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Prescribed fire regimes subtly alter ponderosa pine forest plant community structure

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Abstract. Prescribed fire is an active management tool used to address wildfire hazard and ecological concerns associated with fire exclusion and suppression over the past century. Despite widespread application in the United States, there is considerable inconsistency and lack of information regarding the extent to which specific outcomes are achieved and under what prescribed fire regimes, particularly in regard to ecological goals related to plant community structure. We quantify differences and patterns in plant functional group abundance, species richness and diversity, and other key forest components through time from a unique long-term (15-yr) experiment within the Malheur National Forest of Oregon. Treatments included five fire regimes: fall and spring 5-yr burning, fall and spring single burn, and no burning. Original burns were conducted in the fall of 1997 and spring of 1998, and plant data were collected every five years starting in 2002. Many perennial plant group responses were neutral, subtle, and ephemeral. Total cover increased marginally in response to the first burn, but this response disappeared within a decade. Three 5-yr reburns did not increase or decrease total plant cover, richness, or diversity. Some plant groups with fire resistant and resilient traits, such as annual forbs, exotic forbs, open bunchgrasses, and rhizomatous and resprouting perennials, showed some short-term positive responses to initial burning and 1–2 reburns, but not 3. The moderately more severe fall burns generally impacted plant responses more than spring burning, but many patterns were legacies from the original higher severity burns. Burn frequency was more important for less severe spring burning. Overall, we document that most native perennial plant functional groups were able to resist or recover from burning and reburning, but did not necessarily strongly respond. This may be due to the importance of other overriding forcing factors and ecosystem inertia not easily overcome by very low-severity prescribed burns. Results from our study are important for practitioners using prescribed fire to achieve biodiversity, conservation, and habitat goals that hinge on a vigorous native perennial plant response, as such outcomes are not certain even with frequent burn regimes.

Key words: disturbance; fire frequency; fire regime; forest understory; fuel treatment; long term; plant community; ponderosa pine; prescribed fire; restoration; season of burn.

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INTRODUCTION

It is well recognized that the temporal and spatial patterns of fires, or fire regimes, play a critical role in synergistically shaping the vegetative and fuel structure and function of landscapes across the globe (Agee 1993, Bond et al. 2005, Bradstock 2010, Archibald et al. 2013, Haslem et al. 2016).

Fire regimes are dynamic, but typically characterized by long-term patterns of fire frequency, seasonality, size, extent, and intensity (Agee 1993, Bond and Keeley 2005, Archibald et al. 2013). Fire suppression, fire exclusion, cessation of cultural burning, and land-use changes over the past 150 yr have dramatically altered many historical fire regimes and led to concomitant and frequently undesirable changes in vegetative and fuel structure (Covington and Moore 1994, Hessburg et al. 2005, 2015, Varner et al. 2005, Prichard et al. 2017). These changes are now interacting with global rising temperatures, extended droughts, and lengthening fire seasons, setting the stage for increases in annual area burned and uncharacteristic wildfire effects on natural resources and damage to human life and property (Hessburg et al. 2005, 2015, Savage et al. 2013, Dennison et al. 2014, Mitchell et al. 2014).

Reestablishing historical fire regimes in areas that are considered to be in fire deficit (sensu Marlon et al. 2012) is an active management approach used to address fuel and wildfire hazard concerns (Fernandes and Botelho 2003, Agee and Skinner 2005, Varner et al. 2005, Schwilk et al. 2009, Arkle et al. 2012, Cochrane et al. 2012, Vaillant and Reinhardt 2017), as well as explicit or implicit ecological goals such as the restoration or creation of certain ecosystem processes and forest structural patterns, including range or wildlife habitat, increased species abundance and biodiversity, or other desired conditions (Converse et al. 2006, Dodson and Peterson 2010, Strahan et al. 2015, Yeiser et al. 2015, Kalies and Yocom Kent 2016). In the United States, prescribed burning is commonly used in forests dominated by ponderosa pine or other dry pines to both reduce fuels and achieve ecological and restoration goals (Covington and Moore 1994, Hessburg and Agee 2003, Noss et al. 2006*a*). In the last decade, the U.S. Forest Service has implemented a number of policies, initiatives, and associated congressional funding designed to accelerate fuel treatments and forest restoration using activities such as forest thinning and prescribed fire (USDA Forest Service 2016, Schultz et al. 2017). Almost 2.6 million ha of federal and state lands were burned in 2017 using prescribed fire (NIFC, *public communications*).

Despite widespread prescribed fire application in the western United States, there is considerable inconsistency and lack of information regarding the extent to which specific outcomes are achieved and under what prescribed fire regimes, particularly in regard to ecological goals related to biodiversity and understory restoration and conservation (Driscoll et al. 2010). Other than a handful of studies focusing on combustible fuels and overstory trees (Busse et al. 2000, Thies et al. 2005, Schwilk et al. 2006, Higgins et al. 2015, van Mantgem et al. 2016), manipulative replicate testing of fire regimes remains limited, particularly for fire frequency. Yet use of unsuitable prescribed fire regimes could negatively alter some ecosystem components, and species that thrive under one fire regime may become vulnerable under another (Fisher et al. 2009, Keeley et al. 2011). Fire can directly consume combustible components (litter, coarse woody debris), cause significant damage or mortality to plant species, and indirectly alter biotic (e.g., competition, germination) and abiotic processes (light, substrate exposure; Davis et al. 2000, Copeland et al. 2002, Koerner et al. 2015, Holland et al. 2017).

Fire-prone landscapes tend to support plant species that have fire resistant and resilient traits, and shorter fire return intervals select for species with these types of traits, compared to landscapes with less frequent fire (Brown and Smith 2000, Keeley et al. 2011, Pausas and Keeley 2014, Bowd et al. 2018). For example, studies from the southeastern and mid-continental United States reveal that burn frequency can control herbaceous vs. woody dominance (Glitzenstein et al. 1995, Peterson et al. 2007, Varner et al. 2007) as well as understory species richness (Varner et al. 2003, Peterson and Reich 2008). Studies in southern U.S. pine forests and mid-continental grasslands document that vegetation patterns and species dominance in response to burn season can also vary markedly (Platt et al. 1988, Sparks et al. 1998, Brockway et al. 2002). However, similar relationships between the fire regime and plant community patterns should not be assumed for different ecosystem types (Scheintaub et al. 2009). Indeed, limited studies in the western United States indicate that fire season appears to be a relatively minor factor for many of the plant species that have been studied, and that the intensity and resulting severity of the fire often have a greater impact (Kerns et al. 2006, Knapp et al. 2009, Ellsworth and Kauffman 2017).

While prescribed fire regime studies remain limited in the western United States, a significant body of knowledge regarding the temporal and spatial patterns of historical fires has accrued over the past 25 yr. This information is often invoked to guide prescribed fire regime choice (Agee 1996, Noss et al. 2006*b*). However, estimates of historical fire regimes for ponderosa pine-dominated ecosystems vary both among and within regions, and quantitative techniques continue to improve our understanding (Heyerdahl et al. 2001, Baker 2017, Reilly et al. 2017, Baker and Williams 2018).

Even with reliable and geographically relevant historical fire regime information in hand, applying past regimes to contemporary landscapes may not be possible or appropriate, given competing social and management goals, operational constraints, and potential unknown interactions with new disturbances, stressors, and environmental change (e.g., herbivory, invasive species, global warming, predation, fragmentation, human development, threatened or endangered species; Jackson and Hobbs 2009, McKenzie et al. 2009, Ryan et al. 2013). For example, prescribed burns today in the interior western United States are frequently conducted in the spring and fall under relatively high-fuel-moisture conditions and low temperatures, and when fire crews are available to conduct burns. Yet the majority of lightning-caused wildfire ignitions occur in July and August in conjunction with the hottest and driest time of year (Westerling et al. 2003, Littell et al. 2009). While it is likely that indigenous people ignited some fires outside of summer based on similar concerns about extreme fire behavior, studies suggest the majority of historical fires burned in the summer (Knapp et al. 2009, Ryan et al. 2013), although seasonal fire scar patterns can vary strongly within regions (Heyerdahl et al. 2001). Regardless, the complexity of defining and using historical fire regimes for prescribed fire application underscores the need for long-term studies in contemporary landscapes.

