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FACTORS CONTRIBUTING TO THE SOIL SEED BANK SIZE OF TWO  
OBLIGATE SEEDING *CEANOOTHUS* SPECIES IN NORTHERN CALIFORNIA

SUSAN E. O'NEIL<sup>1</sup> AND V. THOMAS PARKER

Department of Biology, San Francisco State University, 1600 Holloway Avenue,  
San Francisco, CA 94132

ABSTRACT

In fire-prone vegetation, non-sprouting, obligate-seeding species depend on a persistent seed bank to reestablish post-fire populations. Thus, for such seeds, seed development and survival in the soil are critical life history stages. The objectives of our study were to examine the structure and composition of *Ceanothus* seed banks, analyze the viability of seeds in the soil, and determine rates of predation before and after seed dispersal. This study focused on populations of *Ceanothus jepsonii* var. *albiflorus* (J. Howell), which is restricted to serpentine soils. We also included data on *Ceanothus cuneatus* (Hook.) Nutt., a widespread, non-restricted species, for comparison. We found that the seed bank of *C. jepsonii* loses seeds due to destruction or removal at several stages of development. Pre-dispersal seed predators attacked 37% of inflorescences included in experimentation and up to 50% of shrubs from which fruits were collected, post-dispersal predators removed over 70% of seeds in the litter. There is a 30% reduction in viability of older intact *C. jepsonii* seeds in the soil compared to seeds collected from plants during the study. A beetle in the genus *Zabrotes*, not previously known to oviposit on *Ceanothus*, was determined to be a causal agent of pre-dispersal seed predation, with other pre-dispersal predators and parasites also possible. These findings suggest that *Ceanothus* seed banks are quite dynamic and subject to a variety of seed losses during several stages prior to germination, which may ultimately be responsible for soil seed banks remaining relatively constant rather than building up over time.

Key Words: chaparral, *Ceanothus*, obligate seeder, seed predation, soil seed bank.

In Mediterranean climates, plant species have developed a variety of mechanisms to cope with and thrive in fire-prone habitats. Some species are able to resprout from vegetative structures not destroyed in fires, such as burls (Keeley and Zedler 1978). Other species retain their seeds in aboveground serotinous structures that open from the heat of wildfire, releasing seeds to re-establish the populations post-fire; this response is more common in *Banksia* and other southern hemisphere genera, but also utilized by some *Cupressus* and *Pinus* species in the northern hemisphere (Ne'eman et al. 1999). Another coping mechanism involves producing a persistent soil seed bank that responds to wildfire after the adult plants have been destroyed. Referred to as obligate seeding (Wells 1969; Keeley and Zedler 1978), this fire response syndrome has evolved in many shrub genera in fire-prone habitats, such as *Arctostaphylos* and *Ceanothus*, in California chaparral. Both genera have species that resprout and species that are obligate seeders. This study will focus on two obligate seeding *Ceanothus* species in Northern California.

In obligate seeding species, adult plants do not have the ability to resprout and are almost always killed in a wildfire. While persistent soil seed banks vary considerably in size (Parker and Kelly 1989), species in both *Ceanothus* and *Arctostaphylos* do

not seem to accumulate a larger seed bank over time once reproductive maturity has been reached (Keeley 1977, 1987a; Zammit and Zedler 1988, 1994). *Ceanothus* species often have substantially smaller seed banks than other chaparral species with persistent soil seed banks, even with the copious flower and fruit production typical in *Ceanothus* species (Keeley 1977; Parker and Kelly 1989; Zammit and Zedler 1994). For obligate seeding species, factors influencing the seed bank may greatly influence the future of the population.

Seeds are vulnerable at different stages from embryo formation through germination (Cavers 1983; Fenner 1985). During development on the parent plant, seeds are subject to pre-dispersal seed predation. Once dispersed, the remaining seeds are then exposed to seed predators (Louda et al. 1990). For seeds that must survive for years in the soil, the length of time prior to germination extends their vulnerability. The longer a seed resides in the soil, the greater its risk of losing viability, or of being eaten, attacked by fungi or pathogens, or removed from a safe site (Cavers 1983; Fenner 1985; Simpson et al. 1989).

