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SEED FATES OF *ARCTOMECON CALIFORNICA*

by

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ABSTRACT

Seed Fates of *Arctomecon californica*

by

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Seed fates were investigated for *Arctomecon californica* a Critically Endangered plant in the State of Nevada. This species is a short-lived rare perennial plant endemic to the Mojave Desert. Conservation plans for the species would benefit by understanding the fate of *A. californica* seeds from seed production, dispersal, and granivory to incorporation within the seed bank. Each year, 18% of the capsules suffered predispersal loss. The average number of seeds per capsule ranged from 87 to 99 seeds. Seed viability ranged from 87.5% to 100% per plant. Seed production was highly dependent on the number of mature capsules per plant and was used to predict seed output per plant. Dispersal from the capsule mainly by the ejection of seeds triggered by wind tended to disperse seeds away from parent plants. Once seeds reached the soil surface, ants were the main agents responsible for seed removal. The role of rodents appeared to be minimal in *A. californica* seed removal experiments. Examination of the potential role of seed elaiosomes in dispersal elicited variable responses from ants. The seed bank of this species was spatially heterogeneous with most seeds found either close to the surface (34%) or deep within the soil column (26%). The proportion of viable seeds tended to be highest within the 6-15 cm depth increment, suggesting the presence of a long-lived seed bank. The distribution of seeds within the seed bank with respect to viability indicated

10.5% were viable seeds while 35.6% consisted of seed fragments or decayed seeds and the rest, 53.9% were filled but non-viable seeds.

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CHAPTER 1

INTRODUCTION

Seed fates determine the future regeneration and persistence of most plant populations. The interaction between seeds and the environment influence the temporal and spatial patterns of plant species (Harper et al. 1970, Harper and White 1974). Thus, knowledge of the links between seeds and the factors that influence successful propagation of the species are important for successful conservation and restoration.

Arctomecon californica Torrey and Fremont is a short-lived perennial plant endemic to the Mojave Desert and is listed as a Critically Endangered plant by the State of Nevada. The species is a member of the Papaveraceae, or poppy family, and one of three members of the genus *Arctomecon* limited in distribution to Southern Nevada and Northern Arizona. The other two species represented in the genus *Arctomecon* include the endangered *Arctomecon humilis,* confined to southwestern Utah (Harper and Van Buren 2004), and *Arctomecon merriamii*, restricted to southern Nevada and southeastern California (MacMahon 1985). The genus *Arctomecon* is derived from *Arctos* (bear), and *mecon*, (poppy) resulting in several vernacular names including the Las Vegas bearpoppy, golden bear-claw poppy, golden bear poppy, yellow bear-claw poppy, yellow-flowered desert poppy, California bearpoppy, and California bearclaw poppy (Phillips and Phillips 1988, Mistretta et al. 1996, Sheldon-Thompson and Smith 1997). The accepted common name is the Las Vegas bearpoppy.

The habitat of *A. californica* consists mainly of gypsum (calcium sulfate dehydrate) outcrops but also inhabits claybeds, high-boron shales (Meyer 1986), alluvium (Drohan and Buck 2006), desert pavement and "gravelly slopes" (Mistretta et al. 1996). The gypsum substrates are referred to as "gypsum barrens" (Swearingen 1981) ranging from 18-69% gypsum within the soils (Myers 1986) that form edaphic habitats intermixed within the *Larrea tridentata* and *Atriplex canescens* communities of the Mojave Desert (Thorne 1976). In addition to *A. californica,* these barrens support other "gypsum-tolerant species" including *Atriplex confertiflora, Atriplex hymenelytra, Anulocaulis leiosolenus, Camissonia multijuga, Enceliopsis argophylla, Ephedra torreyana, Eriogonum corymbosum, Eriogonum inflatum, Eriogonum insigne, Lepidium fremontii, Mentzelia pterosperma, Petalonyx parryi, Phacelia palmeri, Phacelia pulchella, Psorothamnus fremontii, Psathyrotes pilifera* and *Tiquilia latior* (Meyer 1986, Phillips and Phillips 1988, Mistretta et al. 1996, Powell 1999).

By 1994, all surveys documenting historical and current *A. californica* populations were considered complete and revealed a total of 108 populations. In Nevada, habitat destruction in the western portion of the species range from the rapid expansion of the Las Vegas Valley caused the extirpation of 13 *A. californica* populations. The status of four additional *A. californica* populations was unknown but considered lost. This left 91 surviving populations in Nevada estimated at 580,000 plants covering approximately 8,498 hectares between 320-960 m above sea level (asl). However, Mistretta et al. (1996) identified an additional 13 populations in the Las Vegas Valley that were threatened with extirpation in the foreseeable future due to growth. An additional 29 populations have appeared to or will soon experience significant impacts from growth, off-road vehicle use, mining and mineral exploration, animal grazing, and trampling by feral burros and horses. The other 49 Nevada *A. californica* populations located in the eastern half of the species range are under the Federal management of the National Park Service (NPS) and the Bureau of Land Management (BLM) suggesting extinction of the species as a whole appears unlikely (Mistretta et al. 1996, Phillips and Phillips 1988).

