Mechanisms of Persistence of San Diego Thornmint (Acanthomintha ilicifolia)

Final Report

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ABSTRACT

The purpose of this study was to examine the response of *Acanthomintha ilicifolia* (San Diego thornmint) to various levels of competition and light under controlled conditions. The amount of seed stored in the soil at different times of year was estimated, and the germinability of seeds recovered from the soil seed bank was also studied.

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Two competition experiments were completed. In the first experiment, target *Acanthomintha* plants were grown with high or low densities of *Centaurea melitensis* (Tocalote or star thistle) or with no competitors at all. Competitors were planted in two configurations: "near" and "far". Biomass of target *Acanthomintha* plants decreased significantly with increasing competitor density or close competitor proximity. Fecundity was depressed by competition, but planting arrangement had no effect. The relationship between final *Acanthomintha* biomass and the number of seeds produced was positive and significant.

The second competition experiment utilized three levels of competition and three light treatments in order to test for independent and combined effects of these variables on target clusters of nine *Acanthomintha* plants. The competitor species was *Avena barbata*. The effects of both shade and competitor density on final *Acanthomintha* biomass were significant, and the interaction between treatments was significant as well. Without competitors, shade diminished *Acanthomintha* biomass, but in the presence of competitors, shaded plants outperformed unshaded ones. Seed production was reduced by the presence of competitors, but the magnitude of the decrease was dependent on the shade treatment. As with the first competition experiment, seed production increased as a function of biomass.

Soil seed storage was determined directly by recovering seed from soil samples and indirectly by germinating seeds from soil samples. Seeds recovered from the soil were tested for germinability. Seed storage in the soil was highly variable from sampling date to sampling date, and between the two field sites. In general, it was a small fraction of the likely seed rain, based on earlier studies of the fecundity of plants in the field (Bauder and Sakrison 1997). The number of seeds found in the fall-collected samples was inversely proportional to the amount of precipitation in the previous growing season. Germinability of soil-stored seed was low except for those recovered in the fall of 1998.

Weeding in the field had a significant effect on *Acanthomintha* survivorship only at one site in one year (1997/1998), suggesting that the growth of weedy competitors was favored by that year's high precipitation and longer-than-average growing season. This is consistent with the results of the second controlled experiment which indicated that shade damped the growth and competitive effect of *Avena*, which otherwise caused a significant reduction in *Acanthomintha* biomass and fecundity.

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The results of these experiments, combined with those of the earlier study (Bauder and Sakrison 1997), indicate that weeds can have a significant negative impact on *Acanthomintha ilicifolia* biomass and fecundity, especially in years that favor weedy growth. Many of the common weeds grow rapidly early in the wet season and can quickly overtop slower-growing thornmint plants. Because some of the weeds grow taller than *Acanthomintha* plants, it might be possible to cut off the weeds prior to their seeding without impacting the *Acanthomintha*. The primary negative impact would be trampling of young thornmint plants. Populations near developed land need to be protected from irrigation runoff.

Little seed seems to be stored in the soil and plants harvested late in the summer retain a large amount of seed in the dried calyces. Seed that has been shed likely remains on the soil surface until the rainy season begins. Consequently, fire could have a detrimental effect on *Acanthomintha* populations by diminishing the seed available for the next growing season. Fires might favor some weed species. If the fire effectively reduced weed densities, surviving seedlings should have a higher probability of producing greater biomass and a larger seed crop.

CHAPTER 1. INTRODUCTION

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1.1. PURPOSE OF THIS STUDY

Acanthomintha ilicifolia (San Diego thornmint) is Endangered in the State of California, and on the federal list of threatened plants (CDFG 2000, FWS 1998). Only about 30 natural San Diego thornmint populations survive out of 50 recorded occurrences, and less than half of these are protected (Bauder, McMillan and Kemp 1994). Its range is limited to western San Diego County and northern Baja California, Mexico, and within this limited geographic range it is further restricted to isolated patches of clay soil, sometimes derived from gabbroic rocks (Oberbauer 1993). Typically, these clay patches occur in gently sloping, open, grassy areas surrounded by chaparral vegetation (Bauder et al. 1994).

Little is known about the basic biology of *Acanthomintha ilicifolia*, so that it is difficult to make important management decisions and prioritize preservation measures. Our earlier work (Bauder and Sakrison 1997) addressed seed germination requirements, the effects of weeds on survivorship and fecundity in the field, and insect visitors. The purpose of this study is to build upon the results of the earlier one by focusing on the response of San Diego thornmint under controlled conditions to various competitors and levels of light, and to estimate the amount of seed stored in the soil at different times of the year. Germinability of seeds recovered from the soil seed bank was also examined. Our field research site was at Goodan Ranch/Sycamore Canyon Open Space Preserve, San Diego County, (Department of Fish and Game EO #32: sites 1E and 2 in Bauder, McMillan and Kemp 1994)(Figure 1).

1.2. BACKGROUND

Our recent work indicated San Diego thornmint germination is inhibited by warm temperatures (Bauder and Sakrison 1997). Optimal conditions for germination include a long, daily cool period (c. 10 deg C or 50 deg F)(Bauder and Sakrison 1997). Germinability is related to seed age, with fresh seeds having the lowest germinability and the narrowest range of suitable conditions. As seeds age, the overall percentage germinating increases, and the range of suitable conditions broadens to include higher temperatures. Darkness inhibits germination, more so in younger seeds and at higher temperatures.

