

ECOLOGICAL STUDIES OF MORRO MANZANITA (*ARCTOSTAPHYLOS MORROENSIS*):
SEED ECOLOGY, AND REPRODUCTIVE BIOLOGY

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I) Abstract

Arctostaphylos morroensis is a shrub that is native and restricted to the coastal maritime chaparral and coastal dune scrub of San Luis Obispo County, California. *A. morroensis* is an obligate seeder; that is, it does not resprout, and maintains itself solely by reproducing from seed. Currently, seedlings and young shrubs are rare in and adjacent to mature stands, suggesting that reproduction in this species is fire-dependent. In order to gain information about the ecology of this species, we conducted studies on its seedbanks, germination behavior, and reproductive biology. This report presents results of our studies conducted 1997 - 1998.

To predict the response of *A. morroensis* seeds to fire, we conducted experiments on seed germination in the laboratory. We found highest germination rates following simulated fire (heating plus addition of charate), reduced rates with only heat or charate, and lowest rates following simulated wet-season burn (wetted seeds exposed to heat plus charate).

We collected and analyzed soil seed bank cores from the Elfin Forest area. Seeds collected under live shrubs had very low viabilities (1%), reinforcing the pattern that was suggested by our previous work. We also sampled under large dead shrubs, and found extremely low numbers of viable seeds in the soil seed bank (less than half that under nearby live shrubs). If projected rates of seed loss continue, we conjecture that it is likely these shrubs will not be replaced by *A. morroensis* after a fire. This pattern might result from the combination of low seed densities and altered fire effects in gaps where dead *A. morroensis* are found; most of these gaps have been invaded by the succulent *Conocosia*.

We present results of preliminary studies on the reproductive biology and seed predation of *A. morroensis*. Our main findings were: 1) bumblebees were the most common pollinator, though these were not generally abundant; 2) *A. morroensis* does not self-pollinate; 3) plants produced an average of 108 flowers and 10 fruits per stem (on stems selected haphazardly), with a mean 10% fruit set; 4) we found no difference in flower or fruit characters among sites; 5) fruit predation was occurring at all 3 sites, and was especially high at the Elfin Forest (85% fruit lost within 7 weeks.)

We used data on fruit production and fruit predation to estimate the 1997 contribution to the soil seed bank. The number of seeds added to the Elfin Forest was lowest (316 seeds/m²), moderate at the Hazard Canyon site (912 seeds/m²), and highest at the Dune site (1608 seeds/m²). Based on the densities of seeds currently in the soil seedbank, it would take many years of seed accumulation to acquire the observed densities (Elfin Forest - minimum 57 years, Hazard Canyon - minimum 47 years, Dune

site - minimum 10 years.) This indicates that the interval between fires must be long enough to allow this obligate-seeder to accumulate sufficient seed populations to ensure its regeneration following fire. Thus it would be important that any prescribed burn, or wildfire, be followed by a long period of fire exclusion.

Understanding the response of *A. morroensis* to fire is of critical importance to managing the species, because stands will eventually burn, either during wild or prescribed fires. Here we provide recommendations for studies to be conducted in a prescribed burn. These recommendations include the goals and methods for preburn sampling of vegetation and the *A. morroensis* seedbank, and postburn analysis of fire intensity, the *A. morroensis* seedbank, and seedling establishment.

We also provide recommendations for future research, including a) prescribed burn studies described above, b) comparative studies of viability and germinability of seeds from different sites and sources (i.e., intact fruits on shrub, intact fruits and fresh seeds in litter layer, and seeds in the soil), and c) continued studies on the reproductive biology of *A. morroensis*.

II) Introduction

Arctostaphylos morroensis is a narrowly endemic species restricted to a portion of coastal area in San Luis Obispo County. It is an erect shrub (family Ericaceae) which becomes arborescent with old age; it can be distinguished from other species of co-occurring manzanitas by its persistent shreddy bark and densely hairy lower leaf surfaces (Fig. 1).

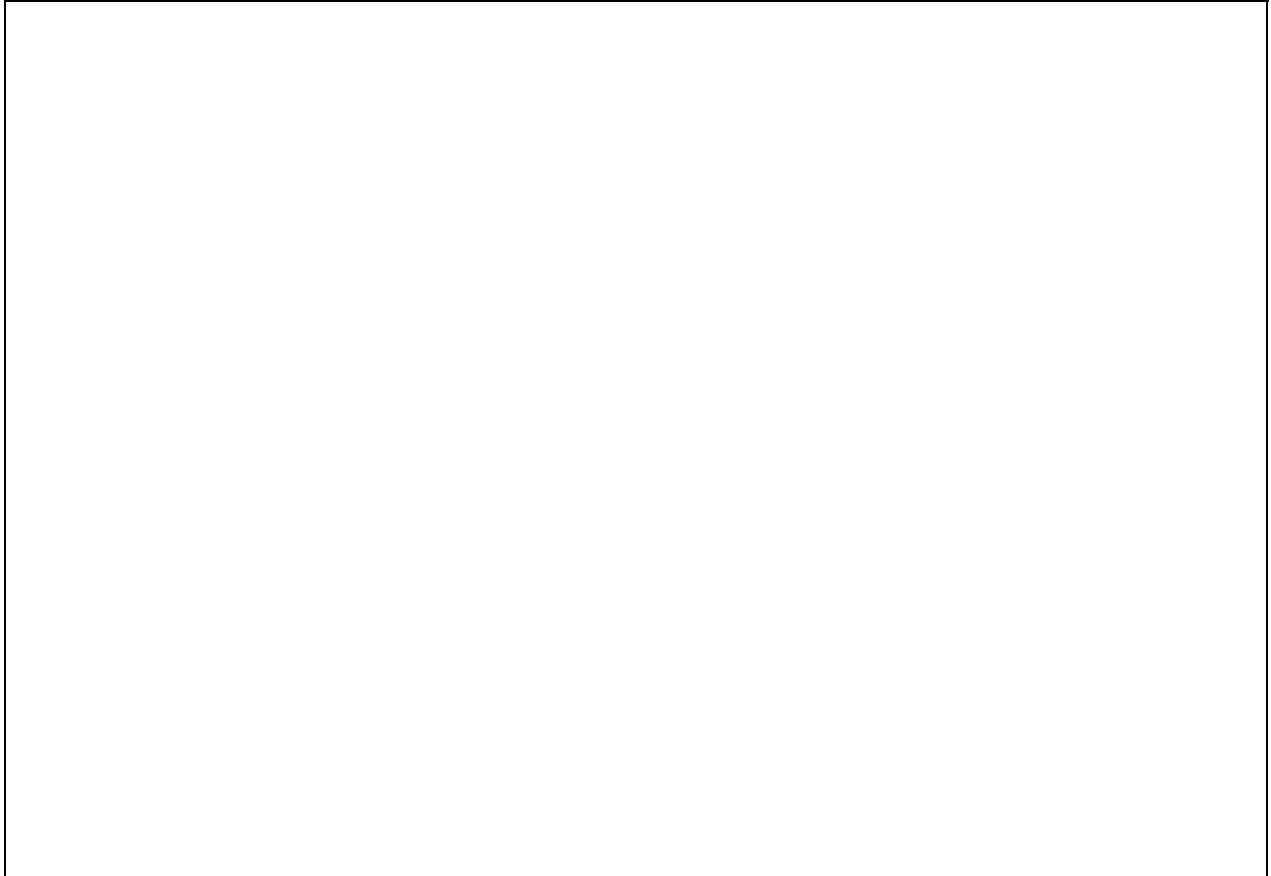


Figure 1. Photographs of *A. morroensis*. Note shreddy bark, and leaf shape. Photos by C. Tyler

The major threat to *A. morroensis* is urban development. This species has been listed by the California Native Plant Society as a plant that is "rare, threatened or endangered in California."

