



Responses of Fendler ceanothus to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest

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Abstract

Overstory tree thinning and prescribed fire are used to restore ecosystem structure and function in ponderosa pine (*Pinus ponderosa* Laws.) forests of the southwest but little research has examined constraints on population-level responses of understory plants. In order to study growth and reproduction of a common shrub species after forest restoration treatments, we monitored Fendler ceanothus (*Ceanothus fendleri* Gray) plants from 1999 to 2002 in thinned and unthinned overstory units. To study effects of tree thinning, we analyzed relationships of overstory stand density (Reineke's SDI) and current-year branch length, number of branches, and biomass, and also evaluated the importance of mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus*) herbivory (Browsing) as a predictor in linear models. To study effects of prescribed fire, we examined mortality, seedling emergence, and growth response on experimentally burned and unburned plots. SDI and browsing were significantly and negatively correlated with *F. ceanothus* current-year branch length, biomass, and leaf area but relationships were generally weak. Across the 4 years, browsing appeared to be consistently more important than SDI in explaining variation in growth. Although SDI and browsing were significant predictors of growth in years with near normal precipitation, models failed in drought years. Burning resulted in 17–32% mortality whereas 0–5% of plants died on unburned plots. Mortality of burned plants was positively related to amount of forest floor consumed during prescribed fires. One growing season after fire, surviving burned plants responded by producing long resprouts. Current-year branches were consistently longer on burned than unburned plants only where plots were protected from large herbivores. Unburned plants had more current-year branches and greater biomass than burned plants. No seedlings emerged on unburned plots but were found on 44% of burned plots. A quadratic function represented the relationship between seedling emergence and forest floor consumption. Our results suggest that restoration treatments in ponderosa pine forests of northern Arizona can help increase abundance of *F. ceanothus* but population responses may be slow, particularly when constrained by ungulate herbivory, fire-related mortality of plants and dormant seeds, and drought.

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1. Introduction

It is well known that tree thinning and opening of dense overstory canopies alters understory microclimate by increasing light transmission, throughfall precipitation, and soil temperature. (Anderson et al.,

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1969; McLaughlin, 1978; Vales and Bunnell, 1988; Groot and Carlson, 1996). Reduction of overstory density can also increase available soil moisture and nutrients (Covington et al., 1997; Kaye and Hart, 1998). These changes can be beneficial to herbaceous and woody understory plants and increased community production is commonly observed after overstory thinning (Jameson, 1967; Ffolliott and Clary, 1975; Uresk and Severson, 1989). Response of understory communities to changes in overstory density can be expressed by negative linear or curvilinear functions (Ffolliott and Clary, 1975). For example, in northern Arizona ponderosa pine (*Pinus ponderosa* Laws.) forests, forage production increased linearly as values of Reineke's stand density index (SDI; Reineke, 1933) decreased below 400–550 (Moore and Deiter, 1992). At higher SDI values, understory production responses to variations in stand density were minimal.

Quantification of overstory–understory relationships allows forest managers to predict outcomes of ecological restoration treatments that use thinning to reduce overstory densities to levels more like those of presettlement forests (Covington and Moore, 1994; Covington et al., 1997; Moore et al., 1999). In some cases, however, other interactions may be as important as stand density in constraining understory plant growth and reproduction. For example, we previously showed that Fendler ceanothus (*Ceanothus fendleri* Gray) not protected from browsing mule deer (*Odocoileus hemionus*) and Rocky Mountain elk (*Cervus elaphus*) had less than one-fourth the current-year biomass as protected plants in ponderosa pine stands that had been thinned as part of an ecological restoration experiment (Huffman and Moore, 2003). Additionally, severe drought may override potential benefits of forest thinning in these semi-arid ecosystems (Fulé et al., 2002). Finally, seeds of plants with seedbank strategies often require scarification or other cues to initiate germination (Harper, 1977). For these species, recruitment of new genets into populations may not occur as a result of overstory thinning alone.