Pre-dispersal seed predation typically involves insect adults or larvae eating a seed, effectively destroying it before dispersal from the parent plant. These reductions in seed production are variable, but seed loss from the potential seed bank exceeds 90% in some species (Fenner 1985; Auld and Myerscough 1986; Hegazy and Eesa 1991; Sallabanks and Courtney 1992; Sheppard et al. 1994).

<sup>1</sup> Current address: National Park Service, 1 Bear Valley Road, Point Reyes Station, CA 94956. Email: segoneil@yahoo.com

While researchers have noted pre-dispersal seed predation as an important factor in seed bank dynamics in chaparral, few have actually documented it (Zammit and Zedler 1993; Boyd 2003). Previous studies have noted pre-dispersal seed predation on *Ceanothus sanguineus* in Idaho caused by a seed wasp (*Eurytoma squamosa*), a seed weevil (*Phyllotrox rutilus*), and a caterpillar (probably Gelechiidae) (Furniss et al. 1978). Huffman (2002) found seed predation by the same seed wasp, *Eurytoma squamosa*, on the resprouting *Ceanothus fendleri* in Arizona.

Once a seed is dispersed from the parent plant, it faces a high probability of predation while in the soil seed bank. Experiments on seed predation in chaparral suggest that vertebrates and invertebrates significantly reduce the size and modify the composition of soil seed banks (Keeley and Hays 1976; Evans et al. 1987; Mills and Kummerow 1989; Kelly and Parker 1990; Borchert et al. 2003). *Ceanothus* seeds are larger in size than most other chaparral species; therefore, they may be more attractive to predators such as rodents, birds and harvester ants (Price 1983; Mills and Kummerow 1989; Hoffmann et al. 1995). In a study by Smith (1942), *Ceanothus* seeds were found in the stomach contents of a large number of brush field pocket mice (*Perognathus parvus mollipilosus*).

*Ceanothus jepsonii* E. Greene (Rhamnaceae) is an obligate seeding species in the subgenus *Cerastes* and is restricted to serpentine soils. There are two varieties, both endemic to northern California. The range of *Ceanothus jepsonii* var. *jepsonii* includes Marin, Sonoma and western portions of Lake and Napa Counties. *Ceanothus jepsonii* var. *albiflorus* J. Howell (hereafter *C. jepsonii*) is found in eastern Lake, Napa, Yolo and Solano Counties and is the focal taxon of this study. Plants are erect, evergreen shrubs that are typically 1 m tall at the study site. Flowering typically begins in April and mature seeds are explosively dispersed in July–August. The seed rain of *Ceanothus* extends from under the canopy to a maximum distance of 9 m from the parent shrub (Evans et al. 1987), but seeds are most often found 1–3 m from the parent plant (Parker and Kelly 1989). The average seed size is 3–4 mm. The species is not currently considered threatened or endangered, but future conservation may be of concern because it is restricted to a specific habitat and soil type, which is undergoing development as people move into the wildland urban interface.

For comparison, we include data on *Ceanothus cuneatus*, an obligate seeding species also in the subgenus *Cerastes*. It is not restricted by soil type and has a wide range from Oregon to Baja California. Phenology and seed rain are similar to that of *C. jepsonii* (Evans et al. 1987). Mature *C. cuneatus* shrubs can be up to twice the height of *C. jepsonii* at the study site. The seeds of *C. cuneatus* are typically 25% smaller than those of *C. jepsonii*.

Species in the subgenus *Cerastes* may live up to 100 years (Keeley 1975), and are dominant shrubs in the mature chaparral stands that were used for experimentation.

The focal objective of our study was to examine the structure and composition of *Ceanothus* seed banks, using a restricted and a non-restricted species. Based on our findings, we: 1) Analyzed the viability and location of seeds in the soil seed bank; 2) Determined the impact, timing, selectivity and causal agent(s) of pre-dispersal seed predation; and 3) Examined the rates of post-dispersal seed predation in *C. jepsonii* seed banks.

