical clarity. We set $\alpha = 0.10$ because we are willing to accept a higher probability of making a Type I error than 0.05. We also present *F* and *t* statistics, their appropriate degrees of freedom, and *P*-values for overall tests, when practical and when such a presentation does not interfere with graphical clarity. We used Fisher's Protected LSD for multiple comparisons for the reburn treatment component, which has three factor levels.

Compositional analyses were done using PC-ORD 5.10 (McCune and Mefford 2006). We used the Multi-Response Blocked Permutation Procedure (MRBPP) to examine whether burn and grazed plots differed from one another in community composition before the reburn and grazing exclusion (2002), and after (2003, 2004, and 2007) (Mielke 1984, 1991, Biondini et al. 1988, McCune and Grace 2002). The MRBPP is used for testing the hypothesis of no difference between two or more groups of entities. It is a nonparametric data dependent permutation based procedure that uses Euclidean distance. No assumption about the underlying data distribution is required. Species with only one

occurrence were removed and blocking was based on stand. If MRBPP results were significant, indicator species analysis was used to interpret these results by determining which species were most abundant and frequent within each treatment. Indicator species analysis (ISA) can be used to describe species relationships to experimental groups (Dufrêne and Legendre 1997, McCune and Grace 2002). For each year and for each stand, we looked at indicator species for each treatment, then summarized the results and report general commonalities. For each analysis, statistical significance was evaluated by a Monte Carlo Method using 4999 randomizations. We restricted our attention to species with $P < 0.10$ and indicator values > 50 (relative abundance \times relative frequency; values range from 0 to 100) (McCune and Grace 2002). For both the MRBPP and ISA analyses, cover data for all species were used and data were square-root transformed.

Non-metric multidimensional scaling ordinations were used to graphically display compositional similarities in vegetation based on treatment and other environmental variables (Kruskall 1964, Minchin 1987). All species were included in the analysis, except species that occurred on less than 4% of the plots were omitted from the ordinations and cover data were square-root transformed and relativized by species maximums. We used the Bray-Curtis distance measure (Faith et al. 1987) with random starting configurations, the "slow and thorough" autopilot setting, 50 runs with real data, a maximum of 250 iterations per run, and a stability criterion of 0.00001. Optimal dimensionality was based on choosing the number of axes beyond which reductions in stress were small (McCune and Grace 2002). A final three-dimensional solution with a stress of 13.8 was selected after inspecting stress values at each dimension. As an interpretive aid, we report Pearson correlation coefficients with each ordination axis for environmental variables (e.g., overstory cover, ground cover, soil, aspect, and fire severity) if $r^2 > 0.20$.

RESULTS

Fire effects

There was no significant difference in percent-

age area blackened between the spring (mean 73.6, CL 41.2, 106) and fall 5-year reburns (mean 79.8, CL 47.4, 112; $F_{1,3} = 1.15$, $P = 0.36$). Most spring reburns were recorded as low fire severity, and most fall reburns were recorded as moderate, indicating that the fall reburns were slightly more severe, although no high fire severity was actually recorded. Previous work documented that prior to burning, no differences were detected in overstory tree structure (Thies et al. 2005, 2006). But for the first round of prescribed fires (1997/1998), the fall burns were more severe, increasing tree mortality, reducing tree basal area, coarse woody debris cover, and litter cover and depth (Thies et al. 2005, 2006, Kerns et al. 2006). However, the reburns conducted in 2002/2003 did not result in any significant changes to tree structure (*unpublished data*). Tree canopy cover results show no difference for either burning or grazing treatment across the sampling period (Table 4).

Changes in ground cover conditions from the original 1997/1998 prescribed fires were evident in 2002 (Table 4). The original fall burns reduced litter cover and depth, and increased bare soil cover, whereas the spring burns did not have this effect. In 2007, similar ground cover patterns as 2002 were found, and the differences were more pronounced. For grazing, there were no differences in 2002 prior to treatment establishment, except that the ungrazed treatment had more coarse woody debris cover. This difference was also present in 2007. For O-horizon depth, a significant interaction (as shown in Fig. 2, Grazing \times Reburning), was found between reburning and grazing in 2007 ($F_{2,9} = 5.44$, $P = 0.03$). Areas open to cattle grazing had reduced litter depth compared to the no grazing treatment, but this was only true for the unburned controls (Table 5). Areas open to cattle grazing were also rockier than areas with no grazing.

We found no significant interaction between reburning and grazing for soil pH ($F_{2,9} = 0.66$, $P = 0.54$). Soil pH values in 2007 for the control were lower, presumably because of increased tree litter cover and depth, compared to the spring reburning, but not fall reburning (Table 5). Areas closed to grazing had higher pH values than areas that were grazed, a result that is counter-intuitive given that these tended to have more litter accumulation than areas open to grazing. It

Table 4. Results comparing overstory tree cover, ground cover and mineral soil data in relation to burning treatments; fires occurred in fall 1997/2002 and spring 1998/2003.

Characteristic	Control		Spring		Fall		$F_{2,6}$	P
	Mean	CL	Mean	CL	Mean	CL		
Tree cover (%)								
2002	34.0	(24.5, 43.6)	38.3	(28.8, 47.8)	30.0	(20.4, 39.5)	1.15	0.38
2007	43.0	(31.7, 54.3)	46.0	(34.7, 57.3)	34.0	(22.8, 45.3)	1.83	0.24
Ground cover (%)								
2002								
Bare soil	1.8 ^A	(0.5, 6.4)	1.7 ^A	(0.4, 6.1)	6.7 ^B	(1.8, 21.4)	12.64	<0.01
Rock	0.4 ^A	(0.1, 1.2)	1.5 ^{AB}	(0.5, 4.9)	1.6 ^B	(0.5, 5.0)	3.81	0.09
CWD†	1.9	(0.9, 3.4)	0.8	(0.2, 1.9)	0.6	(0.1, 1.5)	2.99	0.13
Litter	87.9 ^A	(79.3, 96.6)	87.4 ^A	(78.7, 96.1)	81.0 ^B	(72.3, 89.6)	4.75	0.06
O hz depth‡	4.6 ^A	(3.5, 6.2)	3.4 ^A	(2.6, 4.5)	2.4 ^B	(1.8, 3.2)	11.06	<0.01
2007								
Bare soil	1.9 ^A	(0.8, 4.3)	1.9 ^A	(0.9, 4.3)	5.0 ^B	(2.2, 10.7)	10.66	0.01
Rock	1.2 ^A	(0.7, 2.3)	2.6 ^B	(1.4, 4.7)	3.4 ^B	(1.9, 6.3)	12.10	<0.01
CWD	1.4	(0.4, 3.0)	0.6	(<0.1, 1.7)	1.0	(0.2, 2.4)	1.03	0.41
Litter	91.2 ^A	(87.9, 93.6)	89.9 ^A	(86.2, 92.6)	83.5 ^B	(78.1, 87.8)	13.28	<0.01
O hz depth‡	16.5 ^A	(13.7, 19.4)	12.9 ^{AB}	(10.1, 15.8)	9.1 ^B	(6.2, 11.9)	10.2	0.01§
Mineral soil								
2007								
pH	6.23 ^A	(6.1, 6.4)	6.57 ^B	(6.4, 6.8)	6.41 ^{AB}	(6.2, 6.6)	6.4	0.03
C (%)	3.50	(2.2, 5.5)	3.27	(2.1, 5.1)	3.56	(2.3, 5.6)	0.29	0.76
N (%)	0.18	(0.1, 0.3)	0.17	(0.1, 0.3)	0.19	(0.1, 0.3)	0.26	0.78

Notes: Data are means or back-transformed means followed by 95% confidence limits (CL) in parentheses. Significant differences are in bold; letters denote pairwise significance ($P < 0.05$).

