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Response of antelope bitterbrush to repeated prescribed burning in Central Oregon ponderosa pine forests☆

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ABSTRACT

Antelope bitterbrush is a dominant shrub in many interior ponderosa pine forests in the western United States. How it responds to prescribed fire is not well understood, yet is of considerable concern to wildlife and fire managers alike given its importance as a browse species and as a ladder fuel in these fire-prone forests. We quantified bitterbrush cover, density, and biomass in response to repeated burning in thinned ponderosa pine forests. Low- to moderate-intensity spring burning killed the majority of bitterbrush plants on replicate plots. Moderately rapid recovery of bitterbrush density and cover resulted from seedling recruitment plus limited basal sprouting. Repeated burning after 11 years impeded the recovery of the bitterbrush community. Post-fire seed germination following the repeated burns was 3–14-fold lower compared to the germination rate after the initial burns, while basal sprouting remained fairly minor. After 15 years, bitterbrush cover was 75–92% lower on repeated-burned compared to unburned plots. Only where localized tree mortality resulted in an open stand was bitterbrush recovery robust. By controlling bitterbrush abundance, repeated burning eliminated the potential for wildfire spread when simulated using a customized fire behavior model. The results suggest that repeated burning is a successful method to reduce the long-term fire risk imposed by bitterbrush as an understory ladder fuel in thinned pine stands. Balancing the need to limit fire risk yet provide adequate bitterbrush habitat for wildlife browse will likely require a mosaic pattern of burning at the landscape scale or a burning frequency well beyond 11 years to allow a bitterbrush seed crop to develop.

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1. Introduction

Antelope bitterbrush (*Purshia tridentata* [Pursh] DC.; herein referred to as bitterbrush) is a common woody shrub found extensively on forest and range lands in the western United States and southern British Columbia (Hormay, 1943). Interest in its autecology and management has been keen for many years given the shrub's extensive distribution and numerous ecological roles (Young and Clements, 2002). Bitterbrush is perhaps best known as a high protein, digestible winter browse for mule deer (*Odocoileus hemionus*) and other large ungulates (Young and Clements, 2002). Many rodents and birds also rely on bitterbrush seed for part of their diet (Nord, 1965; Vander Wall, 1995; Smith and Maguire, 2004). Other ecological functions include (1) supplying up to 50% of the annual nitrogen input in pine forests via symbiotic N fixation (Busse, 2000), and (2) acting as a highly flammable ladder fuel to increase crown-fire risk in dry forests.

Bitterbrush is a fire-sensitive species, preferring open-canopy pine stands with seedbeds relatively free of surface organics for seedling establishment (Sherman and Chilcoate, 1972; Edgerton, 1983). How it responds following fire, however, is difficult to predict. Martin (1983) found fairly rapid regeneration of bitterbrush at 19 ponderosa pine (*Pinus ponderosa*) sites in Central Oregon following prescribed burning and suggested that fire is a useful tool for developing young, vigorous stands of bitterbrush. Similarly, Ruha et al. (1996) found that bitterbrush remained the dominant understory plant after moderate- to high-intensity burns in a case study site near Bend, OR. In contrast, others have shown a poor recovery by bitterbrush following burning that presumably reflects the plant's physiological intolerance to fire and its inconsistent ability to resprout (Hormay, 1943; Nord, 1965; Busse et al., 2000), while Zhang et al. (2008) found little response by bitterbrush to burning in a mixed-shrub, ponderosa pine forest.

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Evidently, any generalities regarding bitterbrush's ability to respond to fire are complicated by site specific factors such as fire intensity and severity, fuel loading, fuel moisture, season of burning, soil type, soil moisture, bitterbrush genetic variability, and plant age (Young and Clements, 2002).

Circumstantial evidence from 19th century photographs and journals indicates that bitterbrush was far less abundant in pre-settlement pine forests compared to present day conditions (Young and Clements, 2002). This suggests that historic burning in Central Oregon, which averaged one fire every 4–24 years (Bork, 1984), may have been largely responsible for limiting the presence of bitterbrush. Frequent fire, while encouraging open stand conditions and minimal forest floor accumulation favored by bitterbrush establishment, likely restricted bitterbrush seed production and promoted a graminoid-dominated understory. Interestingly, it was the disruption of the historic fire cycle along with livestock grazing in the late 19th century which reduced the dominance of graminoids and led to an abundance of bitterbrush (Peek et al., 2001; Riegel et al., 2006).