## METHODS

### Study Site

The study was conducted at the Donald and Sylvia McLaughlin University of California Natural Reserve (McLaughlin Reserve hereafter; lat. 38°51'N, long. 122°24'W). The reserve covers 2,800 ha encompassing parts of Napa, Yolo and Lake Counties in the inner north coast range of California (see Harrison et al. 2003 and Safford and Harrison 2004 for a more detailed description of the site). We selected two primary serpentine sites at the reserve for experimentation, both west-facing with similar slopes: Research Hill and Site B. These study sites were not burned by a 1999 arson fire on the reserve (Safford and Harrison 2004). According to California Department of Forestry and Fire Protection, a significant fire has not occurred on the study sites since at least 1950 when they started recording and mapping fires in the state ([www.frap.cdf.ca.gov](http://www.frap.cdf.ca.gov)). Additionally, local residents estimate that the last fire at the experimental sites was over 30 years ago (pers. comm. Scott Moore, McLaughlin Reserve Manager).

A secondary serpentine site, along Butts Canyon Road in Napa County, California was selected for supplemental data collection. This site was chosen primarily due to accessibility and distance from the primary experimental sites (approximately 48 km from the McLaughlin Reserve). A site on the northern border of the McLaughlin Reserve was selected for non-serpentine *C. cuneatus* experimentation with an additional non-serpentine seed collection site along Morgan Valley Road in Lake County, California. Attributes other than soil type and approximate stand age were not considered in secondary site selection.

### Seed Bank Structure

To determine the depth of seeds in the soil column, we collected soil beneath a total of 31 *C. jepsonii* shrubs in the fall of 2000: 7 at Research Hill, 14 at Site B, and 10 along Butts Canyon Road. At each collection site, a 20-cm by 20-cm frame was placed directly under the outer canopy edge of each shrub. Soil and litter within the frame was collected

in 2-cm layers, and each layer was separated into individual bags. The layers represent 0–2 cm, 2–4 cm and 4–6 cm depths of the soil column. For samples with a litter layer, the litter layer was combined with the first (0–2 cm) layer of soil. At these sites, serpentine soils are markedly shallow and bedrock is often encountered at or before 6 cm in depth. Due to shallow soils, the sample size for the 4–6 cm layer under *C. jepsonii* is 25 rather than 31. Soil samples were dried in paper bags at room temperature.

We determined seed density in each soil layer through germination. Each sample was placed in a 20-cm × 20-cm aluminum pan with small drainage holes and 1 cm of river sand on the bottom to help retain moisture (Zammit and Zedler 1994). Each sample was heated in an oven for 30 min at 100°C to stimulate germination by breaking the seed coat (Keeley 1987b; Bell et al. 1993; Garrett 2002). Thermocouples in the soil samples could not be monitored inside the oven, so 30-minute treatments were timed from when the oven, with the sample inside, reached 100°C. We made the assumption that seeds in the samples would reach a temperature sufficient to break the seed coat within that time period. The samples did not undergo a stratification treatment other than being housed in a non-heated greenhouse during the winter which was presumed to be enough of a stratification treatment to overcome dormancy (Odion and Davis 2000). Samples were watered and monitored daily from January through September of 2001. Each seedling that emerged was identified and clipped or repotted if identification was not possible in the seedling stage. Care was taken not to disturb the soil during transplanting.

Data for genera other than *Ceanothus* are not included in the present study. We used a repeated measures ANOVA to analyze soil column seed density. We report univariate *F*-tests with degrees of freedom adjusted using the Huynh-Feldt  $\epsilon$  to correct for lack of sphericity of the variance covariance matrices (O'Brien and Kaiser 1985).

We repeated the same methods on 31 non-serpentine chaparral samples taken from the site at the reserve's northern boundary for comparison. Each sample was collected directly under the outer canopy edge of a *Ceanothus cuneatus* shrub. Samples were treated and data analyzed in the same manner as for *C. jepsonii*.

#### Seeds in the Soil

To determine the proportions of intact preyed upon and undeveloped seeds in the soil seed bank, we collected another series of soil samples underneath the canopy of nine *C. jepsonii* shrubs at Research Hill in the fall of 2000. The samples were collected using 20-cm × 20-cm frames and were equal in volume (6 cm down soil column). The soil was brought back to the lab and dried at room tem-

perature. *Ceanothus jepsonii* seeds were removed by sifting with a series of soil sieves. Seeds were thoroughly inspected and categorized into intact, preyed upon (hollow with an exit hole), and undeveloped (typically deflated-looking and obviously inviable) (Hoffman et al. 1989; Zammit and Zedler 1993; Huffman 2002). These data were analyzed using a one-way ANOVA.

