SHRUB SEED BANKS IN MIXED CONIFER FORESTS OF NORTHERN CALIFORNIA AND THE ROLE OF FIRE IN REGULATING ABUNDANCE

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ABSTRACT

Understory shrubs play important ecological roles in forests of the western US, but they can also impede early tree growth and lead to fire hazard concerns when very dense. Some of the more common genera (*Ceanothus*, *Arctostaphylos*, and *Prunus*) persist for long periods in the seed bank, even in areas where plants have been shaded out. To determine shrub seed density and investigate the feasibility of managing shrub abundance by regulating the size of the soil seed bank with fire, we sampled the seed bank in 24 mixed conifer forest stands throughout northern California. Twenty stands were unburned, two had recently burned in wildfires, and two (McCloud and Jennie Springs) were subjected to experimental prescribed fires with unburned controls. Seeds were extracted from duff and soil that was collected in six layers, to a depth of 10 cm in the mineral soil. *Ceanothus* seeds were the most abundant (mean = 246 seeds m^{-2}), noted at all sites and at 88 % of sampling locations within unburned sites. *Arctostaphylos* and *Prunus* seeds were less abundant (mean = 29 seeds m^{-2} and 6 seeds m^{-2}, respectively), but still recorded at 64 % and 45 % of the unburned sites, respectively. The depth of seed burial varied at all unburned sites, but some seed was present even at the deepest (6 cm to 10 cm) soil layer, where seed mortality due to heat from burning is least likely. Seed density was substantially reduced, but not eliminated, by October prescribed burns at both McCloud and Jennie Springs, while seed density following July burns at Jennie Springs did not differ from the control. The abundance of buried seed indicates that restoring shrubs to forest understory should be possible even in areas where they are currently lacking. If preventing shrubs from colonizing a site is the management goal, the effectiveness of a single prescribed fire may be limited.

INTRODUCTION

Shrubs play a vital ecological role in mixed conifer forests of the western United States by providing cover and forage for wildlife (Sampson and Jesperson 1963, Conard *et al.* 1985), fixing nitrogen and improving soil fertility (Conard *et al.* 1985, Busse *et al.* 1996), and

providing beneficial microenvironments for tree seedling establishment (Dunning 1923, Tappeiner and Helms 1971, Gratkowski 1974). Historically, shrubs were a common yet often patchy component of the forest understory. For example, in 1929, Hasel *et al.* (1934) found tall shrubs including ceanothus (*Ceanothus* sp.) and manzanita (*Arctostaphylos* sp.) to cover 22 % of the forest floor of an old-growth mixed conifer forest in the central Sierra Nevada. The scattered distribution of shrubs within forests was apparently due to both the high light requirements of many shrub species (Cronemiller 1959, Conard *et al.* 1985), and the heterogeneity of the canopy, with many small gaps occurring amongst tree groups of varying age and density (Show and Kotok 1924). Fires burning every 5 yr to 30 yr (Skinner and Taylor 2006, van Wagtendonk and Fites-Kaufman 2006) likely helped to produce and maintain this structural complexity. In the absence of fire, conifers have invaded the gaps, overtopping and replacing the shrubs in many areas (Gruell 2001, Nagel and Taylor 2005).

Large numbers of shrub seeds have been found in the soil, even where living mature plants have long been shaded out (Quick 1956). Such seed may be able to persist for hundreds of years in the seed bank (Gratkowski 1962). When overstory trees are harvested or killed by high severity wildfire, extensive shrub fields often result (Fowells and Schubert 1951, Gratkowski 1974). Competition with dense shrubs has been shown to slow the initial growth of tree seedlings (Conard and Radosevich 1982, Lanini and Radosevich 1986, Oliver 1990, Stuart *et al.* 1993, McDonald and Fiddler 2001). Shrub patches may also burn at higher intensity than fuels in surrounding forest vegetation (Skinner and Taylor 2006), at least under low live fuel moisture conditions.

Shrubs of mixed conifer forests are well adapted to fire. Germination of *Ceanothus* has been shown to be stimulated by heat (Quick and Quick 1961, Kauffman and Martin 1991), whereas charate from partially burned wood promoted germination in *Arctostaphylos*

(Keeley 1987). Some species of *Prunus* also form a seed bank (Marks 1974, Morgan and Neuenschwander 1988, Oakley and Franklin 1998), and while the stimulus for germination in these species is not as well understood, the abundance of bitter cherry (*P. emarginata* [Douglas ex Hook.] D. Dietr.) seedlings after fire (Morgan and Neuenschwander 1988) suggests that similar mechanisms of establishment may apply.

While fire promotes germination, too much heat can also kill seed. Shrub seedlings are therefore often less abundant in areas within fires where the most fuel was consumed (Kilgore and Biswell 1971, Weatherspoon 1988, Moreno and Oechel 1991, Huffman and Moore 2004, Knapp *et al.* 2007). Whether fire kills seeds or stimulates them to germinate depends on both the intensity of the fire as well as the location of the seed in the seed bank. Seed in the organic fermentation and humus horizons are likely to be killed by fires that consume the duff. Seed in the upper soil layers may also be subjected to excessive heating if a large amount of overlying fuel is consumed, especially if the soil is dry (Frandsen and Ryan 1986, Busse *et al.* 2005, Busse *et al.* 2010).

Shrubs have been the focus of management in cases where there are both too few and too many. Whether fire is effective for increasing the cover of shrubs in areas where they are currently lacking will depend, in part, on the presence of seed in the soil. Conversely, the presence of seed in the soil can hamper the long-term effectiveness of some methods of controlling shrub abundance, such as mastication, hand cutting, or herbicides. Managing shrubs by manipulating the size of the seed bank with fire has also been suggested (Biswell *et al.* 1955, Weatherspoon 1988). Whether using fire is a viable strategy to manage shrub abundance in forests will depend on improved understanding of seed bank size, depth of seed burial, and how both are affected by fire under varying burning conditions.

Our study objectives were to 1) quantify the size of the shrub seed bank in mature mixed conifer forest stands; 2) determine where in the duff and upper mineral soil layers shrub seed is most likely to be found; 3) evaluate whether size of the seed bank or location of seeds within the seed bank could be predicted by stand age, stand structure, or site topographic variables; and 4) investigate the effect of prescribed fire and wildfire on the abundance of seed that is located at different depths in the seed bank.

METHODS

Field Data Collection

We chose second growth as well as unlogged stands in mixed conifer forests in northern California, at elevations between 915 m and 1890 m, to sample (Figure 1, Table 1, Appendix 1). The majority of stands were located on medium to high productivity lands adjacent to recently harvested or burned areas, where shrubs had become an important component of the understory after the disturbance. All of the sampled stands were either slated for harvest or sufficiently mature to harvest (i.e., average trees were conifers >25 cm diameter). At most sites, we sampled the seed bank at 10 points within the stand in either 1987 or 1988. Time limitations resulted in only five sample points at the Mt. Hope location. Sampling points were located 30 m apart along a transect oriented in a random direction, with no sampling point less than 10 m from the edge of the stand. If the edge of the stand was reached, we placed the subsequent sampling point at a 90 degree angle in the direction away from the stand edge. We collected three duff and soil subsamples per collection point, each 1 m from the center in random directions, which we then composited.