Weeding of field plots had little detectable effect on survivorship of Acanthomintha ilicifolia, but a positive impact on fecundity (Bauder and Sakrison 1997). In general, field



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Figure 1. Location of Sycamore Canyon.

survivorship in the 1995/1996 rainfall year was high, exceeding 80 percent for both Sycamore Canyon populations (EO 32)(EO = Element Occurrence in the CDFG Natural Diversity Data Base). Weeded plots had more seeds per survivor compared to unweeded plots (x = 115 vs. 86 seeds per survivor). The seed rain in 1996 was over 5, 000 seeds/m² at Site 1 (EO 32) and nearly twice that number at Site 2 (EO 32).

Insect visitors to San Diego thornmint plants included checkered beetles (Cleridae), bee flies (Bombyliidae), and various bees. The most common visitors were the bees and to a lesser extent the beetles. Both may be transferring pollen from flower to flower and plant to plant. There do not appear to be any narrowly distributed or specialized insects visiting the plants, but additional work, especially on the bees (Hymenoptera), will be necessary before any conclusions can be made.

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Work on another species in the genus, *Acanthomintha duttonii*, has been in progress for over 6 years (Pavlik and Espeland 1991, Pavlik, Espeland and Wittman 1992, Pavlik and Espeland 1993, and Pavlik and Espeland 1994). In these studies, survivorship and fecundity of plants were monitored in the field, laboratory seed germination trials were conducted and the plant was reintroduced to an unoccupied site. Steeck (1995) compared the reproductive biology of *A. duttonii* and *A. obovata* ssp. *cordata* in her master's thesis.

1.2.1. <u>Habitat</u>

Acanthomintha species all are found in grasslands, often on serpentine or gabbro derived clay soils (Jokerst 1993). Pavlik, Espeland and Wittman (1992) did a comparative analysis of serpentine-derived clay soils supporting *A. duttonii*; non-serpentine soils collected from a Monterey County site with *A. lanceolata*; soil from an unidentified site in San Diego County that supported *A. ilicifolia*; and potting soil. As would be expected, the potting soil was highest in NPK. It also was high in Ca and Mg compared to the other soils. The primary difference between the serpentine and non-serpentine native soils was in the Ca/Mg ratio, with a higher ratio in the non-serpentine soils.

Contrary to published floras, *Acanthomintha ilicifolia* is not associated with vernal pools but is usually found on moderate slopes with a slope angle rarely greater than 20° and commonly less than 15° (Bauder, McMillan and Kemp 1994). Clayey soils (sometimes gabbro derived, but probably of various origins) with large, deep fissures during the dry season

appear to be an obligate substrate. The clay fraction of soils supporting San Diego thornmint at Sycamore Canyon is 35 percent (Bauder and Truesdale 2000). Sometimes these soils have a very distinct polygonal pattern of cracks. The soils' structure is crumbly, and when moist they often feel spongy underfoot, unlike vernal pool soils that are generally very dense and plastic when wet (Greenwood and Abbott 1980). Small pockets of soil with San Diego thornmint plants frequently occur on the uphill side of rocks. There is no evidence that water actually ponds in San Diego thornmint habitat as it does in vernal pools, nor that its habitat is found in close association with Mima mound topography as vernal pools frequently are (Bauder 1989, Cox 1984).

Thriving San Diego thornmint populations generally have limited disturbance and relatively sparse weedy competitors (Bauder, McMillan and Kemp 1994). Native geophytes are especially common in and around *A. ilicifolia* plants. Examples are *Allium* spp., *Bloomeria crocea*, *Calochortus concolor* and *C. splendens*, and *Chlorogalum parviflora*. The native grass, *Nasella pulchra*, and possibly other *Nasella* species, are common associates. Annual herbs frequently found with *Acanthomintha ilicifolia* are *Aplastrum angustifolium*, *Calycadenia tenella*, *Corethrogyne filaginifolia* var. *virgata*, *Chorizanthe fimbriata* var. *fimbriata*, *Hemizonia fasciculata* and *Harpagonella palmeri*. Shrubby species often in association are *Adenostoma fasciculatum*, *Eriogonum fasciculatum*, *Heteromeles arbutifolia*, *Malosma laurina*, *Rhamnus crocea*, *Yucca whipplei*, various *Rhus* species and several *Salvia* species. The difference between the plant community where San Diego thornmint is found and the coastal sage scrub vegetation type is that thornmint habitat is more open and has a greater density of grasses and herbaceous species and a lower density of shrubs, soft-leaved or otherwise.

The exotics that are closely associated with *A. ilicifolia* are the grasses *Avena* (several species), *Bromus hordeaceus* and *B. madritensis* ssp. *rubens*; thistles such as *Centaurea melitensis* and *Cirsium vulgare*; and the annual herbs, *Anagallis arvensis*, *Brassica nigra*, *Hypochaeris glabra*, and *Sonchus oleraceus*. The possible negative effect on San Diego thornmint of dense exotic herbs was noted by Taylor and Burkhart (1991, 1993, 1994) in various reports on a mitigation project related to loss of several *Acanthomintha ilicifolia* populations due to development.

1.2.2. The Species

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Acanthomintha ilicifolia (San Diego thornmint) is a small herbaceous mint (family Lamiaceae) that is endemic to western San Diego County and northwestern Baja California,

Mexico. The genus *Acanthomintha* has only four species (five taxa), all of which are found in the California Floristic Province, an area to the west of the Sierra Nevada Mountains and extending from southern Oregon into northern Mexico (Jokerst 1993). Thornmints are all short-stemmed (2-3 dm) annuals with bilabiate white flowers tinged with rose or lavender and subtended by spiny bracts, the origin of the name "thornmint".