† CWD = coarse woody debris.

‡ O hz depth = O horizon: the organic soil layer above mineral soil, measured in cm.

§ A significant interaction was found between reburning and grazing; a significant difference due to grazing was found only between the unburned controls.

Table 5. Results comparing overstory tree cover, ground cover and mineral soil data in relation to grazing treatments; 2002 data are pretreatment.

Characteristic	Ungrazed		Grazed		$F_{1,9}$	P
	Mean	CL	Mean	CL		
Tree cover (%)						
2002	32.7	(25.7, 39.7)	35.5	(28.5, 42.5)	0.44	0.52
2007	39.9	(31.7, 48.0)	42.1	(34.0, 50.3)	0.22	0.65
Ground cover (%)						
2002						
Bare soil	2.9	(0.9, 9.0)	2.6	(0.8, 8.0)	0.24	0.63
Rock	1.0	(0.4, 2.5)	0.9	(0.4, 2.1)	0.16	0.70
CWD†	1.8	(1.0, 2.7)	0.5	(0.2, 1.1)	10.46	0.01
Litter	83.8	(76.2, 91.4)	87.1	(79.4, 94.7)	2.86	0.12
O hz depth‡	3.7	(2.9, 4.6)	3.1	(2.4, 3.8)	2.93	0.12
2007						
Bare soil	2.3	(1.1, 4.7)	3.0	(1.5, 6.1)	1.89	0.20
Rock	1.9	(1.1, 3.2)	2.6	(1.5, 4.5)	3.83	0.08
CWD	1.5	(0.7, 2.7)	0.6	(0.1, 1.4)	4.16	0.07
Litter	88.7	(85.4, 91.3)	88.4	(85.1, 91.1)	0.05	0.83
O hz depth‡	14.3	(12.6, 16.0)	11.4	(9.7, 13.1)	16.23	<0.01§
Mineral soil						
2007						
pH	6.50	(6.4, 6.6)	6.31	(6.2, 6.5)	5.53	0.04
C (%)	3.57	(2.4, 5.4)	3.62	(2.2, 5.0)	0.61	0.46
N (%)	0.18	(0.11, 0.26)	0.18	(0.12, 0.26)	0.06	0.81

Notes: Data are means or back-transformed means followed by 95% confidence limits (CL) in parentheses. Significant differences are in bold.

† CWD = coarse woody debris.

‡ O hz depth = O horizon: the organic soil layer above mineral soil, measured in cm.

§ A significant interaction was found between reburning and grazing; a significant difference due to grazing was found only between the unburned controls.

Table 6. Results comparing litter and duff and woody fuels (metric tons ha⁻¹) by fuel class in relation to burning treatment for each sampling period; fires occurred in fall 1997/2002 and spring 1998/2003.

Fuel class	Control†		Spring		Fall		F _{2,6} ‡	P
	Mean	CL	Mean	CL	Mean	CL		
2002, 5-yrns post first burn								
Litter/duff (cm)	5.4 ^A	(4.0, 6.8)	4.7 ^A	(3.3, 6.0)	2.2 ^B	(0.7, 3.5)	9.30	0.015
1 Hour	0.2	(0.1, 0.3)	0.1	(0.0, 0.2)	0.1	(0.0, 0.2)	2.42	0.17
10 Hour	5.4	(3.7, 7.1)	4.2	(2.5, 5.9)	3.9	(2.2, 5.6)	1.64	0.27
100 Hour	6.3	(3.8, 8.8)	4.3	(1.8, 6.8)	4.6	(2.1, 7.1)	2.57	0.16
1000 Hour	6.4	(1.9, 10.9)	6.7	(2.2, 11.3)	7.8	(3.3, 12.4)	0.18	0.84
Total	18.3	(11.5, 25.2)	15.5	(8.5, 22.2)	16.5	(9.7, 23.4)	0.31	0.75
2003, post first 5-yr reburn								
Litter/duff (cm)	5.4 ^A	(3.9, 6.9)	4.2 ^{AB}	(2.7, 5.7)	2.3 ^B	(0.8, 3.8)	6.74	0.03
1 Hour	0.2	(0.1, 0.3)	0.1	(0, 0.2)	0.1	(0, 0.2)	2.28	0.18
10 Hour	5.1 ^{Aa}	(3.5, 7.5)	2.0 ^B	(1.4, 2.9)	3.3 ^{Cc}	(2.3, 4.8)	17.9	0.003
100 Hour	6.3 ^A	(5.0, 7.6)	3.2 ^B	(1.9, 4.5)	2.8 ^B	(1.4, 4.1)	40.1	<0.001
1000 Hour	6.4	(3.1, 9.7)	6.1	(2.9, 9.4)	5.1	(1.8, 8.3)	0.32	0.74
Total	18.3	(14.9, 21.7)	11.5	(0, 24.2)	11.3	(0, 24.0)	1.06	0.35
Percentage consumption								
Litter/duff	NA	NA	40.3	(32.7, 47.9)	22.1	(14.5, 29.7)	29.0	0.01
1 Hour	NA	NA	−18.2	(−115, 79)	28.9	(−68, 126)	2.1	0.24
10 Hour	NA	NA	50.3	(21, 79.7)	13.1	(−16.2, 42.4)	29.3	0.01
100 Hour	NA	NA	19.2	(−9.3, 47.6)	37.4	(8.9, 65.8)	10.8	0.05
1000 Hour	NA	NA	3.5	(−37.9, 45)	25.3	(−16.2, 66.8)	1.41	0.32
Total	NA	NA	23.2	(−1.7, 48.1)	25.6	(0.8, 50.5)	0.11	0.76

Notes: Fuels were collected in 2002 prior to the second fires. Data are means with lower and upper 95% confidence limits (CL) in parentheses. Negative percentage consumption indicates a fuel increase. Significant differences are in bold; letters denote pairwise significance (lowercase $P < 0.10$, uppercase $P < 0.05$).

† Data for controls are from 2002.

‡ Degrees of freedom for percentage consumption analyses are: denominator 1, numerator 3.

is possible the increase in pH may be related to the increase in plant abundance and grass biomass (see *Results: Understory response*), overriding the relatively small effect of litter accumulation.

Fuel loadings tended to be highest in controls in 2002, although the only fuel class that showed a difference was litter and duff (Table 6). In 2003, spring reburns had reduced litter and duff, and fall reburns slightly increased litter and duff. However, litter and duff were still reduced in the fall reburn compared to the control and spring. Looking at percentage consumption, spring burning consumed more litter and duff, largely because there was more litter and duff to consume. Both reburn treatments reduced 10-hr fuels. The spring reburn caused the greatest reduction in this category, and this result is reflected in percentage consumption as well. Both reburn treatments reduced 100-hr fuels and percentage consumption was greater in fall burns. No effect was detected for the largest 1000-hr fuel categories, and no effect was detected for all fuels combined (Table 6).

Understory response

We recorded 217 species in the study area throughout the sampling period, although only 172 were actually found on subplots. Many species (48) were in the Asteraceae family, including the second most common species (based on subplot frequency), the native perennial forb *Achillea millefolium* spp. *lanulosa*. Although more than half of all the species were native perennial forbs, the most common species was the native perennial grass *Elymus elymoides*.