Arctomecon californica is an herbaceous perennial plant composed of a mosaic of live and dead rosettes ascending from a taproot. A single stalk arises from each rosette bearing multiple yellow flowers. Plants flower yearly from March to June generally within 1 to 2 years of establishment. They are commonly self-incompatible plants requiring cross-pollination of the flowers for seed set (Sheldon 1994). There is no vegetative reproduction (Meyer 1987, Mistretta et al. 1996). Flowers are pollinated by bees, wasps, beetles and ants. The most important pollinators are the rare Mojave bee (*Perdita meconis*) and the Adrenid Bee (*Megandrena enceliae*; Hickerson 1998).

This species is considered to have a high reproductive output with 91.3 ± 3.5 seeds per mature fruit (Meyer 1987). Seeds appear to be dispersed by strong winds indicative of the Mojave Desert from May to June (Mistretta et al. 1996). Once seeds are shed from the parent plant they tend to disappear. Germination occurs during the late winter months indicating seeds may require cold stratification for dormancy release (Meyer 1987). Meyer (1987) and Sheldon (1994) both found that the seedling stage suffered the highest mortality rate. Plants that survived to flower, tended to live an average of 4 to 5 years (Meyer 1987). The combination of a short life span coupled with infrequent germination events resulting from insufficient rainfall are the primary causes for the extreme year-to-year fluctuations observed in *A. californica* population densities (Meyer 1987).

In the past, areas that had once supported *A. californica* plants but no longer appeared to have any live plants were no longer considered habitat for the species. This led to the development or uses other than conservation for these unoccupied areas resulting in the loss of *A. californica* habitat over time. Following the death of the live plants, the population may persist for many years as seed bank with a return of live plants following cold winter rains that stimulate germination (Meyer 1987, Powell 1993). This suggests a long-lived seed bank (Meyer 1987, Mistretta et al. 1996). However, preliminary soil seed bank analyses conducted by Science Applications International Corporation (2001) at Bearpoppy Hill, located near the intersection of Lake Mead Boulevard and PabCo Tram road in the Sunrise Management area of Clark County, Nevada (east of Las Vegas, Nevada) concluded that the soil was "depauperate" of *A. californica* seeds. Another *A. californica* seed bank study considered the most intensive to date was conducted by Megill et al. (2007). This study near Eglington Preserve in North Las Vegas, Nevada, found 1.44 seeds per m^2 in an area occupied sporadically by live *A. californica* plants over the past several years (Megill et al. 2007).

Although the existence of a long-lived soil seed bank explains the disappearance and re-appearance of *A. californica* plants on certain sites over time, concern over a decline of *A. californica* populations for the past several years in the Las Vegas Valley due to urbanization has escalated (E. Powell pers. comm.). There has been limited success with transplanting *A. californica* plants (Winkle 2004) and germination of the species had been extremely difficult as well (Powell and Walker 2003). The concern over the decline in *A. californica* populations is even more pronounced in years with limited germination events which cause proponents to push for endangered species status. Then in those years in which germination events due occur, there is the perception that the species may not be rare at all and does not warrant designation as an endangered species. However, extirpation of *A. californica* populations due to urbanization in the Las Vegas Valley has caused a decline in the number of populations of this species. Other factors that may contribute to this decline include intrinsic biological attributes that constrict plant distribution such as life history traits, limited seed dispersion (Meyer 1987) lack of genetic variability (Hickerson and Wolf 1998), pathogens (Mistretta et al. 1996, Meyer 1996), seed predators (Pantone et al. 1995), or lack of pollinators (Hickerson and Wolf 1998).

Overall, there is a general lack of knowledge regarding the fate of *A. californica* seeds. The unknown fate of *A. californica* seeds provides an information gap in conservation management plans that is critical to the preservation of the species (Powell and Walker 2003). It appears that the species survives as a seed bank for part of its life cycle and understanding this is necessary for preservation of habitat where live plants have disappeared and survive only as a seed bank. Also, once seeds are shed from the parent plant they tend to disappear suggesting possible predation by ants and rodents or possible dispersal off-site. Current mitigation measures consist of soil salvaging, an expensive measure to aid in re-colonization of the disturbed area. If removal of *A. californica* seeds off-sites by processes not yet understood occurs then current mitigation measures would be seriously undermined. Therefore, the objective of this research was to determine the seed fates of *A. californica* from seed production, seed dispersal, and granivory to incorporation within the soil seed bank. The following questions were addressed in this research study: (1) Are there physical attributes of *A. californica* plants that can predict seed production? (2) What are the dispersal patterns of the seeds? (3) Do elaiosomes on the seeds promote dispersal by ants? (4) Is there a seed bank of *A. californica* seeds; are those buried seeds viable and what is the vertical distribution of the seeds?