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Plants vary in size from only a few centimeters tall with just a few branches, to nearly 2 dm tall, several dozen branches and a spread of 5 dm when growing conditions are favorable. Flowers are produced in clusters (called glomerules) at the stem nodes. Fecundity is affected by the number of nodes, the number of flowers per node and the seeds produced per flower. In common with other members of the mint family, each flower produces only four ovules and therefore has a maximum output of four seeds. Seeds are held singly in schizocarps, or fruitlets, derived by separation, upon maturity, of the four one-seeded carpels composing the flower's ovary. The number of flowers produced per node is indeterminate and can vary greatly depending on growing conditions. The number of nodes per plant is correlated with the number of branches and the length of the branches. Spindly plants with little branching will have a lower reproductive output than plants with numerous branches (Pavlik and Espeland 1993).

In common with the other thornmint species, San Diego thornmint is a winter annual which germinates during the winter rainy period, flowers in late spring and sets seed and dies in early summer. When flowering, it may be quite showy because of dense populations of plants with relatively large and numerous flowers. However, Steeck's (1995) work on *A. duttonii* indicated relatively low rates of insect visitation. This thornmint is self-compatible and capable of autogamy. Autogamous seed production equaled that of plants both cross- and hand-pollinated. *A. obovata* sp. *cordata*, on the other hand, appears to be self-compatible but not as likely to self-pollinate as *A. duttonii*. For these two thornmint species, likely pollinators are medium and large-sized bees, with bumble bees the most common visitors (Steeck 1995). Nothing is known of the breeding system of *Acanthomintha ilicifolia*. Insect visitors were observed and identified in the first study (See "Background").

CHAPTER 2. GREENHOUSE EXPERIMENTS: RESPONSES TO COMPETITION AND LIGHT CONDITIONS

2.1. EXPERIMENT 1: RESPONSES TO COMPETITION WITH CENTAUREA MELITENSIS

2.1.1. Methods

Experiment 1 tested the responses of *Acanthomintha ilicifolia* to three levels of competitor (high, low, and none) of the weed, *Centaurea melitensis* (Tocalote or star thistle), and two levels of competitor proximity (near and far) within the competition treatments.

Twenty-four plastic bins (53 cm x 43 cm x 30 cm deep) were prepared as plant containers by drilling nine drainage holes in each, cleaning with a dilute bleach solution, and then rinsing with water. Each bin was filled with a mixture of potting soil and river sand (3:1) over a 1-2 cm layer of gravel. Bins were placed on outdoor tables in the greenhouse complex at SDSU, watered several times to settle the soil, and then rewetted until soil was saturated. Five to eight *Acanthomintha* seeds were planted in the center of each bin. Treatment combinations included *Centaurea melitensis* seeds planted at either high density (36 seeds) or low density (eight seeds) in a small-diameter (10 cm) or large-diameter (22 cm) circle centered on the *Acanthomintha*, for the "near" and "far" density treatments (Figures 2 A-D). Four bins received no *Centaurea* seeds. Treatments were assigned randomly to bins. (Figure 3) All seeds were collected from DFG EO #32, sites 1 and 2 at Sycamore Canyon during September 1996, and stored in sealed containers at room temperature until this experiment was begun in January of 1997.

After planting, seeds were misted with water to ensure good seed/soil contact. Germination of both species was complete within 2 weeks. After seedlings were established, the *Acanthomintha* was thinned to one target plant per bin and either four or 24 *Centaurea* plants in treatments with competitors. A few *Acanthomintha* were transplanted to bins with no surviving seedlings. Plants were watered as needed until flowering, then left to dry. When all plants were dry, they were clipped at the soil surface and placed in large paper bags, one per bin and dried to constant mass in a drying oven. The total biomass of each species from each bin was determined. *Acanthomintha* seeds were also counted.



Figure 2A. Spatial arrangement of plants within one bin in the low density/near competitor treatment (Competition experiment 1).



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Figure 2B . Spatial arrangement of plants within one bin in the low density/far competitor treatment (Competition experiment 1).



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Figure 2C. Spatial arrangement of plants within one bin in the high density/near competitor treatment (Competition experiment 1).



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Figure 2D. Spatial arrangement of plants within one bin in the high density/far competitor treatment (Competition experiment 1).

A THE NUMBER		
	2- LO, FAR	3- HI, NEAR
4- NO COMPETITORS	5- HI, FAR	6- LO, FAR
7- HI, NEAR	8- LO, FAR	9- HI, FAR
10- LO, NEAR	11- NO COMPETITORS	12- HI, FAR
13- HI, FAR	14- LO, NEAR	15- LO, NEAR
16- HI, NEAR	17- NO COMPETITORS	18- NO COMPETITORS
19- LO, NEAR	20- LO, NEAR	21- HI, NEAR
22- HI, FAR	23- LO, FAR	24-LO, FAR

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HI = 24 COMPETITOR PLANTS LO = 4 COMPETITOR PLANTS

NEAR = 5 CM RADIUS FAR = 11 CM RADIUS

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Figure 3. Layout of treatments in the first competition experiment.

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San Diego thornmint (*Acanthomintha ilicifolia*) grown with star thistle (*Centaurea melitensis*) had significantly different biomass, depending on competitor density (p < .0001, F = 47.625, df = 2, 18 on log transformed data)(Figure 4). With no competition, the biomass of *Acanthomintha* per bin ranged from 6.0 to 44.9 g (x = 25.3 g); bins with low competition yielded from 0.97 to 3.7 g (x = 2.5 g); and the maximum in the high competition treatment was 0.67 g (x = 0.30 g).

Proximity (near and far) and density (high and low) both had a significant effect on target plant biomass(proximity: p = 0.0291, F= 6.014, df = 1,13 and density: p < .0001, F-47.487, df = 1,13 on log transformed data)(Figure 4). Acanthomintha plants with competitors in the "near" position had less than half the biomass of plants with "far" competitors (x = 0.92 g vs. x = 2.08 g), and those with a high density of competitors had mean biomass about 12% of those with a low density (x = .30 g vs. x = 2.50 g).