Compared to areas open to grazing, grazing exclusion significantly increased total plant cover and perennial forb cover, and there were no interactions between the reburning and grazing treatments for these response variables ($P > 0.60$) (Fig. 3 A, D). Because we did not find significant interactions, we are able to discuss main factor effects independently and interpret effects directly. For total cover, the grazing effect varied by year. Prior to the grazing exclusion treatment in 2002, there was no difference in total plant cover between grazed and ungrazed plots. In 2004, total plant cover was reduced overall compared to 2002 because of burning, but it was higher

(5%) where grazing was excluded. However, cover also dropped in the unburned areas as well in 2004 (about 3%). The mechanism for the dip in the controls is not clear, as 2004 was actually the wettest year we sampled (based on water year annual precipitation). Other factors, such as prior year's moisture, winter snow accumulation, timing of spring snowmelt, and timing of spring precipitation may be driving this response. However, total cover in 2004 was not significantly different than 2002 or 2007. Total plant cover increased across all treatments in 2007, and the effect of grazing exclusion was even more pronounced, increasing cover almost 12%. For perennial forbs, again the grazing effect varied by year (Fig. 3D). Grazing exclusion increased perennial forb cover in 2004, and by 2007 the effect was more pronounced. Plots with grazing exclusions had significantly lower annual forb cover in 2002 (Fig. 3E). This difference was still present in 2007, although it is hard to interpret given the existing pretreatment difference. Grazing exclusion did not increase grass, sedge, or exotic species cover. However, grazing exclusion increased maximum grass leaf height, maximum flower height, and the number of flowering stems, even after this latter metric was divided by cover (Fig. 4). We found no interactions between reburning and grazing for these response variables ($P > 0.60$). Grass leaf height and flowering stem density were not affected by reburning (Fig. 4).

To confirm that we measured vegetation largely prior to cattle utilization, we removed 23 quadrats (out of 288; less than 10%) that impacted nine subplots from the analysis in 2007 that showed evidence of grazing, and three quadrats (1% of quadrats) that impacted 3 subplots in 2004. No subplots were actually removed from the analysis; rather subplot means were calculated without the quadrats with demonstrated utilization. We reran the analysis for total cover and found that removal of these subplots did not change the results ($P = 0.03$ all, $P = 0.02$ with subplots removed). Therefore we are fairly confident that the small amount of utilization that we measured is insignificant. Moreover, because we cannot distinguish wildlife grazing from cattle grazing, this analysis is conservative. As with total cover, we obtained similar results for maximum grass leaf height, maximum flower

height, and the number of flowering stems when quadrats with observed cattle utilization were removed. Therefore, all subplots were used in subsequent analyses.

Sedges, annual forbs, and exotics showed a significant response to reburning (Fig. 3C, E, F). We found no interactions between reburning and grazing for these response variables ($P > 0.60$). Burning reduced sedge abundance. Sedge cover was already reduced in burned areas in 2002, significantly so for spring burning, and spring and fall reburning further reduced sedge cover. For annual forbs, an increase in cover owing to the first fall burns remained in 2002, and fall reburning increased cover, but only in 2004. For exotics, cover increased in response to the first fall burns (Fig. 3F). Reburning in the fall again increased exotic cover as compared to the spring and control treatments in 2004. Unlike the ephemeral rise in native annual cover observed, exotic cover increased on the fall burn units slightly in 2007. This pattern was largely driven by the lower productivity stands located in the eastern part of the study area. Throughout the sampling period, the control and spring burn treatments had similar exotic plant cover. Interestingly, reburning had no significant impact on total plant cover, or on perennial grasses and forbs. Trends for forbs and grasses were very different and forbs may be more sensitive to fall burning than grasses (Fig. 3B, D).

For shrubs, grazing exclusion increased cover of *Ceanothus velutinus*, resprouter fire increasers and non-resprouters (Fig. 5). No significant interactions between reburning and grazing were found for these response variables ($P > 0.20$). Fall reburning increased *Ceanothus velutinus* cover, and spring burning had no effect (Fig. 5A). No response to burning was detected in 2007 for the other shrub species and our shrub groups, although expected trends in response to reburning in 2007 are apparent (Fig. 5). For regenerating conifers, the first fall burn reduced density ($t_{36} = 2.1$, $P = 0.045$), but spring burns had no effect ($t_{36} = 1.1$, $P = 0.27$). Regenerating conifer density increased steadily in the control throughout the sampling period but was only significantly greater than the fall ($t_{36} = 3.8$, $P < 0.001$) and spring ($t_{36} = 2.4$, $P = 0.02$) in 2004.

Species richness and community composition.—No difference in total species richness was