Bitterbrush management in Oregon faces a fundamental challenge. Much of the dietary needs of the region's large mule deer population are met by bitterbrush (Gay, 1998), underscoring the importance of sustaining and promoting bitterbrush habitat. As well, encouraging fire-resilient forests is a foremost objective of public and private landowners, made even more critical by recent wildland-urban expansion. Limiting the abundance of shrubs such as bitterbrush is one of few practical options for reducing fire risk, short of thinning overstory trees. Thus, increasing our scientific understanding of bitterbrush and its response to fuel management is a necessary step to resolve this predicament.

Presently, few data exist on the long-term response of bitterbrush to repeated burning (see Blaisdell and Mueggler, 1956). Our objective was to quantify bitterbrush population response to repeated burning after 11 years. Two experimental sites in thinned, second–growth pine forests with understories dominated by bitterbrush were selected, and post-fire measurements of bitterbrush cover, density, and biomass were taken on a 3-year interval between 1993 and 2006. In addition, we assessed whether the presence of bitterbrush would increase the predicted wildfire spread and fire intensity using a fire behavior model customized to the stand conditions from our sites.

2. Materials and methods

2.1. Site descriptions

The study was conducted on the Bend/Fort Rock Ranger District of the Deschutes National Forest, in the rainshadow of the Central Oregon Cascades. Two ponderosa pine-bitterbrush sites were selected from a larger experiment, the Bend Long-term Site Productivity Study (Bend LTSP; Busse and Riegel, 2005): (1) East Fort Rock, a moderately-low productive site located 17 km southeast of Bend, OR, and (2) Sugar Cast, a moderately productive site located 5 km east of Sunriver, OR. Site index for ponderosa pine is 21 m at East Fort Rock and 24 m at Sugar Cast on a 100-year basis (Barrett, 1978). Bitterbrush is the dominant understory plant at both sites, averaging 13% cover at East Fort Rock and 22% cover at Sugar Cast. Other common species include greenleaf manzanita (*Arctostaphylos patula*), western needlegrass (*Achnatherum occidentale*), bottlebrush squirreltail (*Elymus elymoides*), and Idaho fescue (*Festuca idahoensis*). Peak-season biomass of the herbaceous layer is quite low, averaging 10–20 kg ha^{-1} (Busse, unpublished).

Plant growth is limited by low annual precipitation, which occurs primarily during winter months and is estimated at 41 cm $year^{-1}$ at East Fort Rock and 49 cm $year^{-1}$ at Sugar Cast (http://www.prism.oregonstate.edu). The growing season lasts from approximately mid-May to late August and has an average maximum temperature of 25 °C. Soils at both sites (cryic Vitrands) developed from wind blown deposits of pumice and ash following the eruption of Mt. Mazama approximately 7700 years before present (Soil Survey of Upper Deschutes River Area; http://soildatamart.nrcs.usda.gov). Soil horizon development is weak, with an 8–10 cm loamy-sand surface horizon (4% organic matter; 0.14% total N; pH 6.2) above a 30–40 cm transition horizon (1% OM; 0.02% total N; pH 6.2) and an undeveloped C horizon (Busse, unpublished).

Ponderosa pine regenerated naturally at both sites following railroad logging in the 1930s. The sites have been free of major disturbance since seedling establishment with the exception of pre-commercial thinning operations in the late 1960s and again in 1989 at the onset of the Bend LTSP Study. Thinning from below in 1989 targeted damaged trees plus the smallest trees on each plot. In 1991, the stand age at East Fort Rock was 59 years and mean basal area was 16.9 m^2 ha^{-1} with a stocking of 242 trees ha^{-1} (Busse, unpublished). Stand age at Sugar Cast was 54 years, mean basal area was 15.9 m^2 ha^{-1}, and stocking was 221 trees ha^{-1} (Busse, unpublished).

2.2. Experimental treatments and burn conditions

Two treatments (burned and unburned) were replicated three times at each site in a completely randomized design. Plot size was 0.4 ha with a minimum buffer width between plots of 20 m. Experimental burns were prescribed by District personnel and ignited between late May and early June 1991, and were repeated in early June 2002. The selection of the reburn year was based on the build-up of ladder fuels following the 1991 burns, primarily bitterbrush plants containing needle drape from overstory trees.

Fuel loads were measured before and after burning to estimate fuel consumption. Woody material was measured using a modified version of the planar intercept method (Brown, 1974). Downed wood (1, 10, 100, and 1000 h fuel classes) was counted on 12 systematically located transect lines, 15 m in length, per plot. Litter and duff depths were measured both pre- and post-fire at 60 systematic locations per plot and converted to mass using average bulk density values determined for each plot ($n = 4$ for pre- and post-fire). Post-fire duff measurements were taken within 1 month of burning. Fuel loading and consumption values for the 1991 burns are from Shea (1993). Crown scorch was determined for the 1991 burns by measuring live crown length on all trees prior to burning and again at the end of the first growing season after burning with an optical dendrometer. Crown scorch was not measured following the 2002 burns, although visual inspection of all trees failed to detect substantial crown damage at either site.