Competition depressed fecundity as well. Seed production of plants with a low density of competitors was an order of magnitude larger than plants with a high competitor density (x = 95.40 vs. x = 9.71), and two orders of magnitude greater with no competition (x = 864)(p= .0003, F= 13.054, df = 2,18 on log transformed data)(Figure 5). Low density plantings did not differ from those with no competitors). A 2-factor ANOVA using log transformed data indicates that competitor density was significant (p = .0006, F = 19.888, df = 1, 13) but planting arrangement was not (p = 0.3335, F = 1.009, df = 1, 13). Final biomass was a good predictor of seed production. A regression analysis of number of seeds on final biomass, using log transformed data, was significant (p = .0001, F = 51.817, df = 1, 20)(Figure 6).

2.2. EXPERIMENT 2: COMBINED EFFECTS OF COMPETITION AND LIGHT TREATMENTS

2.2.1. Methods

The second experiment utilized three levels of competition and three light treatments in order to test for independent and combined effects of these variables. A total of 45 bins were prepared as before, and arranged in three groups: full sun or those shaded with 50% or 70% shade cloth. Within these three light treatment groups, "high density", "low density" or "no



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Competitor density and proximity

Figure 4. Acanthomintha biomass production under varying competitor , density and proximity treatments (Experiment 1).

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Competitor proximity and density

Figure 5. Acanthomintha seed production with different competitor proximity and density treatments (Experiment 1).





competitor" treatments were randomly assigned (Figure 7). As before, all seeds used were collected from Sycamore Canyon populations the previous year (1998).

Twenty-five Acanthomintha seeds were planted in a 12-cm diameter circle in the center of each bin. Avena barbata was planted around them in densities of 25 seeds ("low competitor" treatment) or 75 seeds for the "high competitor" treatment. (Figure 8 A and B). The Acanthomintha seedlings were thinned to nine per bin, and the shade cloth was installed after the seedlings were established. Bins were watered as necessary until plants had flowered, then allowed to dry. When the Acanthomintha plants were dry, they were harvested by clipping them at the soil surface, dried at room temperature in paper bags for 3-5 days and in a drying oven for 24 hours at 60 deg C, and then weighed. Seeds were separated from the plants and tallied for each bin. For bins with a large number of seeds (c. >1000), the number of seeds was estimated by weighing the seeds and extrapolating, using the mass determined for a given number of seeds.

2.2.2. Results

The effects of both shade and competitor density on final biomass of *Acanthomintha* were significant (shade: p < .0001, F = 37.333, df = 2, 36 and competitor density: p < .0001, F = 176.118, df = 2, 36). There was a significant interaction between shade and density of competitors (p < .0001, F = 19.940, df = 4, 36). Without competitors, shade diminished *Acanthomintha* biomass 28-31 percent, but in the presence of competitors, shaded plants outperformed unshaded ones. Higher shade resulted in higher (58-150 percent) biomass than did low shade (5-8 percent)(Figure 9). Seed production was reduced by the presence of competitors, but the magnitude of the decrease was dependent on the shade treatment. Without shade, high density competitors resulted in no *Acanthomintha* seed production. When shade was low, seed production was nearly equal in the two competitor density treatments, but with the high shading treatment, seed production decreased with increasing competition (shade: p < .0001, F = 21.118, df = 2,36 and competitor density: p < .0001, F = 82.733, df = 2, 36). The interaction between shade and competition experiment, seed production was a function of final per plant biomass (p < .0001, F = 467.406, df = 1, 44).(Figure 11).

2.3. CONCLUSIONS AND DISCUSSION

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San Diego thornmint (*Acanthomintha ilicifolia*) biomass and seed production (fecundity) were depressed by the presence of competitors in both controlled experiments.

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No Shade		hi	no	10	hi	no	no	hi	no
70% Shade		10	hi	10	no	lo 	10	hi	
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Figure 7 Spatial arrangement of bins at greenhouse showing the location of shade treatments and competitor density (Experiment 2).



Figure 8A. Spatial arrangement of plants within one bin in the low competitor density treatment (Competition experiment 2).



Figure 8B. Spatial arrangement of plants within one bin in the high competitor density treatment (Competition experiment 2).

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No Shade

Low Shade

High Shade

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Competitor density

Figure 9. Mean biomass of *Acanthomintha ilicifolia* target plants as a function of competitor density and shade treatment (Experiment 2).



Competitor density

Figure 10. Mean seed production of *Acanthomintha ilicifolia* target plants grown with different competitor densities and shade treatments (Experiment 2).

 $Y = 2.107 + 1.093X; R^2; p < .0001$

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Close proximity of competitors intensified the effect on biomass, but not on seed production, even though seed production had a significant positive relationship with biomass. The response to shading (beyond that created by competitors) was less clear but offered some interesting clues. It appears that moderate and high shading depressed the growth of the competitor, *Avena barbata*, resulting in improved *Acanthomintha* performance, compared to the unshaded treatments. Weedy competitors usually have rapid growth rates, allowing them to exhaust soil moisture or overtop slower growing plants. The shade cloth reduced the growth rate of *Avena* and ameliorated its competitive effects on San Diego thornmint. The two experiments also suggest that *Avena* neighbors have a greater negative effect on *Acanthomintha* growth and fecundity than do *Centaurea melitensis* plants (Table 1). *Centaurea* eventually develops a woody main stem, and drops its lower leaves. This allows light to penetrate the encircling competitors and reach *Acanthomintha*. *Avena* plants develop many stems and an abundance of linear leaves which create and maintain dense shade throughout the growing season.