Each duff and soil subsample was collected from within a 20.9 cm × 20.9 cm metal frame that we placed onto the forest floor sur-
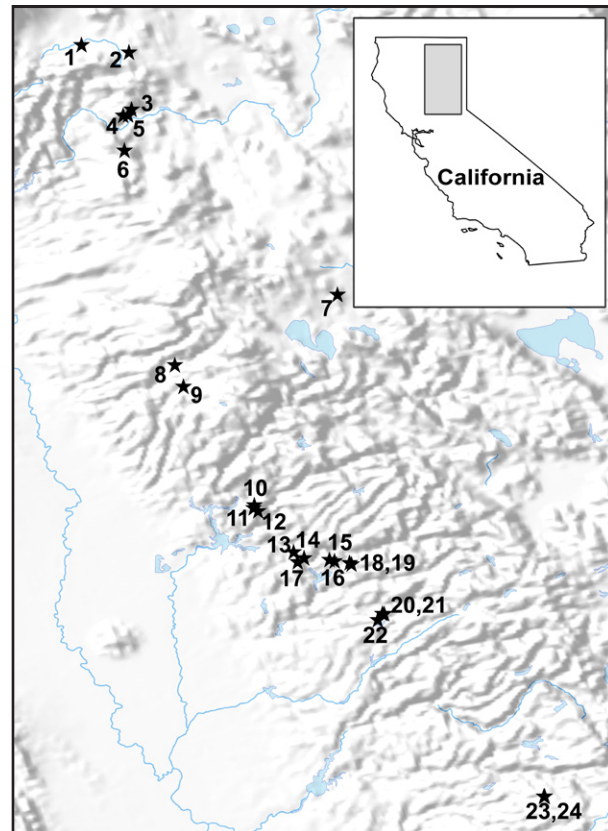

Figure 1. Location of shrub seed bank sampling sites, with site number from Table 1. Prescribed burning experiments were conducted at the McCloud (#1) and Jennie Springs (#7) sites.

face after first removing and discarding litter and small woody fuels. We used a knife to cut the duff (consisting of fermentation and humus layers) and soil vertically along the outer edge. After excavating one side of the square to expose the duff and soil, we extracted six successive forest floor and soil layers within the sampling frame with the help of a spatula and trowel. Each layer was bagged separately. The first layer was of variable thickness, containing all duff located 2 cm or more above the mineral soil boundary, and the second layer was the lower duff from 2 cm down to mineral soil. Layer three was the first 2 cm of mineral soil, layer four went from 2 cm to 4 cm into the soil, layer five went from 4 cm to 6 cm into the soil, and layer six went from 6 cm to 10 cm into the soil.

Table 1. Sites in northern California at which the shrub seed bank was sampled, arranged from north to south, listing land ownership, date of most recent fire (wildfire or prescribed burn), date sampled, and topographic attributes. Most sites had no record of fire (dashes indicate no record, or were last burned >15 yr ago). Each sample consisted of three composited subsamples, except at the McCloud site where only one collection was made per sample. At the McCloud site, half of the samples were collected from adjacent unburned areas. At the Jennie Springs site, six of the samples were collected from unburned patches within the burn units. NF= National Forest; BLM = Bureau of Land Management.

Site No.	Site name	Land ownership	Last burned	Date sampled	Samples (*n*)	Aspect (degree)	Slope (%)	Elevation (m)
1	McCloud	Shasta-Trinity NF	Oct 88	1 Nov 88	56	270	2	1150
2	Horse	Shasta-Trinity NF	-	10 Aug 88	10	82	5	1410
3	Big Poison	Lassen NF	-	12 Jul 88	10	141	14	1210
4	Underground	Shasta-Trinity NF	-	21 Jul 87	10	268	21	1282
5	Flower	Shasta-Trinity NF	-	2 Aug 82	10	52	18	1380
6	Hatchet	Ukiah District BLM	-	4 Aug 88	10	313	3	1545
7	Jennie Springs	Lassen NF	Jul, Oct 83	Sep 87	19	135	<10	1890
8	Rush	Lassen NF	-	6 Sep 88	10	55	13	1160
9	Soda	Lassen NF	-	7 Sep 88	10	95	8	1120
10	Galen	Plumas NF	-	7 Jul 87	10	254	31	1020
11	Brush	Plumas NF	-	17 Aug 88	10	186	11	1025
12	Bald	Plumas NF	-	23 Aug 88	10	258	14	980
13	Mt. Hope	Plumas NF	-	24 Aug 88	5	294	27	960
14	Hamburger	Plumas NF	-	16 Aug 88	10	3	9	930
15	Bridger	Tahoe NF	-	21 Sep 88	10	223	6	995
16	Pendola	Tahoe NF	-	19 Sep 88	10	98	10	975
17	Cummings	Plumas NF	-	30 Jun 87	10	82	27	960
18	Sleighville1	Tahoe NF	Mar 88	29 Aug 88	10	241	20	1035
19	Sleighville2	Tahoe NF	-	30 Aug 88	10	313	8	1075
20	Washington	Tahoe NF	-	27 Sep 88	10	251	11	1190
21	White Cloud	Tahoe NF	-	12 Sep 88	10	335	12	1220
22	Five Mile	Tahoe NF	-	14 Sep 88	10	139	12	1150
23	Pilliken	Eldorado NF	Aug 73	28 Jul 87	10	270	28	1770
24	Dennis Spring	Eldorado NF	-	14 Jul 87	10	200	10	1770

At each sampling point, we recorded the elevation, topographic position (ridge top, upper third, mid-slope, lower third), aspect, and percent slope. We estimated basal area by tree species in the surrounding stand with a 20-factor prism. We visually estimated height, density, and cover of woody understory species within a 2 m radius circular plot around each sampling point. To estimate the age of the stand, we either collected increment cores from the largest dominant or co-dominant trees at each site, or we counted rings on stumps in adjacent cut-over areas. Two sites had previously burned in wildfires (Pilliken in a summer 1973 wildfire, and Sleighville1 in a late winter 1988 escaped site-preparation burn). At these two locations, we collected seed bank samples both within the burn perimeter and in adjacent unburned areas. The Dennis Spring (unburned) site is across a road from the Pilliken site, and the Sleighville2 (unburned) site is about 1 km from the Sleighville1 site.

In order to evaluate the effect of prescribed burning on the shrub seed bank, we established a replicated experiment at the McCloud site. We also sampled the soil seed bank in units

that had been burned in the early summer and fall at the Jennie Springs site.

McCloud Prescribed Burning Experiment

The forest at the McCloud site was a relatively young mixed conifer stand dominated by white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), which grew after the largest conifers were logged (Appendix 1). Shrubs found nearby included bitter cherry, greenleaf manzanita (*Arctostaphylos patula* Greene), and snowbrush (*Ceanothus velutinus* Douglas ex Hook.). We established four 5.5 m × 5.5 m burn units in close proximity to each other in gaps between trees. Shortly before the burns, we sampled the shrub seed bank at eight points just outside the perimeter of each unit, using the same procedures outlined previously except without subsampling. We installed duff pins, which consisted of sections of rebar pounded into the ground flush with the upper surface of the litter, at nine points within each unit in order to determine the percentage of the forest floor removed by the burns. To estimate amount of heating at different forest floor and mineral soil depths, we inserted four 20.2 cm long tiles that were painted with vertical strips of heat-sensitive Tempilaq® paints (temperatures (degrees Celsius) of 52, 59, 66, 79, 93, 149, 260, 427, and 482; Tempil Company, Plainfield, New Jersey, USA) into a cut through the litter, duff, and soil near the corner of each unit. The top of the tile was flush with the top of the litter. We estimated the moisture of the forest floor and upper 10 cm of soil by collecting samples at two to four locations outside of each plot at the time of the burn. The forest floor was separated into the upper forest floor (litter plus fermentation horizons) and lower forest floor (humus) samples. We placed all samples in airtight plastic containers, weighed them wet, and weighed them again after oven drying at approximately 100 °C until the weights no longer changed.