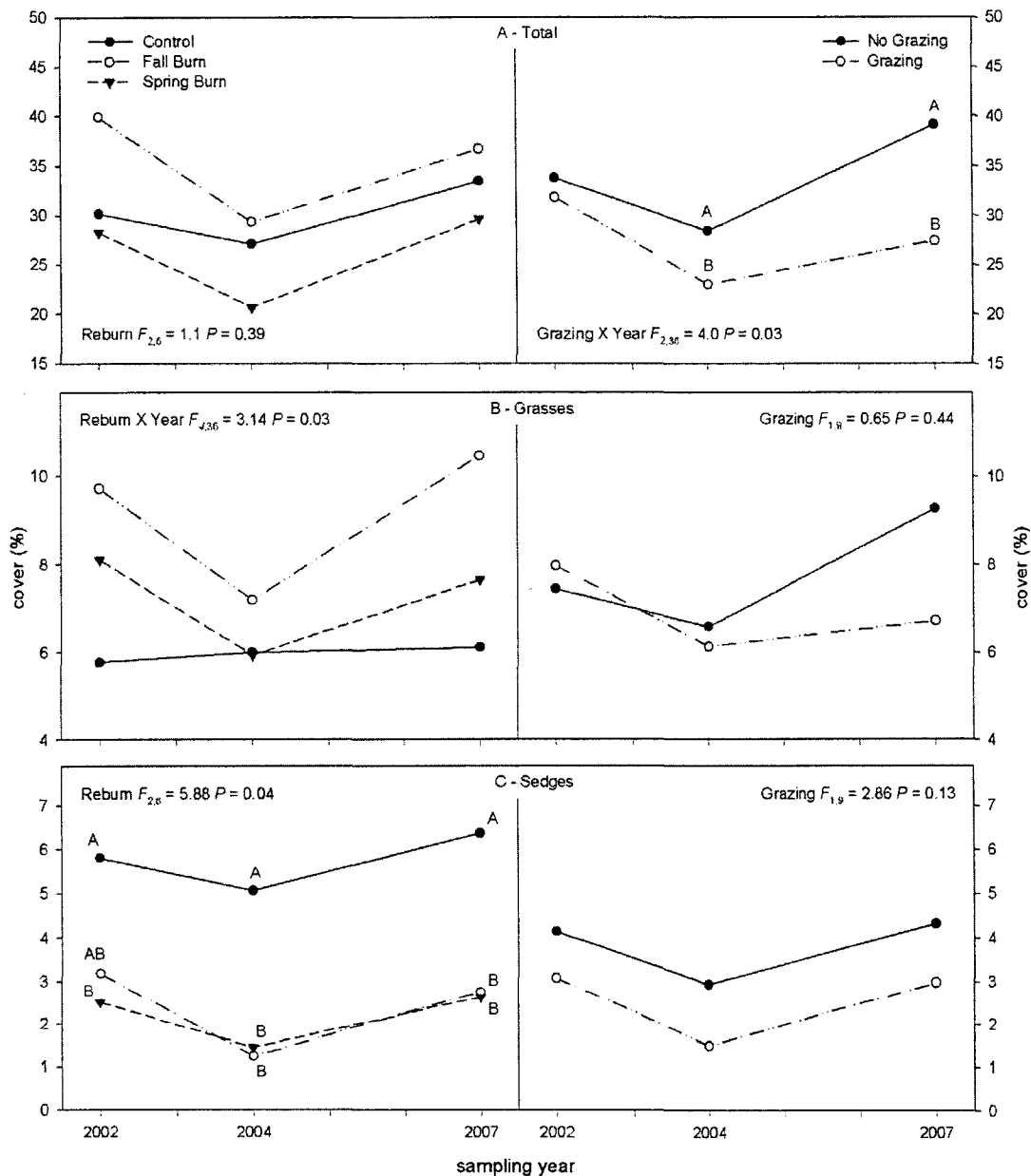


Fig. 3. Trends in understory plant functional group response to burning and grazing treatments through time. The Y-axis shows plant cover, and sampling year is on the X-axis. Each horizontal panel shows a functional plant group response, with fire on the left and grazing on the right. (A) total plant cover; (B) perennial grasses; (C) perennial sedges; (D) perennial forbs; (E) annual forbs; (F) exotics. Fires occurred in fall 1997/2002 and spring 1998/2003. Letters denote statistical significance between treatments within each year (lowercase $P < 0.10$, uppercase $P < 0.05$) and do not relate to differences between years. Note: the grass group significant global effect for reburning is attributed to changes between years, not between treatments.

detected for either grazing or burning treatments showed a change in richness in response to ($P > 0.52$). The only functional group that treatment was for exotics in relation to burning,

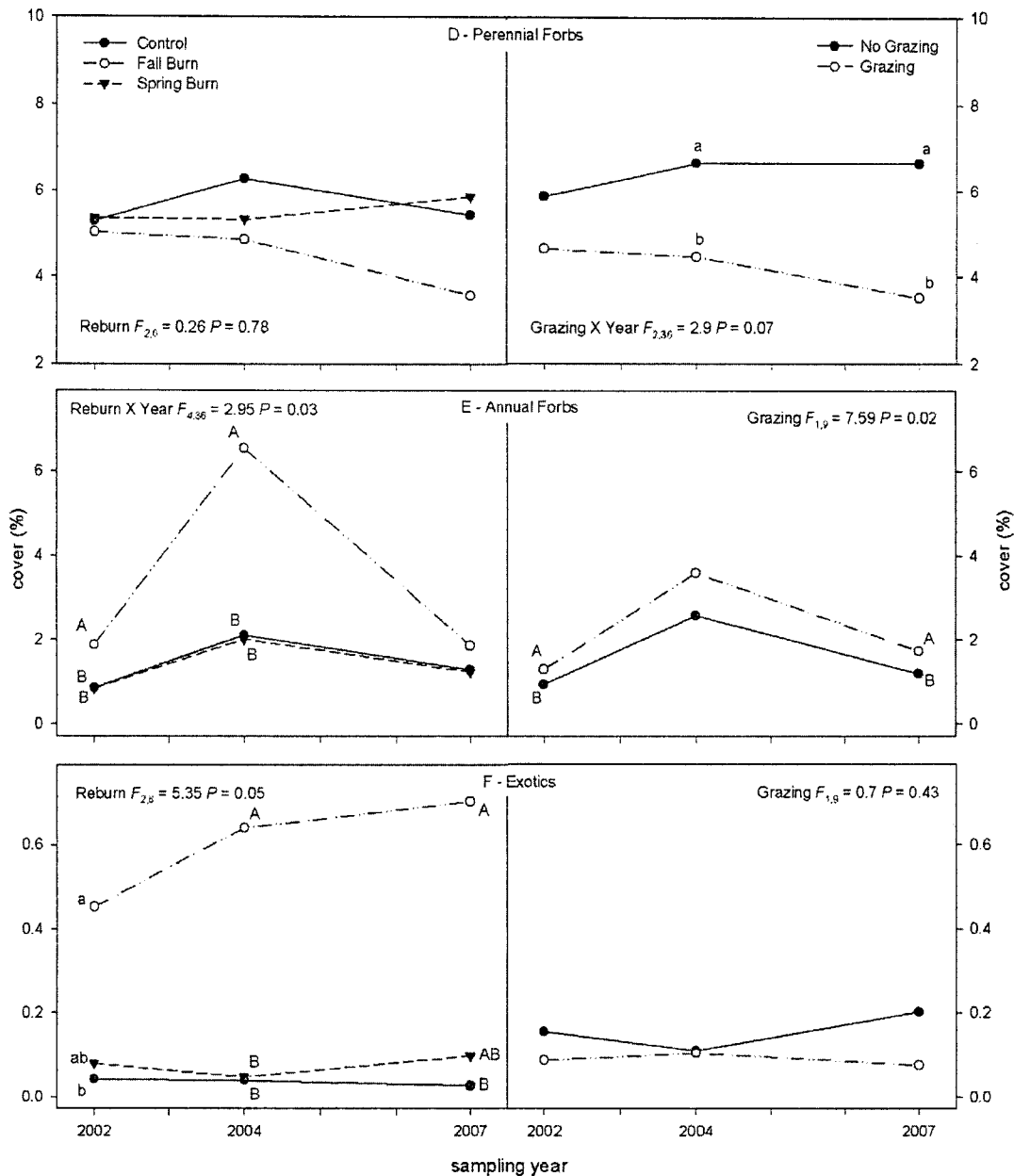


Fig. 3. Continued.

and the response varied by year ($F_{4,6} = 4.5$, $P = 0.005$). Increased exotic species richness ($t_{36} = -6.8$, $P < 0.0001$) was found in 2002 for the fall burns as compared to the spring and control (fall mean = 2.6 species, CL 1.9, 3.2; control mean = 0.79, CL 0.13, 1.5; spring mean = 0.71, CL 0.05, 1.4). This pattern was also detected in 2004 and 2007, although exotic richness had dropped

below the 2002 value by 2007 (fall mean = 1.8 species, CL 1.2, 2.5; control mean = 0.83, CL 0.18, 1.5; spring mean = 0.71, CL 0.05, 1.4). Spring burning had no effect on exotic richness.

Differences related to community composition were largely associated with burning and re-burning, and these differences were only between the fall and control treatments (control vs.

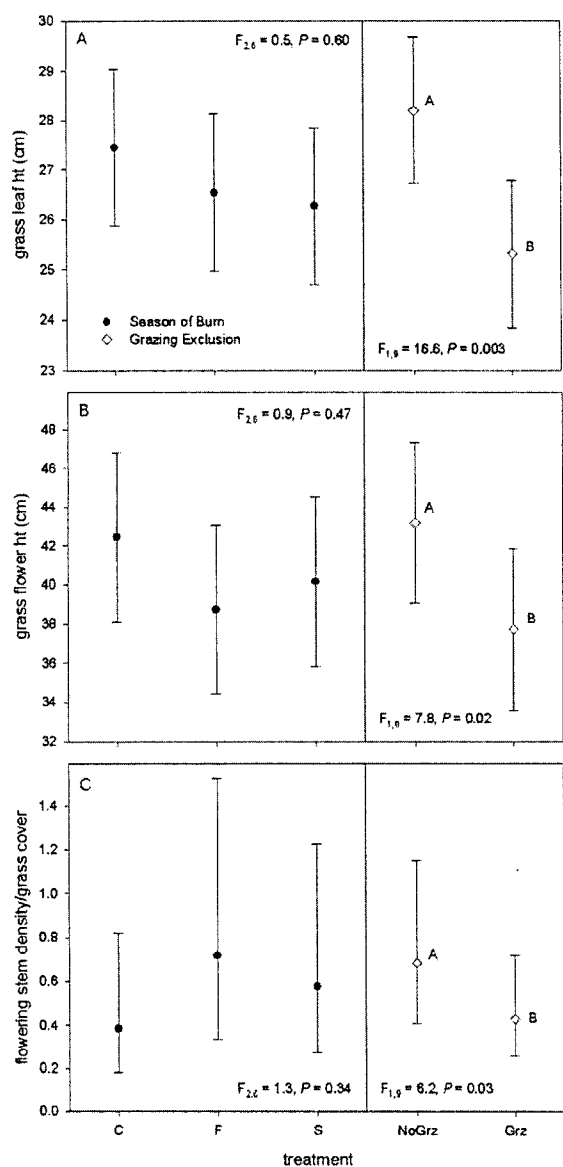


Fig. 4. Results for grass maximum leaf (A) and flower height (B) and flowering stem density (divided by cover) (C) in 2007 in relation to burning and grazing treatments. Data are means or back transformed means and 95% confidence limits. Letters denote statistical significance between treatments (uppercase $P < 0.05$).