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The high seed yields of most plants grown in bins with adequate moisture and nutrients and no competitors could be construed as the realization of maximum fecundity under optimal growing conditions. Field grown plants also show high between-plant variability in seed production. The high variability among plants suggests that apparency to pollinators and efficacy of pollinators may be important factors in determining the amount of seed produced.

Data from field transect weeding experiments indicated a negative effect of weedy competitors on the fecundity of *Acanthomintha ilicifolia* (Bauder and Sakrison 1997). Seed production/survivor in the "low competitor density" treatment in the controlled greenhouse experiments was comparable to that found in field plants (Table 1). *Acanthomintha* plants grown in bins without competitors were in some cases an order of magnitude more fecund than those grown with "low competitor density" or those found in the field, although the variability among plants was very high. A single plant in the first experiment's "no competitor" treatment had exceptionally high seed production (3165 seeds), strongly suggesting that pollinator efficacy may be a factor in the highly variable per plant seed production. Another high-biomass plant in this experiment produced only 34 seeds.

An additional, unexpected result of both experiments was observed in the plastic growth response of *Acanthomintha* under cultivation. In its native habitat, an individual *Acanthomintha* plant generally grows to about 5-20 cm in height, and it is often either unbranched or with up to 4 or 5 short branches. An especially large plant may produce cover in a circle of c. 30 cm diameter. In potting soil, with no competitors and adequate water, some plants grew to the size

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	Seeds/Survivor (mean)	Range
Controlled experiments		
Experiment 1		
No competitors	864	34 - 3165
Low density competition	95	25 - 305
High density competition	10	0 - 28
Experiment 2*		
No competitors	874	557 - 1269
Low density competition	30	2 - 74
High density competition	0	0
Field transects (1996)		
Weeded plots		
Site 1	103	<1 - 716
Site 2	132	2 - 491
Unweeded_plots		
Site 1	<u>6</u> 6	2 - 221
Site 2	110	16 - 535

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Table 1. Comparison of seeds/survivor in controlled outdoor experiments at a greenhouse and on field transects in natural habitat. *Underestimate; assumes survivorship of all nine target plants. For sample sizes, see methods.

of small sprawling shrubs, with many densely-leaved branches and abundant flowers and seeds. In the second experiment, branches that "escaped" the shade of *Avena*, became up to 0.5 m long without branching.

CHAPTER 3. SOIL SEED BANK

3.1. METHODS

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To estimate the extent of the soil seed bank of San Diego thornmint (*Acanthomintha ilicifolia*) and its yearly fluctuations, transects for collecting soil samples were established in September 1996 at DFG EO #32, sites 1 and 2 in Sycamore Canyon. These lines avoided the transects used for the field competitor weeding study (Bauder and Sakrison 1997), but passed through comparable habitat and density of *Acanthomintha*. Samples were collected five times at both sites: September 1996, June 1997, May and October of 1998, and June 1999. Additional samples were collected from the competition/weeding transects on the October 1998 and June 1999 sampling dates. No samples were collected during winter or early spring, to avoid site damage due to wet soil.

The samples collected from the soil sampling transects in September 1996, June 1997, and May 1998 were 1 dm² x 2 cm deep. Five were collected from Site 1 and 11 from Site 2. On the remaining two dates, 12 samples were taken from each site, each measuring 2.5 dm² x 2 cm deep. Half of these were from the soil sample transects and half were from the plant competition/weeding transects. No quadrat was sampled for soils more than once during this study.

All mature *Acanthomintha* plants were removed each year from the competition/weeding transects. We wanted to see if minimizing the seed rain reduced the number of seedlings in subsequent years. To determine the extent of the seed rain and compare the seed rain to the soil seed bank, plants removed in October 1998 from sampled squares prior to soil removal were collected in paper bags, and the seeds were counted.

After air-drying for at least a week, each set of soil samples was stored in plastic ziplock bags at room temperature until processed. To recover seeds from the soil, samples were first washed through a fine sieve onto a screen to separate coarse organic matter from clayey soil. This screen was then inverted and washed through a paper coffee filter to catch remaining

seeds and debris. The filter was spread flat on a paper towel and allowed to air dry for several days, then examined under a dissecting scope to find and retrieve any Acanthomintha seeds. All seeds recovered were then tested for germinability. Seeds from each sample were placed on filter paper in a Petrie dish and wetted with distilled water. These were then incubated in a germination chamber with 11 hours light and 13 hours darkness and a constant temperature of 10° C. These conditions were chosen as optimal for germination of Acanthomintha ilicifolia, based on our previous experiments (Bauder and Sakrison 1997). After 2 weeks, the total number germinated for each sample was recorded. All samples except those collected in June 1999 were processed in this way. We also germinated pre-soaked seeds and unsoaked seeds of two ages to determine if the washing procedure itself affected germinability. One-year old and 2-year old seeds were used. A total of 7 replicates of 50 seeds each were prepared for each of the four treatment combinations. Pre-soaked seeds were placed in distilled water for 1 hour, dried for 1 week at room temperature and then re-wetted and germinated in a chamber set with alternating daytime/nighttime temperatures of 22° C/10° C. Unsoaked seeds were wetted at the time of treated seeds and placed in the same chamber. Emerged seedlings were counted after 2 weeks.

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We processed the last set of soil samples (June 1999) differently from those collected earlier. The soil samples were spread 1.25 cm thick over a sub-layer of sand in pony packs which was saturated with distilled water. Packs were incubated in the germination chamber at a constant 10° C for 3 weeks. Emerged seedlings were counted as they appeared.