A. morroensis is an obligate seeder; that is, it does not resprout, and maintains itself solely by reproducing from seed. In our previous study (Tyler and Odion 1996), surveys of existing stands and historical air photos suggested that stands of *A. morroensis* are likely to have established after fire. In the field, we found very few young individuals

(seedlings or saplings) in, or adjacent to, mature stands. These findings indicate that fire likely plays a crucial role in the establishment and persistence of this species. Information about the cues which stimulate germination of *A. morroensis* seeds would be useful in predicting seedling regeneration after fire, and would be valuable to the development of an appropriate fire management plan. In addition, sampling seed banks under large dead manzanitas (common in the Elfin Forest) would be important in predicting the patterns of postfire establishment in these patches if they were burned.

Data we obtained previously on seed viability and seed populations (Tyler and Odion 1996) indicated that isolated populations of *A. morroensis* had lower seed densities and viabilities, suggesting reproductive stress. Further seedbank sampling in these stands would provide data on the effects of population fragmentation. Information on the reproductive biology of *A. morroensis* could also determine factors contributing to reduced seed populations.

The objective of this study was to gather information on several aspects of the ecology of Morro Manzanita (*Arctostaphylos morroensis*) that may be useful in preparing recommendations for the management of this species. This report includes: 1) results of experiments on the germination of *Arctostaphylos morroensis*; 2) estimates of seed densities and viabilities in isolated stands and under dead manzanitas; 3) results of preliminary studies on the reproductive biology of this species; 4) design recommendations for studies in prescribed burns; and 5) recommendations for future research.

III) Response of *A. morroensis* seeds to burning

Seed germination in the genus *Arctostaphylos*

Past research on the germination behavior of manzanitas provides useful comparative information for the present study. Seeds of obligate seeders, such as *A. morroensis*, have been found to be refractory (Sweeney 1956, Keeley 1992), that is, germination is completely inhibited until primary dormancy is released by a specific fire-related mechanism. Refractory seeds are long-lived. Seeds of *Arctostaphylos* have hard seedcoats and dormant embryos (Berg 1974). When the seed germinates, the hypocotyl is forced through a channel at the basal end (Berg 1974). The tissue plugging this channel is softer than the surrounding endocarp wall. Germination can proceed if the softer tissue is dissolved artificially using acid, or if the endocarp is cracked by heat or mechanical means. Germination of manzanita seeds subjected to various levels of heating was studied by Sampson (1944). Germination rates were found to be greatly enhanced with heat up to a threshold, beyond which mortality occurred. Even with heating, however, germination percentages were found to be low (11% for Common Manzanita, *A. glauca* and 9% for *A. parryi*, both obligate seeders). Germination percentage following

immersion in sulfuric acid was found to be 3-5% for *A. glauca*, an obligate seeder, 3-8% for *A. glandulosa* a sprouter, and 20% for *A. patula* (sprouter) (Berg 1974). All of these test results are apparently from seed that was freshly collected and dried and stored following standard procedures.

In a review of chaparral seed germination, Keeley (1992) did not include *Arctostaphylos* among species requiring heat for germination, but indicated that cold stratification is necessary, and that charred wood eliminated dormancy in some species. (Keeley et al. 1985, Keeley 1987b). Parker (1987) obtained 14% germination for *A. canescens* seeds extracted from the soil and then incubated with an aqueous leachate of charred wood; interestingly, charred wood did not release fresh seed of this species from dormancy, so the charred wood/smoke dormancy release mechanism(s) apparently can change as seeds age in the seed bank. Odion (1995) found that charate significantly enhanced germination over heat alone for soil-stored seed of the maritime chaparral endemic *Arctostaphylos purissima*. Unfortunately, the percentage of total viable seeds that germinated after treatment by heat and charate could not be determined.

In our previous studies, we found that *Arctostaphylos morroensis* stands most likely dated back to the most recent fire at each site (Tyler and Odion 1996). Because of the importance of post-fire regeneration from seed, and lack of sprouting ability in the shrub, knowledge of the fire-related germination behavior of *A. morroensis* seed is critical to understanding the maintenance of this species. For example, should fire continue to be absent from manzanita stands, it could become desirable for managers to induce seedling establishment. This would require knowledge of how to treat seed banks to achieve maximum germination of seeds. Furthermore, if prescribed burning of *A. morroensis* stands were to be undertaken, it would be imperative to be able to predict the response of seeds under different prescription conditions. For example, from a safety perspective, it may be desirable to burn chaparral after fall rains, or during winter or spring. However, Sweeney (1956) found that a number of chaparral species with seed that imbibes water became sensitive to heating after imbibition, despite having high heat tolerance in the dry condition. Parker and Roger (1987) studied the seedling regeneration of obligate seeding *Arctostaphylos montana* following winter burning and found poor regeneration and decreased heat tolerance of moistened seed.

We initiated germination studies in order to determine the response of *A. morroensis* seeds to dry-season and out-of-season burning and to heat and charate. If the seeds could be induced to germinate with charate alone, this could be added to soils as an effective restoration procedure. We also studied the response of untreated seeds to help predict whether some seedling emergence could occur following manual clearing.

Methods

We used seed that had been collected for previous studies on seed density and viability (Tyler and Odion 1996). This seed was collected from the area north of Hazard Canyon, which supported a mix of chaparral, *Quercus agrifolia*, and dense stands of *A. morroensis*; cover of *A. morroensis* ranged from 50 to 100%. Seed was collected below the litter layer from the top 5.1 cm of soil, under adult *A. morroensis* shrubs. We sorted the intact seeds from the soil, and assessed viability in a sub-sample of seeds, which were cut open and examined under a dissecting microscope. The viability for seeds used in this experiment was estimated to be 4.4%.

Treatments were as follows: 1) control, 2) heated, and charate added, 3) heat only, 4) charate only, 5) wet, then heated and charate added. For all treatments, seeds were placed on filter paper (Whatman #1, 110mm circles), which were on top of untreated sponges in trays filled with approximately 1" of deionized water. Water was added as needed to maintain this level. This allowed the filter paper to remain moist for the duration of the germination trial. Trays were kept inside dark growth chambers because light has been shown to inhibit germination in some *Arctostaphylos* species (Keeley 1987). To provide cold stratification, which is necessary for germination in some species of *Arctostaphylos*, temperatures in the chambers were programmed to alternate between cold and warm cycles: 14 hours at 5°C followed by 11 hours at 20°C. After three weeks the temperature was held constant at 20°C for 24 hours per day because no further cold stratification was needed, and embryo growth was expected to be more rapid with warmer temperatures. In addition, after 3 weeks, all seeds were sprayed periodically with Physan (0.4% solution) to control the growth of fungus.

For heat treatments, seeds were placed on enamel pans in an oven at 100° C for 5 minutes. For treatments that received charate, we used 0.2g spread evenly on the germination medium (filter paper). We placed the seeds on top of the treated paper. Charate was collected in the field from chaparral in the Santa Monica Mountains that had burned in a wildfire; several weeks after the fire, charred wood was scraped directly from chamise stems (*Adenostoma fasciculatum*) that remained. For treatment #5, we soaked the seeds for 24 hours in deionized water, then removed the seeds, and heat- and charate-treated them as above.

We used a total of 1050 seeds, 200 in each treatment, except treatment #5 (wet, heat and charate) which had 250 seeds. Seeds were checked every 3 days; germinated seeds were recorded and removed. The experiment was terminated 75 days after initiation.