fall: 2002, $P = 0.07$; 2007, $P = 0.06$), except for 2004. In 2004, we found differences in species composition for all comparisons (control vs. fall, $P = 0.04$; control vs. spring, $P = 0.08$; spring vs.

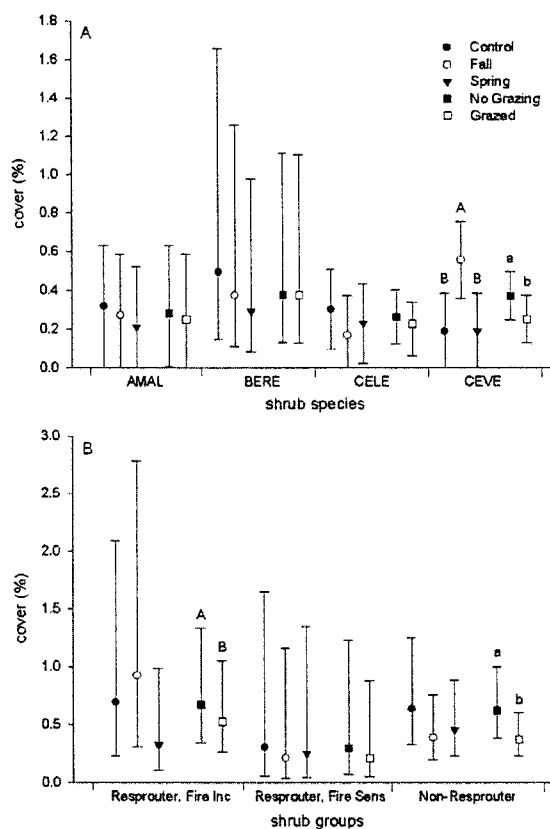


Fig. 5. Trends in shrub species cover (A) and shrub group cover (B) response to burning and grazing treatments from 2007. Fires occurred in fall 1997/2002 and spring 1998/2003. CEVE = *Ceanothus velutinus*; AMAL = *Amelanchier alnifolia*; BERE = *Berberis repens*; CELE = *Cercarpus ledifolius*. Data are means or back transformed means and 95% confidence limits. Letters denote significance between treatments (lowercase $P < 0.10$, uppercase $P < 0.05$).

fall, $P = 0.06$). Indicator species analyses revealed that the fall burn treatments had the strongest indicators (more species with values > 50 and closer to 100) and the most commonalities among the sites. Fall burns and reburns were characterized by known native fire increasers such as *Ceanothus velutinus*, short-lived natives, and exotics such as *Bromus tectorum* and *Cirsium vulgare*. Spring burns and reburns had weak indicators, with no common species across the stands, but indicators included only native perennial grasses and forbs. Control burn units showed some strong indicators which reflect the

floristic differences among the stands. The only common indicator species among the stands for the controls were the perennial native sedge *Carex rossii* and ponderosa pine. Indicators for the control also reflected temporal floristic richness patterns (e.g., species associated with wet springs). For grazing, there were no differences in species composition found until 2007 ($P = 0.04$). Strong indicator species did not emerge in relation to grazing, but ponderosa pine and annual forbs frequently characterized grazed areas and native *Poa* spp. and perennial forbs characterized ungrazed areas.

Non-metric multidimensional scaling ordinations revealed compositional patterns in relation to the floristic differences among the stands (Fig. 6). The clustering evident in Fig. 6 suggests that the major differences in the understory communities were between the eastern and western study areas. Similarities related to burn treatment were also evident, with controls and spring burns more compositionally similar to each other than either was to the fall reburns. Patterns related to grazing treatment were not apparent. Only four variables were correlated to the ordination ($r^2 \geq 0.2$), although correlations were not strong. All were associated with axis 1 and 2 and patterns related to stand location and season of burn (Fig. 6). These results are consistent with the differences noted in our analysis of these variables in relation to stand and reburn treatment (Tables 1, 4), and reflect productivity, disturbance, and resource gradients.

DISCUSSION

We demonstrate that using fire to increase understory plant cover and grass reproductive capability may be more successful if cattle are excluded. But cattle exclusion alone would likely lead to the same outcome even in the absence of burning. For all reburn treatments (spring, fall, unburned), five growing seasons of cattle grazing exclusion significantly increased (1) total vegetative cover, (2) native perennial forb cover, (3) grass stature, (4) grass flowering stem density, and (5) the cover of some shrub species and functional groups. By the end of the sampling period the increase in total vegetative cover we document is considerable (about 12%) given the relatively low total plant cover within these

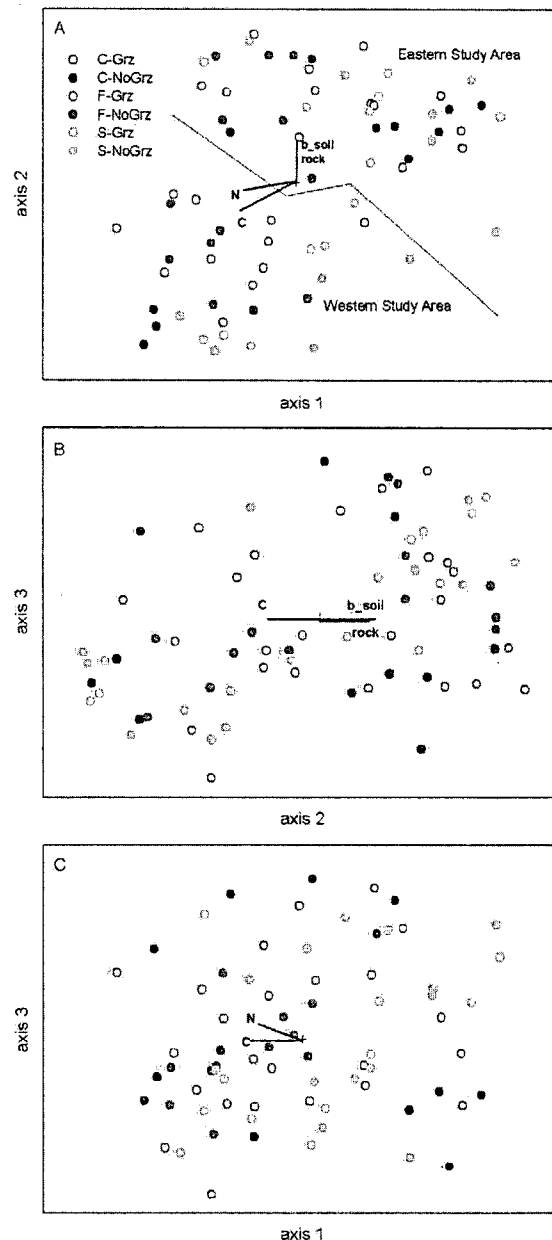


Fig. 6. Non-metric multidimensional scaling ordination results using plant cover from 2007 illustrate similar (clustered) composition in relation to stand and burn treatment. Four variables were correlated ($r^2 > 0.20$) to the ordination: Axis 1: % Carbon (C) $r^2 = 0.24$, % Nitrogen (N) $r^2 = 0.21$; Axis 2: bare soil cover (b_soil) $r^2 = 0.24$, % C $r^2 = 0.20$, % rock cover (rock) $r^2 = 0.20$.