3.2. RESULTS

Seed storage in the soil was highly variable from sampling date to sampling date, and between the two sites (Table 2). In general, it was a small fraction of the likely seed rain. From the October 1998 sampling date, we estimated a seed rain ranging from 589-1863 seeds/m², and a seed bank of 8-100 seeds per m² x 2 cm deep soil volume. The ratio of seeds in the soil to seeds held on the plant ranged from a low of 2:1000 to a high of 47:1000 in the 18 plots where plants survived to reproduction. In six quadrats no plants survived to reproduce. We expected soil seed storage to be at its lowest after the season's germination ceased during the winter and prior to possible dispersal of newly ripened seed, e.g. in June or July, but no clear seasonal pattern emerged. Examination of the relationship between precipitation and the magnitude of the spring seed bank yielded few clues, partly because the two sites responded differently, but the number of seeds/m² in the fall-collected samples was inversely

	Site 1		Site 2				
	# seeds/ ge (m²)	% erminated	# seeds/ ger (m²)	% minated			
Sampling Date							
11/30/1996	1540	21	855	5 5			
6/24/97	840	14	180	25			
5/20/98	120	0	618	33			
10/23/98	30	7 3 _.	100	71			
6/16/99	<1*	NA .	15	NA			

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Table 2. Seeds per m² recovered from the soil sampling transects and the percentage germinating. For information regarding sampling plot sizes and number of samples taken per site, see the Methods (3.1). * Based on the number of seedlings germinated from the soil.

proportional to the amount of the season's precipitation (Figure 12). When total precipitation during the rainfall season was exceptionally high, the number of *Acanthomintha* seedlings and survivors at Site 2 was generally lower compared to years with less precipitation, but no clear pattern emerged at Site 1 (Figure 13).

Germinability of soil-stored seeds was low, except those recovered in the fall of 1998 (Table 2). The sample size was quite small that year, so the higher percentage germinated may not be meaningful.

Seed soaking and drying prior to germination had no significant effect on the percent of seeds that germinated (p = .1671, F= 2.030, df = 1, 24), nor did the seed age (p = .1020, F= 2.890, df = 1, 24)(2-way ANOVA on arcsine square root transformed data).

3.3. CONCLUSIONS AND DISCUSSION

High precipitation could lead to a large seed crop which would not be "flushed" from the seed bank if the succeeding year had low precipitation. These are the conditions that prevailed prior to fall 1996: high precipitation in 1995, low precipitation in 1996. The fall of 1996 had the soil seed sample with the highest number of seeds. Another possibility is that some seeds could have been shed by the end of September, augmenting the seed bank before we sampled. This is unlikely because the matured seeds are held tightly within the calyx.

CHAPTER 4. SUMMARY OF TRANSECT DATA

4.1. METHODS

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Two sites in Sycamore Canyon, sites #1-E and #2 (Figure 1), were chosen to test the impacts of non-native herbaceous plants on San Diego thornmint (*Acanthomintha ilicifolia*). Three transects were laid out across the site #1-E and two at site #2 in 1996 (Bauder and Sakrison 1997). Sampling quadrats were 0.5 m by 0.25 m, divided into two 0.25-m² plots, one on each side (north and south) of the transect line. A total of 130 quadrats (260 plots) were delineated on the five transects combined. All *A. ilicifolia* seedlings in each plot (or one-half quadrat) were counted in 1996, 1997, 1998 and 1999. Half of the quadrats, chosen at random, were weeded of all exotics, except in 1999. Natives were not removed. *Avena* (several species) and other exotic grasses were by far the most common plants in the quadrats,



Figure 12. Number of *Acanthomintha ilicifolia* soil-stored seeds per m^2 of soil surface, as a function of precipitation. Data are from both sample sites.

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Figure 13. Number of surviving Acanthomintha ilicifolia seedlings per m^2 as a function of precipitation. Data are from the weeding/population transects.

aside from San Diego thornmint. Other exotics removed included Anagallis arvensis, Brassica nigra, Bromus hordeaceus, B. madritensis ssp. rubens, Centaurea melitensis, and Sonchus sp., Weeding was completed in March 1996 and 1997 (Bauder and Sakrison 1997) and May of 1998. The weeding was delayed in 1998 because the rainy season extended into April, leaving the ground too soft for access to the plots earlier in the spring.

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In June of each year, when the A. ilicifolia had set seed and dried, the surviving plants in each plot were counted and collected in paper bags, one bag for each plot (Bauder and Sakrison 1997). Originally, we had hoped to collect each plant separately in its own bag, but this proved to be unrealistic considering the large number of surviving plants, their brittleness and intertwined branches. The collected survivors were stored in their paper bags in sealed containers kept at room temperature, and the number of seeds in each bag was counted for the 1996 harvest only (Bauder and Sakrison 1997).

One temperature data logger (Optic Stowaway by Onset Computer Corp.) was installed at each site on May 15, 1998. Data were recorded at 2-hour intervals from this time until June 29, 1999. The dataloggers were installed just below the soil surface. The maximum temperature that can be recorded is 40° C or 104° F. Data from the dataloggers was compared with US Weather Service temperature data from Lindbergh Field and Gillespie Field. Precipitation data for these two stations were examined as well. Gillespie Field is 10 km south of Sycamore Canyon. The distance inland from the coast is comparable. The Sycamore Canyon research sites are higher than the EI Cajon weather stations, c. 183 meters in elevation, compared to 125 meters for the El Cajon fire station and 117 meters for the Gillespie Field tower.