Burns were conducted on 28 October 1988. Winds were light and temperatures averaged 7 °C. Relative humidity averaged 66 %, and woody surface fuels were moderately dry (10 hr fuel moisture = 13 %). Fuels were consumed with a backing fire after ignition at the highest elevation in each unit. Flame lengths were generally 15 cm to 30 cm.

After the burns, we measured the distance from the top of the duff pin to the surface of unburned litter or duff (if any), and to mineral soil. We removed the heat tiles and evaluated the depth of heat penetration into the duff and soil by noting where each paint melted, indicating that the thermal threshold was exceeded. Four days after the burns, we collected duff and soil samples within each burn unit (two at each corner, approximately 1 m inside the unit), adjacent to and paired with collections previously made outside of the burn units. If the sampling point within the unit did not burn, the pair was not used, which resulted in a total of 56 samples (28 burned, 28 unburned) for seed bank processing.

Jennie Springs Prescribed Burning Experiment

The forest at the Jennie Springs site was composed of predominantly 60- to 70-year-old white fir that established within a brush field after a stand-replacing fire (Appendix 1). The emerging conifers eventually shaded out the shrub layer, and some shrub skeletons were still visible in the understory. The dominant shrub species adjacent to the study area were snowbrush and bush chinquapin (*Chrysolepis sempervirens* [Kellogg] Hjelmqvist), but greenleaf manzanita and pinemat manzanita (*Arctostaphylos nevadensis* A. Gray) were also present. The burn units sampled at this site were part of an existing larger study involving three levels of thinning and multiple burning treatments, including: fall burn, early summer burn, and unburned control, all replicated twice in adjacent blocks (Weatherspoon 1985).

Each unit was 0.2 ha and surrounded by an approximately equal-sized buffer. We only sampled the seed bank in the unthinned units that were burned once in either July or October.

Prescribed burns were completed 20 to 22 July, and 12 to 20 October 1983. The July burns were conducted when the fine surface fuels were dry but the lower duff layer was still moist, while the October burns were conducted after rain had dampened the fine surface fuels but the lower duff was still dry. Moist surface fuels at the time of the October burns resulted in a patchy burn pattern; however, forest floor consumption in areas that did burn was nearly complete. The lower duff (humus) layer was generally not consumed by the July burns. Actual fuel moisture values were not available.

We collected forest floor and soil samples for seed bank analysis in September 1987, approximately four years after the burns were completed. We stratified sampling according to burn depth: six samples were deep (October burn), seven samples were intermediate (July burn), and six samples were from unburned patches inside the July and October burn units. Each sample consisted of three subsamples randomly selected from areas within 5 m of the sampling point and composited by layer. Even though samples were collected in multiple burn units, the level of replication was insufficient for the treatment to be considered replicated.

Extracting Seeds from Duff and Soil

We extracted shrub seeds from the duff and soil samples collected in 1987 using procedures modified from those of Quick (1956). After air drying, we sieved the samples, retaining the 1.0 mm to 4.8 mm fraction. We discarded material <1.0 mm, which was assumed not to contain shrub seeds. Material larger than 4.8 mm was first examined for the occasional cluster of *Arctostaphylos* seed still attached to the raceme before discarding. We then removed seed from the retained fraction

using a mechanical seed aspirator that consisted of an industrial vacuum cleaner, mesh screens, and a series of Plexiglas® (Rohm and Haas Company, Philadelphia, Pennsylvania, USA) tubes, which separated the lighter organic particles from the seed. We conducted tests with known amounts of seed placed within soil and duff samples that showed that nearly all fully developed and potentially viable shrub seeds could be extracted using this method. We assessed potential viability of all seeds collected in 1987 and a subset of seeds collected in 1988 by cutting them in half and visually examining them for an intact healthy endosperm.

Data Analysis

We converted seed data to seeds m^{-2} ground surface (summed across all layers), and to the number per unit volume of soil (seeds per 0.01 m^3; i.e., 1 $m^2 \times 1$ cm deep). We used one-way analyses of variance to evaluate differences in seed density (seeds m^{-2}) and seed viability (percentage) among all unburned sites. For data where seed number was segregated into duff and soil layers, we used a mixed model analysis of variance to determine the significance of the site (random) and layer (fixed) main effects, as well as the site × layer interaction. Samples collected from unburned areas within the McCloud and Jennie Springs prescribed burning experiments were included in these analyses. Samples collected from sites that experienced recent wildfire (Sleighville1 and Pilliken) were not analyzed together with data from unburned sites, and we include numbers in Appendix 2 for illustrative purposes only.

In order to evaluate whether stand age, stand structure, and site environment variables were related to the size of the seed bank, we performed a mixed-model analysis of variance, with seed density for each of the three major genera (*Ceanothus*, *Arctostaphylos*, and *Prunus*) as the dependent variables. Explana-

tory variables (fixed effects) were: heat load, percent slope, elevation, stand age, basal area, percentage of basal area composed of fir species (white fir and red fir [*Abies magnifica* A. Murray bis]), percentage of basal area composed of broadleaf tree species (California black oak [*Quercus kelloggii* Newberry], tanoak [*Lithocarpus densiflorus* {Hook. & Arn.} Rehder], and Pacific madrone [*Arbutus menziesii* Pursh]), and percent cover of that shrub genus in the stand at the time the seed were collected. We summarized all variables at the plot level and included site in the model as a random effect. To estimate stand age, we averaged the ages of the three oldest trees sampled at each site. The relative heat load index (unitless) was calculated from aspect, slope, and latitude, using equations given in McCune and Keon (2002). We dropped elevation because it was highly correlated with the percentage of basal area composed of fir species.

We also used mixed-model analyses of variance to investigate whether the depth of the seed bank was associated with stand age, stand structure, or site environment variables. Percentage of seed in the duff layers, percentage of seed in the upper (0 cm to 4 cm) layer of soil, and percentage of seed in the lower (4 cm to 10 cm) layer of soil were dependent variables, with the same explanatory variables described above (except using total shrub cover rather than cover by genus).

For the McCloud prescribed burn experiment, block and pair nested within block (paired being burned and unburned samples taken just inside and outside of the burn unit) were considered to be random variables, with treatment, layer, and treatment × layer fixed. Samples were not paired in the Jennie Springs burn experiment, and only the block effect was considered random. Because the variance for the fall burn treatment at both sites was an order of magnitude less than the variance for the unburned treatment (and July burn treatment at Jennie Springs), we made treatment a grouping variable to specify heterogeneity in the co-

variance structure. For all models, we considered "layer" to be a repeated term with a first order autoregressive structure, meaning that seed densities in adjacent layers were more likely to be correlated. We estimated the denominator degrees of freedom using the Satterthwaite approximation (Satterthwaite 1946). To improve normality, seed number was natural log transformed ($\ln(n + 1)$) and dependent variables expressed as percentages were arcsine square root transformed prior to analysis. All analyses were performed using SAS 9.1 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Seed Abundance

Seed density of all three shrub genera differed significantly among sites (Figure 2). *Ceanothus* seeds were by far the most abundant, averaging 246 seeds m^{-2} (range = 24 seeds m^{-2} to 1383 seeds m^{-2}), and found at all unburned sites sampled (Figure 2). Based on vegetation in openings in the vicinity, the species represented in the seed bank likely included: deerbrush, prostrate ceanothus (*C. prostratus* Benth.), whitethorn ceanothus (*C. cordulatus* Kellogg), and snowbrush (Appendix 1). Seeds from the genus *Arctostaphylos* (likely mostly greenleaf manzanita, sticky whiteleaf manzanita [*A. viscida* Parry], and pinemat manzanita) averaged 29 seeds m^{-2} (range = 0 seeds m^{-2} to 209 seeds m^{-2}), and were found at 14 of the 22 unburned sites (Figure 2). *Prunus* seeds (most likely bitter cherry) represented a relatively minor portion of the shrub seed bank (average = 6 seeds m^{-2}), and were found at 10 of the 22 unburned sites (Figure 2). *Prunus* was abundant only at the Dennis Spring site, where 96 seeds m^{-2} were counted.