We describe the outcomes and implications from a unique long-term (15-yr) experiment designed to examine the effects of different prescribed fire regimes on ponderosa pine-dominated forest vegetation and other components in the intermountain western United States. The prescribed fire regimes, or treatments, include a single spring and fall burn, very frequent (5-yr) spring and fall reburning, and no burning. Our objectives are to quantify differences and patterns in plant functional group abundance (cover), species richness and diversity, and other key forest components as related to our experimental treatments. Our research questions include the following: (1) How does burning in the fall or spring differ from not burning? (2) How do spring and fall responses differ based on burn frequency? (3) How do spring and fall burning differ from each other? (4) Which burn regime increases native plant cover, richness, and diversity as compared to not burning? We expected that responses will differ markedly based on burn season and frequency and plant functional group, and hypothesized that burn regimes more aligned with historical fire regimes (fall burning) will produce more abundant and diverse native plant understories compared to less historically representative burn regimes (spring burning), and that very frequent burning will favor herbaceous species over woody species and favor resprouting and rhizomatous species generally, but decrease diversity compared to a single burn. Lastly, we explore the implications of our results as related to common dry forest restoration goals and policies in the intermountain western United States.

METHODS

Study area

The study was initiated in 1997 within the Malheur National Forest, at the southern end of the Blue Mountain Ecoregion (Bailey, USDA Forest Service 1994) in Oregon using five upland forested stands differentiated by district staff based on past management history (Thies et al. 2005; Fig. 1A). The five stands span a productivity gradient; the eastern area stands have lower overall plant cover and more xeric type vegetation (understory dominated by bunchgrasses such as *Pseudoroegneria spicata* and *Elymus elymoides*) than the two western stands (understory dominated by *Carex geyeri* and forbs such as *Arnica cordifolia*) located 18 km to the west. While differences in understory floristics from the untreated units among the stands are apparent (Kerns et al. 2006), the overstory is more compositionally homogenous, dominated largely by

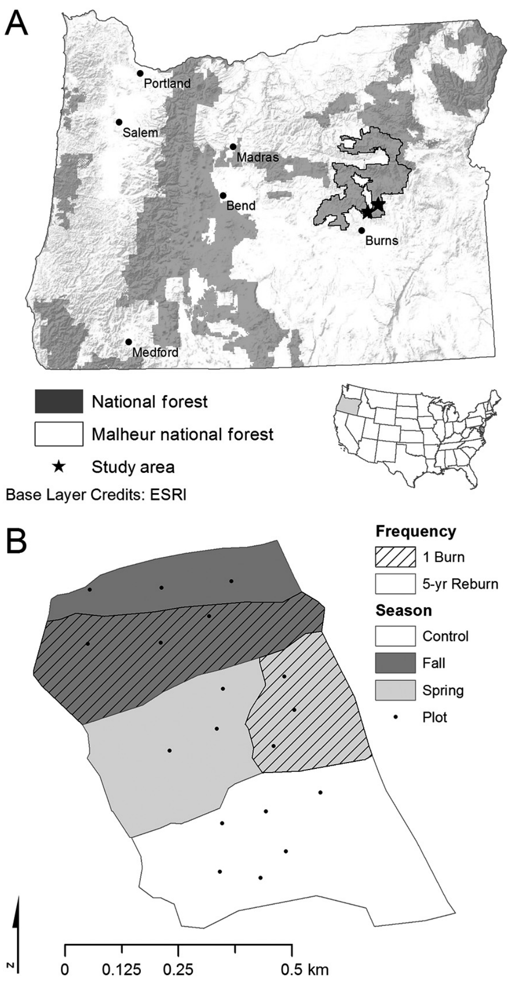

Fig. 1. (A) Location of the Malheur National Forest in eastern Oregon and the western and eastern ponderosa pine stands used (n = 5) as the study area. (B) Example study design for one stand (block) with season (control = no burning; spring; or fall) and frequency (single or 5-yr interval) prescribed burning.

mixed-aged ponderosa pine, with occasional *Juniperus occidentalis*, *Cercocarpus ledifolius*, and rarely *Abies grandis* and *Pseudotsuga menziesii*. As typical of most dry forested public lands in western North America, the stands are open to cattle grazing for approximately six weeks in the summer, and were not rested after the burns in this study. Soils are generally dominated by Mollisols, but Inceptisols and Alfisols are also present (Carlson 1974, Hatten et al. 2008) and soil texture among the stands is quite similar (Hatten et al. 2012).

Mean annual precipitation is 464 mm per year (1981–2012) with only about 24% falling during the growing season as is typical of a Mediterranean climate. Snowmelt typically occurs late May to 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 and biomass are usually in early July, and most plants are dormant by mid-to-late August. Fall rains may bring short-lived greening, but rains are typically followed closely by freezing temperatures.

Experimental design

This study design has been described in detail in previous work (Thies et al. 2005, Kerns et al. 2006, 2011). The first burns were conducted in the fall of 1997 and spring of 1998 three years following a thinning from below treatment. Prior to these first burns, the five stands were each divided into three units (averaging 8 ha in size) and randomly assigned a burn treatment (spring, fall, and control or unburned). In 2002, the study was expanded and the burned experimental units were bisected with one half randomly selected to be reburned every five years and the other half receiving only the original single burn. Thus, the experiment contains five treatments: control (C), fall reburn (FRB), fall single burn (F1B), spring reburn (SRB), and spring single burn (S1B) (Fig. 1B). There are three 10 m radius vegetation sample plots within each treatment (six plots in the unburned treatment) that were established systematically along transect bearings in 1997.

The single burn treatments were burned in early fall of 1997 and late spring of 1998. The 5-yr interval fall reburns were conducted in early fall 2002 and 2007 and the spring 5-yr interval reburns in mid-to-late spring of 2003 and 2008. Prescribed burns were maintained by hand-carried drip torches using a multiple-strip head-fire pattern maintaining a 60 cm flame length if possible. Westlind and Kerns (2017) noted that there was a difference in air temperature during the burns between spring and fall, with the mean spring temperatures estimated to be 6.22°C higher than fall temperatures. There were no differences between spring and fall burns for mean relative humidity, wind speed, or flame length.

Field sampling

Vegetation measurements were designed to assess plant responses without destructive sampling. Current-year understory herbaceous plant canopy cover was visually estimated and recorded by species to the nearest percentage point on eight 1-m^2 quadrats using a marked (0.10 m) PVC square. Quadrats were arranged 5 m and 6 m from the plot 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. Presence of all species was recorded on the entire 10 m radius plot. In 2007 and 2012, shrub cover was recorded by species on the whole plot. We measured overstory tree canopy cover using a moosehorn densiometer at the plot center, and 5 and 15 m from the center in each cardinal direction (total of nine points for each plot).

Plant functional groups

The functional group framework we used is based on the literature, specifically relevant for fire regime studies (e.g., Bowd et al. 2018), was designed to avoid excessive variability associated with coarser groups (e.g., all herbaceous species, graminoids; Willms et al. 2017), and is simple and useable for restoration practitioners to aid in understanding plant response to fire regimes across ecosystems (Pyke et al. 2010, Laughlin et al. 2017). Because ecological resistance to disturbance is case specific (D'Antonio and Thomsen 2004), fine-scale functional groups relevant to managers were developed in consultation with local experts and informed by existing frameworks that use plant traits important for fire resistance and resilience: location of perennating buds, growth form, plant height and architecture, reproductive strategy, life history and origin, and nutrient capture (e.g., McIntyre et al. 1999, Pyke et al. 2010; Tables 1 and 2). Only morphological, physiological, and phenological traits that impact fitness indirectly via their effects on growth, reproduction, and survival, the three components of individual performance, were used (Violle et al. 2007). Traits for the 119 species in our study area also needed to be easily determined from online reference databases, floras, literature, field data, or local expert knowledge, or clearly measurable. For cover analyses, each species was assigned a fine-scale functional group. Coarser-scale functional groups were used for richness analyses based on life history, growth form, and origin only: graminoids (all grasses and sedges), annual forbs, perennial forbs, shrubs, and exotics.