Results

The first germination was observed 28 days after the initiation of the experiment. Most germination (88%) occurred within the first 36 days. Percent germination was low overall (1 - 4.5%), and varied among treatments (Fig. 2.) We can logically assume that the maximum potential germination should be equal to the viability rates (i.e., the number of seeds germinating cannot exceed the number that are viable.) Note that the maximum potential germination, as predicted by viability rates of previously analyzed samples, was also low (4.4%). Germination with heat and charate equaled the “potential maximum”; that is, the number of seeds that germinated under this treatment is the number that was predicted to be viable based on previous estimates of viability of seeds in this sample. Surprisingly, the next most effective treatment was the control. Unexpectedly, germination was reduced for both heat alone and charate alone treatments. Seeds soaked in water for 24 hours prior to heat and charate treatment had substantially lower germination than the unmoistened heat and charate treated seed.

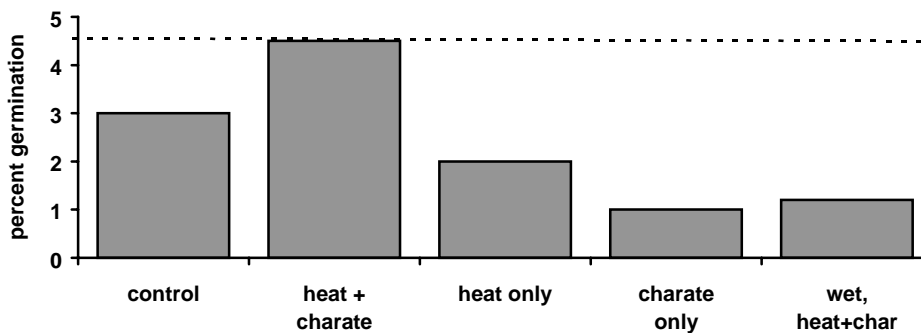


Figure 2. Effects of experimental treatments on germination of *A. morroensis*. Dashed line indicates the estimated percent viability (hence, maximum potential germinability) of seeds in these samples.

Discussion: predicted regeneration after fire

Previous studies (Parker 1987, Keeley and Fotheringham 1998) have demonstrated that the germination behavior of soil stored seed (i.e., from the soil seedbank) could differ from that of fresh seed (i.e., from seed in the litter layer or fruits still on the shrubs). In this experiment we used soil stored seed rather than fresh seed, because we were interested in predicting the post-fire germination response of this species. Following fire, both above-ground vegetation and litter are incinerated, and thus the sole source of seed that could potentially germinate is buried in the soil. Since

germination behavior of fresh *A. morroensis* seed may or may not be representative of seed that survives fire, studying soil stored seed avoids the potential uncertainty.

Our results indicate that appropriate levels of heat and combustion-related chemicals present in charate can induce virtually all viable seed of *A. morroensis* from the soil seed bank to germinate. This explains the strong post-fire response of this species. However, it is clear that fires that occur when soils are moistened will produce substantially reduced germination. Further, it is possible that if seeds are moistened for longer than 24 hours, additional loss in heat tolerance may occur. Late fall or early winter prescribed burns may have particularly negative effects on post-fire germination for the following reason. Early season rains that are sufficient to wet the top several cm of sandy soil, where seeds are found, may not be sufficient to raise fuel moisture levels in woody shrubs (i.e., 2 - 4 cm of rain). Under these conditions, combined with warm air temperature and low humidity, fires could cause high levels of soil heating to occur when the seeds are in the moistened condition; thus, given the results of this study, high seed mortality would be expected.

The poor germination obtained with charate alone contrasts with Keeley's (1992) conclusion that manzanitas require charate, but not heat. Our results indicate that charate alone does not stimulate germination, and this would not be a sufficient treatment for seed banks to be used in restoration/revegetation projects involving *A. morroensis*. Treating seeds to both heat and charate may not be practical for revegetation/restoration of any sizable area. Obtaining seed bank samples from a manzanita stand that happens to burn during the dry season would be an efficient, effective way to procure large quantities of seed for such projects. The optimum time for undertaking revegetation is after such fires take place. Advance planning and recognition of the need for prescribed burning, or serendipity following wildfires would be prudent elements of conservation planning for *A. morroensis*.

Surprisingly, we found relatively high rates of germination for untreated seed. This is particularly interesting given that in the field, seedling establishment of *A. morroensis* without fire is relatively rare. Although we have observed some seedlings (in the dune site, and on a site that had been cleared in the housing development north of Hazard Canyon), their numbers are extremely low given the abundance of seed, and densities of adult shrubs that occur, or had occurred, on the site. There are several mechanisms that may prevent seedlings from establishing in the absence of fire. First, the environmental conditions where seed occurs may be unsuitable for emergence or establishment. The vast majority of *A. morroensis* seed is under the adult shrubs (Tyler and Odion 1996). The environment under live *A. morroensis* canopy is one of low light and deep leaf litter. Thus, failed emergence or early mortality of seedlings might be responsible for the lack of establishment in the field. Second, it is possible that seeds present in the soil (unburned), simply do not germinate -- perhaps due to an environmental cue, such as allelochemicals in the soil. Chou and Muller (1972) found

that the presence of adult manzanita shrubs inhibits germination, and argued that allelochemicals present in the leaves of *A. glandulosa* was the mechanism that prevented seed germination.

Given the rates of germination we found in our control samples, it would be worthwhile to test the use of untreated seed from the soil seed bank for use in restoration/revegetation. In addition, it would be valuable to know whether seed in the litter, and seed freshly collected from shrubs would have high germination without treatment. It is likely that this seed (as opposed to seed in the soil seed bank) will only germinate with the fire treatment, since attempts to propagate *A. morroensis* from seed without treatment have been unsuccessful (Pete Wallberger, pers. comm.).

IV) Estimates of seed densities in isolated stands, and under dead manzanitas

In our earlier studies, we found relatively low densities and viabilities of seeds in samples collected from the Elfin Forest (Table 1). One hypothesis to explain this pattern is that there is poor reproduction due to inbreeding effects in the small population of isolated manzanitas in this area. In order to test this hypothesis we first wanted to determine, more conclusively, whether densities of viable seed were significantly low in these stands relative to the other sites. To increase our sample size, we collected and analyzed more seed bank samples under live adult shrubs in the Elfin Forest area.

In addition, we observed that many of the large manzanitas in this area had recently died. With no input of seeds into the seed bank under the decomposing manzanita skeletons, seed populations will decrease. To determine whether populations of viable seed may become too depleted to support recolonization at locations where canopy of *A. morroensis* once stood, we also sampled and analyzed soils from under the dead plants. Unfortunately, it is not possible to determine how long ago each shrub died, and use this information to develop a seed population decay rate. However, because many of the branches on the shrubs were still intact, we suspect that the shrubs had died within the last few years (probably < 10 years prior to our sampling), and the rate of reduction in seed numbers since then might be projected to a similar time period in the future.

Methods

We collected soil samples in the late summer/early fall of 1997 in the Elfin Forest and nearby areas (e.g., the stand east of South Bay Blvd - across the road from the Elfin forest). Samples were collected from under 5 dead, and 5 living, isolated *A. morroensis*.