Prescribed fire is often used with thinning as an ecological restoration tool in ponderosa pine forests of the Southwest (Covington et al., 1997; Moore et al., 1999; Allen et al., 2002). Low-intensity fire can mineralize accumulated forest floor litter layers,

release nutrients bound in detritus, reduce heavy fuel loads, and rejuvenate plant populations by stimulating sprouting and germination of dormant seeds (Whelan, 1995). Importantly, low-intensity fire was a critical process that influenced structure and function of presettlement ponderosa pine forests of the southwest and returned at mean intervals ranging from 2 to 20 years (Fulé et al., 1997). Thus, fire should be reintroduced when restoration of functional attributes of these ecosystems is a goal (Kaufmann et al., 1994; Covington et al., 1999).

Presettlement fires likely burned quickly through abundant grassy fuels and transferred little heat to soil systems in southwest ponderosa pine forests. Low fuel loads, high fuel moistures, high relative humidity, low daytime temperatures, and low wind speed are needed to safely reintroduce fire in these forests where it has been excluded for nearly 130 years (Sackett et al., 1996; Fulé et al., 1997). Otherwise, initial fires can smolder in slash and deep layers of accumulated forest floor debris and transfer lethal levels of heat to soils (Covington and Sackett, 1990; Sackett et al., 1996). Thus, fire behavior and severity during prescribed burns are likely to be important determinants of successional trajectories for understory communities. Further, easily measured variables predictive of fire effects on understory species can help land managers formulate prescriptions that both reduce accumulated fuels and accomplish ecological objectives related to vegetation structure and composition.

Our objective in this study was to quantify the effects of overstory density and prescribed fire on *F. ceanothus*, a semi-evergreen, nitrogen-fixing shrub common in understories of ponderosa pine forests throughout the southwest, Rocky Mountains, and into South Dakota (Story, 1974; Conard et al., 1985). Scattered populations of *F. ceanothus* provide understory structural heterogeneity and wildlife habitat, particularly browse for mule deer and elk (Huffman and Moore, 2003). Resprouting of *F. ceanothus* after disturbances such as fire appears to be common (Pearson et al., 1972; Ffolliott et al., 1977; Vose and White, 1991) although detailed descriptions of vegetative characteristics and variation of response to fire behavior are presently lacking. Similar to congeneric species, its seeds are forcibly ejected from dehiscing capsules and likely remain in forest floor seed banks for years until heat from fire allows germination

(Kearney and Peebles, 1951; Quick and Quick, 1961; Reed, 1974; Krishnan, 1989). Here we report *F. ceanothus* growth and reproduction under a range of forest overstory densities and the importance of herbivory and drought in constraining response. We also describe mortality, production, and seedling recruitment on experimentally burned plots one growing season after burning.

2. Materials and methods

2.1. Study site

We conducted our study during 1999–2002 on the Fort Valley Experimental Forest (35°16'N, 111°41'W) in Coconino County approximately 10 km northwest of Flagstaff, AZ. Elevation of the study area was around 2300 m above mean sea level. Aspect of the site was southerly and the topography was gentle with average slopes of approximately 5–10%. Soils are developed on tertiary basalt parent material and are moderately well drained. Annual precipitation at the site averages around 52 cm and is typically bimodal in distribution with July–September rain and December–March snow. In 1999, precipitation was 96% of the long-term (51 years) average of 41.3 cm for January–September (Western Regional Climate Center, 2003). In 2000, 63% of the long-term average fell in these months. In 2001, precipitation was 91%, but in 2002 only 54% of the long-term average for January–September occurred. Thus, 1999 and 2001 had near average precipitation whereas 2000 and 2002 were droughts.

Forest overstories were comprised of ponderosa pine and common understory species included the grasses Arizona fescue (*Festuca arizonica* Vasey), mountain muhly (*Muhlenbergia montana* (Nutt.) A.S. Hitchc.), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) and pine dropseed (*Blepharoneuron tricholepis* (Torr.) Nash); the forbs lupine (*Lupinus* spp.), fleabane (*Erigeron* spp.), buckwheat (*Eriogonum* spp.), yarrow (*Achillea millefolium* L.), and pussytoes (*Antennaria* spp.); and shrubs *F. ceanothus* and woods rose (*Rosa woodsii* Lindl.). No domestic livestock were present at the study site and primary large herbivores were mule deer and Rocky Mountain elk.