2.3. Bitterbrush measurements

Three permanent belt transects (5 m × 20 m) were located systematically in each plot to estimate bitterbrush density, cover, and biomass. All plants within the belt transects were measured on a 3-year basis beginning in 1993 and the transect values were combined to determine plot averages. Canopy length and width of each plant were measured, and cover was estimated for each shrub assuming a rectangular-shaped canopy. Total cover was calculated by summing the cover of all plants within the three transects. Because the number of germinants was high following the 1991 burns, their coverage was estimated as the product of their population count and their average canopy size, determined by measuring 20 randomly selected seedlings per plot.

Table 1
Predictive equations of bitterbrush aboveground biomass and age as a function of canopy diameter. Fifty plants representing the range of size classes found at each site were measured for canopy dimensions, and destructively sampled to determine biomass and age. Stepwise regression analysis was used to select the canopy measures for estimating bitterbrush biomass and age.

Site	Variable[a]	Predictive equation[b]	R^2
East Fort Rock	ln(Biomass)	(2.374 ln(Canopy)) − 4.610	0.94
	ln(Age)	(0.9774 ln(Canopy)) − 1.412	0.85
Sugar Cast	ln(Biomass)	(2.911 ln(Canopy)) − 7.303	0.96
	ln(Age)	(0.949 ln(Canopy)) − 1.221	0.79

[a] Units are g plant^{-1} for biomass and years for age.
[b] Canopy = canopy diameter (cm), determined by the average of the longest canopy axis and its perpendicular axis.

Bitterbrush biomass and age were estimated using non-destructive equations developed for each site in 1990. Fifty plants per site, representing the full range of canopy size classes, were measured for canopy length and width, total height, and stem diameter at ground level prior to destructive sampling for dry weight (60 °C for 72 h). Plant age was determined by counting the annual rings at ground level (cross-dating techniques were not used to verify plant age). Stepwise regression analysis (SAS, 2000) was used to predict biomass and age as a function of the four canopy variables (Table 1). Total biomass per hectare and age-class distribution were then determined using non-destructive canopy measurements of all plants within the belt transects.

Post-fire basal sprouts were counted in the second growing season following the 1991 and 2002 burns. Sprouting success was determined as the percentage of burned plants per plot that sprouted and remained alive through the second growing season.

2.4. Overstory canopy cover as a predictor of bitterbrush abundance

Overstory canopy cover was estimated in 1997 to examine the relationship between shading and bitterbrush abundance. Tree canopy diameter and stem diameter at breast height (DBH) were measured on 15 randomly selected trees per plot, representing all size classes. Canopy diameter was measured along the two cardinal axes of each tree, and the average was used to determine canopy area assuming a circular shape. DBH was the independent variable in regression analysis (SAS, 2000) for predicting the canopy area of a given tree. Correlation coefficients for individual plots ranged from 0.34 to 0.92, with a median of 0.72. All trees within each plot were then measured for DBH, and total canopy cover was calculated as the sum of the individual canopy areas from the regression equations. We did not account for the possible overestimation of canopy cover due to overlapping tree canopies. However, this error was likely small due to the wide spacing between trees.

2.5. Predicted wildfire behavior

The effect of repeated prescribed burning on wildfire behavior was simulated using the wildfire behavior model, BehavePlus 3.0 (Andrews et al., 2005). This is a deterministic (non-random) model that, similar to most fire models, uses the Rothermel fire-spread algorithm (Rothermel, 1972) to estimate fire-line intensity and rate of spread of a surface fire based on site characteristics. Our interest was to determine if repeated burning altered the predicted wildfire spread by its affect on vegetation and fuels. Flame length and rate of spread were predicted using vegetation and fuel data from the two sites. Separate simulation runs were made for (1) no burning (No burn); (2) a single burn in 1991 (Single burn); (3) repeated burning in 1991 and 2002 (Repeated burn) at each site. Plot conditions in 2006 were used for No burn and Repeated burn treatments, while plot conditions prior to the repeated burns in 2002 were used to predict the effect of a single burn on wildfire behavior. Input variables (plot data from the current study or from Busse, unpublished) for each run included fuel load (1-, 10-, and 100-h woody fuel), average fuel bed depth, herbaceous biomass, bitterbrush biomass, tree height, and crown ratio (live crown length:total crown length). Common variables for all runs included: 5%, 6%, and 7% moisture content for 1-, 10-, and 100-h fuels, respectively; 25% moisture of extinction; 30% live herbaceous moisture content; 50% live shrub moisture content; and 28 °C air temperature. The values for the common variables were recommended by W. Johnson of the Deschutes National Forest fire staff to approximate late summer conditions in Central Oregon. Flame length and rate of spread for the customized models were compared with standard fuel models SH3 (Moderate Load, Humid Climate Shrub) and TU2 (Moderate Load, Humid Climate Timber-Shrub) for the no burn treatment, and TL1 (Low Load, Compact Conifer Litter) for the repeated burn treatment (Scott and Burgan, 2005).