Table 1. Understory plant functional groups used for analysis and associated traits.

Descriptive name used in text†	Growth form	Life history	Propagation	Origin	Nitrogen fixation
Total	All	All	All	All	All
Annual forbs	Forb	Annual/Biennial	Seed	Native	No
Non-rhizomatous forbs	Forb	Perennial	Seed, bulbs, corm	Native	No
Rhizomatous forbs	Forb	Perennial	Rhizomatous, seed	Native	No
N-fixing forbs	Forb	Perennial	Seed	Native	Yes
Exotic forbs	Forb	Varies; most biennial	Seed	Exotic	No
Dense bunchgrass	Grass	Perennial	Seed	Native	No
Open bunchgrass	Grass	Perennial	Seed	Native	No
Rhizomatous grass	Grass	Perennial	Rhizomatous, seed	Native	No
Perennial, exotic grass‡	Varies	Perennial	Varies	Exotic	No
Sedges	Sedge	Perennial	Rhizomatous, seed	Native	No
Non-resprouting shrubs	Shrub	Perennial	Seed	Native	No
Non-resprouting, N-fixing shrubs	Shrub	Perennial	Seed	Native	Yes
Resprouting shrubs	Shrub	Perennial	Resprouting, seed	Native	No
Resprouting, N-fixing shrubs	Shrub	Perennial	Resprouting, seed	Native	Yes
Unassigned‡	Varies	Unknown	Unknown	Unknown	Unknown

Notes: Traits used were based on commonly used plant attributes (e.g., Pyke et al. 2010), discussions with local experts, and attention to traits relevant for resistance and resilience to fire.

† Exotic annual grasses are reported in Kerns and Day (2017).

‡ Not analyzed.

Table 2. Dominant species for each plant functional group based on average total stand cover in 2012.

Descriptive name used in text†	Code used in graphs	Dominant species
Total	Total	*Carex geyeri, Elymus elymoides, Arnica cordifolia, Bromus tectorum, Festuca idahoensis*
Annual forbs	Ann	*Epilobium minutum, Collinsia parviflora, Collomia* spp., *Gayophytum heterozygum, Montia perfoliata*
Non-rhizomatous forbs	NonRhiz	*Fragaria virginiana, Eriogonum heracleoides, Erigeron corymbosus, Senecio integerrimus, Antennaria microphylla*
Rhizomatous forbs	Rhiz	*Arnica cordifolia, Thalictrum fendleri, Kelloggia galioides, Achillea millefolium, Silene menziesii*
N-fixing forbs	Nit	*Lupinus caudatus*
Exotic forbs	Exo	*Taraxacum officinale, Cirsium vulgare, Lactuca serriola, Verbascum thapsus*
Dense bunchgrass	Dense	*Festuca idahoensis, Pseudoroegneria spicata, Achnatherum occidentale, Acnatherum lemmonii, Deschampsia elongate*
Open bunchgrass	Open	*Elymus elymoides, Bromus carinatus, Poa secunda, Elymus glaucus, Koeleria macrantha*
Rhizomatous grass	Rhiz	*Poa wheeleri, Calamagrostis rubescens, Leymus cinereus, Melica fugax, Melica bulbosa*
Perennial, exotic grass	NA	*Thinopyrum intermedium, Poa bulbosa, Poa pratensis*
Sedges	Sedge	*Carex geyeri, Carex rossii, Carex hoodii*
Non-resprouting shrubs	NoResp	*Ribes cereum, Artemisia tridentata*
Non-resprouting, N-fixing shrubs	Nit	*Cercocarpus ledifolius, Purshia tridentata*
Resprouting shrubs	Resp	*Berberis repens, Symphoricarpos* spp., *Chrysothamnus nauseosus, Amelanchier alnifolia, Chrysothamnus vscidiflorus*
Resprouting, N-fixing shrubs	CEVE	*Ceanothus velutinus*
Unassigned	NA	Unknown forb, unknown grass seedlings, one occurrence of an unknown brome

† All grasses possess the C_3 photosynthetic pathway. Exotic annual grasses are reported in Kerns and Day (2017); exotic perennial grasses were too few to report.

Each plant functional group needed to be statistically robust, or analyzable, across the experiment. Some plant groups were considered more relevant or desirable for certain management goals (e.g., wildlife habitat, forage production), including native perennial bunchgrasses, sedges, and shrubs. Results for exotic grasses, notably cheatgrass, are published elsewhere (Kerns and Day 2017), as are results for tree seedlings (Westlind and Kerns 2017). We note that there are no warm-season or native annual grasses in the study area, no exotic shrubs, and too few tree species to analyze for richness (Table 1). Tree overstory canopy cover was analyzed, but understory tree density results are presented elsewhere (Westlind and Kerns 2017).

Analysis

The experiment is a randomized block, incomplete split-plot with repeat measures with season of burn as the whole plot (control, fall, and spring or C, F, and S), frequency of burn as the split or subplot (5-yr reburning or RB; and a single burn, 1B), and year as the repeat measure. The unburned control treatment is the incomplete split, as these plots were not burned; however, there are six plots within the unburned treatment, matching the sampling as if they were split. Treatment was defined as the combination of burn season and frequency (e.g., fall reburn, FRB). Univariate abundance responses were plant functional group cover (Table 1), functional group richness, inverse Simpson's diversity, Simpson's evenness, and Berger-Parker dominance. Other forest components included litter cover, organic horizon depth, soil cover, and overstory cover.

All variables were averaged for each plot from the quadrat cover data, then averaged at the experimental unit scale for each sampling year based on the three plots within each treatment type in each block (controls are represented twice to represent the experimental structure, but without representing the two levels of the reburn effects), and analyzed with a repeated-measures mixed-model ANOVA using Proc MIXED in SAS 9.4 and the Satterthwaite degree-of-freedom method and a heterogeneous compound symmetry covariance structure. Treatment and year and their interaction were fixed effects, and stand (block) and nested stand within season of burn were random. Year was the repeat measure with the subject defined as the split or subplot. Differences were assessed with pairwise comparisons within year only. We used an alpha of 0.05 for figures and tables and present significant P values in prose, including marginal contrasts ($0.05 < P < 0.10$), using a dash for clarity (e.g., F1B – C). All statistical results (F values, degrees of freedom) are presented in Appendix S1. Assumptions of normality and constant variance were checked graphically via residual plots. All response measures demonstrated reasonable symmetry, and only a few required relaxing the assumption of constant variance; thus, we did not transform any of our response variables. Plant responses are presented for 2002, 2007, and 2012 except shrub cover data are available only from 2007 and 2012. Data from 2002 represent the five-year growing-season response to the first fall 1997/spring 1998 burns. Because the treatments have not yet been reburned, comparisons between burn frequency treatments for the fall and spring confirm that there were no differences due to the burn frequency treatment assignment, and comparisons between burn intervals only represent the effect of season in 2002. Data from 2007 represent a 10-yr response for the single burn treatment (S1B, F1B), and maximum recovery after two 5-yr reburns for the RB treatment (SRB, FRB). The 2012 data demonstrate the fifteen-year response to the single spring and fall burns, and maximum recovery following three burns for the reburn treatments. We had no a priori interest or research questions associated with F1B – SRB or S1B – FRB contrasts, although the statistical results are shown in figures and tables for clarity.