2.2. Sampling methods

2.2.1. Experimental design

F. ceanothus patches were located in three forest units undergoing ecological restoration treatments and three adjacent untreated (control) units in March 1999. Forest restoration units were 14–16 ha in size and were thinned in late winter 1998. Before thinning, basal area was 34–38 m²/ha and density was 955–1492 trees/ha for trees greater than 1.37 m in height. Thinning from below reduced basal area by 35–56% and left 140–243 trees/ha in scattered groups to emulate presettlement spatial structure (Fulé et al., 2001).

Ten discrete patches of *F. ceanothus* were found in each of the forest restoration and control units ($N = 60$) and these were used to examine effects of overstory density on *F. ceanothus* growth and reproduction. Patches were generally no more than 2 m in area and comprised 1–15 *F. ceanothus* stems. *F. ceanothus* can expand vegetatively and sprout from belowground branches and root crowns (Vose and White, 1987; Huffman, pers. obs.). It is not known whether patches comprised more than one clone. Hereafter, we refer to stem populations in these patches as *F. ceanothus* “plants”. Circular plots (1 m²) were established at the center of *F. ceanothus* patches and metal rebar was used to mark plot centers for relocation.

We established an additional 50 *F. ceanothus* plots in each of the restoration units and used these to study effects of prescribed fire ($N = 150$) and interactions with herbivory on growth and reproduction. Effects of prescribed fire could only be examined within the thinned forest units due to extreme fuel hazard in control units. Forest floor depth was estimated to the nearest 0.1 cm at plot center. In restoration units, plots were randomly assigned to herbivore protection and experimental burning treatments in a 2 × 2 factorial design.

2.2.2. Herbivore protection

Fenced exclosures, 2 m × 2 m in area and 1.4 m in height, were constructed in spring 1999 around plots selected for herbivore protection. Exclosures were made of wire fence (5 cm × 10 cm mesh) and T-bar posts. The small size of the fenced area discouraged deer and elk from jumping over the fencing and large mammal herbivory was effectively eliminated within

exclosures. From 0.6 to 5% of terminal buds on current-year branches were damaged or removed, apparently by invertebrates, within exclosures across the 4 study years.

2.2.3. *Experimental burning*

In order to burn selected plants, fire lines were constructed around all *F. ceanothus* plots in restoration units. Fire lines were continuous fuel breaks approximately 25–50 cm in width wherein all vegetation and forest floor material was removed exposing the mineral soil. The area protected by fire lines, and which encompassed each *F. ceanothus* plot, was approximately 4 m². Additionally, all downed woody debris larger than 5 cm in diameter was removed from plots in order to control fire behavior and severity.

F. ceanothus plots were experimentally burned in April 2000 and May 2001 in coordination with United States Forest Service's (USFS) broadcast burning of the larger forest units. In April 2000, 24 *F. ceanothus* plots (12 protected from herbivores, 12 unprotected) were burned in one of the restoration units (called overstory unit 3T). Drip-torches filled with a diesel-gasoline mixture were used to ignite forest floor material around edges of the plots and fires were allowed to burn until naturally extinguished. Due to extreme fire danger in spring 2000, burn plans were cancelled before we could complete our experiments. We were able to resume experimental burning in May 2001. At this time, 65 additional plots (33 protected from large herbivores, 32 unprotected) were burned in the 2 remaining restoration units (called overstory units 1T and 2T).

Average and maximum flame lengths on plots were estimated during burning. To assess fire behavior, forest floor depth on plots was measured within 2 months of burning following methods used at plot establishment.

2.2.4. *F. ceanothus* measurements

Length and number of *F. ceanothus* stems on plots were measured in March 1999 (pretreatment). Subsequently, *F. ceanothus* stems were measured annually in September each year from 1999 to 2002. Stem length, basal diameter, current-year branch length (estimated average and longest), and number of current-year branches were measured. Current-year biomass and leaf area was estimated from stem length relationships

developed from separate destructive sampling (Huffman and Moore, 2003).