#### Seed Viability

To assess the viability of fresh intact seeds versus older intact seeds from the soil, two batches of *C. jepsonii* seeds were subjected to tetrazolium-chloride (TZ) testing. One batch included 192 fresh seeds collected directly from adult plants at Site B during 2001. A second batch consisted of 112 seeds collected during the previously mentioned seed type study. These seeds were intact and solid but showed signs of aging such as discolored or scratched seed coats. The TZ test is a method of assaying seed viability that can be done on dormant seeds (Moore 1962). If a seed has functioning mitochondria, the tissue will stain red (Freeland 1976). Respiring seeds were considered viable. The test was conducted by the Oregon State University Seed Laboratory following specifications normally used for hard-coated seeds.

#### Timing of Pre-dispersal Seed Predation

In the spring of 2001, we excluded insects from inflorescences starting at different times throughout the flowering season to assess the timing of pre-dispersal seed predation during seed development. Prior to the placement of exclosures, we hand-pollinated and flagged five inflorescences on a total of 30 shrubs at Research Hill and Site B. Hand pollination was done using fine paint brushes and transferring pollen from the flower of one shrub to the exposed style of a flower on another nearby shrub. The inflorescence branches were covered with 2-inch by 3-inch insect mesh sleeves to prevent insects from accessing the developing seeds at approximately two-week intervals starting at the onset of blooming through fruit maturation (Andersen 1988; Greig 1993).

The 30 shrubs chosen for experimentation were categorized phenologically into early- and late-blooming cohorts. The early-blooming cohort (10 shrubs at Research Hill and 10 shrubs at Site B) received their first treatment on March 30. The late-blooming cohort received their first treatment on April 11. The fifth and final exclosure treatment for all 30 plants was installed on June 22. Seeds covered during the final treatment were exposed to seed predators throughout development on the parent plant. All exclosures, acting as seed traps during dispersal, were collected on July 1. Fruits and seeds were brought back to the lab and the seeds of each inflorescence were dissected. If at least one seed per inflorescence had a larva inside, the inflores-

cence was considered attacked. In some cases, once an inflorescence was considered attacked, further seed dissection was halted and the remaining seeds were monitored for adult insect emergence for identification. Unfortunately, this precluded us from analyzing predation rates by seed rather than by inflorescence.

#### Host Specificity and Distribution of Pre-dispersal Seed Predator

After determining that pre-dispersal seed predator(s) were attacking *C. jepsonii* at Research Hill, we then set out to evaluate if the predation was occurring on *C. cuneatus* at the same site and if it occurs on both species in other locations. We collected fruits from 10 co-occurring *C. cuneatus* shrubs at Research Hill. We also collected fruits from 10 *C. jepsonii* shrubs from a serpentine chaparral site 48 km from Research Hill, and from 10 *C. cuneatus* shrubs growing on non-serpentine soil 7 km from Research Hill. All fruits were placed in direct sun for 10 hours to dry and explosively expel seeds from the capsule. Fruits that did not explode were cracked using pliers and the seeds removed.

We monitored all seeds collected in summer 2001 for insect emergence. Because no insect activity was detected by mid-March 2002, we dissected half of the seeds from each sample. Prior to insect emergence, attacked seeds often looked identical to unaffected seeds on the surface. We determined presence/absence of predation for each inflorescence by slicing into fully formed seeds and checking for larvae inside. Again, because dissection was halted for an entire sample when at least one seed was found to be infested, results are expressed as number of attacked shrubs rather than number of attacked seeds.

#### Post-dispersal Seed Predation

In the fall of 2001, 19 pairs of trays containing fresh seed were buried level with the soil surface at 19 random sample sites at Research Hill to estimate rates of post-dispersal seed predation. Each pair of 20-cm by 20-cm trays contained 3–4 cm of sand, covered with 1 cm of leaf litter, and 50 seeds mixed into the litter layer. The seeds used in this study were not tested for presence of insect larvae. They were collected from adult shrubs using seed traps during the summer of 2001, presumably reflecting similar densities, viability and insect infestation as seeds in the litter surrounding the trays. We covered one tray per pair with 0.5-cm by 0.5-cm wire mesh to prevent vertebrates from removing seeds and the other tray was left open. After 10 weeks and prior to the onset of the rainy season, the trays were brought back to the lab. Seeds not removed during the experiment were recovered by sifting through the sand and litter in the laboratory. Seed count data were analyzed using a paired *t* test.