RESULTS

Effects of fall burning

Fall burning vs. no burning.—In 2002, total mean cover was 11–16% higher in response to the first fall burns; however, only the single burn treatment was marginally different from no burning (F1B – C $P = 0.07$; Fig. 2; F and P values for all contrasts for all variables are shown in Appendix S1). After 2002, there was no difference detected for total plant cover as compared to no burning for either fall burn treatment. For open bunchgrasses, cover was about two to three times higher in response to the first burn, although the difference was only marginal for the single burn treatment (F1B – C $P = 0.07$; Fig. 2). By 2007, cover was similarly higher for both fall treatments, but again these differences were marginal (F1B – C $P = 0.06$; FRB – C $P = 0.09$), and by 2012 were not significant. In 2007, sedge cover was marginally reduced over 50% by reburning (FRB – C $P = 0.08$), a pattern that continued in 2012 following the third reburn, although the difference was not significant (Fig. 2).

Annual forb cover more than tripled in 2002 in response to the first fall burns compared with no burning (F1B – C $P = 0.006$; FRB – C $P = 0.03$; Fig. 3). In 2007, annual cover was again three times higher than unburned but only for the repeat burn treatment (FRB – C $P = 0.005$). By 2012, no differences were detected for annual forbs as compared to no burning for either treatment. Exotic forb cover was over 170 times higher in response to the first fall burns, although only significantly for the established reburn treatment (although the reburning treatment had not yet been applied; FRB – C $P = 0.02$; Fig. 3). This response disappeared with reburning and was not found in 2007 or 2012. However in 2007, the single burn treatment now had marginally higher cover compared to no burning (F1B – C $P = 0.06$).

Resprouting N-fixing shrub (CEVE) cover was over four times higher due to the single and repeat fall burns in both 2007 and 2012 (respectively: F1B – C and FRB – C both $P < 0.001$; F1B – C and FRB – C both $P < 0.0001$; Fig. 4). The cover of non-resprouting N-fixing shrubs decreased by seven times in 2007 in response to reburning (FRB – C $P = 0.02$), but this pattern was less pronounced and non-significant in 2012.

The first fall burns marginally increased total richness about 14% in 2002 for the single burn treatment compared with no burning (F1B – C $P = 0.07$; Fig. 5). There were about 60% more native annual forb species in 2002 in response to the first fall burns (F1B – C and FRB – C both $P < 0.02$). This response was short-lived and was not found in 2007 or 2012 (Fig. 5). We document a marginal increase in shrub richness associated with fall reburning in 2007 (FRB – C $P = 0.08$), but not in 2012. While mean exotic richness remained low across the study area, it more than tripled after the first fall burns (F1B – C and

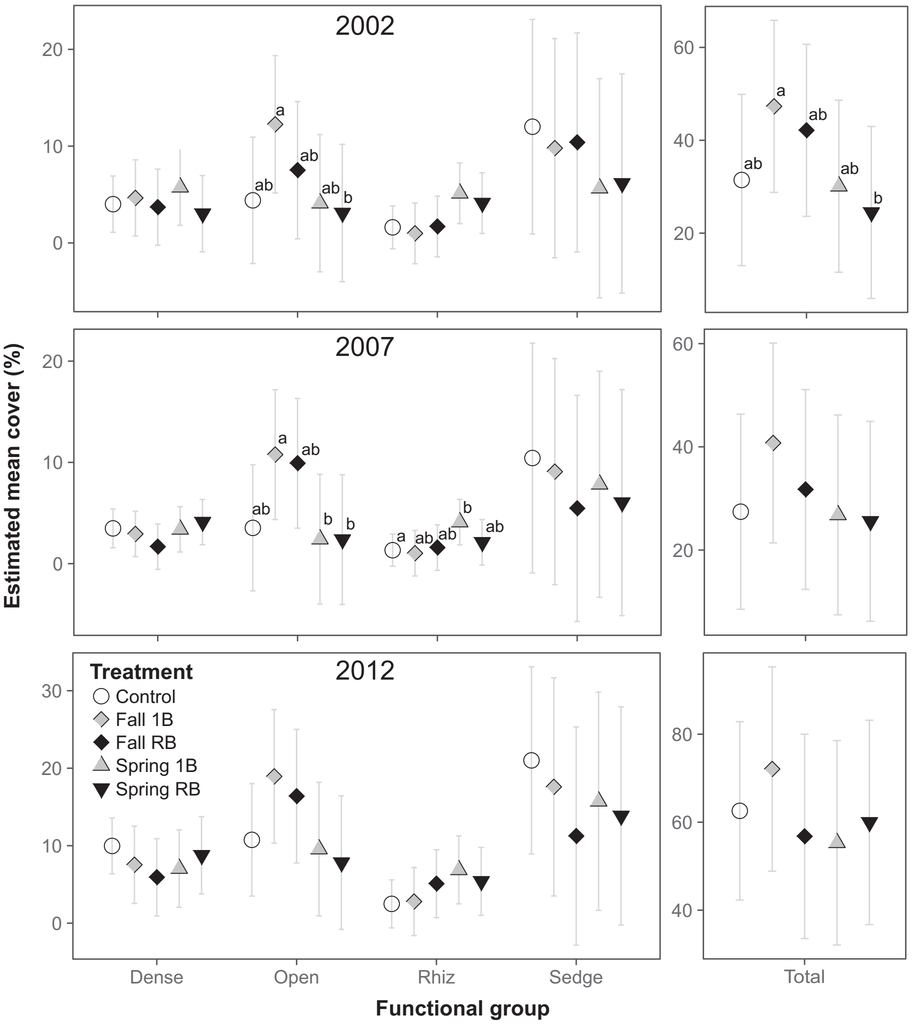

Fig. 2. Total (right panels) and graminoid functional group cover response to season (control = no burn) and frequency (1B = single burn; RB = 5-yr interval) of prescribed burning by sampling year. See Tables 1 and 2 for functional group code descriptions and species examples. Different letters indicate significant differences where $P < 0.05$. Vertical lines denote 95% confidence intervals.

FRB – C both $P < 0.0001$), a pattern that was still significant in 2007 (F1B – C $P = 0.004$) but gone by 2012. However, reburning maintained higher exotic richness in both 2007 and 2012 (F1B – C $P = 0.0007$, $P < 0.000$, respectively). Neither fall burn regime altered any of the diversity metrics as compared to no burning (Table 3).

Other forest components showed considerable impacts as a result of fall burning (Table 4). The soil organic (O) horizon depth was reduced by about 50% compared with no burning in 2002 in response to the first fall burns (F1B – C and FRB – C both $P < 0.002$), and this pattern held for both 2007 and 2012 (F1B – C, both years $P < 0.01$). Reburning similarly reduced O horizon depth in 2007 and 2012 compared with no burning (both years, FRB – C $P < 0.004$), but because there were no differences between the fall burn treatments in 2007 and 2012, the effect of reburning is likely a legacy from the first burns. Both single and repeat fall burning reduced litter cover in 2007 (F1B – C $P = 0.04$; FRB – C $P = 0.007$) and 2012 (F1B – C $P = 0.03$; FRB – C $P = 0.004$). Bare soil cover was three to four times higher following the fall first burns in 2002 (F1B – C $P = 0.05$; FRB – C $P = 0.01$), but the effect of the single first burn

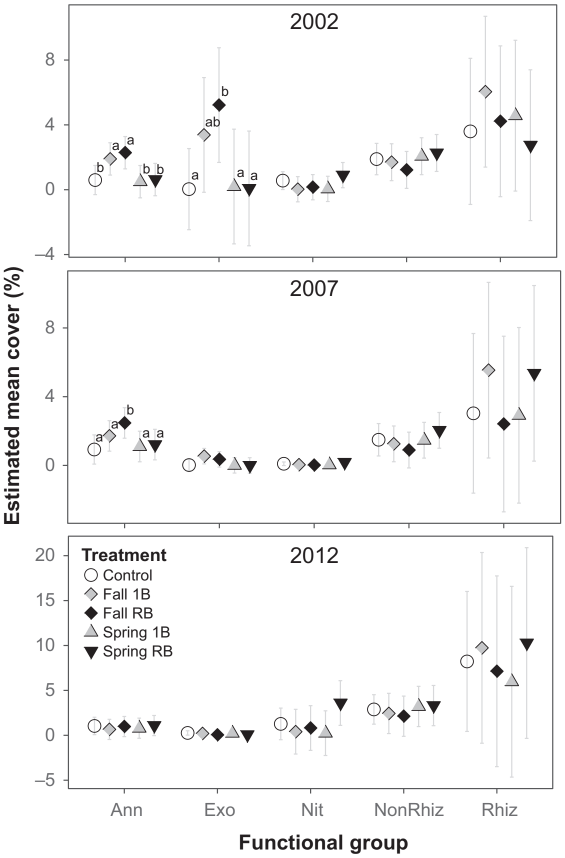

Fig. 3. Forb functional group cover response to season (control = no burn) and frequency (1B = single burn; RB = 5-yr interval) of prescribed burning by sampling year. See Tables 1 and 2 for functional group code descriptions and species examples. Different letters indicate significant differences where $P < 0.05$. Vertical lines denote 95% confidence intervals.

was gone in 2007. Fall reburning more than doubled bare soil cover in 2007 (FRB – C $P = 0.001$) and 2012 (FRB – C $P = 0.04$) compared with no burning. Overstory tree canopy cover was reduced by 11% in 2012 by repeated fall burning, almost a one-third reduction from the unburned control (FRB – C $P = 0.04$).