2.6. Statistical analysis

The effects of burning on bitterbrush cover, density, and biomass were analyzed on a plot basis by repeated measures analysis using PROC MIXED (SAS, 2000) with an autoregressive covariance structure. Data for bitterbrush density and woody fuel mass at the Sugar Cast site were log transformed to correct for unequal variances and non-normality of residual values. Means and standard errors for these variables were back-transformed for presentation purposes. All other data were normally distributed. Treatment effects within a given year (Student's *t*-test) were performed using the SLICE command. Significance for the statistical analyses was at $\alpha = 0.05$.

3. Results

3.1. Fire characteristics and fuel reduction

The burns in 1991 were low- to moderate-intensity with average flame lengths ranging from 0.5 to 1.2 m at both sites (Shea, 1993). Corresponding fire-line intensities ranged from 81.1 to 458.1 kW m^{-1}. Consumption of fine woody material (<7.5 cm diameter) averaged 60% at East Fort Rock and 59% at Sugar Cast, while consumption of the forest floor (O horizon; litter + duff) was 43% at both sites. No tree mortality was found at either site with the exception of a single plot at Sugar Cast. Here, a fairly large opening was created in the center of the plot as swirling winds fueled the fire, killing 11 out of 34 trees. The 2002 burns were low intensity, with average flame lengths of 0.5 m. Fine woody fuel mass was low prior to burning (4.2–6.1 Mg ha^{-1}) and was reduced 54% at East Fort Rock and 65% at Sugar Cast by burning. Reductions in forest floor depth averaged 38% at East Fort Rock and 45% at Sugar Cast. Repeated burning reduced the forest floor depth at both sites from a pre-fire average of 4.3 cm in 1991 to 1.1 cm following the 2002 burns.

3.2. Post-fire seed germination and basal sprouting

Seed germination accounted for 68% and 100% of bitterbrush recruitment following the 1991 burns at East Fort Rock and Sugar Cast, respectively (Table 2). Seedlings were particularly numerous at Sugar Cast following burning. Basal sprouting of burned plants accounted for the remaining 28% of bitterbrush recruitment at East Fort Rock.

Table 2
Bitterbrush recruitment following the 1991 and 2002 burns at two ponderosa pine sites. Measurements were made in the second growing season after burning, with the number of successful basal sprouts counted on a whole-plot basis and the number of germinants summed across 3, 100-m^2 belt transects per plot. Values are means (n = 3) and S.E. in parentheses.

	East Fort Rock		Sugar Cast	
	1991 Burn	2002 Burn	1991 Burn	2002 Burn
Pre-burn density (plants ha^{-1})	2070 (505)	3399 (285)	2517 (506)	8355 (3441)
Post-burn recruitment (plants ha^{-1})				
Basal sprouts	244 (68)[a]	300 (68)	4 (28)	355 (28)
Germinants	522 (95)	189 (95)	3230 (387)	223 (387)

[a] Common standard errors within a site and recruitment type determined by Proc Mixed (SAS).

Seedling counts were low following the 2002 burns, declining 2.8-fold at East Fort Rock and 14.5-fold at Sugar Cast relative to the 1991 burns (Table 2). Again, the number of basal sprouts was low after the 2002 burns: successful survival was found for 8.8% of burned plants at East Fort Rock and 4.2% of burned plants at Sugar Cast.

3.3. Bitterbrush cover, density, biomass, and age-class distribution

Bitterbrush canopy cover was significantly lower on burned than unburned plots at both sites during the entire study ($p < 0.001$). Canopy cover between 1993 and 2006 averaged 4% for burned plots and 19% for unburned plots at East Fort Rock, and 7% and 29%, respectively, at Sugar Cast (Fig. 1). Burning in 1991 resulted in a near collapse of bitterbrush cover as less than 1% cover was found at the two sites by 1993. A steady increase in cover was found in the succeeding 6 years, however. By 1999, bitterbrush cover approached 50% of that found on unburned plots at both sites.