4.2. RESULTS

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Weeding effects on seedling survivorship were not significant at Site 1 for any of the 3 years we applied the weeding treatment (Table 3)(Figure 14 A). At Site 2, weeding had a significant, positive effect on Acanthomintha seedling survivorship only during the 1997/1998 growing season (Table 4)(Figure 14 B). This positive effect on survivorship persisted into the next season, even though there was no weeding in 1998/1999. Precipitation at San Diego's Lindbergh Field was substantially below average in each year except the 1997/1998 rainfall season, an El Niño year. Total precipitation for that year was nearly double the long term mean. Canyon with adequate records (National Weather Service), have a long-term mean of 33.3 cm

compared to 25.5 cm at Lindbergh Field (National Weather Service). Each year's removal of Gillespie Field and an adjacent fire station in El Cajon, the nearest weather stations to Sycamore the current year's plants with their seed crop did not produce a noticeable decline in the number of surviving seedlings in either the weeded or unweeded plots at Site 2, but at Site 1 a decline was observed (Figure 14).

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Analysis of weather data indicated that Gillespie Field, compared to the coastal Lindbergh Field weather station, has greater annual precipitation and less moderate temperatures (Figure 15). In El Cajon, the November-March nighttime temperatures are in the range that favors *Acanthomintha ilicifolia* germination (5-10° C.), as indicated by germination experiments under controlled conditions (Bauder and Sakrison 1997)(Figure 15). The most moderate daytime temperatures occur between December and March. Temperatures over 25° C. inhibit or prevent germination, especially in newly matured seed. Seeds older than 1 year, germinate more readily at warmer temperatures, but are still inhibited by temperatures over 25° C.

Nighttime surface soil temperatures recorded by the dataloggers were below 15° C. at both Sycamore Canyon sites at the end of November 1998, throughout December 1998, and into January 1999 (Figures 16 and 17). Daytime soil temperatures regularly exceeded 25° C. in the fall of 1998 until November, and began to exceed 25° C. again in March of 1999 (Figures 18 and 19). During the summer months, air temperature recorded at Gillespie Field was nearly always higher than the surface soil temperature recorded by the dataloggers (Figures 18 and 19).

The cooler months (November-March) are also the wettest, averaging a total of 29.11 cm of precipitation, or 87% of the average yearly amount at Gillespie Field (Table 6). The three winter months of January, February, and March have the highest precipitation of any months of the year.

			Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power	
-	Weeding trt	1	.014	.014	.070	.7917	.070	.058	
	Residual	144	29.110	.202					

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1997

		Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1	.278	.278	1.115	.2927	1.115	.173
Residual	144	35.845	.249				

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1998

		Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1	.509	.509	3.050	.0829	3.050	.394
Residual	144	24.043	.167				

1999

		Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1	.276	.276	2.162	.1436	2.162	.292
Residual	144	18.368	.128				

Table 3. ANOVA tables for the number of *Acanthomintha ilicifolia* survivors per plot over a 4-year period at Site 1, Sycamore Canyon. No weeding was performed in 1999.



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Figure 14. Survivorship in weeded and unweeded plots on transects at two sites in Sycamore Canyon. Plants and seeds were removed from plots each year. No weeding was performed in 1999.

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		Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1	.014	.014	.070	.7917	.070	.058
Hesidual	144	29.110	.202				

1997

		Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1	.278	.278	1.115	.2927	1.115	173
Residual	144	35.845	.249				

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1998

		Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1	.509	.509	3.050	.0829	3.050	394
Residual	144	24.043	.167				

1999

146- W		Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
weeding trt	1	.276	.276	2.162	.1436	2,162	292
Residual	144	18.368	.128				

Table 3. ANOVA tables for the number of *Acanthomintha ilicifolia* survivors per plot over a 4-year period at Site 1, Sycamore Canyon. No weeding was performed in 1999.



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Figure 14. Survivorship in weeded and unweeded plots on transects at two sites in Sycamore Canyon. Plants and seeds were removed from plots each year. No weeding was performed in 1999.

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	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1	.425	.425	1.279	.2605	1.279	.190
Residual	112	37.247	.333				

1997

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1.	.034	.034	.128	.7210	.128	.064
Residual	112	29.872	.267				

1998

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1	3.091	3.091	14.671	.0002	14.671	.980
Residual	112	23.597	.211				

1999

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Weeding trt	1	1.439	1.439	6.111	.0149	6.111	.690
Residual	112	26.365	.235				

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Table 4. ANOVA tables for the number of *Acanthomintha ilicifolia* survivors per plot over a 4-year period at Site 2, Sycamore Canyon. No weeding was performed in 1999.



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Figure 15. Comparison of long-term monthly averages for temperature and precipitation at San Diego's Lindbergh Field and Gillespie Field in El Cajon.



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Figure 16. Daily minimum temperatures for ambient air (Gillespie Field) and surface soil (Sycamore Canyon, Site 1).

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Figure 17. Daily minimum temperatures for ambient air (Gillespie Field) and surface soil (Sycamore Canyon, Site 2).



Figure 18. Daily maximum temperatures for ambient air (Gillespie Field) and surface soil (Sycamore Canyon, Site 1).

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1. 1. 1. 1. Figure 19. Daily maximum temperatures for ambient air (Gillespie Field) and surface soil (Sycamore Canyon, Site 2).

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Jul		Aug	Sep	Q	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
0.15 0.05 0.0	0.05 0.0	0.0	0	0.20	1.73	0.94	18.67	7.09	18.95	. 3.58	1.63	0.46	53.44
0.05 0.00 0.00	0.00 0.00	0.00	_	0.00	0.48	1.93	3.86	8.15	6.02	1.27	0.05	0.00	21.82
0.13 0.00 0.00	0.00 0.00	0.00		2.29	4.72	3.48	8.81	1.40	0.00	0.84	0.00	0.00	21.67
0.05 0.00 2.16	0.00 2.16	2.16		0.08	4.19	3.43	6.45	26.29	9.22	2.82	3.07	0.33	58.09
0.51 0.00 0.08	0.00 0.08	0.08		0.20	2.08	1.70	4.70	1.57	1.63	3.23	0.00	0.28	15.98
0.13 0.05 0.46	0.05 0.46	0.46		1.12	3.66	3.56	7.39	6.88	7.62	2.03	0.43	0.28	33.60

Table 5. Monthly precipitation (cm) at Gillespie Field, El Cajon, California. *based on at least 15 years from 1979-1999. Bold indicates data from Lindbergh Field were substituted for missing values.