Most of the *Ceanothus* seeds at the four unburned sites sampled in 1987 were potentially viable (mean = 97.5 % of tested seeds having an intact endosperm when cut in half) and no significant differences in the percentage
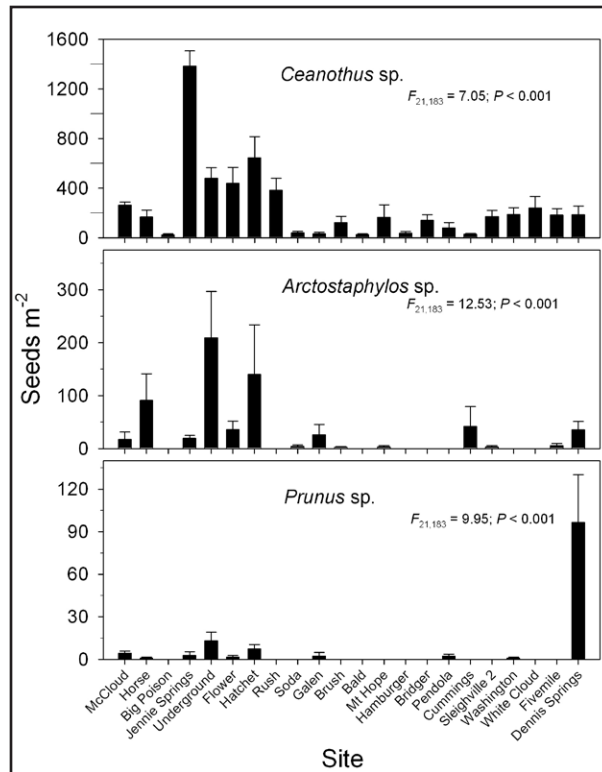
Figure 2. Average number of seeds m^{-2} of the three dominant shrub genera (*Ceanothus, Arctostaphylos,* and *Prunus*) at 22 forested sites in northern California without a history of recent fire (>15 yr), arranged from north to south. Error bars indicate the standard error.

of seeds with intact endosperm existed among sites ($F_{3,31}$=1.38; $P = 0.475$). Conversely, only a small portion (12.5%) of the *Arctostaphylos* seeds collected at the four unburned sites in 1987 showed evidence of viability. While the percentage with an intact endosperm ranged from 4.5% at the Cummings site to 24.3% at the Underground site, differences among sites were not statistically significant ($F = 1.73, P = 0.192$). Percentage of presumed viable *Prunus*

seeds was intermediate (mean = 32.2%), and did not differ between the two sites having enough seeds to be included in the analysis (Dennis Spring [36.6%] and Underground [27.8%]; $F = 1.26, P = 0.322$). We only spot-checked for the presence of an intact endosperm in the 1988 seed collections, but viability numbers were similar to those found in 1987.

Seed density at the two sites sampled within areas burned by wildfires within the past 15 years was considerably lower than in adjacent unburned areas. Sleighville1, burned in the late winter (six months prior to sampling) when the soils were presumably still moist, contained only 16.5 seeds m^{-2} of the three major genera, compared to 174.2 seeds m^{-2} found at Sleighville2, located outside of the burn boundary. Samples collected within the Pilliken burn contained 10.8 seeds m^{-2}, or only 3.4% of the seeds of the three major genera found on the adjacent Dennis Spring site (316.9 seeds m^{-2}), even though the Pilliken burn occurred 14 years prior to the samples being collected.

Seed Depth

The significance of the site × layer interaction for all three genera demonstrated that the location of seeds in the forest floor and soil layers differed among sites (Table 2). For example, while over 50% of the *Ceanothus* seeds at the Horse site were in the duff layers, all seeds at the Cummings site were located in the underlying mineral soil (Appendix 2). At two sites (Cummings and Underground), over 50% of the seeds were located within the deepest two soil layers (4 cm to 6 cm and 6 cm to 10

Table 2. Mixed model analysis of variance of three genera of shrub seeds 0.01 m^{-3} (1 m^2 × 1 cm depth) in six layers from the top of the forest floor to 10 cm into the mineral soil at 22 unburned forested sites in northern California. Degrees of freedom (df) are shown for both the numerator and the denominator.

Term	*Ceanothus*			*Arctostaphylos*			*Prunus*		
	df	F	P	df	F	P	df	F	P
Site	21, 281	14.81	<0.001	21, 351	11.28	<0.001	21, 319	14.53	<0.001
Layer	5, 812	45.67	<0.001	5, 783	3.53	0.004	5, 784	1.63	0.150
Site × layer	105, 812	1.84	<0.001	105, 783	1.45	0.004	105, 784	2.22	<0.001

cm), and therefore presumably better protected from heating with fire. For *Arctostaphylos*, seed location similarly ranged from shallow (all seeds in the duff layers at the Brush site), to more deeply buried (over 70 % of the seeds in the soil) at the remaining 10 of 13 sites (Appendix 2). For *Prunus*, all seeds were located in the duff layers at four sites (McCloud, Horse, Flower, and Washington), compared with 85 % and 100 % of seeds located in the mineral soil at the Dennis Spring and Underground sites, respectively (Appendix 2).

Because of the variation in the seed community composition among sites, we analyzed the data for each genus separately; comparisons among genera are therefore only illustrative. *Ceanothus* and *Arctostaphylos* seeds were both, on average, most abundant in the first 2 cm of mineral soil (Figure 3). *Ceanothus* seed appeared to be somewhat more deeply buried than *Arctostaphylos* seed, with a higher percentage (10.6 % vs. 5.1 %) found in the deepest (6 cm to 10 cm) soil layer. Although a smaller percentage of *Prunus* seed appeared to occur in the duff layers, *Prunus*

also contained the smallest percentage in the deepest (6 cm to 10 cm) soil layer (4.5 %), with the majority found in the upper 0 cm to 4 cm of mineral soil (Figure 3).

Factors Associated with Seed Abundance and Depth

Ceanothus seed was generally most abundant at sites with the least slope, sites with higher cover of *Ceanothus* in the understory, and sites with the greatest fir relative basal area (Table 3). The only variable significantly associated with the abundance of *Arctostaphylos* seed was fir relative basal area. None of the variables tested were significantly associated with *Prunus* seed density. Age of the oldest trees sampled in the stand, which may indicate the amount of time since shrubs dominated the understory, was not significantly associated with seed abundance of the three genera.