CHAPTER 2

METHODS

Study Sites

The study sites were located throughout the natural range of *A. californica* in the northeastern portion of the Mojave Desert along the western edge of Lake Mead National Recreation Area (LMNRA) and the Frenchman Mountains, near Las Vegas, Nevada (Fig. 1). Sites 1-3 (Rainbow Gardens) were gypsum evaporite deposits, or badlands, at an elevation of 585 m above sea level (asl) in the Frenchman Mountains and were at least 100 m apart. Sites 4-5 (Stewarts Point) were characterized by exposed rocky gypsum outcrops covered in alluvial gravel at 373 m asl (Powell 2003). These were at least 500 m from each other and 97 km from Sites 1-3. All the gypsum outcrops are located within the southern Basin and Range Providence and derived from the Muddy Creek geologic formation (Phillips and Phillips 1988) deposited during the Permian to Quaternary age (Meyer 1986). The average annual temperature is 20 ° C with extreme temperatures ranging from -13 ° C to 47 ° C. Precipitation varies from 14 mm to 272 mm with an annual average of 114 mm (National Weather Service 2006).

In April 2004, at each of the five sites, I established one 100 x 20 m plot that had at least 15 flowering *A. californica* plants and was minimally disturbed by off-road vehicle traffic or human activities. All data were collected within these plots. I measured seed production, seed dispersal, and granivory at Sites 1-4 from March-September 2004 and

2005 and seed bank at Sites 1-5 from January-March 2005. Site 5 was added for the seed bank study to increase statistical power.

Seed Production

I sampled seed production from March-July in both 2004 and 2005. Five different reproducing *A. californica* plants were randomly chosen per site each year. All mature capsules were removed from the parent plant prior to dispersal (methods from Myerscough and Marshall 1973) and the following capsule measurements were recorded for each capsule in cm: the length, diameter (greatest width across each capsule), volume and the number of seeds per capsule. Estimated capsule volume was based on the capsule shape and calculated using each of the following volume equations: cone = $\frac{1}{3}\pi r^2 h$, cylinder = $\pi r^2 h$ and sphere = $\frac{4}{3}\pi r^3$. The following plant characteristics were recorded for each reproductive *A. californica* plant within each plot during May-June 2004-2006: the number of flowers, capsules, stalks, and rosettes per plant, plant diameter (avg. two perpendicular measurements) and plant size based on the area of a circle (πr^2).

Seed production samples from 2005 were stored at room temperature in coin envelopes for six months in a closet. Viability was tested on a subset of seeds with 2, 3, 5-triphenyl tetrazolium chloride solution following ten hours of soaking in distilled water (AOSA 2000). After soaking, seeds with pink-stained embryos were considered viable. Preliminary viability testing of seeds encased in capsules with obvious fungal infection resulted in 90% mortality of infected seeds therefore, those capsules were discarded from the data set due to bias.

Seed Dispersal

I measured plant-based seed dispersal using seed traps placed around five different randomly chosen plants that differed from those used for seed production at Sites 1-4 (methods from Chambers and MacMahon 1994). In spring 2004, I trapped seeds using 10x10 cm squares of cardboard coated with Tanglefoot®, a sticky adhesive substance. Each sticky trap was placed randomly within four equal-sized quadrats designated by their center point as North (0°), South (180°), East (90°) and West (270°) in three concentric rings (20 cm, 40 cm, and 60 cm radius) from the edge of the plant (Fig. 2). To obtain proportional sampling of area amongst rings, four traps were placed in the smallest ring (0-20 cm), 12 in the middle ring (20-40 cm) and 20 in the outer ring (40-60 cm). The total area sampled by plot-level sticky traps was 1.8 m^2 or 0.09 % of each plot.

In spring of 2005, I repeated this study but added an additional two concentric rings that extended the design out to a radius of 100 cm from the edge of each plant to increase the chances of capturing the tail-end of the primary seed dispersal curve (Fig. 2). This resulted in 100 traps instead of 36 traps around each of the five targeted plants and 2.5% of each plot covered with traps. Additionally, the five study plants were dissected once natural dispersal concluded to determine the average number of seeds trapped within plants during seed dispersal. The seeds within the plants were not used in any analyses because I was unable to determine if the seeds were from the current year or an accumulation of past years. These seeds likely accumulated over past years because numerous seeds were lodged in decayed rosettes. Also, seeds from nearby plants may have inflated the number of seeds trapped around seed dispersal study plants during 2004; therefore I removed all capsules from all plants within 200 cm of the 2005 seed dispersal plants to try an minimize any potential bias.