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4.3. CONCLUSIONS AND DISCUSSION

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The lack of a difference in number of survivors between weeded and unweeded plots may have resulted from the impacts of the weeding itself which negated any beneficial effects of reduced competitor density. It is also possible that weed growth in neighboring plots affected the survivorship within the sampled plots. We do not believe that either of these possible explanations is likely. The response to weeding in the wet year (1997/1998), particularly at Site 2, suggests that the growth of weedy competitors was favored by the high amount of precipitation and consequently, the effects of weeding were more pronounced. This is consistent with the results of the second controlled experiment which indicated that *Acanthomintha* plants in competitive effect of *Avena*. The number of seeds recovered from the soil was the lowest in the fall of 1998. If weedy growth had the same effects in the field on morphology and apparency to pollinators as we observed with the controlled competition experiments, the El Niño year may have resulted in lower fecundity despite greater-than-average moisture.

Seeds lying immediately beneath the soil surface experience a different temperature regime compared to ambient temperatures, if the air temperature data taken from nearby Gillespie Field are comparable to conditions at the two research sites in Sycamore Canyon. In the summer, soil temperatures substantially exceed air temperatures, and they are out of the range favoring *Acanthomintha ilicifolia* germination. Seeds would thus be protected against untimely germination in the event of an uncommon summer rainstorm. During winter months, soil temperatures are generally cooler than air temperatures, favoring germination during the rainiest period of the year.

CHAPTER 5. SUMMARY CONCLUSIONS, DISCUSSION, AND RECOMMENDATIONS

5.1. SUMMARY CONCLUSIONS

In both competition experiments, *Acanthomintha* biomass and fecundity decreased with increasing competitor density. Final *Acanthomintha* biomass was a good predictor of seed production, with greater biomass associated with higher seed set. The effects of shade were more complex. Without competitors, shade diminished *Acanthomintha* biomass, but in the

presence of competitors, shaded plants outperformed unshaded ones. The magnitude of the decrease in seed production was dependent on the shade treatment.

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Seed storage in the soil was highly variable from sampling date to sampling date, and between the two field sites. In general, it was a small fraction of the likely seed rain, based on earlier studies of the fecundity of plants in the field (Bauder and Sakrison 1997). The number of seeds found in the fall-collected soil samples was inversely proportional to the amount of precipitation in the previous growing season. Germinability of soil-stored seed was low except for those recovered in the fall of 1998.

Weeding in the field had a significant effect on *Acanthomintha* survivorship only at one site in one year (1997/1998), suggesting that that year's high amount of precipitation and longer-than-average growing season favored the growth of weedy competitors. This is consistent with the results of the second controlled experiment which indicated that *Avena*, caused a significant reduction in *Acanthomintha* biomass and fecundity, unless it, too, was shaded.

5.2 DISCUSSION AND MANAGEMENT RECOMMENDATIONS

The results of the competition and soil seed bank experiments, combined with the work in the earlier study (Bauder and Sakrison 1997), indicate that weeds can have a significant negative impact on *Acanthomintha ilicifolia* biomass and fecundity, especially in years or under conditions that favor weedy growth. Many of the common weeds, such as the star thistle (*Centaurea melitensis*) and wild oats (*Avena barbata*) used in this study, grow rapidly early in the wet season and can quickly overtop slower-growing thornmint plants. Because these weeds grow taller than *Acanthomintha* plants, it might be possible to cut off the weed tops prior to their seeding without adversely impacting the *Acanthomintha*. Care would need to be taken to minimize trampling of San Diego thornmint plants during the weed cutting.

Our studies indicate Acanthomintha ilicifolia transplantation efforts are likely compromised by inadequate weed control, shading by ornamentals, and irrigation runoff. These conditions could partially explain the decline or demise of four transplanted populations (EO 38, 39, 41, and 42)(Bauder, McMillan, and Kemp 1994). Fertilizers likely encourage weeds and pesticides may eliminate native pollinators. Lack of native vegetation nearby could result in the absence of suitable pollinators or decline in pollinator populations. Low densities of *Acanthomintha* plants (reducing apparency to pollinators) may adversely affect long-term population trends. Disrupted soil structure could also contribute to the failure of transplanted

populations. The mechanisms producing the strong association of San Diego thornmint with clayey soils are still unexplored, and the effects of the disrupted soil profile and structure on soil moisture relations and root growth of both *Acanthomintha* and weedy competitors are unknown. The lack of a substantial soil seed bank indicates that the soil cannot be depended upon to provide sufficient seed to establish a transplanted population or to expand existing populations into restored habitat. Seed must be harvested from plants.

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Fire during summer or fall could have a detrimental effect on *Acanthomintha* populations by diminishing the seed available for the next growing season because little seed is stored in the soil, and plants retain a large amount of seed in the dried calyces until the rainy season begins. Seed that has been shed likely remains on the soil surface. Fires could potentially favor some weed species. Also, a dense stand of weeds would inflate the fuel load in the openings where *Acanthomintha* naturally grows. On the other hand, if a fire effectively reduced weed densities, *Acanthomintha* seedlings should have a higher probability of producing greater biomass and a larger seed crop. Prior to a controlled burn, copious *Acanthomintha* seed would need to be collected. More needs to be known about the effects fire would have on *Acanthomintha* seeds, plants used by insects associated with *Acanthomintha*, and on the various weeds growing in association with it.

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