F. ceanothus seedling recruitment was assessed twice per year (July and September) and emerging seedlings were counted at each plot within the 2 m × 2 m areas encompassed by fire lines and herbivore exclosures. Emergent seedlings were identified by their small stature (stem diameter < 0.5 mm, length < 5 cm) and the presence of cotyledons.

Overstory density was measured in 2001 at each plot using point sampling (Avery and Burkhart, 1983). Wedge prisms of 4.6 basal area factor (BAF; m²/ha) were used for tree tallies. All tally trees were measured for diameter at breast height (1.37 m) and recorded in 4 cm diameter classes.

2.3. *Data analyses*

Linear regression was used to analyze relationships between *F. ceanothus* growth variables and overstory density and browsing. Significance level selected for regressions was 0.05. *F. ceanothus* growth variables analyzed were stem number, current-year branch length (average and longest), current-year biomass, and current-year leaf area for each of the 4 years of the study. Overstory density values were derived using Reineke's stand density index (SDI; Reineke, 1933) and tree diameters from point samples. Browsing values were calculated as the number of current-year branches browsed divided by the total number of current-year branches counted on each plot. Data were natural log-transformed when examination of residual plots indicated increasing variance with increasing estimated values.

One-way analysis of variance (ANOVA) was used to test for effects of prescribed burning within restoration units (no plots were burned in untreated units). Since significant differences in stem number, size, and current-year biomass and leaf area had developed between protected and unprotected plots by the time they were burned (Huffman and Moore, 2003), effects of burning were analyzed for these two groups separately. Further, effects of burning were analyzed separately for the 2 burn years (2000 and 2001). To analyze fire effects in 2000, data from burned and unburned plots in overstory unit 3T were used. To analyze fire effects in 2001, data from burned and unburned plots in overstory units 1T and 2T were used. In ANOVA

tests for burn-year 2001 plots, overstory unit was included as a blocking factor. *F. ceanothus* response variables analyzed were stem number, population change, current-year branch number and length (average and longest), and current-year biomass. Data were natural log-transformed when necessary to normalize data distributions and homogenize variances. Significance level for tests was 0.05.

Logistic regression was used to test for relationships between *F. ceanothus* mortality (categorical) and flame length and amount (cm) of forest floor consumed in burning. Linear regression was used to analyze the relationship between seedling emergence and forest floor consumption.

Seedling establishment was assessed by evaluating: (1) emergence, defined as the number of first-year seedlings counted on a plot. Such seedlings typically had cotyledons and one or more true leaves; (2) 1-year survival, defined as the number of seedlings counted for emergence divided by the number of seedlings remaining on the same plot after the next growing season multiplied by 100 (e.g. (emergence 2000/remaining 2001) × 100); (3) 2-year survival, defined as the number of seedlings counted for emergence divided by the number remaining on the same plot after two growing seasons multiplied by 100 (e.g. (emergence 2000/remaining 2002) × 100). Two-year survival assessment only applied to plots in the overstory unit (3T) that was burned in 2000.

3. Results

3.1. Overstory density, herbivory, and drought

Values for SDI ranged from 124 to 1754 across all plots (thinned and control forest units) sampled. Although SDI contributed significantly ($P < 0.05$) to models and was negatively related to *F. ceanothus* growth, its importance was generally low ($\beta_1 \leq 10.0041$) compared to that of browsing (proportion of current-year stems browsed; $\beta_2 \leq 10.0181$) (Table 1). In 1999, a year of near normal (96%) precipitation January–September, SDI and browsing together explained 60% of variation in current-year biomass. Neither SDI nor browsing was significantly related to number of current-year branches in 1999 (Table 1). In 2000, a drought year (63% normal precipitation

Table 1
 r^2 , regression coefficients, and P -values for models of *F. ceanothus* current-year growth (Y) on plots not protected from large herbivores and not burned, as related to ponderosa pine stand density (SDI^a) and proportion of current-year branches browsed (browsing)