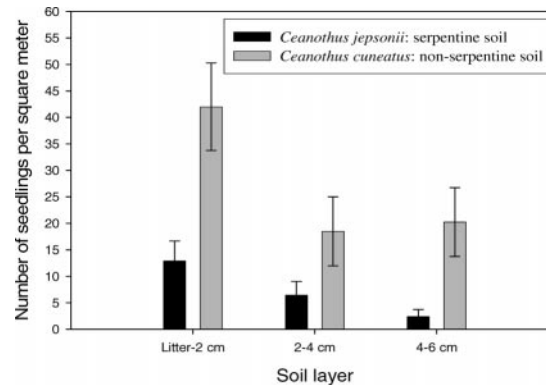


FIG. 1. Mean number (with standard error) of *C. jepsonii* and *C. cuneatus* seedlings to emerge in greenhouse soil layers, 2000 (*C. jepsonii*  $n = 31$  per soil layer, except for 4–6 cm  $n = 25$ ; *C. cuneatus*  $n = 31$  per soil layer).

## RESULTS

### Seed Bank Structure

*Ceanothus jepsonii* seed density declined with an increase in depth down the soil column. We found a significant difference between each adjacent soil layer ( $F_{1.77, 53, 18} = 4.26$ ,  $P = 0.023$ ). There were few *C. jepsonii* seedlings to emerge overall (Fig. 1). The top layer, 0–2 cm, averaged  $12.9 \pm 3.7$  seedlings/m<sup>2</sup>. The two lower soil layers had even lower numbers of seedlings emerging ( $6.5 \pm 2.6$  seedlings and  $2.4 \pm 1.3$  seedlings/m<sup>2</sup> respectively).

The non-serpentine soil containing *C. cuneatus* had significantly more seedlings in the top layer than in any other layer ( $42 \pm 8.2$  seedlings/m<sup>2</sup>), but seed density did not decline in a constant fashion down the soil column as in *C. jepsonii* (Fig. 1). The lowest layer, 4–6 cm down the soil column, had approximately the same number of seedlings on average as the middle layer, 2–4 cm ( $20.3 \pm 6.5$  seedlings/m<sup>2</sup> and  $18.5 \pm 6.5$  seedlings/m<sup>2</sup> respectively). *Ceanothus cuneatus* seeds which were collected from non-serpentine soil had greater seedling emergence than *C. jepsonii*. Over three times as many *C. cuneatus* seedlings germinated in the top layer of soil as *C. jepsonii*.

### Seeds in the Soil

Seeds with insect exit holes (i.e., preyed upon) averaged  $525 \pm 126$  seeds/m<sup>2</sup> and intact seeds averaged  $480 \pm 127$  seeds/m<sup>2</sup> in the soil seed bank (Fig. 2). No significant difference occurred with respect to density of the three seed types: preyed upon, intact and visibly inviable seeds ( $F_{1.77, 14, 17} = 0.236$ ,  $P = 0.77$ ). Intact seeds represented 34% of the total seeds; the two inviable categories combined for 66% of the total seed bank (Fig. 2). Because seeds that have been preyed upon are hollow and fragile, some were possibly destroyed during the sifting process.

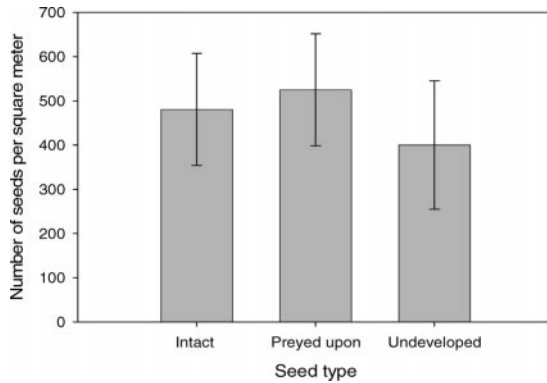


FIG. 2. Mean number of seeds (with standard error) recovered from *C. jepsonii* soil seed bank by seed type ( $n = 9$ ). Proportions were statistically similar at 34% intact, 37% preyed upon and 29% undeveloped.