Recovery of bitterbrush cover was poor following the second burn at East Fort Rock. Canopy cover remained under 2% between 2002 and 2006. This weak recovery contributed to a significant treatment $\times$ year interaction in repeated measures analysis ($p = 0.05$). In contrast, bitterbrush recovery was fairly strong at Sugar Cast following the second burns, reaching 10% canopy cover by 2006. Variation between plots was high, however. Bitterbrush cover in 2006 was 23% on the plot with high tree mortality, while the other burned plots averaged 3% cover. Overstory canopy cover was also variable, ranging from 18% on the plot with tree mortality to an average of 32 $\pm$ 2% (standard error) on the other burned plots and 29 $\pm$ 3% on unburned plots in 1997.

Bitterbrush density and biomass were also significantly lower on burned than unburned plots between 1993 and 2006 (Fig. 1). The only exception was that burning in 1991 did not significantly reduce bitterbrush density at Sugar Cast ($p = 0.197$) due to the high number of post-fire germinants. Average bitterbrush density at Sugar Cast between 1993 and 2006 was 4732 plants ha^{-1} for burned versus 7633 plants ha^{-1} for unburned plots. Average bitterbrush biomass between 1993 and 2006 was 4–5-fold lower on burned compared to unburned plots at both sites ($p < 0.001$).

Most bitterbrush plants were 10 years of age or younger on the burned plots by the end of the experiment (Fig. 2), reflecting the near-complete burning pattern across each plot. Interestingly, a similar skew in age-class favoring young plants was also found for

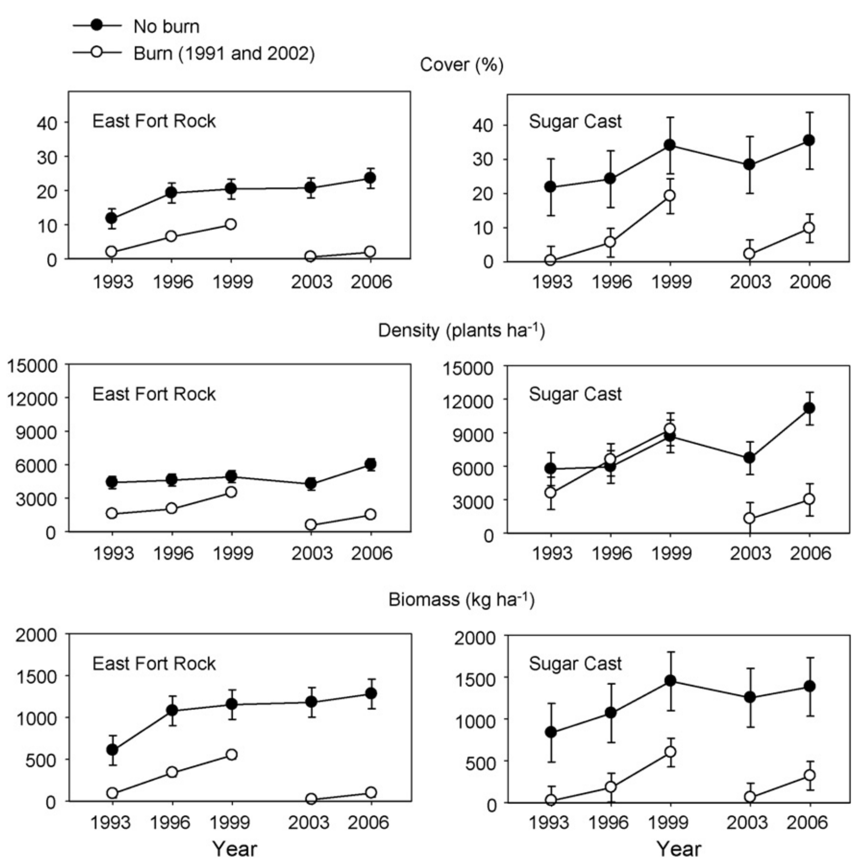

Fig. 1. Effect of initial burning in 1991 and repeated burning in 2002 on bitterbrush cover, density, and biomass at two ponderosa pine sites in central Oregon. Standard error bars (n = 3) are presented except when smaller than the symbol size.