	1999			2000			2001			2002				
	r^2	β_1	β_2	r^2	β_1	β_2	r^2	β_1	β_2	r^2	β_1	β_2	P	
Mean branch length (cm)	0.47	-0.001	-0.014	<0.001	0.11	-0.008	0.008	0.42	-0.002	-0.011	<0.001	ns	ns	ns
Longest branch (cm)	0.47	-0.001	-0.014	<0.001	ns	ns	ns	0.34	-0.002	-0.010	<0.001	ns	ns	ns
Number of branches ^b	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.01	-0.002	ns
Stem biomass (g)	0.60	-0.002	-0.018	<0.001	0.13	-0.015	0.003	0.24	-0.003	-0.017	<0.001	ns	ns	ns
Stem leaf area (cm ²)	0.19	-0.001	-0.010	0.001	0.08	-0.009	0.022	0.14	-0.002	-0.011	0.008	ns	ns	ns
Plot biomass (g m ⁻²)	0.27	-0.004	-0.012	<0.001	0.14	-0.002	0.007	0.16	-0.004	ns	0.002	0.12	-0.004	ns
Plot leaf area (cm ² m ⁻²)	0.18	-0.003	-0.005	0.001	0.09	-0.002	ns	0.10	-0.003	ns	0.012	0.14	-0.003	ns

When both SDI and browsing were significant ($P < 0.05$) in the regression, statistics for the full model (full model in the form: $\ln(Y) = \beta_0 + \beta_1(X_1) + \beta_2(X_2)$, where $X_1 = \text{SDI}$ and $X_2 = \text{browsing}$) are presented. When either SDI or browsing was not significant ($P \geq 0.05$) in the regression, statistics for the partial model (partial model in the form: $\ln(Y) = \beta_0 + \beta_1(X_1)$ or $\ln(Y) = \beta_0 + \beta_2(X_2)$; where $X_1 = \text{SDI}$ and $X_2 = \text{browsing}$) are given.

^aReineke's (1933) stand density index.

^bSquare-root transformed.

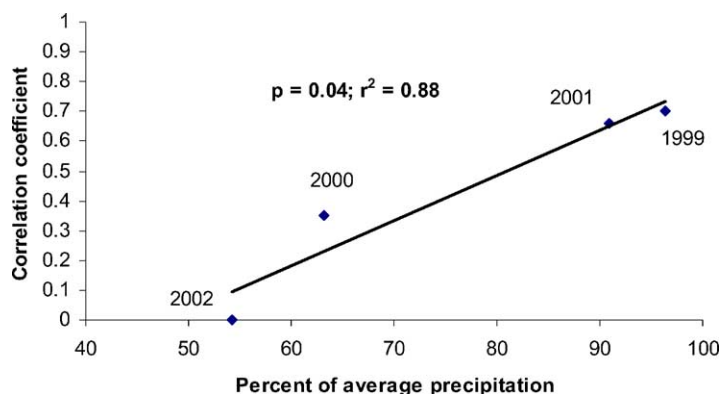


Fig. 1. Relationship of *F. ceanothus* growth model correlation coefficient and percent of average precipitation for months of January–September. Model is: $\ln(\text{current-year branch length}) = \beta_0 + \beta_1(\text{SDI}) + \beta_2(\text{browsing})$; where SDI is Reineke's (1933) stand density index, and *browsing* is percent current-year branches browsed by large ungulates (see also Table 1).

January–September), SDI was only significantly ($P < 0.05$) related to current-year biomass and leaf area on plots. Browsing in 2000 was significantly ($P < 0.05$) related to all growth variables except the longest current-year branch length, number of current-year branches, and current-year leaf area on plots (Table 1). In 2001, a year of near normal (91%) precipitation, results were similar to those of 1999 and the full model generally provided the best predictions of growth. In 2002, a year of extreme drought (54% normal precipitation January–September), SDI was significantly related to number of current-year branches and current-year biomass and leaf area on plots. Browsing was not significantly ($P \geq 0.05$) related to any growth variable in 2002.