#### Seed Viability

A tetrazolium-chloride test showed that 91% of fresh seed (collected from shrubs and tested in the same season) was viable. The second batch, consisting of aged seeds recovered from the soil seed bank, showed only 63% viability.

#### Extent and Timing of Pre-dispersal Seed Predation

Of inflorescences exposed to the predator(s) for the entire flowering season, 37% were attacked. No inflorescences were attacked on or before April 11. All attacks occurred between April 22 and June 22 regardless of when the individual shrubs began to bloom (Fig. 3). The pre-dispersal seed predator(s) were active at the site and ovipositing during this time while seeds were still developing on the parent plant.

Plants were unable to escape predation through differences in flowering time. Early- and late-blooming cohorts had approximately the same number of shrubs attacked by the predator throughout the season. The two early-blooming cohorts showed four and five of 10 shrubs attacked respectively at each site. Four of the 10 late-blooming shrubs at Research Hill were attacked during the season. Early-blooming shrubs showed an increase in predation rates over the season, while late-blooming shrubs showed a mostly steady rate of predation after May 4 (Fig. 3). Some shrubs had only one inflorescence with beetle predation, while others had up to three of the five inspected inflorescences attacked. Inflorescences which were covered early on in the experiment had very low successful pollination rates with few or no seed/fruit developing and few remnant flowers left at the end of the season (80% and 60% for the first two treatments of early-blooming shrubs). It is probable that we were ineffective artificial pollinators and inflorescences covered later in the season with close to

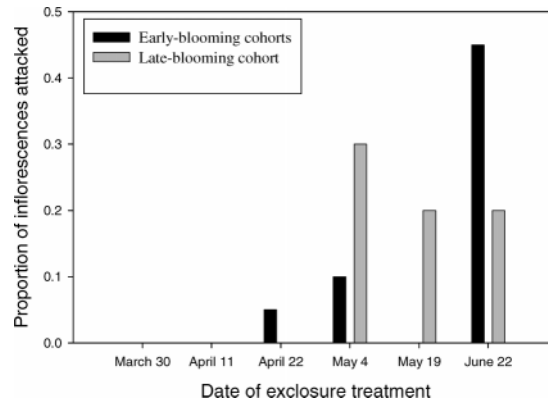


FIG. 3. Proportion of attacked inflorescences for early- and late-blooming cohorts throughout the season, 2001 (early-blooming  $n = 20$ , late-blooming  $n = 10$ ). Plants were assigned to a cohort based on phenology. The date indicates when enclosures were installed on one of five branches of each plant. The early-blooming cohort did not receive a treatment on May 19.

100% seed production (with some aborted/undeveloped) had been pollinated by insects prior to enclosure installation.

#### Host Specificity and Distribution of Pre-dispersal Seed Predator

A beetle in the genus *Zabrotes* was found to be at least one of the pre-dispersal seed predators on *C. jepsonii* and *C. cuneatus*. Three beetles emerged from stored seeds (collected in 2000) and were identified by the USDA Systematic Entomology Lab, Beltsville, MD as belonging to *Zabrotes* (Coleoptera: Bruchidae: Amblycerinae). It is probable that there are more predators and/or parasites active at the site. The exit holes in the seeds and other evidence of attacks resemble those described by Furniss et al. (1978) and Huffman (2002) on *Ceanothus* seeds attacked by seed wasps. The larvae in the examined seeds were translucent, taking up the entire volume of the seed with no frass inside the seed. In some instances only one seed per fruit was attacked, in others all seeds appeared attacked. Some, but not all, fruits also had exit holes indicative of a seed wasp or weevil (Furniss et al. 1978).

Results from *C. cuneatus* showed that the pre-dispersal predator(s) are not just attacking *C. jepsonii*. At both the serpentine and non-serpentine sites, 30% of *C. cuneatus* inflorescences were attacked. Four of 10 *C. jepsonii* inflorescences collected from Butts Canyon Road site were attacked. During the 2001 blooming period, the proportion of shrubs attacked by the beetle appeared to be relatively homogeneous at different sites on different species (30–50%). Our study indicates that the pre-dispersal predator(s) are not restricted by host species or location.