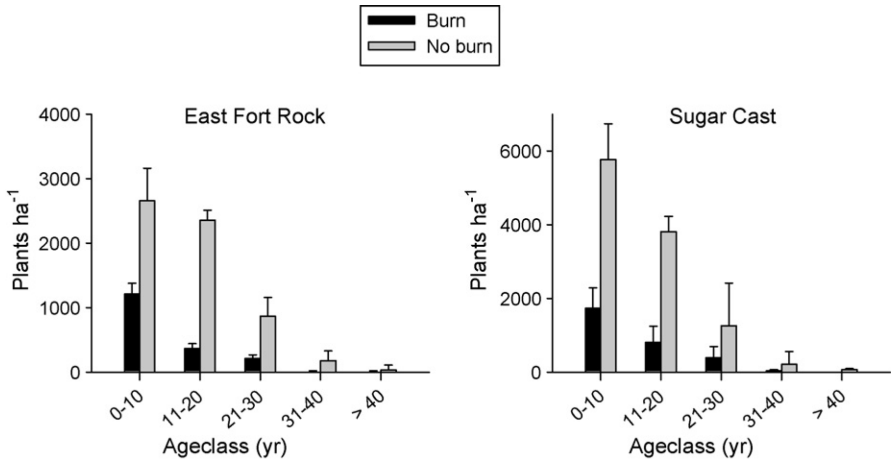

Fig. 2. Bitterbrush age-class distribution in 2006. Shrub ages were estimated non-destructively using the predictive equations presented in Table 1, with individual canopy dimensions of each shrub within the 100-m^2 belt transects used as input.

unburned plots. More than 80% of all plants were 20 years old or younger at the two sites without burning, which corresponds with the timing of the thinning operations in 1989.

3.4. Predicted wildfire behavior

Input variables for the wildfire behavior runs are shown in Table 3. Model inputs and outputs were similar between sites, so only the results for Sugar Cast site are presented. Bitterbrush mass and fuel bed depth (average shrub height) varied considerably between treatments. Woody fuel mass also varied by treatment; however the absolute values were low and did not contribute substantially to the predicted wildfire behavior. Repeated burning essentially eliminated the potential for wildfire spread by its affect on bitterbrush (Fig. 3). In comparison, a single burn produced fire behavior conditions nearly comparable to no burning due to the recovery of bitterbrush following the 1991 burns. Ponderosa pine mortality was 18% (the minimum predicted value in BehavePlus) and no crown scorch was predicted for any treatment. Predicted fire behavior from our customized runs was similar to the output from standard fuel models SH3, TU2, and TL1 from Scott and Burgan (2005).

4. Discussion

Bitterbrush is a multi-functional species in its range throughout the western United States. Its presence affects wildlife foraging and hiding cover, fire behavior, and soil fertility (Nord, 1965; Gay, 1998; Busse, 2000). Results from our 15-year study showed that the presence of bitterbrush was significantly altered by repeated burning. The initial burns resulted in a short-term collapse in bitterbrush cover followed by a fairly rapid recovery period. This finding agrees with results from earlier studies that suggested bitterbrush will respond favorably to burning if given a sufficient recovery period (Martin, 1983; Ruha et al., 1996). Repeated burning in 2002, although it did not eliminate bitterbrush from the forest understory, substantially reduced seedling recruitment and total cover. Average recruitment (seed germination plus basal sprouting) was 2–6-fold lower after the 2002 burns compared to the 1991 burns, and bitterbrush cover was particularly low at East Fort Rock (<2%) in the 5 years following the repeated burns (Fig. 1). Thus, our results suggest that repeated burning is an effective tool to reduce the presence of bitterbrush and modify its function as both a wildlife browse and a ladder fuel. Proof of this claim will

Table 3
Input variables used to predict fire behavior in central Oregon ponderosa pine stands previously treated with either no burning, a single prescribed burn, or repeated burning on an 11-year cycle. Data represent the range of values found at Sugar Cast ($n = 3$).

Model parameter	No burn	Single burn	Repeated burn
Bitterbrush mass (kg ha^{-1})	780–1839	382–1124	50–642
Fuel bed depth (m)	0.5–0.6	0.4–0.6	0.0–0.1
1-h Fuel mass (Mg ha^{-1})	0.1–0.5	0.2–0.5	0.4–0.5
10-h Fuel mass (Mg ha^{-1})	2.1–4.7	2.1–3.1	1.2–1.4
100-h Fuel mass (Mg ha^{-1})	1.2–1.6	0.7–1.7	0.4–0.8
Tree height (m)	18.6–19.9	18.3–20.4	18.4–20.1
Live crown ratio (%)	70–74	50–67	50–67
Slope (%)	1–2	1–3	1–3
Live herbaceous mass (kg ha^{-1})	2–26	14–24	19–32