Single vs. repeat burning in the fall.—Few of the plant functional groups responded even marginally differently to fall burn frequency in any year we measured (Figs. 2–4). Annual forb cover was 1.5 times higher in the reburns compared to a single burn in 2007 (FRB – F1B $P = 0.03$), but this difference was not found in 2012 after the third burn (Fig. 3).

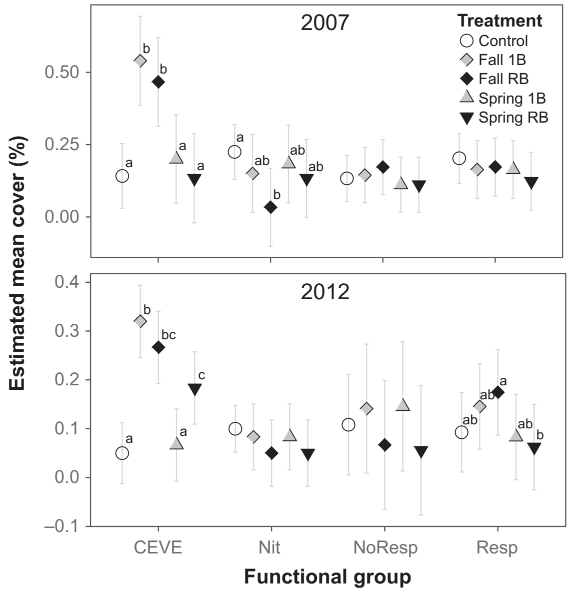

Fig. 4. Shrub functional group cover response to season (control = no burn) and frequency (1B = single burn; RB = 5-yr interval) of prescribed burning by sampling year. See Tables 1 and 2 for functional group code descriptions and species examples. Different letters indicate significant differences where $P < 0.05$. Vertical lines denote 95% confidence intervals.

There were few differences found for species richness and diversity metrics based on fall burn frequency for any of our sample years (Fig. 5, Table 3). In 2002, the fall burn treatments differed marginally with about 1.5 more native perennial forb species in the single burn treatment (F1B – FRB $P = 0.09$) although both treatments at this point had experienced a single fall burn; this difference remained in 2007 ($P = 0.10$), but disappeared in 2012, as richness had risen slightly with reburning. In 2012, two intervals of reburning increased exotic richness by about one species (F1B – FRB $P = 0.002$). Simpson's evenness in 2002 was marginally higher in the reburn treatment, even though both treatments had received only a single burn (F1B – FRB $P = 0.08$). However, this difference disappeared by 2007.

Few differences were found for other forest components related to fall burn frequency (Table 4). Bare soil cover was twice as high due to fall reburning in 2007 (F1B – FRB $P = 0.04$) and marginally so in 2012 (F1B – FRB $P = 0.098$).

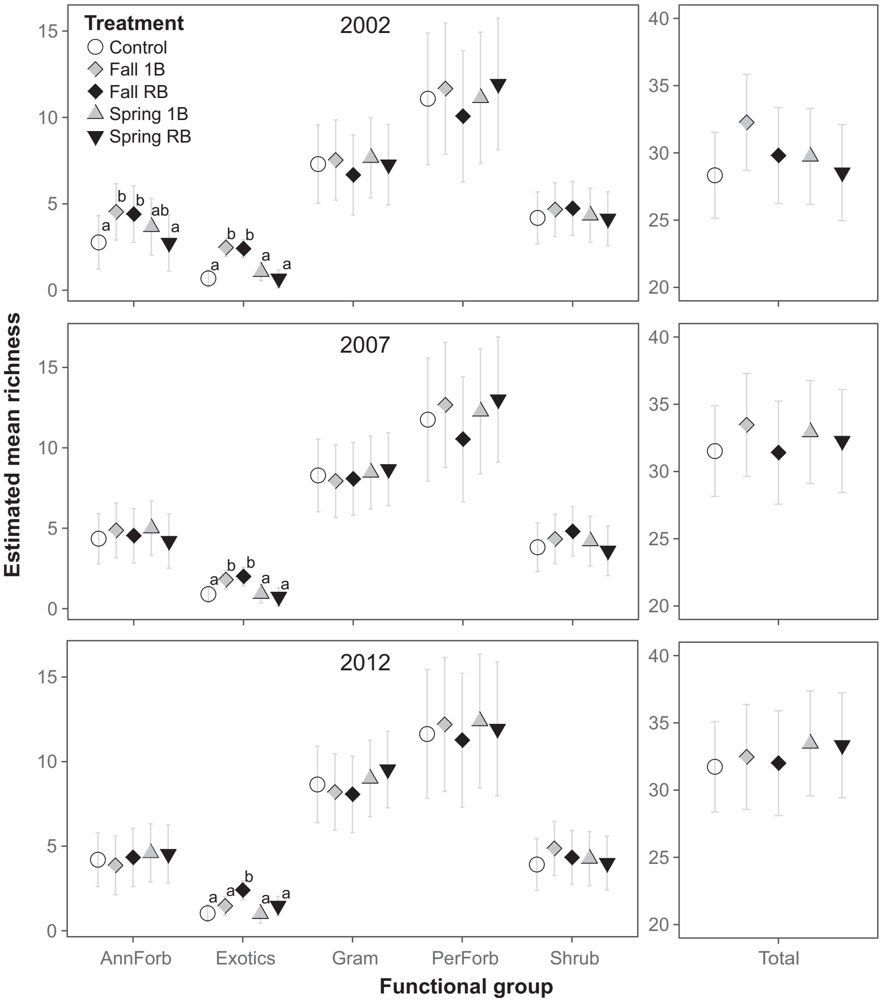

Fig. 5. Total (right panels) and coarse functional group richness response to season (control = no burn) and frequency (1B = single burn; RB = 5-yr interval) of prescribed burning by sampling year. See Tables 1 and 2 for functional group code descriptions and species examples. Different letters indicate significant differences where $P < 0.05$. Vertical lines denote 95% confidence intervals.

Effects of spring burning

Spring burning vs. no burning.—Rhizomatous grass cover more than tripled due to the first burns in 2002, although the difference was marginal (S1B – C $P = 0.07$; Fig. 2). This pattern was present in 2007 (S1B – C $P = 0.05$), but was gone by 2012. Most other perennial plant groups showed a lack of response to spring burning (Figs. 3 and 4), although resprouting N-fixing shrubs increased in response to reburning by 2012 (SRB – C $P = 0.002$; Fig. 4).

Richness and diversity metrics showed no response to spring burning compared with no burning (Fig. 5, Table 3). Spring burning also did not impact most other forest structural components, although O horizon depth was slightly and marginally lower after the first burn in 2002 (S1B – C $P = 0.06$), but this pattern was not long-lived.