TABLE 1. Mean and standard error of total number of seeds and number of viable seeds per sample (237.6 cm² x 10.3 cm), percent viability, percent infertile seeds, and estimated seedbank size and number of viable seeds per m². P-values are results of one-way analysis of variance to determine differences among sites (df: site, error = 3, 16). **From Tyler and Odion 1996.**

<u>SITE</u>	1 <u>Dune area - Montaña de Oro</u>	2 <u>N. of Hazard Canyon</u>	3	4 <u>Elfin Forest</u>	<u>P</u>	<u>all sites combined</u>
n	5	5	5	5		20
Total number of seeds per sample	362 (61)	1072 (131)	1011 (99)	512 (127)	< 0.001	739 (86)
Viable seeds per sample	17 (4)	48 (6)	68 (15)	9 (3)	< 0.001	36 (7)
% Viability	6 (2)	5 (1)	7 (1)	2 (1)	0.076	5 (1)
% Infertile	47 (2)	42 (4)	45 (4)	49 (5)	0.679	45 (2)
Estimated seedbank size (no. per m ²)	15,224 (2552)	45,134 (5529)	42,569 (4181)	21,551 (5358)		31,119 (3636)
Estimated # viable seeds per m ²	719 (152)	2017 (245)	2876 (631)	390 (132)		1501 (281)

For each sample we took 6 soil cores; the cylindrical soil corer was 7.1 cm in diameter, and 10.3 cm deep. Thus the total amount of soil collected per shrub was $237.6 \text{ cm}^2 \times 10.3 \text{ cm}$. Litter was removed prior to extracting soil and the corer was inserted so that it was flush with the mineral soil surface. In the laboratory, we homogenized the six samples, passed the soil through a No. 12 USA Standard Testing Sieve (mesh size = 1.70 mm), and then retrieved seeds from the remaining mix of litter, pebbles, and other small debris. We cut open all seeds and examined the chamber for viable embryos using a dissecting microscope. Embryos that were white and fleshy were counted as viable. This visual technique of assessing seed embryo viability has been shown to yield results consistent with tetrazolium testing (Parker, pers comm.). Many of the seeds were intact, but the chamber lacked an embryo, or the dried remains of an embryo. We scored these seeds as infertile, since apparently no embryo development had ever occurred.

Results

Analysis of samples collected under live manzanitas in the Elfin Forest area confirm our previous findings that seed density and viability are especially low at this site (Table 2). Seed densities ranged from 96 - 792 per sample and the number of viable seeds per sample from 0 - 18. One of the samples, which came from a shrub that was small, had a particularly low total seed density (96), and no viable seeds. Because percent seed viability is so low in these stands (average 1%), the complete lack of viable seeds in this sample may be a function of small total seed number. Out of 20 samples in our previous study (Tyler and Odion 1996), only one was found to be lacking viable seeds; that sample was also from a small shrub and likewise, the total population of seeds under that shrub was low.

	mean	s.e.
Total number of seeds per sample	349	128
Viable seeds per sample	7	3
% viability	1.7	0.7
% infertile	45.6	3.3
estimated seedbank size, #/m ²	14,710	5,368
estimated # viable seeds per m ²	295	145

Table 2. Mean and standard error of seedbank parameters for samples under live *A. morroensis* in the Elfin Forest area; collected 1997. Samples were $237 \text{ cm}^2 \times 10.3 \text{ cm}$. N = 5.

T-tests comparing our “new” Elfin Forest samples with our previous samples from this area, revealed no significant differences. Therefore we combined these two data sets, to provide a revised, more complete assessment of seed densities and viabilities at our study sites (Table 3).

Under dead manzanitas, there were an average of 12,027 seeds/m², about 65 percent as many as found under live shrubs in the same area (Table 3). Percentage viability was slightly lower than under live shrubs as well (0.9% vs. 1.5% - no statistically significant difference), and two samples had no viable seed. As a consequence, the mean density of viable seed remaining under dead shrubs as of summer/fall 1997 was only 112/m², about one third the number under nearby live *A. morroensis*.

We conducted analysis of variance on seed bank parameters of all sites, and results were consistent with our previous study (Table 3). We found significant differences in numbers of seeds per sample, and numbers of viable seeds per sample ($P < 0.001$). Post-hoc comparison tests (Tukey) revealed that the stands in the Dune Area and the Elfin Forest (both live and dead shrubs) had significantly lower densities than the sites north of Hazard Canyon. The Dune Area is the youngest site (~39 years), and we suspect that the Elfin Forest is the oldest (Tyler and Odion 1996). Percent viability also varied among sites, with the lowest at the Elfin Forest. We have proposed that the low numbers of viable seeds in the soil seed bank at the Elfin Forest may be a result of reproductive stress. However, preliminary studies on the reproductive biology suggest that fruit production is not particularly low at this site (see section V.d. and e.) Rather, intense seed predation may be the primary factor resulting in low numbers of viable seeds at this site. Low numbers of viable seeds in the Dune Area may be a function of stand age.

Implications for seedling regeneration following fire

Studies on postfire seedling establishment in chaparral provides information on *Arctostaphylos* seedling densities and survival rates after a burn. Sampson (1944) studied plant succession at several burned chaparral sites in northern California. In plots dominated by Eastwood Manzanita (sprouter/seeder), an average about 25 seedlings per m² were found, and about 9 per m² of the obligate seeding Common Manzanita (*A. glauca*.) At another site dominated by Common Manzanita, an average of 6 seedlings per m² were found. These sites were monitored for five years after which 38 percent of the Common Manzanitas persisted at one site, but 94 percent at another. Survival of Eastwood Manzanita was 72 percent after 5 years. Horton and Kraebel (1955) studied vegetation development after fire in southern California. At a site described as dominated by *Adenostoma fasciculatum* and *Arctostaphylos glandulosa* (seeder/sprouter), seedling density of *Arctostaphylos glauca* (obligate seeder) was about 6 per m². All of the manzanita seedlings in this study had died by fifteen years after the burn. Odion (1995) studied establishment of *Arctostaphylos purissima* in maritime chaparral. An average of 14 seedlings/m² were found after fire where gaps (n = 15) in the chaparral cover had

TABLE 3. Mean and standard error of total number of seeds and number of viable seeds per sample (237.6 cm² x 10.3 cm), percent viability, percent infertile seeds, and estimated seedbank size and number of viable seeds per m². P-values are results of one-way analysis of variance to determine differences among sites (df: site, error = 4, 26). Means with different letters are significantly different (Tukey post-hoc comparison tests.)

<u>SITE</u>	1 <u>Dune area - Montaña de Oro</u>	2 <u>N. of Hazard Canyon</u>	3	4 <u>Elfin Forest</u>	5 <u>Elfin forest dead</u>	<u>P</u>
n	5	5	5	10	6	
Total number of seeds per sample	362 (61) a	1072 (131) b	1011 (99) b	431 (89) a	286 (49) a	< 0.001
Viable seeds per sample	17 (4) a	48 (6) b	68 (15) b	8 (2) a	3 (1) a	< 0.001
% Viability	6 (2) a	5 (1) a, c	7 (1) a	2 (1) b, c	1 (1) b, c	0.001
% Infertile	47 (2)	42 (4)	45 (4)	47 (3)	36 (2)	0.089
Estimated seedbank size (no. per m2)	15,224 (2552) a	45,134 (5529) b	42,569 (4181) b	18,131 (3753) a	12,027 (2059) a	< 0.001
Estimated # viable seeds per m2	719 (152) a	2017 (245) b	2876 (631) b	343 (94) a	112 (60) a	< 0.001

occurred prior to burning. Where there had been a shrub canopy prior to fire, an average of 8.7/m² were found. Along a 47m transect where pre-burn shrub cover was high 3.3/m² were found. These were strongly concentrated in areas of lower soil heating during fire. Survival after 5 years varied among these locations between 11 and 15 percent in the gap areas, where seedlings of all species were much more abundant.

It is difficult to predict the density of *A. morroensis* seeds required to produce enough seedlings that would become established individuals to replace those present before the fire (i.e., to maintain a steady population size). A certain percentage of *A. morroensis* seed will be killed by fire depending on seed depth distribution. A portion of viable seed surviving may not receive sufficient heat, and/or be exposed to chemicals in charate, and/or cold stratification treatment to break dormancy (i.e. if it is too deeply buried, or is somehow isolated from fire effects). Some seed may be too deeply buried to emerge if it does germinate. Mortality among manzanita seedlings that do emerge may be close to 80 percent after 5 years in maritime chaparral. Most of this mortality will likely occur the first summer after fire (Tyler and D'Antonio 1995, Odion 1995). For *Arctostaphylos purissima*, an obligate seeder found in Pleistocene sands just south of Morro Bay, Odion (1995) found a density of 290 germinable seeds/m² in the seed bank prior to fire under the canopy, 48.4/m² after fire, and a density of 0.5 seedlings/m² in the same plots 5 years after fire. If the probability of establishment were roughly the same for *A. morroensis*, then it would be necessary for there to be minimum of about 580 germinable seeds/m² of *A. morroensis* to be present in the seed bank before fire in order to produce a density of 1 established individual/m² after 5 years.