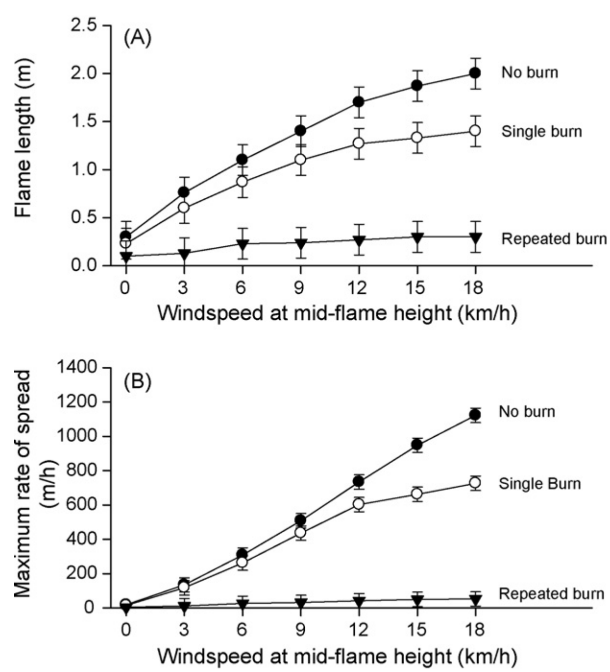

Fig. 3. Predicted wildfire behavior based on vegetation and fuel conditions at Sugar Cast in 2006 for unburned plots (No burn) versus plots burned in 1991 and 2002 (Repeated burn). Plot conditions prior to the repeated burns in 2002 were used to estimate the effects of a single fire on wildfire behavior (Single burn). Flame length (A) and rate of spread (B) of a surface wildfire were predicted using the fire behavior model, BehavePlus 3.0.

require further field monitoring since bitterbrush abundance was quantified for only five growing seasons after the repeated burn. Whether an 11-year cycle of prescribed burning is still needed to maintain low bitterbrush cover, or whether the fire-return interval can now be extended beyond 11 years remains to be seen.

Competition with understory vegetation for site resources was assumed to be a minor factor affecting post-fire bitterbrush recovery. Greenleaf manzanita was the most common species besides bitterbrush, yet averaged less than 3% cover on burned plots during the experiment (data not presented). Herbaceous species were even less abundant; their average biomass during peak season between 1992 and 2003 was less than 20 kg ha^{-1} (Busse, unpublished). Therefore, the 15-year response of bitterbrush to repeated burning is best discussed by reviewing the shrub's ability to (1) resprout following burning, (2) recruit new seedlings from the seed bank and from rodent seed caching, or (3) compete with overstory trees for light, water, and nutrients.

Sprouting of burned plants was trivial at both sites. Sprouting success increased from essentially none following the 1991 burns to 4% following the 2002 burns at Sugar Cast, and was approximately 10% at East Fort Rock following both burns (Table 2). This finding concurs with previous reports showing post-fire bitterbrush sprouting under 10% in interior Oregon pine forests (Driscoll, 1963; Sherman and Chilcoate, 1972; Martin, 1983). Only Busse et al. (2000) reported mild sprouting success following prescribed burning in the region. They found an average of 25% resprouting following early season spring burning when soil moisture was presumably high. While acknowledging the complexity of biotic and abiotic factors that regulate bitterbrush sprouting (Martin and Driver, 1983), the collective evidence suggests that sprouting is not a dominant recovery mechanism for bitterbrush following underburning in interior Oregon pine forests.

Post-fire seed germination, in contrast, was the primary mechanism of bitterbrush recovery following the initial burns. This was particularly evident at Sugar Cast where bitterbrush density was similar between burned and unburned plots between 1993 and 1999. At East Fort Rock, bitterbrush density on burned plots reached 70% of the density found on unburned plots by 1999. Again, this highlights the ability of bitterbrush to respond favorably to a single burn. Surprisingly, post-fire seed caching by rodents as a pathway of seed dispersal and germination appeared to be minor at both sites. Seed caching is considered the primary mechanism of seedling establishment by bitterbrush (West, 1968; Vander Wall, 1994), as rodents bury seed clusters which develop into multiple-stemmed shrubs when left undisturbed. By concealing seeds in the surface mineral soil, rodents unwittingly encourage seed germination in a seedbed having favorable temperature and moisture content (Young and Clements, 2002). While single-seed caches are possible, Vander Wall (1994) found they account for only 5% of all bitterbrush seedlings. As a comparison, visual inspection showed that all seedlings on the burned plots were single stemmed and, presumably, derived from non-cached seed. This follows the view expressed by Nord (1965) in his treatise on bitterbrush autecology that seedling establishment is "spasmotic" and is an expression of a complex set of environmental conditions required for seed production, seed germination, and seedling survival. What remains unclear from our study and from literature is the longevity of the bitterbrush seedbank in forests where seed caching is uncommon. Can bitterbrush seed remain dormant for many years before conditions are ripe for germination, or are they viable only for a limited time following production?