upland bunchgrass and *Carex geyeri* dominated forests. Because we are comparing cattle grazing exclusion to grazed areas that are measured largely prior to utilization, these results probably reflect chronic grazing impacts rather than simple utilization. We found no interaction between reburning and grazing treatments for all the variables we measured (except for litter depth). In the case of grazing, the lack of an interaction with reburning indicates that the grazing exclusion effect was consistent across all the reburning treatments, including the areas that were not burned, and that cattle did not seem to preferentially select either spring or fall reburned areas.

Our findings are consistent with the grazing studies from the Western U.S. cited in our introduction. Our results related to grass cover, which did not increase with grazing exclusion, are inconsistent with some studies but are consistent with observations that (1) perennial plants subjected to grazing (particularly heavy grazing) are typically shorter and more prostrate than ungrazed or lightly defoliated populations, often either not changing or actually increasing cover in response to grazing; and (2) little time is required for grazing selection pressure to differentiate ecotypes of perennial grasses (McNaughton 1979, Tomas et al. 2000). But Bates et al. (2009) recently concluded that carefully and properly applied livestock grazing after low-severity prescribed fire did not hinder the recovery of herbaceous plant communities in a sagebrush steppe ecosystem. However, Bates et al. (2009) used very small treatment plot sizes, strictly controlled short-duration grazing periods (5–10 days), and the study area was rested from grazing the first year after the fires, conditions that are not typical or comparable to our operational grazing study. It is also unclear if the area had a long prior cattle grazing history, or if the areas were being grazed for the first time. In addition, the authors point out that the lower seed production in several of the grazing treatments could affect future recruitment of new plants and that grazing after fire in larger pastures and for longer duration would likely have resulted in areas of differential use and levels of herbaceous recovery.

In contrast to other studies, areas open to grazing did not have increased plant richness

when compared to communities that were not grazed. We observed significant but weak compositional patterns in relation to grazing at the end of the sampling period, but found no changes in richness. It is possible that our grazing exclusion treatment may yet result in changes in species composition, but that these changes will take additional time to emerge. Although species compositional changes and changes in richness receive considerable attention, management activities often influence the relative abundances of species more frequently than the presence or absence of species (Chapin et al. 2000). This is certainly true for grazing effects in our study. However, changes in plant relative abundance might warrant increased attention because these changes progress more rapidly than compositional changes and have important consequences for ecosystems long before species may be threatened by extirpation or extinction (Chapin et al. 2000).

In contrast to what we observed for grazing exclusion, prescribed fire reburning had no effect on total plant cover or on native herbaceous perennial cover and richness, regardless of season of burn. Reburning had few effects on shrubs (except *Ceanothus velutinus*), and areas reburned in the fall had greater cover of colonizing species and exotics, and more exotic species. Lack of a strong response from the native plant community might be why we see no evidence that cattle preferentially select burned areas (i.e., we detected no grazing and fire interaction). Native plants may not be responding to prescribed fire reburning, even in the absence of grazing, because of other various stressors and dispersal limitations. There is often a paradoxical assumption that highly changed ecosystems subject to numerous contemporary perturbations will respond quickly and favorably once a historical disturbance process is restored, but this does not appear to be the case in our study area at this point in time. In addition, over a century of fire exclusion, extensive grazing, tree encroachment, forest floor accumulation, climate change, competition from invasive species, and legacies from past management practices may have caused some ponderosa pine communities to cross a threshold and to reside now in different steady states (Tiedemann et al. 2000).

Land managers have expressed concern that

novel spring burning may reduce understory abundance or richness as compared to more historically appropriate early fall burning. We found little statistical evidence to support this (except for sedges) although spring burn areas tended to have lower plant cover in general. Spring burning is often a concern because plants are thought to be particularly susceptible to damage and mortality during growth initiation and prior to carbohydrate assimilation (Brockway et al. 2002; see Knapp et al. 2007 for a relevant forest ecosystem review). Our results show that plant abundance and compositional patterns in the spring burn units were actually very similar to controls, indicating that spring burns did not change these plant communities.

Outcomes from the reburns depended largely on pre-reburn trajectories, many of which were established during the first burns in our study area. Previous work documented that for the first round of prescribed fires, burns conducted in the fall were more severe (including more overstory mortality), effects that were still evident 10 years later. Consequently, fall burning and subsequent reburning had a more significant impact on species cover and composition than spring reburning. Although fall reburns better emulate the historical disturbance regime, they could potentially create a persistent early successional state, and at least for the duration of this study, do not appear to be increasing native perennial plant species cover or richness. This pattern was also strongly reflected compositionally for the fall burn units, as species indicators included native and exotic post-fire colonizers. This pattern may be ephemeral for native colonizing forbs, but exotic cover was stable and even slightly increasing five years after reburning in fall treatment areas. However, average exotic cover and richness in the study area are still low. Yet localized patches of high exotic cover exist and are of concern because these areas serve as source populations. For example, a new population of Canada thistle (*Cirsium arvense*) was discovered in 2003 in a fall burn unit. Although repeat burning using short burn cycles may potentially assist fuel management efforts (Youngblood et al. 2006), and mimic some historical burn cycles, short-interval fall repeat burning could lead to eventual dominance by exotic invasive plant species in this setting. This outcome is highly

dependent on the severity of the first burn, available source propagules, post-fire conditions, and changes in environmental conditions.

We show that five years of cattle grazing exclusion after spring and fall prescribed fire reburns and in control areas increased total plant cover, increased the stature and reproductive capability of grasses, and increased the cover of some native perennial shrubs. While we document potential chronic impacts of cattle grazing, repeat burning had few effects on the native perennial plant community and promoted early successional communities that included invasive weeds. The prescribed fire treatments in this study are representative of the types of restoration treatments that are being conducted throughout the interior West to reduce hazardous fuels. In application, prescribed fire is typically used as a coarse-filter strategy, meaning that the reintroduction of fire alone is intended to restore multiple ecosystem components. While we note that we have only measured effects after two burn cycles, and that a significant understory cover response may take more time, we document that the release from the long grazing history that these stands have experienced caused a greater degree of change for the understory than the initial reintroduction of fire. If one goal of ecological restoration in these forests is increased cover of native perennial plants, and the potential for increased native perennial grass reproduction through enhanced flowering, then cattle grazing exclusion, or potentially a change in cattle grazing management, could provide critically important options in restoration plans.