Using these probabilities, we predict that the seed bank found under dead manzanitas (112 viable seeds/m²) would produce about 0.2 established seedlings/m². Thus, at the time of our sampling there was probably sufficient viable seed to replace dead individuals, assuming this seed receives fire-related germination cues to overcome dormancy. However, this assumption may not be accurate. Vegetation invading the bare space under the dead shrubs is dominated by the succulent exotic *Conocosia pugioniformis*. At the time of our sampling this ground-hugging plant averaged 32 percent cover, and this may increase over time. Soil heating within these gaps during fire will probably be much lower than would typically occur with burning of *A. morroensis* stands. With its high water content, *Conocosia* would absorb some of the heat that would be generated by the burning of the surrounding chaparral. In addition, there is little litter in the gaps. The shrub skeletons continue to be consumed by termites, and to decompose, reducing the fuel provided by the dead manzanitas. It is possible that these patches would not be successfully ignited by the surrounding chaparral during a fire. Thus, the seeds, especially those buried relatively deeply, may not be treated to byproducts of combustion required to release them from dormancy. In addition, viable seed populations may continue to drop by about 50 percent every 5 years in the future (i.e. the present rate of decline). Considering these factors and the low likelihood that the stand will burn in the

foreseeable future, it is possible that dead manzanitas will not be replaced unless management action is taken before too much time is allowed to pass.

V) Reproductive Biology of *A. morroensis*

The goal of this set of pilot studies on the reproductive biology of *A. morroensis* was to examine the reproductive output of this species, and to determine the factors that influence recruitment of individuals in extant populations and that contribute to differences in reproductive output among stands. These studies were conducted in the spring and summer of 1998. We examined pollinators, self-fertilization, fruit set, seed set, numbers of mature fruits that reach the soil, and the effect of predation on fruit survival.

Study sites

We examined aspects of reproductive biology in three sites. The first site was the Elfin Forest, north of Santa Ysabel Ave. and west of South Bay Blvd. This area is a mix of maritime chaparral, coastal scrub, and oaks. The percent cover of *A. morroensis* is low, ranging from <1% to 5-25%. The manzanita stands at this site are older than 47 years, and some individual manzanitas appear to be very old. Previous studies (Tyler and Odion 1996) found that the seeds in the soil seed bank here had particularly low seed densities and low viabilities, suggesting that potential reproductive stress is occurring in this stand.

The second site was the dunes area west of Pecho Valley road in Montaña de Oro State Park, where the stand age was estimated at 37 years. This site is a mix of maritime chaparral and coastal scrub. The percent cover of *A. morroensis* in this site (according to Mullany 1990) ranged from 25-50% to 75-100%.

The third site was north of Hazard Canyon, east of Pecho Valley Road in Montaña de Oro State Park. This site is a mix of *Quercus agrifolia* and dense *A. morroensis*. The percent cover of *A. morroensis* ranged from 50-75% to 75-100%. This stand of manzanita is intermediate in age between sites 1 and 2. It is located relatively close to site 2 (<400 m), but upslope and farther from the ocean.

Pollinators

Pollinators were observed on seven days during March and April 1998. Insects were captured and collected for identification. Specimens will be identified to species in 1999 following additional collections. Counts of pollinators visiting plants were recorded for each site.

The most abundant pollinators observed visiting *A. morroensis* flowers were bumblebees (*Bombus* sp.). Other pollinators included Halictid bees and Anthophorid bees. Twenty-two periods of observation of at least 10 minutes per period, when at least one pollinator was observed, were conducted on seven different days. During 18 observation periods only bumblebees were observed. During the remaining four periods, in addition to bumblebees, a *Colletes* sp., Halictid bees, and a Syrphid fly were observed visiting *A. morroensis* flowers.

Pollinators were generally not abundant on the *A. morroensis* blooms. On one occasion at the second site in the dunes area (on April 4, 1998, somewhat late in the bloom season), no pollinators were observed during a one-half hour period even though abundant blooms were present on many plants.

Self-fertilization

To determine whether *A. morroensis* is capable of self-fertilization, inflorescences were bagged to exclude all pollinators. Open flowers were removed from the inflorescence prior to bagging and closed buds were counted. Bags were left in place until all of the flowers within the bag had senesced. The stems were then examined for fruit.

A total of 1243 flowers on 53 stems on 14 plants were bagged to exclude cross pollination. Inflorescences were covered beginning on March 3, 1998, until all of their flowers dropped their corolla. Out of 1243 total flowers monitored, 1235 flowers did not set fruit, while 8 flowers did set fruit. Out of the 53 stems that were bagged, 48 of the bagged inflorescences did not set fruit, as compared to 5 bagged inflorescences that did set one or two fruits. This result indicates that *A. morroensis* can not self pollinate. It is likely that the eight bagged flowers that did set fruit were in fact open before bagging and missed when other open flowers were removed, and thus perhaps they had already been pollinated.

Fruit set

To examine fruit set, six plants were selected haphazardly within each site and ten stems were selected and banded for identification on each plant. Stems were selected that were new in bud, and these were followed weekly to determine the full count of flowers produced by the stem from February through April. Buds were marked or noted and new buds were added to the total when they occurred. Fruits were counted on stems from March through the first week in June. By June many fruits had fallen off the stems, so the highest count taken for each stem was used as the fruit production number for that stem.

The counts of flowers and fruit on the ten stems on each plant were used to determine a mean value for flower number and fruit number per stem for each plant. The ratio of fruit number to flower number was calculated to determine the average fruit set per plant. We used one-way analysis of variance (ANOVA) to detect statistically significant differences in flower production, fruit production and fruit set among study populations.

Results

The mean number of flowers produced per stem per plant ranged from 80 to 135 (Table 4). The Elfin forest site had the lowest number of flowers produced per stem, and the Hazard Canyon site the highest, but we detected no statistically significant differences among the sites (ANOVA: $P = 0.243$, $n = 18$).

Means Table for mean no. of flowers per stem, per plant
Effect: location

	Count	Mean	Std. Dev.	Std. Err.
Elfin forest	6	79.6	19.9	8.1
Dune	6	111.3	75.8	31.0
Hazard Cyn	6	134.6	51.6	21.1

ANOVA Table for mean flowers per stem

	DF	Sum of Squares	Mean Square	F-Value	P-Value
location	2	9137.6	4568.8	1.556	0.243
Residual	15	44053.5	2936.9		

Table 4. Mean number of flowers per stem on six plants at each study site, and results of analysis of variance to detect differences among treatments.

Fruit production averaged between 8 - 12 fruits per stem (Table 5). Highest numbers of fruits produced per stem were found in the dune population, but this difference was not statistically significant (Table 5).

Fruit set over all study populations averaged 10.0% (Fig. 3). The Hazard Canyon site had less than half the fruit set of the Dune site; however this difference was not statistically significant (ANOVA: $P = 0.125$, $n = 18$). The pattern of lower fruit set in this stand resulted from both higher flower production and lower fruit production at Hazard Canyon compared to the other two sites. Further study is required to determine whether this difference among stands would be significant with greater sample size. Differences among the Dune and Hazard Canyon sites would be particularly interesting because these 2 areas are relatively close to one another.