Values of r^2 for growth models were generally higher in years 1999 and 2001 than in 2000 and 2002. Annual precipitation played a significant role in determining the importance of overstory tree density and browsing on *F. ceanothus* growth parameters. Although only four growing seasons were available to assess the relationship, a significant ($P < 0.05$) positive trend was observed between correlation coefficients of *F. ceanothus* growth models (current-year branch

length response variable) and percent of average long-term precipitation for the months January–September (Fig. 1).

3.2. Experimental burning

In general, fire behavior and severity were similar on plots burned in 2000 and 2001 (Table 2). In 2000, burning resulted in mortality of 17% (4 of the 24 burned) of *F. ceanothus* plants whereas no plants died that were not burned in forest unit 3T. In 2001, 32% (21 of the 65) of the burned plants died whereas 5% of plants died that were not burned in units 1T and 2T. For all burned plots combined, probability of mortality was significantly ($P < 0.001$) related to amount of forest floor consumed (Fig. 2). Probability of plant death increased dramatically after about 3 cm of forest floor consumption and no plants survived on plots where more than 6 cm of forest floor was consumed. Average (13–19 cm) and maximum (91–117 cm) flame lengths were not significantly related to *F. ceanothus* mortality.

On plots where burning did not result in *F. ceanothus* mortality (72% survival overall), plants

Table 2
Means (S.E.) for fire behavior and severity characteristics on *F. ceanothus* plots burned in 2000 and 2001

Year	N	Flame length (cm)		Severity rating		Forest floor consumption	
		Average	Maximum	Substrate	Vegetation	Percent	Depth (cm)
2000	24	18.7 (1.5)	48.7 (5.7)	3.1 (0.1)	3.0 (0.1)	50.0 (5.7)	2.7 (0.4)
2001	65	12.6 (0.6)	36.8 (2.3)	3.2 (0.1)	3.3 (0.1)	52.0 (4.0)	2.3 (0.2)

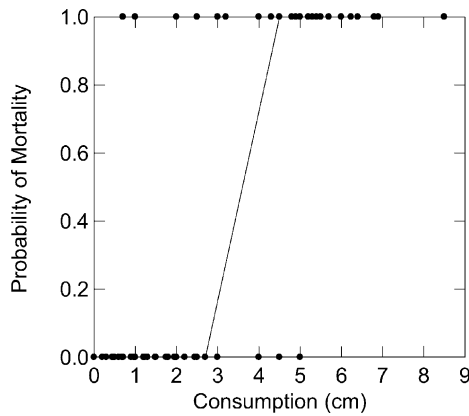


Fig. 2. Probability of *F. ceanothus* mortality as related ($P < 0.001$) to amount (cm) of forest floor consumed in experimental burns. Data are for plots burned in 2000 and 2001 pooled.

resprouted from aerial stem bases or belowground structures within about 60 days from burning. In general, burning converted *F. ceanothus* patches from all-aged stem assemblages to those dominated by first-year sprouts. Where plants survived, burning had varying effects on subsequent stem production. Burning did not significantly ($P \geq 0.05$) affect the number of stems on plots protected from large herbivores. Mean stem number generally increased on protected plots regardless of burning. Stem number did not significantly ($P \geq 0.05$) change on unprotected plots burned in 2000. However, a significant ($P < 0.05$)

increase in number of stems occurred on unprotected plots burned in 2001.

Burned plants generally produced longer current-year branches than unburned plants one growing season after treatment (Table 3). Current-year branches of burned plants were mainly sprouts originating from stem bases or belowground structures. These were long stems (≤ 43 cm) with relatively few lateral shoots. On unprotected plots burned in 2001, there were no significant differences in current-year branch length between burned and unburned plants (Table 3).

Stems of unburned plants had significantly ($P < 0.05$) more current-year branches than those of burned plants one growing season after burning, regardless of herbivore protection (Table 3). More current-year branches on stems of unburned plants translated to significantly ($P < 0.05$) greater current-year biomass for plants burned in 2001 (Table 3). No significant difference in current-year stem biomass was found between burned and unburned plants for those burned in 2000.