Study limitations and future research needs

As with all studies, interpretation and applicability of our results are related to the conditions under which the study was conducted. Our results may be applicable to similar upland bunchgrass and *Carex geyeri* dominated ponderosa pine forests in the West, similar prescribed spring and fall fire regimes, and similar summer grazing regimes. We note that our sites have a long history of cattle grazing, received no post-fire grazing rest period, were grazed each season during the experiment, and that the grazing season coincided with peak graminoid flowering and peak understory biomass. Application of a

different post-fire grazing regime may have resulted in a different outcome. While we have complete data on grazing season of use and number of animals in each area each year during the experimental period, we lack annual utilization data to characterize grazing intensity at the plot or experimental unit scale. Therefore, it is more difficult to make comparisons to other studies that do include utilization data and to make generalizations on that basis. Also, we only measured a relatively short-term understory response to fire and grazing. Long-term effects may be considerably different. For example, there is some evidence that using fire to increase understory species abundance and richness may take 5–20 years, particularly when the initial understory state is depauperate and seed sources limited (Webster and Halpern 2010). In addition, Davies et al. (2009) found that long-term grazing exclusion (60+ years) followed by fire resulted in substantial *Bromus tectorum* and annual forb invasion in sagebrush steppe. The authors suggested that the lack of grazing allowed fine fuels around the crowns of native perennial bunchgrasses to accumulate, increasing the likelihood of fire-induced mortality. We will be assessing the possibility for a similar phenomenon as our study progresses, although we suspect that frequent (e.g., 5-year interval) burning could mitigate this outcome.

As noted in our introduction, few studies have examined the interaction of fire and cattle grazing together in western ponderosa pine forests. Until additional studies are conducted, our results should be interpreted with care. We plan to continue our 5-year reburn cycle, maintain our grazing exclosures, add a 15-yr interval reburn regime, and report longer-term findings. We hope to expand vegetation sampling to include some additional measures such as grass basal cover, standing crop, annual yield and utilization. These types of data would allow a more detailed assessment of the understory response and relationship to grazing intensity. New research could focus on establishing similar studies in other interior coniferous forests that are also grazed by cattle. Our current experiment is not conducive to doing so, but new research could also be designed to test two or more different grazing regimes, rather than just one. This could provide land managers with informa-

tion about understory vegetation responses under a wider range of post-fire grazing regimes and intensities.

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LITERATURE CITED

- Adler, P. B., D. G. Milchunas, and W. K. Lauenroth. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* 41:653–663.
- Agee, J. K. 1993. *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, D.C., USA.
- Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* 12:1418–1433.
- Armour, C. L., D. A. Duff, and W. Elmore. 1991. Position statement on the effects of livestock grazing on riparian and stream ecosystems. *Fisheries* 16:7–11.
- Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62:1165–1183.
- Bakker, J. D., and M. M. Moore. 2007. Controls on vegetation structure in southwestern ponderosa pine forests, 1941 and 2004. *Ecology* 88:2305–2319.
- Barkworth, M. E., L. K. Anderton, K. M. Capels, S. Long, and M. B. Piep, editors. 2007. *Manual of the grasses of North America*. Intermountain Herbarium and Utah State University Press, Logan, Utah, USA.
- Bartuszevige, A. M., and P. L. Kennedy. 2009. Synthesis of knowledge on the effects of fire and thinning

- treatments on understory vegetation in U.S. dry forests. Oregon State University Agricultural Experiment Station Special Report 1095. Corvallis, Oregon, USA.
- Bates, J. D., E. C. Rhodes, K. W. Davies, and R. Sharp. 2009. Postfire succession in big sagebrush steppe with livestock grazing. *Rangeland Ecology and Management* 62:98–110.
- Belsky, A. J., and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conservation Biology* 11:315–327.
- Biondini, M. E., P. W. Mielke Jr., and K. J. Berry. 1988. Data-dependant permutation techniques for the analysis of ecological data. *Vegetatio* 75:161–168.
- Bork, J. L. 1984. Fire history in three vegetation types on the east side of the Oregon Cascades. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Brockway, D. G., R. G. Gatewood, and R. B. Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management* 65:135–152.
- Brown, J. K. 1974. Handbook for inventorying downed woody material. General Technical Report INT-16. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Brown, R. T., J. K. Agee, and J. F. Franklin. 2004. Forest restoration and fire: principles in the context of place. *Conservation Biology* 18:903–912.
- Burns, C. E., S. L. Collins, and M. D. Smith. 2009. Plant community response to loss of large herbivores: comparing consequences in a South African and a North American grassland. *Biodiversity and Conservation* 18:2327–2342.
- Carlson, G. 1974. Soil resource inventory basic soil information and interpretative tables: Malheur National Forest. USDA Forest Service, Pacific Northwest Region, Portland, Oregon, USA.
- Chapin, F. S., III, et al. 2000. Consequences of changing biodiversity. *Nature* 405:234–242.
- Cingolani, A. M., M. Noy-Meir, and S. Díaz. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecological Applications* 15:757–773.
- Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* 68:1243–1250.
- Collins, S. L., and M. D. Smith. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* 87:2058–2067.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–1144.
- Covington, W. W. 2000. Helping western forests heal. *Nature* 408:135–136.
- Covington, W. W., and M. M. Moore. 1994. Post-settlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. *Journal of Sustainable Forestry* 2:153–181.
- Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry* 95:23–29.
- Davies, K. W., T. J. Svejcar, and J. D. Bates. 2009. Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecological Applications* 19:1536–1545.
- DeBano, L. F., D. G. Neary, and P. F. Ffolliott. 1998. Fire: its effect on soil and other ecosystem resources. John Wiley & Sons Inc., New York, New York, USA.
- Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69:57–68.
- Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology* 41:604–614.
- Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications* 7:895–908.
- Gee, G. W., and J. W. Bauder. 1986. Particle size analysis. Pages 383–411 in A. Klute, editor. *Methods of soil analysis. Part 1. Physical and mineralogical methods*. 2nd edition. American Society of Agronomy, Madison, Wisconsin, USA.
- Gildar, C. N., P. Z. Fulé, and W. W. Covington. 2004. Plant community variability in ponderosa pine forest has implications for reference conditions. *Natural Areas Journal* 24:101–111.
- Halpern, C. B. 1989. Early successional pattern of forest species: interactions of life history traits and disturbance. *Ecology* 70:704–720.
- Harris, G. A. 1991. Grazing lands of Washington State. *Rangelands* 13:222–227.
- Harrod, R. J. 2001. The effect of invasive and noxious plants on land management in eastern Oregon and Washington. *Northwest Science* 75:85–90.
- Hatten, J. A., D. Zabowski, A. Ogden, and W. Thies. 2008. Soil organic matter in a ponderosa pine forest with varying seasons and intervals of prescribed burn. *Forest Ecology and Management* 255:2555–2565.