Single vs. repeated spring burning.—There were few significant differences for the plant functional groups in response to spring burn frequency (Figs. 2–4). For N-fixing forbs, mean cover was 14 times higher in 2012 for the reburn treatment as compared to the single burn, although the difference was marginal (S1B – SRB

Table 3. Simpson's diversity and evenness and Berger-Parker dominance responses to season and frequency of prescribed burning.

		C		F1B		FRB		S1B		SRB	
Response	Year	Mean	CI	Mean	CI	Mean	CI	Mean	CI	Mean	CI
Simpson's diversity	2002	4.9	(3.9–5.9)	4.2	(3.0–5.3)	3.8	(2.6–4.9)	4.5	(3.3–5.6)	4.8	(3.7–6.0)
	2007	4.8	(3.8–5.9)	4.2	(2.9–5.5)	4	(2.6–5.3)	5.4	(4.1–6.7)	5.8	(4.5–7.1)
	2012	4.4	(3.4–5.4)	3.9	(2.8–4.9)	3.9	(2.8–5.0)	4.4	(3.3–5.4)	4.5	(3.4–5.5)
Simpson's evenness	2002	0.31	(0.22–0.41)	0.33	(0.2–0.43)	0.4	(0.30–0.50)	0.35	(0.25–0.45)	0.31	(0.21–0.41)
	2007	0.32	(0.23–0.41)	0.34	(0.24–0.44)	0.37	(0.27–0.46)	0.28	(0.18–0.38	0.27	(0.17–0.37)
	2012	0.33	(0.23–0.43)	0.34	(0.23–0.46)	0.39	(0.28–0.50)	0.3	(0.19–0.42)	0.33	(0.22–0.44)
Berger-Parker	2002	0.39	(0.30–0.48)	0.43	(0.33–0.53)	0.48	(0.38–0.57)	0.44	(0.34–0.53)	0.4	(0.30–0.50)
	2007	0.41	(0.32–0.50)	0.45	(0.36–0.55)	0.46	(0.36–0.55)	0.38	(0.28–0.47)	0.35	(0.26–0.45)
	2012	0.41	(0.32–0.51)	0.44	(0.34–0.54)	0.44	(0.34–0.54)	0.4	(0.30–0.50)	0.41	(0.31–0.51)

Notes: Simpson's diversity (D) is presented as inverse diversity (1/D) where higher numbers indicate higher diversity. Simpson's evenness is $D/D_{\max}$. No differences were detected where $P < 0.05$. CI numbers in parentheses indicate 95% confidence intervals. Abbreviations are as follows: C, control/no burn; F, fall; S, spring; 1B, single burn; RB, 5-yr interval; CI, confidence interval.

Table 4. Other forest component responses to season and frequency of prescribed burning.

		C		F1B		FRB		S1B		SRB	
Response	Year	Mean	CI	Mean	CI	Mean	CI	Mean	CI	Mean	CI
Litter cover (%)	2002	87.2	(81.0–93.3)	80.0	(71.7–88.3)	79.7	(71.3–88.0)	84.3	(76.0–92.6)	85.9	(77.6–94.2)
	2007	89.7 a	(85.9–93.5)	84.8 bc	(80.3–89.2)	82.8 b	(78.3–87.3)	87.8 ab	(83.3–92.3)	88.5 ac	(84.0–93.0)
	2012	89.6 a	(86.1–93.1)	85.4 bc	(81.6–89.2)	83.7 b	(79.9–87.4)	88.8 ac	(85.0–92.6)	88.9 ac	(85.1–92.6)
Bare soil cover (%)	2002	2.0 a	(−1.1 to 5.1)	6.9 ab	(2.7–11.2)	8.6 b	(4.4–12.8)	2.3 a	(−1.9 to 6.5)	3.6 ab	(−0.6 to 7.8)
	2007	2.0 a	(0.1–3.9)	3.2 a	(1.1–5.3)	5.7 b	(3.6–7.8)	1.7 a	(−0.5–3.8)	2.9 a	(0.7–5.0)
	2012	1.9 b	(0.0–3.8)	2.1 ab	(−0.1 to 4.4)	4.3 a	(2.1–6.6)	0.9 b	(−1.4 to 3.1)	2.5 ab	(0.2–4.7)
O horizon depth (cm)	2002	4.5 a	(3.7–5.4)	2.2 bc	(1.1–3.4)	2.2 b	(1.0–3.3)	3.8 ac	(2.7–5.0)	3.2 ab	(2.1–4.3)
	2007	4.3 a	(3.7–5.0)	3.0 b	(2.2–3.7)	2.8 b	(2.0–3.6)	4.5 a	(3.7–5.3)	3.6 ab	(2.8–4.3)
	2012	4.3 a	(3.7–4.9)	3.0 bc	(2.3–3.7)	2.7 b	(2.0–3.4)	4.3 a	(3.5–5.0)	4.0 ac	(3.2–4.7)
Tree canopy cover (%)	2002	36.0	(28.6–43.3)	33.9	(25.2–42.7)	33.8	(25.1–42.6)	39.5	(30.8–48.2)	40.0	(30.8–48.3)
	2007	42.6 ab	(34.7–50.5)	33.5 a	(23.4–43.5)	35.3 ab	(25.3–45.4)	48.2 b	(38.1–58.2)	47.9 b	(37.9–58.0)
	2012	37.1 a	(29.9–44.2)	30.5 ab	(22.3–38.8)	25.9 b	(17.6–34.1)	41.9 a	(33.6–50.2)	36.0 ab	(27.7–44.3)

Notes: CI numbers in parentheses indicate 95% confidence intervals. Different letters indicate significant differences where $P < 0.05$. Abbreviations are as follows: C, control/no burn; F, fall; S, spring; 1B, single burn; RB, 5-yr interval; CI, confidence interval.

$P = 0.06$; Fig. 3). Resprouting N-fixing shrub (CEVE) cover was almost three times higher for spring reburning than a single burn (S1B – SRB $P = 0.01$; Fig. 4).

Most of the richness and diversity metrics showed no significant differences (Table 3, Fig. 5). By chance in 2002, the spring reburn treatment had slightly fewer (less than one, S1B – SRB $P = 0.06$) exotic species compared to the single burn treatment. This difference was gone in 2007, but reappears marginally in 2012 ($P = 0.09$); however, the pattern is flipped with slightly more exotic species found with reburning. Spring burning had little impact on other forest components (Table 4), although O horizon depth was 21% lower for the reburn treatment, but only marginally in 2007 (S1B – SRB $P = 0.06$).

Comparison of fall and spring burning

Single fall vs. spring burn.—On average, total cover was about 17% higher in the fall treatments as compared to the spring in 2002 (F1B – S1B $P = 0.06$; FRB – SRB $P = 0.05$; both contrasts reflect the single burn only; Fig. 2), but seasonal differences from the first burn were no longer evident in 2007 and 2012 (i.e., F1B – S1B). Open bunchgrass cover was marginally higher owing to the first fall burn as compared to spring treatments in 2002 (F1B – S1B $P = 0.07$), and this pattern was still evident in 2007 (F1B – S1B $P = 0.04$), but marginal in 2012 (F1B – S1B $P = 0.10$). Rhizomatous grass cover was about five times higher in response to spring burning in 2002 (S1B – F1B $P = 0.07$), and although this difference was marginal, it was also detected in 2007 (S1B – F1B $P = 0.06$), but not in 2012. In 2002, native annual forb cover was higher in the fall treatments as compared to the spring treatments (all contrasts shown, $P < 0.04$; Fig. 3), but the differences for the single burn treatment disappeared in 2007 and 2012. Exotic forb cover was higher in one of the fall treatments as compared to spring in 2002 (FRB – SRB $P = 0.04$), and this pattern was marginal in 2007 for the single burn (F1B – S1B $P = 0.09$) and gone by 2012 (Fig. 3). Resprouting N-fixing shrub cover was 3–4 times higher after a single fall vs. spring burn in 2007 and 2012 (F1B – S1B, both years $P < 0.004$; Fig. 4).