Means Table for mean no. fruit per stem per plant

Effect: location

	Count	Mean	Std. Dev.	Std. Err.
Elfin forest	6	8.8	1.7	0.7
Dune	6	11.6	8.3	3.4
Hazard Cyn	6	8.0	4.9	2.0

ANOVA Table for mean no. fruit per stem per plant

	DF	Sum of Squares	Mean Square	F-Value	P-Value
location	2	44.3	22.2	.691	0.516
Residual	15	480.8	32.1		

Table 5. Mean number of fruits per stem on six plants at each study site, and results of analysis of variance to detect differences among treatments.

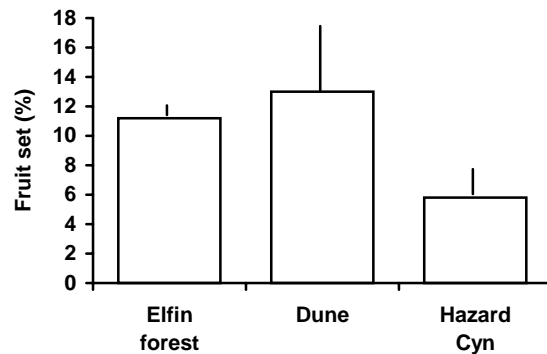


Figure 3. Differences in fruit set among study populations. Data are means of 6 plants per site, + 1 s.e.

Estimate of mature fruit reaching the soil

The average number of fruits falling from a plant was estimated by placing trays under each of the six plants at each site (total number of trays placed in the field = 72). When possible, four trays were placed under the outer canopy edge of each plant in each of the compass quadrants. Trays were 25 cm x 25 cm. They were constructed of wood frames, wire screen bottoms, and hardware cloth tops that were slightly v-shaped; the top was contoured in this way so that fruits hitting the cage would roll toward the center and fall into the tray. Thus, the trays excluded rodents from the fruit once the fruit entered the tray. Fruit falling into the trays was used to estimate the number of fruits that reached soil

per area, under each study plant. Fruits in the trays were counted and emptied throughout the spring and summer until no fruit remained on the plant.

The majority of fruits fell from the plants during June and early July (Figure 4). Of the total 1223 fruits collected at all sites (as of September 25, 1998), 1136, or 93%, were collected by July 18th.

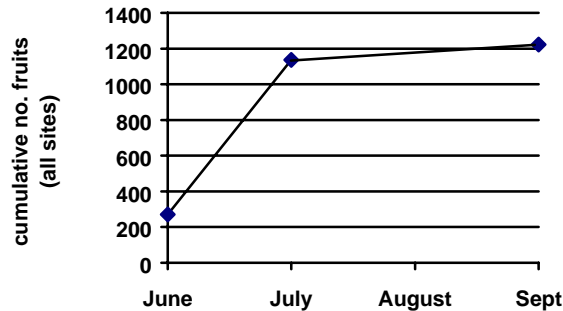


Figure 4. Cumulative number of fruits collected in trays (June - September 1998). Data are total numbers for all sites, all trays (72) combined. Total ground area covered = 4.5 m².

Combining all sites, shrubs dropped an average of 17 fruits per tray (area = 0.0625 m²), or 272 per 1 m². There was no significant difference in the number of fruits reaching the ground among sites, although the Hazard Canyon site, above the road in Montaña de Oro had the lowest number of fruits (Table 6). This is not surprising, given that this site also had the fewest numbers of fruits produced per stem (Table 5). The Elfin Forest site was next lowest, and the dune site below the road in Montaña de Oro was highest.

Means Table for Total fruit dropped per tray (25 cm x 25 cm)
Effect: site

	Count	Mean	Std. Dev.	Std. Err.
Elfin Forest	24	16.5	14.9	3.0
Dune	24	23.8	32.6	6.7
Hazard Cyn	24	10.8	11.8	2.4

ANOVA Table for Total fruit dropped per tray (25 cm x 25 cm)

	DF	Sum of Squares	Mean Square	F- Value	P-Value
site	2	2012.1	1006.1	2.115	.128
Residual	69	32824.9	475.7		

Table 6. Mean number of fruits dropped, and results of analysis of variance to detect differences among treatments.

Interestingly, there was a significant difference in the amount of fruit that reached the ground on different sides of the plant. All four quadrants of the plants were sampled, and the northeast half of the plants had significantly fewer fruits fall from the plant than did the southwest half of the plants (Figure 5). There were no significant differences between north and east, and south and west, so these two directions were lumped for the analysis. It appears that fruit (and flower) production is associated with sun exposure. Related to this phenomenon, we observed that in the Elfin Forest, some of the larger shrubs are bare or dying on the north-facing side of the plant. These patterns of growth and reproduction in relation to exposure may merit further investigation.

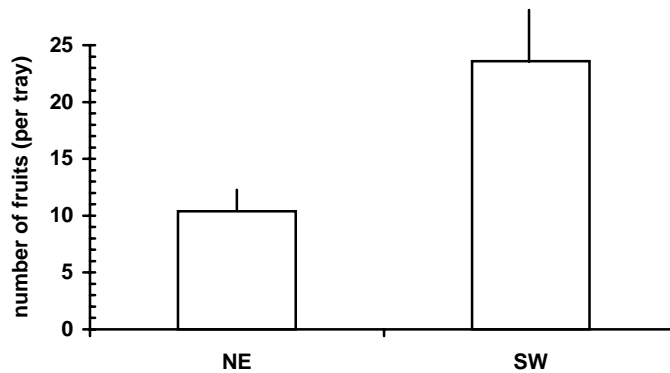


Figure 5. Numbers of fruit that reached the ground from plants at all three study sites when divided by the side of the plant according to compass direction. Data are means (+ 1 s.e.) of total numbers of fruits per tray (25cm x 25cm), all sites combined.

ANOVA Table for total fruit dropped per tray

	DF	Sum of Squares	Mean Square	F-Value	P-value
NE vs. SW	1	3133.7	3133.7	6.919	0.011
Residual	70	31703.3	452.9		

Table 7. Effect of direction on the number of fruit that reach the ground around a plant. Analysis of variance was conducted using all three of the study sites combined.

Fruit and seed predation

The effect of vertebrate predators on fruit survival was examined by experiment. We used 3 treatments to determine the rate of fruit removal from trays in which known numbers of fruit were placed. These treatments were: a) under the plant canopy and screened to prevent vertebrate predator access, b) under the plant canopy and open to

predators, and c) away from the plant canopy (1 - 3 m from canopy edge) and open to predators. The first treatment served as a control to determine whether fruits were lost to a factor other than vertebrate predators. The trays were 10 cm by 20 cm and 3 cm high, made of a wood frame with a screen bottom, and those that prevented predators had hardware mesh tops. Ten mature fruits were placed in each tray; trays were placed in association with each of the six study plants at each of the three sites. The number of fruit and seeds remaining were counted at intervals for six weeks. We looked for differences among treatments in the number of fruits remaining to determine whether vertebrate predators affect the number of fruits that contribute to the seed bank, and whether predation is more intense beneath the cover of a plant, or outside of the cover of the plant.

Results

We found that predators removed a significant number of fruit over the period of the study (Table 8). Combining all sites, after only 46 days, there were an average of 4 fruits remaining per tray in both open treatments (i.e., predators present) compared to 11 fruits in the controls (ANOVA, $P < 0.001$; posthoc Scheffe test indicate that both open treatments were significantly lower than the control, but not different from each other). No loss of fruit in the control trays verifies that the seed loss in the other treatments was in fact due to active seed removal by vertebrates. The addition of an average of 1 fruit per tray to the controls (which started with 10 fruits) most likely resulted from fruit drop from the canopy.

Means Table for Fruit remaining out of 10 - 7/18/98

Effect: Treatment				
	Count	Mean	Std. Dev.	Std. Err.
Open/under plant	30	4.4	3.5	.6
Open/ not under plant	30	4.5	3.9	.7
Screened/under plant	30	11.2	2.6	.5

ANOVA Table for Fruit remaining 7/18/98

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Treatment	2	915.8	457.9	40.591	<.0001
Residual	87	981.5	11.3		

Table 8. Mean number of fruits remaining (out of 10) in trays after 46 days in three experimental treatments and results of analysis of variance to detect differences among treatments.