- Hessburg, P. F., and J. K. Agee. 2003. An environmental narrative of Inland Northwest United States forests 1800–2000. *Forest Ecology and Management* 78:23–59.
- Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecology and Management* 211:117–139.
- Hessl, A. E., D. McKenzie, and R. Schellhaas. 2004. Drought and Pacific Decadal Oscillation linked to fire occurrence in the inland Pacific Northwest. *Ecological Applications* 14:425–442.
- Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: a multi-scale example from the interior west, USA. *Ecology* 82:660–678.
- Heyerdahl, E. K., D. McKenzie, L. Daniels, A. E. Hessl, J. S. Littell, and N. J. Mantua. 2008. Climate drivers of regionally synchronous fires in the inland Northwest (1651–1900). *International Journal of Wildland Fire* 17:40–49.
- Hitchcock, C. L., and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, Washington, USA.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695–713.
- Hobbs, N. T., D. S. Schimel, C. E. Owensby, and D. S. Ojima. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* 72:1374–1382.
- Jones, A. 2000. Effect of cattle grazing on North American arid ecosystems: a quantitative review. *Western North American Naturalist* 60:155–164.
- Kerns, B. K., and J. Ohmann. 2004. Evaluation and prediction of shrub cover in coastal Oregon forests. *Ecological Indicators* 4:83–98.
- Kerns, B. K., W. G. Thies, and C. G. Niwa. 2006. Season and severity of prescribed burn in ponderosa pine forests: implications for understory native and exotic plants. *Écoscience* 13:44–55.
- Knapp, E. E., D. W. Schwillk, J. M. Kane, and J. E. Keeley. 2007. Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest. *Canadian Journal of Forest Research* 37:11–22.
- Kruskall, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1–27.
- Kuenzi, A. M., P. Z. Fulé, and C. H. Sieg. 2008. Effects of fire severity and pre-fire stand treatment on plant community recovery after a large wildfire. *Forest Ecology and Management* 255:855–865.
- Laughlin, D. C. 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. *Rangeland Ecology and Management* 59:135–144.
- Laughlin, D. C., and P. Z. Fulé. 2008. Wildland fire effects on understory plant communities in two fire-prone forests. *Canadian Journal of Forest Research* 38:133–142.
- Laughlin, D. C., J. D. Bakker, M. T. Stoddard, M. L. Daniels, J. D. Springer, C. N. Gildar, A. M. Green, and W. W. Covington. 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. *Forest Ecology and Management* 199:137–152.
- Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. *SAS for Mixed Models*, 2nd edition. SAS Institute Inc., Cary, North Carolina, USA.
- Mack, R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119:757–773.
- Madany, M. H., and N. E. West. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. *Ecology* 64:661–667.
- McCune, B., and J. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon, USA.
- McCune, B., and M. J. Mefford. 2006. *PC-ORD. Multivariate analysis of ecological Data*. Version 5.10 MjM Software, Gleneden Beach, Oregon, USA.
- McIntyre, S., M. Díaz, S. Lavorel, and W. Cramer. 1999. Functional analysis of vegetation response to disturbance: introduction. *Journal of Vegetation Science* 10:604–609.
- McNaughton, S. J. 1979. Grassland-herbivore dynamics. Pages 46–81 in A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago, Illinois, USA.
- Metlen, K. L., and C. E. Fiedler. 2006. Restoration treatment effects on the understory of ponderosa pine/Douglas-fir forests in Western Montana, USA. *Forest Ecology and Management* 22:355–369.
- Metlen, K. L., C. E. Fiedler, and A. Youngblood. 2004. Understory response to fuel reduction treatments in the Blue Mountains of Northeastern Oregon. *Northwest Science* 78:175–185.
- Mielke, P. W., Jr. 1984. Meteorological applications of permutation techniques based on distance functions. Pages 813–830 in P. R. Krishnaiah and P. K. Sen, editors. *Handbook of statistics 4: nonparametric methods*. Elsevier Science Publishers, New York, New York, USA.
- Mielke, P. W., Jr. 1991. The application of multivariate permutation methods based on distance functions in the earth sciences. *Earth-Science Reviews* 31:55–71.
- Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination.

- Vegetatio 68:89–107.
- Moore, M. M., C. A. Casey, J. D. Bakker, J. D. Springer, P. Z. Fulé, W. W. Covington, and D. C. Laughlin. 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. *Rangeland Ecology and Management* 59:135–144.
- Moore, M. M., W. W. Covington, and P. Z. Fulé. 1999. Evolutionary environment, reference conditions, and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications* 9:1266–1277.
- Nelson, D. W., and L. E. Sommers. 1996. Total carbon, organic carbon, and organic matter. Pages 961–1010 in J. M. Bartels, et al., editors. *Methods of soil analysis, Part 3: chemical methods*. 3rd edition. SSSA Book Series 5. American Society of Agronomy, Madison, Wisconsin, USA.
- Oliver, W. W., and R. A. Ryker. 1990. *Pinus ponderosa* Dougl. ex Laws.—Ponderosa pine. Pages 413–424 in R. M. Burns and B. H. Honkala, editors. *Silvics of North America. Volume 1: Conifers*. USDA Forest Service, Washington, D.C., USA.
- Pausas, J. G., R. A. Bradstock, D. A. Keith, and J. E. Keeley. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85:1085–1100.
- Pellant, M. P., P. L. Shaver, D. A. Pyke, and J. E. Herrick. 2000. Interpreting indicators of rangeland health. Version 3. US Department of the Interior, Bureau of Land Management, Interagency Technical Reference TR-1734-6. Denver, Colorado, USA.
- Powers, H. A., and R. E. Wilcox. 1964. Volcanic ash from Mount Mazama (Crater Lake) and from Glacier Peak. *Science* 144:1334–1336.
- Pyke, D. A., J. E. Herrick, P. L. Shaver, D. A., and M. P. Pellant. 2002. Rangeland health attributes and indicators for qualitative assessment. *Journal of Range Management*. 55:584–597.
- SAS Institute Inc. 2008. SAS 9.2. SAS Institute Inc., Cary, North Carolina, USA.
- Schwilk, D. W., et al. 2009. The national fire and fire surrogate study: effects of fuel reduction methods on forest vegetation and structure. *Ecological Applications* 19:285–304.
- Smith, J. E., D. McKay, C. G. Niwa, W. G. Thies, G. Brenner, and J. W. Spatafora. 2004. Short-term effects of seasonal prescribed burning on the ectomycorrhizal fungal community and fine root biomass in ponderosa pine stands in the Blue Mountains of Oregon. *Canadian Journal of Forest Research* 34:2477–2491.
- Staver, A. C., W. J. Bond, W. D. Stock, S. J. van Rensburg, and M. S. Waldram. 2009. Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications* 19:1909–1919.
- Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9:1189–1206.
- Thies, W. G., D. J. Westlind, and M. Loewen. 2005. Season of prescribed burn in ponderosa pine forests in eastern Oregon: impact of pine mortality. *International Journal of Wildland Fire* 14:223–231.
- Thies, W. G., D. J. Westlind, M. Loewen, and G. Brenner. 2006. Prediction of delayed mortality of fire-damaged ponderosa pine following prescribed fires in eastern Oregon, USA. *International Journal of Wildland Fire* 15:19–29.
- Tiedemann, A. R., J. O. Klemmedson, and E. L. Bull. 2000. Solution of forest health problems with prescribed fire: are forest productivity and wildlife at risk? *Forest Ecology and Management* 127:1–18.
- Tomas, M. A., A. D. Carrera, and M. Poverene. 2000. Is there any genetic differentiation among populations of *Piptochaetium napostaense* with different grazing histories? *Plant Ecology* 147:227–235.
- USDA-NRCS. 2009. National Weather and Climate Center SNOTEL data: Oregon Rock Springs site. (<http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=721&state=or>)
- USDA-NRCS. 2010. The PLANTS Database. (<http://plants.usda.gov>)
- United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, producer. 2009. Fire Effects Information System database. (<http://www.fs.fed.us/database/feis/>)
- United States General Accounting Office. 2005. Livestock grazing. Report to Congressional Requesters. GAO-05-869.
- Van Langevelde, F., C. Van De Vijver, L. Kumar, J. Van De Koppel, N. De Ridder, J. Van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, and W. J. Bond. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84:337–350.
- Webster, K. M., and C. B. Halpern. 2010. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. *Ecosphere* 1(5):art9. [doi: 10.1890/ES10-00018.1]
- Weisburg, P. J., and H. Bugmann. 2003. Forest dynamics and ungulate herbivory: from leaf to landscape. *Forest Ecology and Management* 181:1–12.
- Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson. 2006. Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. *Wildlife Society Bulletin* 34:283–292.
- Youngblood, A., K. L. Metlen, and K. Coe. 2006. Changes in stand structure and composition after restoration treatments in low elevation dry forests of northeastern Oregon. *Forest Ecology and Management* 234:143–163.