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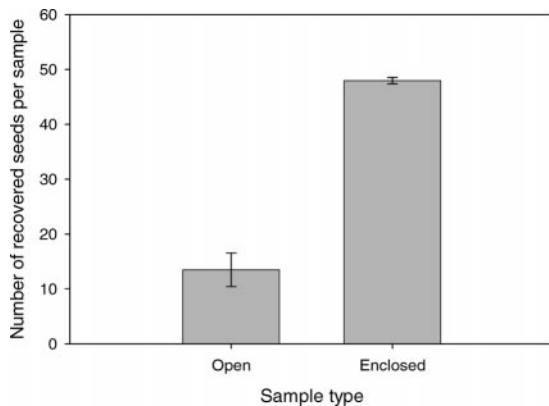


FIG. 4. Mean number (with standard error) of seeds recovered (maximum of 50) from open and caged samples following 10 weeks of exposure to post-dispersal predators, 2001 ( $n = 20$ ).

#### Post-dispersal Seed Predation

Post-dispersal seed predation on *C. jepsonii* seeds was considerable. Significantly more seeds were removed from the open tray in each sample pair (t-test,  $t = -11.080$ ;  $df = 18$ ;  $P = 1.77 \times 10^{-7}$ ). Open samples averaged 73% of seeds removed ( $36.5 \pm 3.05$ ) (Fig. 4). Enclosed samples averaged 5% of seeds removed ( $2.1 \pm 0.57$ ) after 10 weeks in the field.

#### DISCUSSION

Prior to germination and establishment, the critical life history stages of obligate-seeding *Ceanothus* species include seed development and survival in the soil seed bank. Several independent processes were found to reduce the potential number of *C. jepsonii* seeds in the soil seed bank. Pre-dispersal seed predators attacked at least 30% of the shrubs, post-dispersal predators removed over 70% of seeds in the litter, and 38% of the older intact seeds in the soil were inviable. A beetle in the genus *Zabrotes*, not previously known to oviposit on *Ceanothus*, was determined to be one of the causal agents of pre-dispersal seed predation. Other pre-dispersal predators at the site are possible, but were not identified during this study (Furniss et al. 1978; Huffman 2002). While *C. cuneatus* seed banks seem to retain more seeds than *C. jepsonii*, there is strong evidence for a host of removal vectors at different life stages for both species.

Seed density of *C. jepsonii* and *C. cuneatus* decreased with depth in the soil column as expected, as seeds are dispersed on the top layer of soil or litter and slowly are moved down the soil column by gravity, rain and soil movement by animals (Parker and Kelly 1989). Location in the soil is an important factor for seed germination because it affects the heat cue from fire; near the surface, temperatures may be too hot, but with increasing depth

are eventually too cool to stimulate germination. Overall germination rates were low for both species in our experiments, and we probably did not achieve maximum germination rates for either species. All montane *Ceanothus* species require a stratification treatment before they will germinate, and it seems that some coastal species of *Ceanothus* also have higher germination rates with even a brief stratification treatment (Quick and Quick 1961). Higher germination rates in low elevation *Ceanothus* species also have occurred with a stratification treatment, as in *Ceanothus cuneatus* from 762 m elevation (Quick 1935), and even in coastal species like *Ceanothus purpureus* from 500 m in Napa County (Garrett 2002).

However, in this experiment we were interested in relative location of seeds in the soil and a pattern is still discernible even without maximum germination rates. These data show that a high proportion of the seeds are in the top 2 cm of the soil column. Seeds that close to the surface may not survive the heat of a fire (Hasey 1985). A smaller proportion of seeds were found below 4 cm down the soil column which may be too low for germination to occur. *Ceanothus cuneatus* had two to three times more seed in the middle layer (2–4 cm) than *C. jepsonii*. More *C. cuneatus* seedlings emerged in all layers which may be a function of the shrubs being larger than *C. jepsonii* and producing more seeds, *C. cuneatus* responding more favorably without a stratification treatment, or predators preferentially attacking the larger *C. jepsonii* seeds. Flower and/or seed production rates were not examined during this study for either species, but are obviously crucial to understanding the dynamics of the seed banks of these species.