This difference between control and both open treatments was significant as early as 11 days after the initiation of the study (ANOVA, $P < 0.001$).

We conducted two-way analyses of variance to examine both the effects of site and location (under canopy vs. away from canopy) on fruit predation. For these analyses we used only the open treatments (Figure 6). We found no location effect, i.e., there was no significant difference in loss of fruit in trays that were underneath versus away from plant canopies for all sites and for all dates (2-way ANOVA, location: $P = 0.582$). However, the number of fruit lost to predation was significantly higher at the Elfin forest site (predation rate = 85%) than at the two sites in Montaña de Oro for all dates (2-way ANOVA, site: $P < 0.001$). There was no significant difference between the two Montaña de Oro sites (predation rates = 34% and 47%). We found no location by site interaction (2-way ANOVA, location by site interaction, $P = 0.632$).

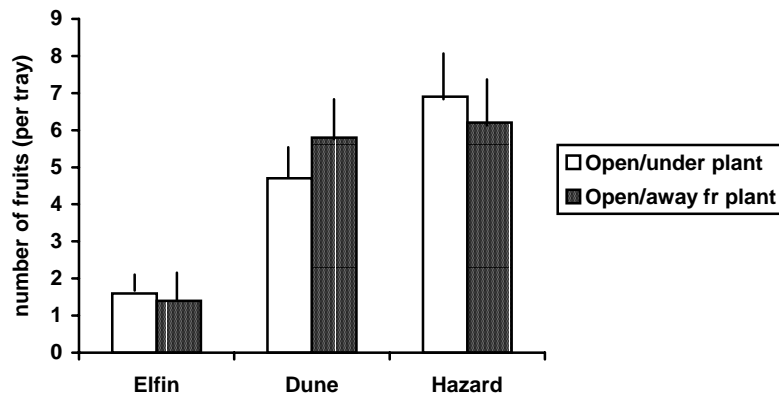


Figure 6. Numbers of fruit remaining (out of 10) in open trays at 3 sites, both under plant canopy and away from adult shrubs. Data are means (+ 1 s.e.) on July 18, 1998 (46 days after study initiation.)

We believe that the dominant fruit/seed predators were woodrats (*Neotoma fuscipes*). This suggestion is based on our observing rat scat in several cages, and on the proximity of large wood rat nests, particularly in the Elfin Forest. We also found brush rabbit scat in some cages at the Elfin Forest site only. Rodents are known to be attracted to fruit and/or seeds (Horton and Wright 1944, Keeley and Hays 1976). Seed predation is probably greater for species with larger seeds (Keeley 1992). Previous studies of seed predation have reported that rates of *Arctostaphylos* seed predation can be as high as 60 percent of the entire seed bank within a 6 month period (Keeley 1977).

Synthesis of seedbank and reproductive biology results - preliminary findings

One question we addressed in this report is whether isolated stands of *A. morroensis* in and near the Elfin Forest are exhibiting signs of reproductive stress, and if so, what factors might explain this pattern. We have demonstrated that this stand does, in fact, have significantly lower numbers of viable seeds in the soil seed bank (Table 3). In our pilot studies on reproductive biology, we found that fruit set was not different from other sites, suggesting that low seed numbers are not a result of poor reproduction (i.e., unusually low flower production or pollination rates.) Rather, the extremely high rates of fruit predation at this site may contribute significantly to the low numbers of viable seeds that are eventually incorporated into the soils seed bank.

Measurement of reproductive characters and rates of seed removal should be monitored over several years before making conclusions about reproductive stress in populations. Pollinator abundance, flower production, and fruit set, is likely to vary among years. For example, flower and subsequent fruit production in *Arctostaphylos* may be determined largely by rainfall during the previous year because buds are set at that time (Keeley 1977). Keeley (1987a) found that fruit production for *Arctostaphylos glauca* (obligate seeder) and *A. glandulosa* (sprouter) varied over a ten year period from near zero to 1100 seeds per m².

We used our data on fruit production, fruit predation, and previous data on numbers of seeds per fruit (Tyler and Odion 1996) to estimate the 1997 contribution to the soil seed bank (Table 9). This estimate was derived with the following formula: number of fruits per m² minus loss due to predation times number of seeds per fruit.) We calculated that the number of seeds added to the Elfin Forest was lowest (316 seeds/m²), moderate at the Hazard Canyon site (912 seeds/m²), and highest at the Dune site (1608 seeds/m²). These are surely overestimates since additional seed predation will probably occur before the seeds become incorporated in the soil. Our rates of seed/fruit predation are based on removal of fruits in a relatively short time period - only 46 days. In addition, at the Elfin Forest seed populations under shrubs that have been dead only a few years were about 60 percent those under live, suggesting that predation of seed continues to be significant long after fruits drop from the shrub.

At the Elfin Forest, based on the observed densities of seeds in the soil (from Tyler and Odion 1996), it would take 57 years of seed accumulation (at the estimated rate of 316/m²) to yield the number of seeds currently in the soil seedbank. This is a very conservative estimate, not only because predation is underestimated, but also because the fruit production and drop was measured under large shrubs; it clearly took many years for these older/large individuals to reach a size in which their total fruit production is as great as it is now. In addition, although it's probable that no germination occurs under shrubs, any germination of seed would further reduce the rate of seed accumulation. Based on this first year of data on fruit production and predation, we speculate that a long fire

interval (probably greater than 50 years) is needed for accumulation of seed at the Elfin Forest to reach present seedbank levels. It should be noted that the present density of viable seeds at the Elfin Forest is quite low compared to other locations. If successive fires were to occur at relatively frequent intervals at the Elfin Forest, the effect could be to reduce the abundance of *A. morroensis* due to what Zedler (1995) has referred to as "Immaturity Risk." Immaturity risk occurs when fire regimes change and result in a fire interval that is too short to allow obligate-seeders to accumulate sufficient seed populations to ensure their regeneration following fire. Although the senescence of large shrubs at the Elfin Forest indicates that a prescribed burn in a portion of the site may help maintain the manzanita population there, it would be important for such a burn, or a wildfire, to be followed by a long period of fire exclusion. This would not appear to be a problem, given that fire has been excluded from the site successfully over many decades; however, increasing abundance of grass fuel, veldt grass in particular, could facilitate ignition and spread of fire into the stand. Thus, there could be an increasing risk of more frequent fire in this site over time.

<u>site</u>	<u># fruits per m²</u>	<u>% loss due to predation</u>	<u># fruits per m² remaining</u>	<u># seeds per fruit</u>	<u># seeds per m² added in 1997</u>	<u>total # seeds per m² in seedbank</u>
Elfin Forest	263.3	85	39.5	8	316	18,131
Dune	379.3	47	201.0	8	1608	15,224
Hazard Cyn	172.7	34	114.0	8	912	42,569

Table 9. Estimates of numbers of seeds added to the seedbank in 1997 at three study sites. All data from the present report, except # seeds per fruit, and total # seeds in seedbank; the latter are from Tyler and Odion 1996.

This scenario applies to the Hazard Canyon population as well, since we calculate that it would take 47 years for seeds to accumulate to the densities measured there in the soil seedbank; however, the density of seeds in the seedbank is much greater, especially for viable seeds, at this site than at the Elfin Forest. At the Dune site, only 10 years of accumulation at the 1997 rate would be required for seed populations to reach their present density; however, seed densities at this site are rather low, and at present may not be sufficient to ensure postfire regeneration of *A. morroensis*. Thus it may require a longer time period for seeds to accumulate to a high enough density to ensure regeneration following fire at this site. Studies conducted in a prescribed burn at one of these sites would provide information about minimum densities of seed in the soil required for successful postfire establishment.