3.3. Seedling establishment

No seedlings emerged on unburned plots in any of the 4 study years. On plots burned in 2000, seedlings emerged on nearly half (45.8%) the plots and a mean of 1.0 (S.E. = 0.3) seedlings per plot (2500 seedlings/ha) occurred. Seedlings were found on 55% of plots burned in 2001 and emergence averaged 5.1 (S.E. = 1.4)

Table 3

Characteristics of current-year growth on *F. ceanothus* stems one growing season after spring burning

	Burned 2000 ^a		<i>P</i> ^c	Burned 2001 ^b		<i>P</i>
	Unburned	Burned		Unburned	Burned	
Protected						
Branch length (cm)	3.2	11.3	**	12.5	19.7	***
Branch number	18.8	3.3	***	12.5	3.1	***
Biomass (g)	0.61	0.83	ns	1.90	1.20	*
Unprotected						
Branch length (cm)	2.5	4.4	**	5.0	5.9	ns
Branch number	6.7	2.8	*	9.1	4.0	**
Biomass (g)	0.14	0.17	ns	0.73	0.28	*

^a Plots ($n = 24$) burned in one experimental forest unit in 2000.

^b Plots ($n = 65$) burned in two experimental forest units in 2001.

^c Level of significance for comparison of unburned and burned plot means.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

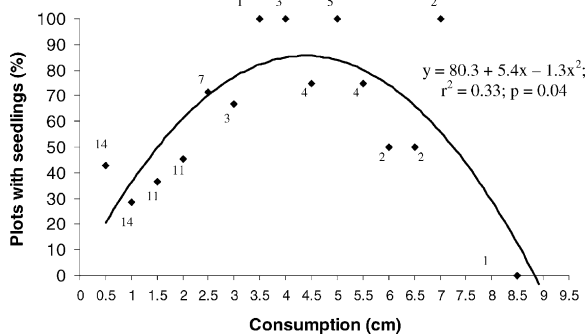


Fig. 3. Relationship between proportion of plots on which *F. ceanothus* seedlings emerged and forest floor consumption during experimental burning. Values shown in association with data points are number of plots in forest floor consumption classes.

seedlings per plot (12,750 seedlings/ha). Protection from large herbivores did not significantly (Mann–Whitney; $P \geq 0.05$) affect the number of seedlings per plot for either burn year. Therefore, summaries for seedling emergence and survival are given for protected and unprotected plots combined ($N = 89$).

The number of seedlings emerging on plots was not significantly related to amount of forest floor consumed. However, a significant ($P < 0.05$) relationship was found between probability of seedling emergence on plots (proportion of plots on which seedlings emerged) and amount of forest floor consumed in 0.5 cm classes (Fig. 3). The form of the relationship was quadratic and probability of emergence was the greatest (45–100%) on plots with moderate (2.5–6.5 cm) amounts of forest floor consumed.

One-year seedling survival was 26.7% (1000 seedlings/ha) on plots burned in 2000. One-year survival on plots burned in 2001 was 11.0% (1250 seedlings/ha). Mean 1-year survival was not significantly ($P \geq 0.05$) affected by protection from large herbivores for plots in either burn year. Two-year seedling survival on plots burned in 2000 was 3.6% (200 seedlings/ha).

4. Discussion

4.1. *F. ceanothus* growth as related to overstory density

Annual growth of *F. ceanothus* was negatively related to overstory stand density (SDI), although

relationships we found were weak. Other researchers have reported similarly weak relationships of shrub production and ponderosa pine density although herbivory was not included in models (Uresk and Severson, 1989; Moore and Deiter, 1992). Over the 4 years of our study, ungulate herbivory appeared to be generally more important than SDI in explaining variation in growth. This was not surprising since we previously reported that *F. ceanothus* shrubs protected from deer and elk retained nearly five times more current-year biomass than that were not protected (Huffman and Moore, 2003). Additionally, full models that included both SDI and browsing as predictors of growth were insignificant, or explained no more than 14% of the variation in *F. ceanothus* growth, during 2 drought years at our site (Table 1). Periodic drought is common in southwestern ponderosa pine ecosystems and appears to constrain understory response to overstory thinning (Fulé et al., 2002). Our results suggest that substantial growth response to restoration treatments may require several years at our site, particularly under intense pressure from large herbivores.