Pre-dispersal seed predation reduced the number of seeds entering the seed bank. Seeds with signs of insect emergence made up the largest proportion of *C. jepsonii* seeds recovered from the soil (37%). We documented attacks on at least 30% of *C. jepsonii* and *C. cuneatus* shrubs in and outside of the reserve. While in some species, insect damage can act as a cue for germination by breaking the seed coat (Hoffman et al. 1989; Ollerton and Lack 1996); this is not the case for *Ceanothus* because the predator destroys the entire seed.

Our study is the first documentation of *Zabrotes* attacking *Ceanothus* species. The genus *Zabrotes* normally feeds on members of the Fabaceae (Romero and Johnson 2000). Other beetle genera in the same subfamily have host records of species in the Rhamnaceae (Romero and Johnson 2000). Attacks by *Zabrotes* were found to occur late in seed development with no differences in attack rates between early- and late-blooming shrubs. A smooth seed coat, characteristic of *Ceanothus*, has been shown to be important for oviposition site selection for Bruchid beetles (Johnson 1981). Bruchids prefer to oviposit on relatively large seeds, which *Ce-*

*anothus* seeds are in comparison to most chaparral species (Moegenburg 1996).

Post-dispersal seed predators removed a significant portion of experimental seeds (>70% during a 10-week period). Seed density in these experiments approximated naturally occurring densities, and seeds were covered with small amounts of litter. We assume that rodents, birds or other vertebrates were responsible for the post-dispersal predation. However, ants may have also contributed to seed removal (caged samples averaged 5% of the seeds removed). The large reduction of seed density by post-dispersal predators is consistent with other experiments in chaparral (Keeley and Hays 1976; Evans et al. 1987; Mills and Kummerow 1989; Kelly and Parker 1990).

Undeveloped seeds accounted for approximately one-third of all seeds found in soil seed bank samples. These shriveled, hollow and obviously inviable seeds were undeveloped, and had no exit hole or other obvious signs infestation. Past studies have called this category 'aborted' (Hoffman et al. 1989; Zammit and Zedler 1993). They may have been seeds that never fully developed due to resource limitations; others may have been aborted due to predation by *Zabrotes* and/or other possible predators (Sallabanks and Courtney 1992) or been attacked by fungi after losing viability while in the soil. A high number of aborted seeds would be consistent with other studies of *Ceanothus* (Keeley 1977; Furniss et al. 1978; Huffman 2002). We also noted a high number of undeveloped seeds in the inflorescences inspected for pre-dispersal predation aside from those flowers that were unsuccessfully artificially pollinated by us.

The relatively small seed bank size compared to other chaparral genera, such as *Arctostaphylos*, is consistent with other studies of *Ceanothus* species (Keeley 1977; Schlesinger et al. 1982; Zammit and Zedler 1988; Parker and Kelly 1989; Zammit and Zedler 1993; Odion 2000; Garrett 2002). Intact seeds represented approximately one-third of seeds in the soil ( $480 \pm 127$  seeds/m<sup>2</sup>). Some seeds recovered from the soil exhibited worn seed coats, appearing scaly or discolored. Viability of the older seeds from the soil seed bank was 30% less than that of freshly collected seeds, suggesting a loss of viability over time. The more widespread, unrestricted species seems better able to utilize the strategy of producing many seedlings post-fire than the serpentine-restricted species that may be of concern for conservation of *C. jepsonii*. However, the seed losses documented here may simply be the mechanisms responsible for keeping soil seed bank numbers level over time rather than representing a recent decline due to new environmental factors and removal vectors (Keeley 1977, 1987a; Zammit and Zedler 1988, 1994).

Whether the current seed bank size and rates of seed removal reflect historic or natural levels is not clear in the context of recent anthropogenic influ-

ence such habitat fragmentation, species introductions and fire suppression. The seed losses, by native or non-native fauna, may be influencing the dynamics of the soil seed bank more than previously suspected. *Zabrotes* could not be identified to species, so more work is needed to determine whether it or the other potential pre-dispersal seed predators at the site are native to northern California. Pre-dispersal seed predation can alter the soil seed bank and the distribution of plants within their range (Louda 1982). As chaparral stands age, *Ceanothus* shrubs are often shaded out by larger shrubs or trees that invade these plant communities with a lack of fire (e.g., Keeley 1992; Zammit and Zedler 1994), further reducing seed input. Our findings suggest *Ceanothus* seed banks are quite dynamic and subject to a variety of seed removal and losses to seed input in a number of stages prior to germination.

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