The plot-level seed dispersal design consisted of 180 sticky traps placed randomly within the plots at Sites 1-3 from March-April 2004 and 2005 (methods from Chambers and MacMahon 1994; Fig. 3). The total area sampled was 1.8 m^2 or 0.09% of each plot. The captured seeds were counted and their trap locations plotted on x, y grids along with the distance to the closest reproducing *A. californica* plant.

Granivory

Exclusion experiments consisted of a two-way factorial experiment with four treatments (excluding ants, rodents, both or neither) at Sites 1-4 conducted 1-2 months after natural dispersal. The granivory experiment consisted of five separate trials conducted in 2004 and 2005: Trial 1: 20-25 July 2004, Trial 2: 27 July-1 August 2004, Trial 3: 13-20 July 2005, Trial 4: 28 August-2 September 2005 and Trial 5: 2-9 September 2005. Each replicate consisted of four petri dishes assigned to each of the four treatments containing 30 seeds each (Fig. 4), and five replications of each treatment per site. Groups of replicates for each treatment were placed randomly throughout the plots at Sites 1-4, irrespective of plants. Several pebbles were placed in each dish to mimic the natural environment. Cages consisting of 10x8x5 cm boxes of wire mesh with an aperture size of 5x5 mm were used to exclude rodents from the seeds. To exclude ants, Tanglefoot® sticky adhesive was applied as a circular moat around cage-free petri dishes containing *A. californica* seeds. To exclude both rodents and ants, rodent exclosures and Tanglefoot® circular moats were placed around the petri dishes. Controls that excluded neither rodents nor ants consisted of petri dishes with seeds placed in the open without cages or moats.

Elaiosome

During preliminary analyses, I noted that many of the *A. californica* seeds had white, fleshy appendages located along the hilum (point of attachment of the seed to the ovary tissue) edge of the seed (Harper and Van Buren 2004). These appendages resembled Beattie and Culver's (1981) definition of an elaiosome i.e. "the general presence of a white or cream-colored, glistening tissue present as a discrete external body..." (Fig. 5). Elaiosomes are an "energy rich" food source made up of proteins, lipids and carbohydrates utilized to promote collection and dispersal by ants (Marshall et al. 1979, Beattie and Culver 1981, Hanzawa et al. 1985, Brew et al. 1989). However, not all tissues on seed coats are adaptations for ant dispersal (Roth 1977). The morphological and functional roles of these appendages on *A. californica* seeds are unknown. To determine how common these putative elaiosomes were, I examined 18,453 *A. californica* seeds taken from Sites 1-4 in 2004 and 2005 that were used in granivory experiments. An additional collection of 4,800 seeds collected from the population at the North Las Vegas Airport, Nevada approximately 40 km NW of Sites 1-3 was provided by the Bureau of Land Management and only included in the elaiosome survey.

I conducted several elaiosome experiments to determine if ants would selectively choose *A. californica* seeds with elaiosomes over seeds without elaiosomes, as suggested by numerous studies (O'Dowd and Hay 1980, Brew et al. 1989, Oostermeijer 1989, Handel and Beattie 1990, Hughes and Westoby 1992). All experiments were conducted after natural dispersal with each treatment placed in separate polyurethane dishes covered with screen to prevent rodent removal and allow air circulation. The first elaiosome experiment consisted of two trials: 14-20 July 2005 and 20-21 July 2005, testing seeds with an elaiosome versus seeds without elaiosomes. The design included five replicates of two treatments per site (n = 4) with 10 seeds per treatment. The second experiment included two trials: 28 August-2 September 2005 and 2-7 September 2005 that differed from the first experiment by nicking the seed coat of all seeds. This nicking accounted for any preferential choice that may result from the accidental nicking of the seed coat when removing the elaiosome. Additionally, special care was taken when removing the elaiosomes to ensure no fragments were left behind. The design consisted of five replications of two treatments (both nicked but with and without elaiosomes) per site ($n = 4$) with 10 seeds per treatment. A third experiment was conducted for five consecutive days from 23-28 September 2005. The design included ten replications of three treatments per site ($n = 4$) with 10 seeds per treatment. Each replication pooled all treatments into a single screen-covered polyurethane dish to increase chances of detecting preferential selection by ants. The three treatments consisted of: (1) intact seeds plus elaiosomes; (2) seeds with elaiosomes removed; and (3) intact seeds with elaiosomes plus nicked seed coat (methods from Brew et al. 1989).