None of the variables tested were significantly associated with percentages of seed in the duff, upper soil, or lower soil layers (analyses not shown). The only variable that ap-
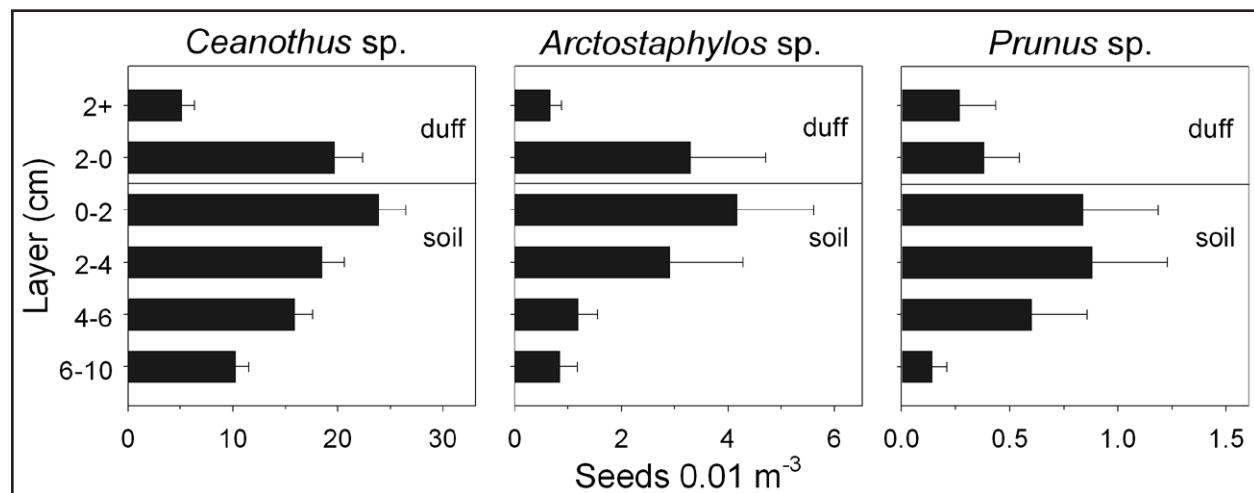

Figure 3. Average number of seeds of the three dominant shrub genera (*Ceanothus, Arctostaphylos,* and *Prunus*) per 0.01 m^3 (1 m × 1 m × 0.01 m depth) in six layers from the top of the forest floor to 10 cm deep in mineral soil at 22 unburned forested sites in northern California. Layer 2+ is the upper duff from the top of the duff to 2 cm above mineral soil, layer 2-0 is the lower duff from 2 cm down to mineral soil, layer 0-2 is the top 2 cm of mineral soil, layer 2-4 is from 2 cm to 4 cm deep, layer 4-6 is from 4 cm to 6 cm deep, layer 6-10 is from 6 cm to 10 cm deep.

Table 3. Results of mixed model analyses of variance for three shrub genera found in the seed bank at 22 unburned forested sites in northern California. Average seed density (seeds m^{-2}) as the dependent variable and independent variables describing stand structure and site environment. Heat load is a relative index calculated from aspect, slope, and latitude (McCune and Keon 2002). Stand age is estimated as the average age of the three oldest trees sampled at each site. "Fir basal area (%)" is the percentage of basal area composed of fir species, and "Broadleaf basal area (%)" is the percentage of basal area composed of broadleaved tree species. Numbers for variables where the relationship with seed density was negative are shown in bold.

Fixed effect	*Ceanothus*	*Arctostaphylos*	*Prunus*
	------------------------ *P* ------------------------		
Heat load (unitless)	**0.547**	0.070	0.820
Slope (%)	**0.016**	0.208	0.591
Stand age (yr)	**0.217**	**0.344**	**0.267**
Basal area (m^2 ha^{-1})	**0.592**	0.800	0.202
Fir basal area (%)	0.030	0.010	0.706
Broadleaf basal area (%)	0.736	**0.103**	**0.137**
Ceanothus cover (%)	0.022*	-	-
Arctostaphylos cover (%)	-	**0.684**	-
Prunus cover (%)	-	-	**0.654**

*Percentage cover was only evaluated for shrubs of the same genus as the seed being analyzed as the dependent variable.

proached significance was shrub cover, with a trend toward a higher percentage of shrub seed found in the duff layer at collection locations with a greater cover of shrubs.

Effect of Prescribed Burning

Prescribed burning at the McCloud site substantially reduced the number of seeds of all three shrub genera. Seed density of *Ceanothus*, *Arctostaphylos*, and *Prunus* within the burn units was nearly 28 times less than the number found just outside the burn units (10.4 seeds m^{-2} vs. 285.9 seeds m^{-2}). The layer × burn treatment interaction was highly significant (Table 4), with the greatest number of seeds per unit volume located in the lower duff layer in the unburned treatment and in deepest mineral soil layer (6 cm to 10 cm) within the burn treatment (Figure 4). Soil and the forest floor were moderately dry at the time of the McCloud burns (moisture of upper litter and duff = 20.3%, of lower duff = 28.6%, and of upper 10 cm of mineral soil = 18.5%). Depth of the forest floor layer averaged 9.1 cm prior to the burns and was completely consumed to

Table 4. Fixed effects in a mixed model analysis of variance of number of shrub seeds 0.01 m^{-3} (1 m^2 × 1 cm depth) of the three most common genera (*Ceanothus, Arctostaphylos,* and *Prunus*) in six layers from the top of the forest floor to 10 cm into the soil with and without prescribed burning at two sites (McCloud and Jennie Springs) in northern California. Treatments at the two sites were: McCloud—fall (October) burn and control; Jennie Springs—fall (October) burn, early summer (July) burn, and control. Degrees of freedom (df) are shown for both the numerator and the denominator.

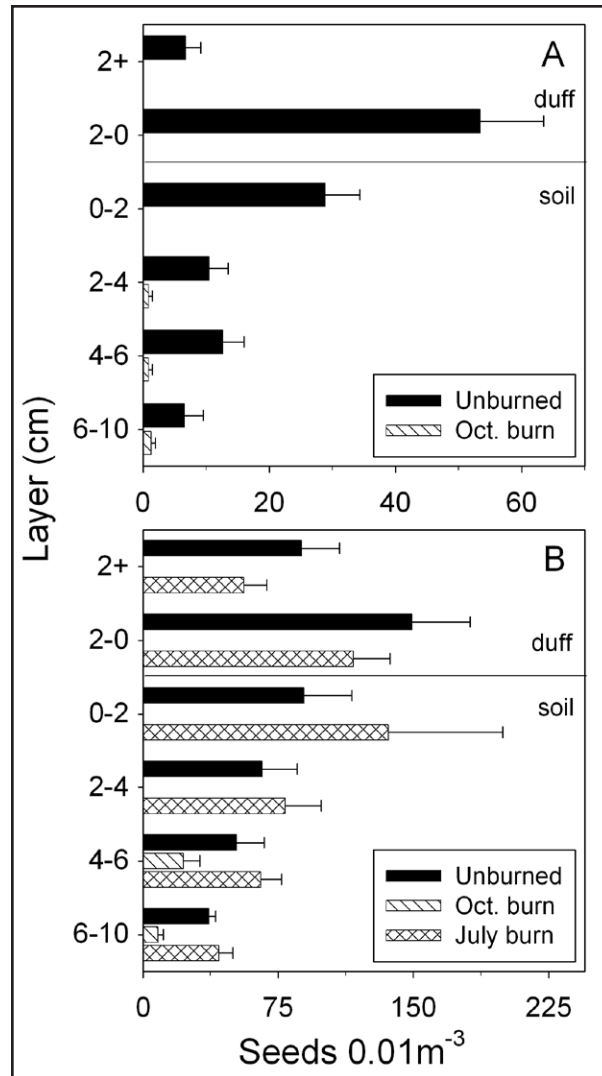| Term	McCloud			Jennie Springs		
	df	*F*	*P*	df	*F*	*P*
Treatment	1, 61.1	120.72	<0.001	2, 67.4	259.93	<0.001
Layer	5, 135	6.49	<0.001	5, 83.2	3.17	0.011
Treatment × layer	5, 135	9.33	<0.001	10, 67.4	7.65	<0.001