Burning after 11 years apparently did not allow sufficient time for the bitterbrush seedbank to restock. Seed germination was 3–14-times lower after the second burns compared to the initial entry (Table 2). As a consequence, bitterbrush density on burned plots was only 26% of the density found on unburned plots by the end of the experiment in 2006. This observation supports the concept that a minimum of 10 years is required before young bitterbrush plants develop a seed crop (Nord, 1965; Young and Clements, 2002). However, we cannot disregard the role of moisture availability as a contributing factor to low seed germination, as the first years following the 2002 burns had lower than average precipitation in Central Oregon (http://www.dri.edu/summary/climsmor.html). Still, the management implications of these results are straightforward: frequent prescribed fire appears to be an effective means to restrict bitterbrush recruitment and, ultimately, ladder fuel accumulation. The corollary implication is that fire frequency should be extended beyond 11 years until a strong seed crop is produced in areas where wildlife habitat is a priority and mosaic burn patterns are not anticipated.

Competition with overstory trees may have influenced bitterbrush recovery following the burns. Robust recovery was found only where fire-induced tree mortality created a large clearing (Sugar Cast plot 2). By 2006, Sugar Cast plot 2 had 10-times greater bitterbrush cover compared to the other burned plots, and was nearly comparable in its cover to the unburned plots. This response cannot be explained simply by greater light interception in the opening, however. All burned and unburned plots were thinned prior to burning, and light was likely adequate (~30% overstory canopy cover) to allow the vigorous bitterbrush growth found on unburned plots. We speculate that several factors in addition to light availability contributed to the response, including (1) higher soil surface temperatures for stimulation of seed germination, (2) lower transpirational use of soil water by overstory trees, and (3) less competition for available nutrients.

By retarding bitterbrush cover and reducing fuel loading, repeated burning essentially eliminated the potential for wildfire spread in these stands. Fire model runs using BehavePlus 3.0 showed that minimal flaming or fire spread would result following repeated prescribed burning. In contrast, both the single-entry burn and no burning produced low to moderate flame lengths (between 0.2 and 2 m) depending on wind conditions. Still, the predicted crown scorch and tree mortality were nominal in these thinned stands regardless of prescribed fire treatment, supporting results from studies showing a low probability of crown-fire spread in thinned stands (Peterson et al., 2005; Ritchie et al., 2007).

Fuel treatment is a priority in Central Oregon second-growth pine forests, as it is in other low-severity fire regimes in the western United States that experienced a build-up of surface fuels during the recent century-long policy of fire suppression (Brown et al., 2004; Schoennagel et al., 2004). The combined use of thinning and prescribed fire has been recommended by several as a restorative treatment for limiting both crown fires and surface fires in these forest types (Stephens, 1998; Fulé et al., 2002; Peterson et al., 2005). As evidence, Raymond and Peterson (2005) found that tree mortality during the 2002 Biscuit wildfire in southwestern Oregon was substantially reduced on research plots that were thinned and then burned under prescription 1 year prior the wildfire. Similarly, Ritchie et al. (2007) found that prior thinning and burning essentially stopped a rapidly moving crown fire in an interior ponderosa pine forest, while thinning alone resulted in a drop from a crown fire to a surface fire with relatively low tree mortality. Our study provides evidence of the restorative success of burning for limiting fire risk in thinned stands. Unlike other studies, woody fuel loads were low at our sites and contributed little to fire risk. Instead, the benefit of prescribed burning from a fire-risk standpoint was to reduce the presence of bitterbrush. Our findings also emphasize the importance of re-treating shrubs, either with fire or an alternative method (mowing, masticating), to impede their rapid recovery.

In summary, repeated burning was responsible for a 15-year reduction in bitterbrush cover, density, and biomass. Low- to moderate-intensity burning reduced bitterbrush to a minor understory presence by the end of the experiment. Much of the decline in bitterbrush cover was attributed to seedbank depletion since insufficient time was permitted between burns to develop and replenish the seed crop. Additionally, post-fire sprouting of burned plants was only a minor contributor to bitterbrush recovery and should not be considered an important recovery mechanism in Central Oregon pine forests. From a management standpoint, these results suggest that repeated burning in thinned pine stands is a successful method to reduce the long-term fire risk from bitterbrush as an understory ladder fuel. Balancing the need to limit fire risk yet provide adequate bitterbrush habitat for wildlife browse will likely require a mosaic pattern of burning at the landscape scale, unless the burning frequency is extended well beyond 11 years to allow a bitterbrush seed crop to develop.

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