Seed Bank

At Sites 1-5, I analyzed the seed bank in 2005 by collecting soil cores within a 20 x 20 m grid subjectively placed within the area of maximum *A. californica* density. At each of 200 randomly located points within each grid, I removed 954.3 cm^3 soil cores (9 cm diameter, 15 cm height, vol. of cylinder) at four depth increments (0-2 cm, 2-4 cm, 4-6 cm and 6-15 cm). The total number of soil cores removed per site was 200 (200 cores * 4 depths = 800 samples) with the total area sampled 1.27 m^2 or 0.32% of each grid surface. The number of seeds were counted for each depth increment and assigned to either one of the following categories based on seed condition: seed fragment (decayed seed), filled seed (firm and plump) or viable seed (tetrazolium test). The total number of seeds found per site within each grid was determined by averaging the four pooled depths for each site ÷ 1.27 m^2 (area sampled per grid) equals the average number of seeds per m^2. The average number of seeds per m^2 within each depth increment was calculated by averaging the five pooled sites for each depth increment ÷ 1.27 m^2 (area sampled per grid). The 6-15 cm depth increment was divided by 4.5 to adjust for volume differences between depths to calculate mean seeds per cm^3.

Seed Fate Model

The *A. californica* seed fate model is based on data collected over the two-year study period and presented as percentages. The number of adults and seedlings ($\leq$ 2 cm) were based on the average of each over two years. Seedling mortality was determined using the proportion of seedling deaths divided by total seedlings * 100 for each site from 2004 to 2005 and averaged. Estimated seed production per plant was determined by applying the seed production predicator equation: No. Seeds = 41.07*(No. mature cap/plant)$^{1.232}$ and averaging the estimated number of seeds produced over two years. Predispersal was the average number of aborted capsules divided by mean number of capsules produced per plant * 100. The percentage of seeds that fell within plants was based on the average number of seeds found within plants divided by the total estimated seeds produced per plant * 100. The percentage of seeds trapped during plant-base dispersal studies was calculated as the total number of seeds trapped per plant ÷ estimated seed production and then extrapolated out to the plot-level. Plot-based dispersal was calculated as seeds trapped per m^2 and as a percentage to determine the approximate number of seeds trapped during seed dispersal based on estimated plot-level seed production. The percentage of *A. californica* seeds lost to granivory was calculated from the proportion of seeds removed from treatments that excluded rodents and no exclusion (control) averaged across Trials 1-5 * 100.

Statistical Analyses

Differences in seed output per plant among years and sites were analyzed using a mixed-model ANOVA. The fixed effects of site, year, and site*year and the random effect of plant (site) were tested. Seed production per plant was derived using regression analysis with total seeds per plant as the response variable and the number of mature capsules per plant as the predicator variable. Within each year, the seed production predictor equations were analyzed for slope differences using analysis of covariance (ANCOVA) with the number of mature capsules per plant as the covariate (Sokal and Rohlf 1981). Where there were no significant effects of year*capsules, data were combined for years to determine a single predictive equation for seed output per plant.

The relationship between seed production per plant versus plant attributes (capsule attributes and plant characteristics) were tested using correlation and regression analysis. Each capsule attribute and some plant characteristics were slightly different variations of one another that were based on the same measurement, which resulted in inter-correlation among variables. To deal with this problem, I selected the variables with the strongest relationships with seed output per plant and when required performed step-wise multiple regression analysis to ensure spurious conclusions were not made.

Plant-based seed dispersal data for both years were analyzed independently due to a design change in 2005. Variables were $\log_{10}$ transformed ($x` = \mathrm{Log}_{10(x+1)}$; Zar 1984)). Each year was analyzed using a mixed-model ANOVA with fixed effects of site, ring, direction, and site*ring, site*direction, site*ring*direction and the random effect of plant(site). Bonferroni adjustments were made when studying pairwise differences.

Treatment differences for exclusion and elaiosome experiments were tested using a mixed-model ANOVA with fixed effects of site, treatment, and their interaction on the number of seeds removed. Replicate group within each site was included as a random effect. Prior to analysis, the dependent variable was $\text{Log}_{10(x+1)}$ (Trial 1 and Trial 3) or $\text{Sqrt}_{(x+3/8)}$ (Trial 4) transformed for exclusion trials to meet assumptions of normal residuals and equal variance (Sokal and Rohlf 1981, Zar 1984). If transformation was not possible, then non-parametric two-factor analysis and extension of the Kruskal-Wallis test was performed (Granivory Section: Trial 2 and Trial 5) with multiple comparison testing (Zar 1984). Elaiosome data was non-normal, therefore all data was transformed using $\text{Sqrt}_{(x+3/8)}$ except for Experiment 1 which was $\text{Log}_{10(x+1)}$ transformed. Bonferroni adjustments were made when studying pairwise differences.