Figure 4. Combined number of seeds of the three dominant shrub genera (*Ceanothus, Arctostaphylos,* and *Prunus*) in six layers within unburned and prescribed burned plots at two sites in northern California: (A) McCloud and (B) Jennie Springs. Layer 2+ is the upper duff from the top of the duff to 2 cm above mineral soil, layer 2-0 is the lower duff from 2 cm down to mineral soil, layer 0-2 is the top 2 cm of mineral soil, layer 2-4 is from 2 cm to 4 cm deep, layer 4-6 is from 4 cm to 6 cm deep, layer 6-10 is from 6 cm to 10 cm deep. Unburned plots at the McCloud site were sampled 28 days prior and burned plots sampled four days after the burn. All sampling at Jennie Springs was done four years after burning.

mineral soil in most places; overall, 95% of the forest floor was consumed. Soil temperatures exceeded 93 °C at 13 of the 15 points

evaluated, and the depth into the soil at which this heating threshold was reached averaged 3.8 cm. Soil temperatures greater than 149 °C occurred at 7 of the 15 points evaluated, and the depth into the soil at which this heating threshold was reached averaged 1.1 cm.

At the Jennie Springs site, significantly more *Ceanothus*, *Arctostaphylos*, and *Prunus* seeds were found in unburned units (1383 seeds m⁻²) than in units burned in October (76 seeds m⁻²) (Figure 4). While patchy, the October burns generally consumed all of the surface fuel down to the mineral soil in areas where the fire carried. Total seed number in the July burn treatment (moister fuel conditions that allowed only partial consumption of the duff) did not differ from the unburned control (Figure 4). The treatment × layer interaction was highly significant, with the greatest number of viable seeds occurring in the lower duff and upper soil layers in the unburned and July burn treatments, and the greatest number of viable seeds found deeper in the mineral soil (the 4 cm to 6 cm soil layer) after the October burns (Figure 4). Seed densities in the unburned treatment and the July burn treatment were not significantly different for any of the duff and soil layers. Unequal sample size and lack of replication at this site means that results should be considered preliminary. However, treatment areas are in close proximity to each other and replicate samples were collected across treatment boundaries; we therefore believe the results to be robust and not confounded by other factors.

DISCUSSION

Our finding that the shrub seed bank within mixed conifer forest stands was dominated by *Ceanothus* species is consistent with a previous study of shrub seed banks at one location in the Sierra Nevada, south of our study area (Quick 1956). Not only did *Ceanothus* comprise 88% of all identified shrub seeds, it was also ubiquitous and found at all 22 unburned sites, representing a broad geo-

graphic range, as well as 88 % of all sampling locations within sites. Quick (1956) found an average of 646 *Ceanothus* seeds m^{-2} in an unlogged mixed conifer stand, which is within the range of values noted across sites in our study (24 seeds m^{-2} to 1383 seeds m^{-2}). However, the average in our study (242 seeds m^{-2}) was somewhat less than reported by Quick (1956). The second most abundant shrub genus was *Arctostaphylos*, with an average of 19 seeds m^{-2}, similar to what Quick (1956) found at one mixed conifer site (16 seeds m^{-2}). An average of 32 % of samples in our study contained *Arctostaphylos* seed, and 15 % contained *Prunus* seed, consistent with the much reduced numbers of seed of these species, relative to *Ceanothus*.

The seed bank under four different *Ceanothus* and *Arctostaphylos* species in southern California were found to range from 87 seeds m^{-2} to 4114 seeds m^{-2} (Keeley 1977). Even larger numbers of seed (4500 seeds m^{-2} to 8422 seeds m^{-2}) have been noted under two *Arctostaphylos* species in northern California (Kelly and Parker 1990). However, these latter two studies are from chaparral ecosystems, and sampling was done directly beneath live shrubs. Our study and Quick's (1956) were conducted in forests that were relatively free of live shrubs. Therefore, the seeds in the seed bank were more likely to have dated to a time earlier in succession when shrubs comprised a greater proportion of the understory, or they resulted from dispersal from outside of the sampled area.

Percentages of seeds that we presumed to be viable were similar to percentages reported by Quick (1956), which were based on actual numbers germinating (97.5 % vs. 77.2 %, respectively, for *Ceanothus*; 12.5 % vs. 15.7 %, respectively, for *Arctostaphylos*). While this suggests that a visual inspection may provide an adequate estimate of viability for these species, actual germination tests would be necessary to verify that this is the case.

Forests dominated by *Abies* tended to have the largest *Ceanothus* and *Arctostaphylos* seed banks. Such forests are found at higher elevations that typically burn less frequently but at higher severity than lower elevation mixed-conifer forests (e.g., Beaty and Taylor 2001). High severity patches create openings and high light environments, which would favor shrub establishment and growth. The reason for more *Ceanothus* seeds in sampling locations with the least slope is not clear. *Ceanothus* seed were most abundant in areas with the greatest *Ceanothus* cover in the understory, suggesting that, without regular inputs from annual seed crops, the seed bank size will decline over time. *Arctostaphylos* and *Prunus* seed densities were not associated with the current shrub composition in the stand, possibly because few sites contained any shrubs of these genera and thus the amount of variation was insufficient to conduct an adequate test. Lack of a relationship may also indicate that abundance of seed of these genera is more dependent on dispersal from outside sources, a residual seed bank from when shrubs last occupied the site, or both. If the shrub seed bank declines over time due to granivory, decay, or other causes (Parker and Kelly 1989, Kelly and Parker 1990), one might expect more seed in younger stands where a shrub phase had occurred relatively recently. However, we saw no evidence of a relationship between stand age and seed bank size for any of the three shrub genera. Admittedly, our estimate of stand age is rough and average age of the oldest trees also may not be a good indicator of the time when shrubs were a more important component of the understory, especially in uneven-aged stands. The lack of a relationship with stand age may indicate that seeds remaining from a previous shrub phase at a site had largely been depleted, especially for some of the older stands. While seeds of these shrub species can remain viable for decades or even centuries (Quick and Quick 1961, Gratkowski 1962), the seed bank is still transient, with

numbers tending to decline substantially with time (Zammit and Zedler 1988, Parker and Kelly 1989). Keeley *et al.* (2005) noted fewer post-wildfire buckbrush (*Ceanothus cuneatus* [Hook.] Nutt.) seedlings in chaparral stands with longer intervals since the previous fire, up to 150 years. This drop may have been due to fewer adult plants of this species in older chaparral, thus less recent input to the seed bank. That more seeds are produced in a single good seed year than are usually found in the seed bank (Keeley 1977) is another indicator of seed loss over time. This loss appears to be mostly due to seed predation and not senescence or decay (Kelly and Parker 1990). As seeds are lost over time, the relationship between input from shrubs that once grew on site and seed bank size may decline, while other mechanisms of seed bank maintenance, such as dispersal, increase in importance. Small mammals have been shown to cache shrub seeds at a considerable distance from the parent plants (Vander Wall 1994, Roth and Vander Wall 2005), and the frequent observation of *Ceanothus* and other shrub seedlings growing in dense clusters (Cronemiller 1959; Vander Wall 1994; E. Knapp, USDA Forest Service, Pacific Southwest Research Station, Redding, California, personal observation) suggests that such animal-mediated dispersal is common.