The above analysis relies on predation data from only one year's observations and that are still incomplete. An item of future research that could greatly improve our understanding of seed predation would be to determine the percent viability of fresh seed. Seed predators are very efficient at eliminating viable seeds (Keeley, pers. comm.). Therefore, the difference in viability between freshly collected seed, and seed in the soil may provide an estimate of the amount lost to predation.

VI) Recommended design for studies in prescribed burn

Understanding the response of *A. morroensis* to fire is of critical importance to managing the species, because stands will eventually burn, either during wild or prescribed fires. Prescribed (i.e., controlled intentional) burns could be deemed necessary to initiate seedling regeneration, diversify stand ages, or to reduce fire hazards at the urban interface. Although *A. morroensis* has co-existed with fire for millennia, and is presumably adapted to regenerating from fire, the environment it exists in today is different than at any time in the history of the species.

In the current environment, there may be impediments to successful postfire regeneration. Perhaps the most threatening change is the presence of exotic species, such as iceplant and veldt grass, that could invade a burn area. The negative interaction that would likely occur between these and young manzanita seedlings (exotic species that threaten *A. morroensis* are discussed in the previous report; see Tyler and Odion 1996). An additional threat is burning when the soil is wet, that is after fall rains occur or in the spring. This could happen either a) because prescribed burning may be considered "safer" when surrounding vegetation is moist, as the fire is then unlikely to spread uncontrollably, and/or b) as a result of the current patterns of ignition sources and fuel over the landscape. With man-made structures, *Eucalyptus* forests, and annual grasslands present, fire now has the potential to spread into chaparral during times of the year and conditions when it might not have previously. Our germination results strongly suggest that there will be poor regeneration after seeds become moistened. However, it is uncertain how much rain is required before seeds reach the sensitive condition each year; for example, it is unknown whether increased mortality would occur after just one moderate rain event initiating the rainy season.

In addition to these concerns, the fuel load (including litter accumulation) in dense stands of *A. morroensis* appears exceptional, especially if most of the aboveground vegetation were to be consumed by fire, as often occurs with obligate-seeders. It is possible the present fuel load exceeds that found during previous centuries when fairly frequent burning by aboriginals and early European settlers occurred. Much of this fuel is large size class material, and it is uncertain how much of this would be consumed by fire, and how much would collapse and smolder on the ground. The litter will also burn by smoldering combustion, and this will produce prolonged soil heating. Given these

conditions, it is possible that soil heating during a fire in dense *A. morroensis* stands in their present condition could lead to excessive seed mortality. The presence of seed at sufficient depth in the soil to survive fire will be critical to seedling regeneration. It is uncertain at what depth seeds need to occur in the soil to be insulated from soil heating that might occur under the present conditions.

Seeds that do survive may be buried too deeply and not be able to emerge. Emergence depth is allometrically related to seed size (Bond and van Wilgen 1995). *A. morroensis* have seed that varies considerably in size. Successful germination results from the balancing of effects of heat and depth (Whelan 1995), but this balance will be altered if soil heating is accentuated, and/or seeds and soils are affected by moisture in excess of that found in the evolutionary past when *A. morroensis* stands burned.

Considering these factors, it is imperative that research be designed to answer the following basic question: is post-burn seed germination and subsequent seedling survival of *A. morroensis* sufficient to ensure maintenance of the species? Research on postfire seedling establishment of *A. morroensis* can be undertaken in a prescribed burn planned for Fall 1998. It is likely that this burn would take place after at least some fall precipitation, allowing an assessment of regeneration after fire in conditions that land managers prefer.

We recommend the following sampling design. Prior to the burn 10 - 15 permanent plots should be established within the proposed burn boundaries in a range of vegetation types: a) dense monospecific stands, b) under isolated individuals, and c) in adjacent vegetation. Preburn and postburn sampling will be conducted in these plots to assess vegetation cover, seedbank characteristics, soil heating and seedling establishment.

Pre-burn

Collect seedbank samples using the methods described earlier in this report; in addition separate the samples collected from the top 5cm of soil from the bottom 5cm to determine effects of soil depth on seed mortality. Seedbank samples should be collected in manzanita plots only because previous studies have shown that seed is limited to under shrub canopy.

Conduct vegetation sampling. Within the permanent plots, record the percent cover of all species present.

Just before fire (i.e., the morning of the burn), set out “water cans” or paint strips to assess soil heating during the burn. Cans are filled with a known volume of water, a hole is drilled in the top, and tape placed over the hole. Relative soil heating with fire can be determined from water loss from cans placed in the burn.

Postburn

As soon as possible after the fire, assess burn intensity in each plot. Collect cans and measure amount of water remaining, or collect paint strips. Describe fire severity qualitatively. This information will be useful in determining the relationship between seed mortality and seedling emergence, and the level of soil heating.

Collect soil seedbank cores (again, only in manzanita plots), keeping top and bottom samples separate. Comparing pre- and post-burn seedbanks will allow one to determine the percent of seed mortality during fire. In addition, information about densities of seed at various depths, along with seed mortality rates, and seedling emergence, will make it possible to determine if emergence rates are affected by seed mortality, seeds being too deeply buried, or some other factor.

In plots where manzanita is absent, particularly where veldt grass is present, add soil from underneath burned manzanita shrubs. In order to evaluate interactions between exotic species and *A. morroensis*, seed bank samples should be taken after fire and moved into target plots where veldt grass or iceplant occur. The performance of seedlings in these new locations should be compared with those unaffected by exotic species. This will also test the efficacy of moving seed banks to restore sites degraded by exotics to manzanita chaparral.

Monitor plots. In late winter and late spring plots should be monitored for a) *A. morroensis* germination and initial seedling survival, and b) percent cover of other species, including exotics. Survival of *A. morroensis* seedlings associated with exotic species should also be studied and compared with areas where these exotics are removed. Mortality in subsequent years, as well as general stand development should continue to be monitored until it is possible to predict the composition of the vegetation that is likely to persist for the remainder of the fire cycle.

VII) Recommendations for future research

In addition to the burn related research just described, there are some other key questions that need to be answered to better understand the ecology of this species.

Further laboratory and greenhouse experiments should be conducted to a), determine whether seeds from isolated stands (i.e. the Elfin Forest), which have lower viability than other sites, also have lower germination rates, b) examine variation in germinability among sites, to determine the best sources of seed to be used in restoration, and c) repeat treatments described in this report (section III.) to strengthen conclusions from this experiment. Because viability of seeds is so low (~4%) many seeds are required to observe even a few germinating, even when conditions are optimal. Therefore, we recommend repeating germination trials when possible.

The present study reports results of seed bank analyses and germination treatments on seeds that would be present following a fire (i.e., seeds in the soil seedbank below the litter layer.) For restoration purposes, it would be useful to determine the “quality” of all seed sources. We recommend that seed viability be assessed within a site at all stages of seed availability, including 1) intact fruits on shrub, 2) intact fruits on ground, 3) seeds in litter layer. These findings could then be compared to data on seed viability in soil seed bank (from this and previous reports).

Our pilot study on the reproductive biology of *A. morroensis* yielded a number of interesting results. Because pollinator abundance and other factors affecting reproductive success can vary strongly among years, we recommend that these studies be continued. The information that should be gathered for another year includes: 1) identification and quantification of pollinators, 2) measurement of flower production, fruit set, and seed set, 3) rates of self-compatibility, 4) measurement of the addition of fruit to the litter (fruit drop), and 5) seed predation rates.

GIS mapping of the Los Osos and Montaña de Oro region could assist in quantifying historical and current distributions and abundances of *A. morroensis*. In addition, this type of mapping and analysis could help to clarify the relationship among physical factors, such as slope, aspect, and soil type, disturbance factors, land use history and presence/cover of *A. morroensis*.

VIII) Literature cited

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