Seed bank analysis yielded data that did not fit known theoretical distributions; therefore an empirical distribution was created using bootstrapping, artificial re-sampling of data 1,000 times (Zar 1984). The total number of seeds found within the seed bank was analyzed using a mixed-model ANOVA with fixed effects of site, depth and site*depth and the random effect of soil core(site). Bonferroni adjustments were made when studying pairwise differences. The proportions of filled and viable seeds per depth versus the total number of seeds found were pooled among sites to test for differences between depths. Multiple comparisons were made using a test analogous to Tukey post-hoc with angular transformations for each proportion (Zar 1984). SPSS was the primary statistical software used for all analyses except for the seed bank analysis in which R software was used. Significance was determined at $P < 0.05$.

CHAPTER 3

RESULTS

Seed Production

Arctomecon californica populations exhibited year-to-year variation in seed production ($F_{1,8} = 29.628$, $P < 0.0001$; Fig. 6). There was approximately a seven-fold increase in the average number of seeds produced from 2004 (429 ± 102.2 seeds) to 2005 (3,374 ± 595.9 seeds) and a five-fold increase in the average number of flowers (20 ± 2.30 to 95 ± 9.29) and capsules (17 ± 1.9 to 82 ± 7.7) per plant. Also, the mean number of seeds per capsule slightly increased from 2004 (87 ± 3 seeds; n = 79 capsules) to 2005 (99 ± 1.5 seeds; n = 634 capsules). In addition to the increase in reproductive structures among years, a random sample of plants (n = 48 plants) which survived both years showed an 85% average increase in plant size. Predispersal loss, the average number of aborted capsules per plant increased more than 4 times from 2004 (3 ± 0.58) to 2005 (14 ± 2.64) which is approximately 18% predispersal loss per plant. Even though differences between years was detected, seed production did not significantly vary between sites ($F_{3,15} = 0.782$, $P = 0.521$) or with the combination of site and year ($F_{3,7} = 0.972$, $P = 0.456$).

In 2005, seed viability was tested on a subset of seeds gathered from seed production studies that were stored for 6 months under normal conditions. Overall, 94 ± 0.84% of the seeds tested across Sites 1-4 were viable. Seed viability ranged from 87.5% to 100% per plant within sites (n = 19 plants; Table 1).

Several plant characteristics were analyzed to determine whether any of the variables were capable of providing a reliable estimate for seed output per *A. californica* plant. In 2004, the results of the Pearson correlation analysis indicated that the number of mature capsules per plant ($r = 0.962$, $P = < 0.0001$; $n = 16$ plants) and the number of flowers per plant ($r = 0.540$, $P = 0.031$; $n = 16$ plants) were significantly correlated with seed production at the plant-level compared to any other plant characteristics (Table 2). All variables were $\text{Log}_{10(x+1)}$ transformed except for the number of flowers per plant to meet normality assumptions. The predicator variables, the number of mature capsules and the number of flowers per plant along with the response variable, number of seeds produced were analyzed in a multiple regression analysis. Multicollinearity was an issue therefore, step-wise multiple regression analysis was performed. This analysis indicated a highly significant model ($F = 355.414$, $P = <0.0001$) with an $r^2 = 0.959$. The regression coefficient was b = no. mature cap/plant = 95.084, $P = <0.0001$ and the y-intercept = -40.100, $P = 0.235$. The regression linear model for 2004 seed production was: No. seeds = 95.084 * No. mature cap/plant (Fig. 7).

The second year results supported those of 2004, the number of mature capsules per plant had the strongest relationship with seed output per plant ($r = 0.955$, $P = < 0.0001$; $n = 20$ plants). Pearson correlation analysis also detected a significant relationship between seed production per plant and plant diameter ($r = 0.788$, $P = <0.0001$), plant size ($r = 0.770$, $P = <0.0001$) and the number of stalks per plant ($r = 0.547$, $P = 0.013$) in the second year, which was not discernible in the first year (Table 2). Also, the strength of the relationship between seed output and the number of flowers per plant slightly increased in 2005 ($r = 0.614$, $P = 0.004$). The predicator variables, the number of mature capsules, flowers, and stalks per plant, plant diameter and plant size along with the response variable, the number of seeds produced were analyzed in a multiple regression analysis. Again, multicollinearity was an issue in the model therefore, step-wise multiple regression analysis was performed. The results of the step-wise multiple regression analysis indicated a highly significant model ($F = 269.721$, $P = <0.0001$) with an $r^2 = 0.934$. The regression coefficient was b = no. mature cap/plant = 109.738, $P = <0.0001$ and the y-intercept = -353.332, $P = 0.185$. The resultant linear model for 2005 seed production was: No. seeds = 109.738 * No. mature cap/plant (Fig. 7).