While the majority of seed of the three main shrub genera were located in the duff or upper mineral soil where they are presumably more vulnerable to being killed by heat of a fire, a substantial portion were also located in deeper soil layers. Differences among species were relatively minor, but the somewhat greater proportion of *Ceanothus* seed located deeper in the soil is consistent with smaller average seed size, which might allow seeds deposited on the surface to settle more rapidly. The generally broad distribution of seed across depths at most sites indicates that at least some would be likely to escape mortality in all but the most severe fires. We expected that a greater proportion of seed would be found in upper layers of the seed bank (i.e., in the duff or upper mineral soil) in younger stands and at locations with more shrubs in the current understory. However, neither stand age nor shrub cover were significant contributors to location in the seed bank in our analyses. It is possible that other unevaluated factors such as seed dispersal and deeper burial through caching by small mammals, or soil mixing due to disturbance from gophers, or frost heaving, or erosion are more important.

Effect of Fire on the Soil Seed Bank

The large reduction in seed density noted after fall prescribed burns and at sites that had experienced wildfire suggests that seeds were not only consumed by the fires, but that heating of the soil was likely sufficient to kill at least some of the seeds stored in the upper soil layers. The lack of an effect of early summer (July) burns at Jennie Springs was likely due to reduced burn severity. July burns were only moderately consumptive, removing the litter and leaving much of the duff intact, while the fall burns, in areas where surface fuels carried the fire, generally consumed the entire forest floor organic layer (including seeds stored in the duff). Drier soils in the fall may have also allowed heat above the level necessary to kill seeds to penetrate more deeply into the soil. For species with seed that is stimulated to germinate by heating, the range of temperatures sufficient to scarify but not kill the seed is relatively narrow. For example, in *Ceanothus*, the greatest germination response has been shown to occur when seeds were exposed to temperatures of 90 °C to 100 °C, while 120 °C was lethal (Quick 1935, Cronemiller 1959, Kauffman and Martin 1991). Soils may become heated to temperatures well over 120 °C to depths of 5 cm or even 10 cm, if the soil is dry and when fuel loading is high (Busse *et al.* 2005, 2010). By bracketing the soil heating values obtained from tiles dabbed with temperature-sensitive paints, we would predict that the average depth

of heating that is lethal to seeds with fall burns at the McCloud site was somewhere between 1.1 cm and 3.4 cm. This is consistent with the post-fire results indicating a lack of seed in the upper 2 cm of mineral soil. We suspect higher soil moisture in July burns at the Jennie Springs site, which would have reduced the depth of lethal soil heating, was likely at least partially responsible for the lack of a significant effect on seed density. It should be noted that while temperature-sensitive paints only show the maximum temperature reached and not the duration, seeds in the soil appear to be more sensitive to exposure to a maximum temperature rather than to the duration of heating in wildfires (Odion and Davis 2000).

In situations where reducing the potential for shrubs to colonize is a management goal, burning has been suggested as an alternative to other more expensive or controversial mechanical or chemical control treatments (Martin 1982, Weatherspoon 1985). Prescribed burning done prior to harvest of trees would kill some shrub seed, both directly through consumption and heating, and indirectly by stimulating them to germinate and rapidly die because of canopy shading, leaving fewer to germinate once the stands are opened up. Demonstrating the potential utility of pre-harvest burning, the July burns in unthinned stands at Jennie Springs caused numerous shrub seed to germinate, and these generally died in the months following germination (Weatherspoon 1985). However, because the size of the seed bank was so high to start with, our sampling three years later failed to detect a significant drop in visibly viable seed. The fall burns killed much more seed but still left a substantial number behind. All other sites we sampled contained deeply buried seed, where heat from even highly consumptive burns would be unlikely to kill them. While some of these sur-

viving seed may be buried too deeply to germinate and emerge successfully, disturbance from logging, fire, or small mammals could readily bring seeds closer to the surface. In addition, even prescribed burns under dry forest floor conditions are likely to be very heterogeneous, with patches that escape fire or burn at reduced severity. Complete effectiveness may therefore not be obtainable or even desirable.

Shrubs play an important ecological role in mixed conifer forests, and historical data (e.g., Hasel *et al.* 1934) suggest that they were, in many areas, once more abundant than they are today. Fire suppression has eliminated one of the main gap-forming processes and caused forests to become increasingly dense, both of which do not favor shrubs. However, the high frequency and density of shrub seed, as well as the broad distribution of seed at different depths in the seed bank shown in our survey, suggest that plenty of seed are likely to remain in most areas to restore the shrub component to the forest understory, if this is a management goal. All that would be required is fire, or thinning followed by fire, to open up the canopy and stimulate buried seeds to germinate.

Because of their need for high light environments, shrubs were historically most abundant in or near canopy openings and were thus patchy and discontinuous. This patchiness likely dampened fire hazard and may have made competition less of an impediment to the initial growth of tree seedlings. A better understanding of the feedbacks between overstory environment and shrub abundance will be useful for developing silvicultural guidelines that capitalize on the ecological benefits of shrubs without producing an extensive and continuous understory shrub layer that could lead to tree seedling competition and fire hazard concerns.

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Appendix 1. Tree species composition, basal area, average age, and shrub understory at 24 seed bank sampling sites in northern California, arranged from north to south. Tree species are listed in order of abundance by basal area. If plantations where trees had recently been removed were located nearby, the shrub species found there were also noted, in visual (approximate) order of abundance.

Site name	Tree species[c]	Basal area (m² ha⁻¹)	Stand age[a] (yr)	Duff depth (cm)	*Arctostaphylos* cover (%)	*Ceanothus* cover (%)	*Prunus* cover (%)	Shrub species in adjacent plantation
McCloud	ABCO	29.8	52	9.3	-	-	-	PREM, ARPA, CEVE
Horse	ABCO, CADE, PSME, PILA, PIPO	49.1	153	7.6	0.0	0.0	0.0	PREM, ARPA, CEVE
Big Poison	PSME, PIPO, CADE, QUKE, ABCO	36.3	259	7.4	0.0	0.0	0.0	CEIN
Underground	ABCO, CADE, PILA	76.7	70	4.3	0.0	0.0	0.0	CECO, ARPA, PREM, CEIN, CEVE
Flower	ABCO, PSME, PIPO, QUKE	42.7	113	6.8	1.0	0.0	3.1	CEVE, PREM, ARPA, CECO
Hatchet	ABCO, PIPO	40.2	84	6.7	0.0	0.0	0.0	ARPA, PREM, CECO, CEPR
Jennie Springs[b]	ABCO, ABMA	74.6	70	8.4	0.0	0.0	0.0	CEVE, ARPA, ARNE
Rush	PSME, ABCO, PILA, PIPO, CADE, ABMA	41.8	134	5.7	0.0	1.4	0.0	CEIN
Soda	PIPO, CADE, PSME, ABMA, ABCO, PILA	59.2	92	7.0	0.0	0.5	0.1	-
Galen	LIDE, PIPO, PSME, PILA, CADE, ABCO, QUKE	55.1	101	4.0	0.0	0.0	0.0	CEIN
Brush	PSME, CADE, PIPO, PILA, ABCO, LIDE	38.1	287	5.2	1.5	0.7	0.0	-
Bald	CADE, PIPO, PSME, ABCO, QUKE, PILA	41.3	118	6.8	0.0	0.0	0.0	-
Mt. Hope	PIPO, CADE, PSME	38.6	82	7.2	0.0	12.8	0.0	-
Hamburger	PSME, PIPO, PILA, QUKE, LIDE, ABCO, CADE	40.4	126	6.5	0.0	0.0	0.0	-

[a] Stand age is estimated as the average age of the three oldest trees sampled at each site.
[b] Data from Weatherspoon (1985)
[c] ABCO = white fir, ABMA = red fir, CADE = incense cedar (*Calocedrus decurrens* [Torr.] Florin), LIDE = tanoak, PILA = sugar pine (*Pinus lambertiana* Douglas), PIPO = ponderosa pine (*P. ponderosa* Lawson & C. Lawson), PSME = Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), QUKE = California black oak. Where adjacent plantations existed, shrub species were noted as an indicator of what might be found in the seed bank at the collection site (ARPA = greenleaf manzanita, ARNE = pinemat manzanita, ARVI = sticky whiteleaf manzanita, CECO = whitethorn ceanothus, CEIN = deerbrush, CEPR = prostrate ceanothus, CEVE = snowbrush, PREM = bitter cherry.