4.2. Vegetative response to prescribed fire

Although short flame lengths suggested low fire intensity, temperatures lethal for *F. ceanothus* shrubs were apparently generated belowground when burning consumed more than about 3 cm of forest floor depth. Detrital layers of 2–4 cm are common in ponderosa pine forests of the southwest although depths of up to 8 cm have been reported where fire has been excluded for many years (Covington et al., 1997; Fulé et al., 2002). Although land managers are often concerned with heat effects from burning in heavy slash (e.g., Fulé et al., 2002), our data corroborates other findings that indicate smoldering combustion in forest floor fuels can have severe effects on important biota (Covington and Sackett, 1984, 1990). Further research is needed to determine if other factors, such as plant age, soils, or climatic conditions after burning, affect *F. ceanothus* response to prescribed fire.

Plants that survived burning resprouted readily and after two growing seasons burned plants were regaining an all-age population structure. Sprouting after disturbance and annual stem recruitment between disturbances are important strategies for persistence in competitive plant communities and where safe sites

for seedling establishment are rare (Keeley, 1977; Kurmis and Sucoff, 1989; Huffman et al., 1994; Tappeiner et al., 2001). For *F. ceanothus*, rapid recovery of vertical stature after fire is accomplished through production of long, unbranched sprouts. This capability was more fully expressed on plots protected from large herbivores. Our findings corroborate to those of Vose and White (1987) who found that burned plants were nearly the same size as unburned plants 1 year after fire. Since flower and fruit production appears to be related to stem size (Huffman, 2003; Huffman and Moore, 2003), a quick return to preburn stature may suggest an adaptive trait that allows *F. ceanothus* to replenish dormant seed pools in the interim periods between frequent fires.

4.3. Regeneration from seed

F. ceanothus seedling emergence was related to depth of forest floor consumed during experimental burns. Probability of emergence was the greatest at moderate depths (>2 and <7 cm) of consumption. These results suggest that dormant seeds in soil seed banks were stimulated to germinate after exposure to heat from fire (e.g., Story, 1974; Krishnan, 1989; Huffman, 2003) but at greater depths of forest floor consumption heat-induced mortality of seeds occurred (Huffman, 2003). A dormant seed strategy is commonly reported for the *Ceanothus* genus (Gratkowski, 1974; Keeley, 1977, 1992; Noste, 1985; Conard et al., 1985), although germination responses to temperature and duration of heat appear to vary among species (Quick, 1935). Although rates of long-term survival and establishment of new genets is uncertain, recruitment may offset fire-related mortality of extant plants at our site.

4.4. Management implications

As additional programs are established to restore ecological function in fire-prone, forest ecosystems, it will be increasingly important to monitor understory plant populations and identify biotic and operational constraints to their recovery. On our site, tree thinning from below and prescribed fire treatments appeared to have potential to increase *F. ceanothus* growth and reproduction. Herbivory and drought, however, were important in constraining plant growth for 4 years after

forest restoration treatments. Herbivory by wild ungulates has been shown to be an important constraint on restoration of other forest types (Augustine and Frelich, 1998; Opperman and Merenlender, 2000). Management options to alleviate ungulate herbivory in ponderosa pine forests include retaining scattered slash after thinning operations to provide plants with temporary protection, or modification of landscape features such as water catchments and roads to modify animal spatial patterns (Reynolds, 1966; Severson and Medina, 1983).

In our study, fuel conditions (i.e., forest floor depth) and fire behavior affected mortality of established plants and seedling emergence. Similarly, Schimmel and Granström (1996) showed that burn depth could be used as an indicator of heat impact to belowground propagules and affect population structure of several understory species in boreal forests. This suggests that burn plans may be formulated to achieve fuel consumption targets as well as produce desired population structures and understory plant community characteristics. In turn, responses of common understory species should be used as feedback in the adaptive process to refine ecological restoration prescriptions.

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