The relationship between the number of mature capsules per plant and the number of seeds per plant was used to estimate seed output per *A. californica* plant for 2004 and 2005. The resultant regression equations for each year in Figure 7 were compared to determine if the two lines might be estimating the same population regression coefficient; therefore, I tested the assumption of homogeneity of ß (slope). An analysis of covariance (ANCOVA) was performed modeling year as a fixed effect, the number of mature capsules as the covariate and the number of seeds per plant as the dependent variable. Even though I observed some heteroscedasticity in the data, there were no significant differences among the slopes ($F_1 = 0.234$, $P = 0.632$; Table 3). For that reason, both years of data $\mathrm{Log}_{10(x+1)}$ transformed were combined into a single predictive equation to estimate seed production per plant. The overall model was highly significant ($F_{1,34} = 819.793$, $P < 0.0001$) with $r^2 = 0.963$. The resultant equation was: $\mathrm{Log}_{10(x+1)}$(No. seeds) =

1.232 * $Log_{10(x+1)}$(No. mature cap/plant) + 1.624. The final model in original form was: No. seeds = 41.07*(No. mature cap/plant)$^{1.232}$ (Fig. 8).

At the population level, I estimated realized seed production (potential output minus aborted capsules) per plant (n = 4 sites) using the number of mature capsules per plant and the derived seed output equation: No. of seeds = 41.07*(No. mature cap/plant)$^{1.232}$ (Table 4). In 2004, the estimated seed output per plant ranged from 510 to 1,406 seeds with an average of 1,171 ± 187.06 seeds per plant. At the site-level, seed production ranged from 3,572 to 41,894 seeds with an average seed production of 443,799 seeds per site. An increase in seed production occurred in the second year, the estimated seed output per plant ranged from 3,931 to 13,4890 seeds with an average of 8,998 ± 1,089.35 seeds per plant. At the site-level, seed production ranged from 154,455 to 1,254,609 seeds with an average seed production of 443,799 seeds per site. On average across years, 234,288 seeds were produced per site. The most dramatic increase in seed output among populations occurred at Site 4 (Stewarts Point) in 2005, where an estimated 1.2 million seeds were produced (Table 4).

I investigated whether or not capsule attributes have unique contributions to predicting seed output within a capsule as well. Spearman rank correlation analysis was performed on 2004 (n = 79 capsules) and 2005 (n = 634 capsules) data because data failed Shapiro-Wilk normality tests and several transformations were unsuccessful. Both years were affected by multicollinearity issues given that most of the capsule measurements were slight variations of one another resulting in redundancy. All capsule attributes were significantly correlated with the number of seeds per capsule in 2004 but none were significant in the second year (Table 5). In 2004, the length of the capsule (cm) had the strongest relationship with the number of seeds per capsule ($r = 0.548$, $P = <0.0001$) compared to the other variables.

Seed Dispersal

In 2004, plot-level seed dispersal studies indicated the seed dispersal curve for *A. californica* was leptokurtic (high peak) with a long right-tail. The seed dispersal curve peaked at 100 cm with the tail-end of the curve extending up to 400 cm away from the closest source plant (Fig. 9). The average distance seeds were trapped away from the assumed closest source plant was 213 ± 44.1 cm. Out of 180 plot-level sticky traps placed randomly within each site ($n = 3$), approximately 2.0 ± 0.2% of the traps caught seeds. The mean number of seeds per trap and per m^2 among sites was Site 1: 0.02 ± 0.014 seeds per trap (2 seeds m^2), Site 2: 0.06 ± 0.056 seeds per trap (6 seeds m^2) and Site 3: 0.02 ± 0.014 seeds per trap (2 seeds m^2). Due to the minimal number of sticky traps that caught seeds among sites, 8 traps in all, the interpretation of the seed dispersal curve and seeds per square meter are preliminary at best.

The second year plot-level dispersal data captured a better representation of the overall seed dispersal curve for *A. californica* plants than previous year data. The distribution was leptokurtic with the peak of the seed dispersal curve 100 cm away from the closest potential source plant followed by a decrease in the number of seeds with increasing distance (Fig. 10). *Arctomecon californica* seeds were found at distances up to 800 cm from a potential source plant. The average distance seeds were trapped away from the closest adult plant was 210 ± 22 cm. The frequency distribution illustrates that 33% of the traps that caught seeds were at distances greater than 200 cm from the source whereas 67% were less than 200 cm (Fig. 11). Approximately, 9.0 ± 0.3% of the plot-level sticky traps caught seeds at each site (n = 180 traps) which was almost a five-fold increase from 2004. The mean number of seeds per trap and per m^2 among sites was Site 1: 0.63 ± 0.240 seeds per trap (63 seeds m^2), Site 2: 0.19 ± 0.060 seeds per trap (19 seeds m^2) and Site 3: 0.33 ± 0.161 seeds per trap (33 seeds m^2).