Few differences in richness or diversity metrics were found when comparing the single fall and spring burns (Table 3, Fig. 5). There were more annual forbs in the fall treatment as compared to spring in 2002 (FRB – SRB $P = 0.03$), but the pattern was short-lived and not evident in 2007 or 2012. Exotic richness was twice as high after the fall burn in 2002 (all spring and fall contrasts, $P < 0.001$; Fig. 5), and this pattern remained in 2007 (F1B – S1B $P = 0.01$) but not in 2012.

Litter cover was reduced for the single fall treatment compared to spring but only marginally in 2012 (F1B – S1B $P = 0.09$; Table 4). Bare soil increased marginally due to the first fall burns compared to spring burns (FRB – SRB $P = 0.09$), but effects from the first burns were not evident in 2007 or 2012 (Table 4). The single fall burn reduced the O horizon depth as compared to spring burning, a pattern that remained throughout the sampling period (2002 F1B – S1B $P = 0.06$; 2007 F1B – S1B $P = 0.008$; 2012 F1B – S1B $P = 0.02$; Table 4). Tree canopy cover was lower for the single fall treatment in 2007 and marginally in 2012 (F1B – S1B $P = 0.04$, $P = 0.06$, respectively).

Repeated spring vs. fall burning.—Note that the effect of burn frequency is not demonstrated until 2007, and is more clearly related to reburning if there was no difference between the FRB and SRB treatments in 2002 (prior to reburning), or if the sign of the difference changes. Although there were seasonal differences in total cover in 2002 due to the first burn (presented above), there were no differences between fall and spring reburning in 2007 or 2012. In 2007, open bunchgrass cover was four times higher in the fall reburn compared to the spring (FRB – SRB $P = 0.06$; Fig. 2), while densely tufted bunchgrass cover was over twice as high in the spring vs. fall reburns (FRB – SRB $P = 0.09$). Although these differences were marginal, neither effect was present in 2002, but these differences disappeared by 2012.

Native annual forb cover was two times higher with fall vs. spring reburning in 2007 (FRB – SRB $P = 0.02$; Fig. 3). It is important to note that these differences were present in 2002 and may reflect the initial entry fire, and the pattern was not detected in 2012. Resprouting N-fixing shrub cover was 3.5 and 1.5 times higher with fall vs. spring reburning in 2007 and 2012 (FRB – SRB $P = 0.004$, 0.07, respectively; Fig. 4). Resprouting shrub cover was almost three times higher in fall vs. spring reburning in 2012 (FRB – SRB $P = 0.05$).

Perennial native graminoid richness in 2012 (FRB – SRB $P = 0.06$) and perennial native fob richness in 2007 (FRB – SRB $P = 0.09$) were marginally higher after spring reburning vs. fall (Fig. 5), while shrub richness was marginally higher in fall vs. spring in 2007 only (FRB – SRB $P = 0.06$). These differences were not found in 2002. Exotic richness was higher in the fall compared to the spring reburn in both 2007 and 2012 (both $P < 0.001$; Fig. 5), although the effect was only based on one species. Shrub richness was marginally higher (but only by one species) in the fall compared to the spring reburn in 2007 (FRB – SRB $P = 0.06$), but this pattern was not evident after the third reburn in 2012. Inverse Simpson's diversity was 1.5 times higher in spring vs. fall in 2007 (FRB – SRB $P = 0.06$), while Berger-Parker dominance was 1.3 times higher in fall vs. spring (FRB – SRB $P = 0.10$; Table 3). Although both differences were marginal, these differences were not detected in 2002.

Litter cover was higher in spring vs. fall after two (2007) and three (2012) repeat burns (FRB – SRB $P = 0.04$, 0.01, respectively), while conversely bare soil cover was marginally higher in the fall reburn treatment in 2007 (FRB – SRB $P = 0.02$; Table 4), although this pattern was marginally evident in 2002 after the first burns (see above) and disappears in 2012. O horizon depth was lower in fall vs. spring reburns by

2012 (FRB – SRB $P = 0.02$), and tree canopy cover was also marginally lower in fall vs. spring in both 2007 and 2012 (FRB – SRB $P = 0.08$, 0.09, respectively).

Discussion

We describe outcomes from a unique 15-yr experiment designed to examine the effects of different prescribed fire regimes on ponderosa pine-dominated forest vegetation and other forest components in the intermountain western United States. We found that most plant functional group responses were not markedly different among our burn regimes or even in comparison with no burning, especially for native perennial herbaceous groups. Many burn treatment results were neutral, subtle, and ephemeral, with either non-significant or statistically marginal responses compared to no burning. Although total plant cover and richness did increase within five years in response to our first fall burns, this pattern disappeared within a decade. Only one plant functional group (CEVE, the resprouting N-fixing shrub *Ceanothus velutinus*) demonstrated a long-term positive response to the single burn. We also failed to document either short- or long-term changes in diversity in response to our single fire treatments or 5-yr reburning as compared to no burning. There was some evidence that fall reburning may actually be detrimental to some native perennial plant groups, such as the trends in lower cover we report for sedges and non-resprouting N-fixing shrub cover. Reburning in both spring and fall also maintained higher exotic species richness, one of the only richness or diversity patterns detectable after 15 yr of reburning. Previous work has shown that reburning resulted in higher cover of the exotic annual grass *Bromus tectorum* compared to no burning, although reburning may be less important than the original entry burn (Kerns and Day 2017).

Our results are consistent with some other recent studies and reviews documenting neutral, ephemeral, or inconsistent responses to single-entry prescribed burns (Nelson et al. 2008, Abella and Springer 2015, Strahan et al. 2015, Kalies and Yocom Kent 2016, Willms et al. 2017), particularly for herbaceous perennials (Rossman et al. 2018). Lack of long-term (15 yr) plant responses to a single-entry burn may be expected in forests that are characterized historically by frequent fire. Inconsistencies or neutral responses may be due to factors such as different spatial and temporal scales at which responses are measured, lack of experimental power, or overriding biotic and abiotic forcing factors (e.g., climate, competitive interactions, other disturbances) that can either obscure plant responses to treatments (Moore et al. 2006, Driscoll et al. 2010, Haslem et al. 2016, Rossman et al. 2018) or homogenize plant community patterns. Others point out that these inconsistencies may reflect the fact that species-specific responses are lost when all taxa are lumped together into very broad categories such as herbaceous plants (Willms et al. 2017, Rossman et al. 2018). For example, some studies show an increase in understory richness and abundance 3–5 yr after fire, especially for short-lived forbs, supporting the notion that use of finer-scale functional groups can help elucidate plant responses to fire, although responses may still be ephemeral (e.g., Metlen and Fiedler 2006, Strahan et al. 2015).

By using relatively fine-scale plant functional groups, we did find that some plant groups possessing traits that may offer greater resistance and resilience to fire responded positively and more strongly to burning. Although differences among some treatments may appear too small to be biologically significant, examination of relative and percentage differences between treatments may suggest otherwise. These groups included annual forbs, open bunchgrasses, exotics forbs, and CEVE for fall burning, and rhizomatous grasses for spring reburning. Many of these species may be damaged or directly killed by even low-severity fire, but are able to recolonize quickly through either persistent seed banks in the soil (annual forbs, exotic forbs) or vegetative structures (rhizomes, resprouts) that are not killed by lethal temperatures or short fire return intervals (Agee 1996, Pyke et al. 2010, Bowd et al. 2018), or are able to resist substantial damage or mortality from fire due to their growth form (open bunchgrasses).