Appendix 1, continued.

Site name	Tree species[b]	Basal area (m² ha⁻¹)	Stand age[a] (yr)	Duff depth (cm)	*Arctostaphylos* cover (%)	*Ceanothus* cover (%)	*Prunus* cover (%)	Shrub species in adjacent plantation
Bridger	PIPO, PSME, CADE, QUKE, ABCO	53.7	80	7.8	0.0	0.0	0.0	CEPR
Pendola	PSME, PIPO, CADE, QUKE, ABCO, PILA	53.7	105	5.3	0.0	0.3	0.0	CEIN, CEPR, ARVI
Cummings	PSME, PIPO, CADE, QUKE, LIDE	47.7	77	3.9	0.0	0.0	0.0	ARVI, CEIN
Sleighville1	PSME, PIPO, QUKE, CADE, PILA, ABCO	47.7	105	2.6	0.0	0.1	0.0	CEIN, CEPR
Sleighville2	PIPO, PSME, CADE, ABCO, LIDE, QUKE	48.2	100	7.6	0.0	0.0	0.0	CEIN, ARVI
Washington	PSME, CADE, ABCO, PILA, PIPO	45.9	171	5.7	0.0	0.5	0.0	CEIN
White Cloud	PSME, ABCO, CADE, PIPO	36.7	82	7.2	0.0	1.2	0.0	CEIN
Five Mile	ABCO, PSMA, PIPO, CADE, QUKE	39.5	111	8.4	0.0	0.0	0.0	CEIN
Pilliken	ABCO, CADE	62.4	77	2.7	0.0	0.0	0.3	ARPA, CECO, CEIN, PREM
Dennis Spring	ABCO, PIPO, CADE, QUKE	67.9	74	5.2	0.0	0.0	0.0	ARPA, CECO, CEIN, PREM

[a] Stand age is estimated as the average age of the three oldest trees sampled at each site.
[b] ABCO = white fir, ABMA = red fir, CADE = incense cedar (*Calocedrus decurrens* [Torr.] Florin), LIDE = tanoak, PILA = sugar pine (*Pinus lambertiana* Douglas), PIPO = ponderosa pine (*P. ponderosa* Lawson & C. Lawson), PSME = Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), QUKE = California black oak. Where adjacent plantations existed, shrub species were noted as an indicator of what might be found in the seed bank at the collection site (ARPA = greenleaf manzanita, ARNE = pinemat manzanita, ARVI = sticky whiteleaf manzanita, CECO = whitethorn ceanothus, CEIN = deerbrush, CEPR = prostrate ceanothus, CEVE = snowbrush, PREM = bitter cherry.

Appendix 2. Number of *Ceanothus, Arctostaphylos,* and *Prunus* seed 0.01 m^{-3} (1 m × 1 m × 0.01 m depth) by collection layer[a] from top of the duff to 10 cm in mineral soil at 24 sites in northern California, arranged from north to south, including two (Sleighville1 and Pilliken) that had experienced wildfire within the previous 15 years. At the McCloud and Jennie Springs sites, data are from samples collected in the unburned treatment only.

| | *Ceanothus* Collection layer (cm) | | | | | | *Arctostaphylos* Collection layer (cm) | | | | | | *Prunus* Collection layer (cm) | | | | | |
| | Duff | | Mineral soil | | | | Duff | | Mineral soil | | | | Duff | | Mineral soil | | | |
Site name	2+	2-0	0-2	2-4	4-6	6-10	2+	2-0	0-2	2-4	4-6	6-10	2+	2-0	0-2	2-4	4-6	6-10
McCloud	6.2	44.6	26.8	10.7	12.7	7.7	0.2	6.0	1.9	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0
Horse	7.7	38.0	15.1	3.3	7.4	1.4	2.8	24.1	4.1	3.7	4.5	0.6	0.0	0.4	0.0	0.0	0.0	0.0
Big Poison	0.7	2.4	2.4	1.2	1.6	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Underground	3.1	20.4	35.0	38.8	61.3	40.9	1.4	22.5	33.1	8.8	12.5	13.4	0.0	0.0	0.8	0.0	4.5	0.6
Flower	10.1	32.7	50.3	33.9	26.2	25.1	2.0	2.0	3.3	7.0	0.4	0.6	0.2	0.4	0.0	0.0	0.0	0.0
Hatchet	12.3	51.9	52.7	61.3	47.4	35.6	5.3	9.4	7.8	29.0	5.3	0.2	0.1	0.8	0.8	1.6	0.0	0.0
Jennie Springs	85.9	148.6	89.3	65.4	51.1	35.1	2.0	0.7	0.0	0.7	0.7	1.0	0.2	0.0	0.0	0.0	0.0	0.3
Rush	5.6	51.6	58.5	28.2	23.7	9.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Soda	0.1	3.7	3.3	2.9	4.9	2.2	0.1	0.0	0.0	0.4	0.8	0.2	0.0	0.0	0.0	0.0	0.0	0.0
Galen	0.0	1.6	5.3	2.0	2.9	1.6	0.0	2.9	7.8	1.6	0.0	0.4	3.3	0.0	0.4	0.0	0.0	0.0
Brush	0.0	9.4	20.4	14.7	6.5	4.7	0.2	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bald	0.4	1.6	3.3	4.1	2.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mt. Hope	4.7	13.1	23.7	12.3	8.2	6.5	0.0	0.0	0.8	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hamburger	0.2	2.0	4.5	2.0	4.1	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bridger	2.1	9.8	22.9	13.1	10.2	5.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pendola	0.0	4.1	7.0	10.6	9.0	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.4	0.0	0.0
Cummings	0.0	0.0	0.8	4.9	4.1	2.0	0.0	0.0	20.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sleighville1	0.8	0.0	1.2	4.5	0.8	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sleighville2	0.0	6.1	11.9	20.0	17.6	14.9	0.0	0.4	0.0	0.4	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Washington	0.1	9.4	20.0	28.6	16.4	9.6	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
White Cloud	4.5	21.7	36.8	24.5	9.8	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Five Mile	1.0	15.5	30.3	20.4	10.6	5.9	0.1	0.4	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pilliken	0.0	0.0	0.8	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	1.6
Dennis Spring	0.5	7.8	32.7	14.5	19.2	8.5	0.3	2.0	5.3	7.8	0.4	0.8	1.6	4.9	14.7	15.9	7.8	2.0

[a] Layer 2+ is the upper duff from the top of the duff to 2 cm above mineral soil, layer 2-0 is the lower duff from 2 cm down to mineral soil, layer 0-2 is the top 2 cm of mineral soil, layer 2-4 is from 2 to 4 cm deep, layer 4-6 is from 4 to 6 cm deep, layer 6-10 is from 6 to 10 cm deep.