Many species that comprise the native perennial grass and shrub plant groups that responded positively to fire are well known as "fire increasers or invaders" (Rowe 1983, Agee 1996). For example, the dominant open bunchgrass in our study area, *Elymus elymoides* (also a dominant across the entire study), is a noted post-disturbance rapid colonizer (Moore et al. 2006), as are rhizomatous species (Youngblood et al. 2006). Annual and exotic forbs possess similar plant traits and responded similarly to the fires in this study—both demonstrating an ephemeral response to a single burn. Interestingly, one or two reburns did not stimulate strong reestablishment as compared to the first fires. The five-year interval used in this study is probably too short to maintain a resilient annual or exotic forb seed bank, or forb responses are highly ephemeral and gone within 5 yr, a potentially constructive result if these species are of concern. Very frequent burning may also be too low severity to promote seed germination and short-lived species establishment. Indeed, the reburns in this study were often difficult to conduct and carry due to fine fuel limitations (Westlind and Kerns 2017). On the other hand, bare soil cover increased and O horizon depth was reduced with fall reburning, as was overstory tree cover, suggesting that burns were of sufficient severity to expose new mineral soil and increase light availability. While we document some important plant functional group responses to burning, it is possible that further differentiation, particularly for perennial plant groups, could provide more insight into plant responses. However, one problem with defining very fine-scale and specific plant functional groups is the lack of reliable trait information for the 119 species that characterized the flora.

Neutral and inconsistent responses from prescribed fire studies may also be due to burn prescriptions, which are designed to control fire behavior within strict guidelines, but can vary widely. It is possible that these regimes may not always generate strong plant community responses, due to either fire season, frequency, intensity, or spatial extent. Our study allows us to examine this issue in light of burn frequency and season and provides weak support for the notion that simply conducting prescribed fires more frequently will increase perennial native plant abundance and diversity in general. Similarly, Scudieri et al. (2010) found little ponderosa pine understory vegetation response to 30 yr of very frequent burning (less than 5 yr) in the southwest, a result the authors attribute to a lack of change in overstory plant cover. However, we document that fall reburning reduced overstory canopy cover to about 26% by 2012, which was significantly lower than the 37% cover found with no burning.

The five-year burn interval implemented in this study is at the very low end of the range of fire regimes reported for the study area (Soeriaatmadja 1966, Bork 1984, Agee 1996). This burn interval was suggested largely due to concerns regarding fuel buildup and discussion of fire history studies and prescribed fire regimes from southwestern ponderosa pine forests (Sackett 1980, Swetnam and Baisan 1996). New fire history data using contemporary techniques that were not available at the time our study was initiated support the notion that mean fire return intervals less than 10 yr are less common (Heyerdahl et al. 2001, Johnston et al. 2017, Reilly et al. 2017). Ironically, 5-yr burning has not reduced woody fuels due to notable overstory mortality that actually increased fuels, although ground fuels (litter and diff) have been reduced (Westlind and Kerns 2017). While we suggest that simply conducting prescribed fires more frequently may not increase perennial native plant abundance and diversity, we acknowledge our burns were still conducted under low-temperature and high-humidity conditions that still may not allow fire to do as much work (North et al. 2007). Westlind and Kerns (2017) suggest that an intermediate fire frequency closer to 10 yr in these types of ponderosa pine forests may offer better outcomes related to fuel reduction goals, and this may hold for some plant goals as well. Some suggest wildfires managed for ecological or other resource goals may provide a viable option as well as recognized tradeoffs (Barros et al. 2018). However, field testing of this hypothesis may be difficult to implement, although some studies focused on tree structure and hazardous fuels are noted (Huffman et al. 2017).

Our results demonstrate that burn season impacted the plant community more than burn frequency for fall burning, but burn frequency was important for spring burning. In addition, many of the patterns that we found were strong legacies from the original burn. These results underscore the importance of fire severity, rather than phenological interactions with burn season, as a major driver shaping vegetation patterns (Knapp et al. 2009, Ellsworth and Kauffman 2017). Haslem et al. (2016) note that while time since the last fire was more important than fire frequency in explaining forest structure patterns in Australia, patterns were strongly mediated by the type of fire and fire severity. The prescribed burns in this study were generally low severity, but fuels are typically drier in the fall, and fall burning creates tangible differences in fire severity, such as more bare soil cover, reduced forest floor depth (both documented in this study), and patchy overstory tree torching and more mortality compared to spring burns (Thies et al. 2005, Kerns et al. 2006). Higher fire severity associated with fall compared to spring burns has been documented in other studies as well (e.g., Sapsis and Kauffman 1991).

Burning in spring is considered outside the historical wildfire season, but does not appear to be strongly detrimental to the plant community even when done frequently. This may be due to the fact that spring burn conditions and plant phenology today may be quite different than in the past (Westerling et al. 2006, Körner and Basler 2010). Many spring treatment plant responses were statistically similar to the unburned treatment, and spring burning actually benefited some plant functional groups such as rhizomatous grasses. However, we caution that our plant functional group approach can obscure species-specific responses.

Some plant functional groups responded in opposing directions to seasonal burn regimes, leading to marginal differences between the seasonal fire regimes but no difference compared to no burning. For example, in 2007, open bunchgrass cover was higher in response to the fall reburn compared to spring, while dense bunchgrass cover was higher in spring vs. fall reburns. Compared to open bunchgrasses, denser bunchgrasses such as *Festuca idahoensis* are typically more sensitive to fire (Zouhar 2000). Diversity results, while also marginal, suggested that spring reburning may lead to higher plant diversity, while fall reburning may increase species dominance and evenness. These trends are consistent with some studies suggesting growing-season fires can favor cool-season species (Platt et al. 1988, Biondini et al. 1989), and lend support to the intermediate disturbance hypothesis, assuming fall reburning represents a higher level of disturbance compared to spring reburning (Grime 1973*a*, *b*, Wilkinson 1999).

Our study is unique in the western United States as we examine five burn treatments, two aspects of fire regime (season and frequency), and long-term responses. There are caveats associated with any ecologically based field study, and our sample size (n = 5) and statistically marginal differences suggest results should be interpreted cautiously. Nevertheless, our results are consistent with a growing number of studies documenting neutral plant responses to prescribed fire particularly for native perennial plant groups. While lack of a strong native plant community response may be viewed positively, in that these treatments also do not appear to be detrimental, practitioners using prescribed fire may have biodiversity, conservation, and habitat goals that hinge on expectations for vigorous plant responses and increases in desired species such as perennial bunchgrasses important for forage production. For example, evaluation of a handful of fuel reduction (thinning and burning) projects analyzed through the NEPA (National Environmental Policy Act) process on the Malheur National Forest showed that goals and desired conditions related to prescribed fire use and upland vegetation were typically focused on altering tree structure and composition to move landscapes more toward reference conditions, as well as creating and restoring vigorous native plant communities, reducing invasive plant populations, and increasing forage availability. Understanding of reference conditions was often based on regionally relevant studies (e.g., Hessburg et al. 2005, Churchill et al. 2017), although information is often limited or non-specific for non-tree forest understory conditions in these types of studies.

Dry forests that historically experienced frequent fire have often undergone decades of fire suppression, historical livestock overgrazing, continued livestock grazing, and other land-use changes, which combined have led to a variety of changes such as increased tree density, forest floor build up, and decreased understory production (Covington and Moore 1994, Hessburg et al. 2005, 2015). Many ponderosa pine forests likely reside in an alternate state, a phenomenon observed in other forest types after long periods of fire-free intervals (Hoffmann et al. 2012), and are now subject to other exogenous forcing factors such as rising CO_2 concentrations, and climatic variability and change. State changes and inertia in these ecosystems may not be overcome easily by using one relatively weak forcing factor and could send systems into unintended trajectories (Kitzberger et al. 2016). These landscapes may be somewhat resistant or resilient to fire due to traits of the remnant native flora, but may lack the native seed source, plant vigor, or environmental conditions necessary to respond strongly and positively to low-severity fire. On the other hand, new invasive species may be well positioned to increase after prescribed fire (Kerns and Day 2017). Successfully disrupting substantial ecosystem inertia and moving systems beyond resisting but not responding may require addressing multiple constraints, careful reconsideration of when, how, and why to intervene, and a shift in focus away from using the past to guide management (Suding and Hobbs 2009, Hobbs et al. 2014). While reestablishing historical fire regimes in areas that are considered to be in fire deficit is increasingly being called for, our study adds a unique and long-term perspective to the growing body of evidence that there is considerable uncertainty about plant community outcomes related to such interventions in an era of increasingly rapid and novel change.

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