The analysis of 2004 plant-based dispersal data indicated there was a significant interaction between site and ring ($F_{6,132} = 2.468$, $P = 0.027$; Table 6). At Site 2, seeds tended to be deposited away from the parent plant (Fig. 12). There were significantly higher numbers of seeds trapped in the 20-40 cm ring (mean = 12 ± 4.4 seeds) as compared to the 0-20 cm ring (mean = 3 ± 1.4 seeds). Seed deposition tended to decrease from the 20-40 cm ring to the 40-60 cm ring (mean = 8 ± 3.4 seeds). Site 1 exhibited the same trend as Site 2, except that no significant differences in the number of seeds trapped were detected between rings. At Site 3, seed deposition tended to increase with increasing distance away from the source plant. Site 4 appeared to have seeds deposited closer to the parent plant with a tendency of fewer trapped seeds in the 20-40 cm ring followed by an apparent increase in the number of seeds trapped in the 40-60 cm ring. Seed deposition was significantly affected by cardinal direction ($F_{3,132} = 12.705$, $P < 0.0001$; Table 6) with more seeds trapped to the North of plants within sites (mean = 6 ± 1.7; Fig. 13).

The percentage of seeds trapped per plant ranged from 1% to 56% (Table 7). There were no significant differences detected in the number of seeds trapped between sites ($X^2_{0.05,2} = 3.906$, $P = 0.142$). Among populations (n = 4 sites), 16 ± 3.6 % of the total number of seeds dispersed were captured. However, the population at Site 4 suffered extreme herbivory therefore the estimated seed output for the two plants may be biased.

In 2005, plant-based dispersal studies indicated the preliminary shapes of the seed dispersal curves for each site were high peaked (kurtosis ≥ 0.52) with long-right tails (skewness ≤ -0.11; Fig. 14). A clear pattern within each site provides a good deal of confidence that most *A. californica* seeds are deposited away from the parent plant, seed deposition tends to increase at distances equal to or greater than 20 cm from the source plant and seeds can disperse up to 100 cm with the potential for further dispersal likely.

The second year plant-based dispersal results indicate all fixed effects were significant (Table 8). There was a significant site*ring interaction ($F_{6,154}= 1.7981$, $P = 0.049$; Fig. 15). At Sites 1 and 4, significantly fewer seeds were trapped in the 0-20 cm ring compared to the 20-40 cm ring where a significant increase in the number of seeds trapped occurred. The numbers of seeds deposited in the 40-60, 60-80 and 80-100 cm rings were not significantly different from each other and were comparable in the numbers of seeds trapped in the 20-40 cm ring. No significant differences were detected between the number of seeds trapped and the distance they were trapped from the source at Sites 2 and 3. Within Sites 1, 2 and 4 the seed dispersal curve appeared to peak 60 to 80 cm away from the parent plant compared to Site 3 which tended to be within 20-40 cm of the source plant.

There was a significant interaction between site and the cardinal direction seeds were dispersed ($P = 0.001$; Table 8). Seeds tended to disperse and collect in greater numbers to the north of plants at Sites 1, 3 and 4 (Fig. 16). At Site 2, significantly more seeds were trapped to the North and East of plants, which were comparable in the numbers of seeds trapped. Even though there was some variation in seed deposition with respect to cardinal direction, it was relatively minor compared to the total number of seeds deposited to the North of plants.

In 2005, the percentage of seeds trapped per plant ranged from 3% to 34% (Table 9). There were no significant differences in the number of seeds trapped between sites during plant-based dispersal studies ($X^2_{0.05, 2} = 0.594$, $P = 0.743$). Among populations (n = 4 sites), 19 ± 2.2% of the total number of seeds dispersed were trapped. Another 1% of seeds were trapped within *A. californica* plants upon dispersal. The number of seeds trapped within the plants ranged from 0 to 215 seeds with a mean of 35.4 ± 10.7 seeds (Fig. 17). The percentage of viable seeds that were ensnared within the plants ranged from 0-96%.

Granivory

The results of the mixed-model ANOVA analysis testing the effect of time despite failing normality, suggested all fixed effects of site, treatment, time and all possible interactions were significant for 2004 and 2005 (Table 10). Therefore, each granivory trial was analyzed separately. The results indicated strong treatment effects occurred most of the time (Table 11) although, two of the five trials had significant site*treatment effect suggesting a variable response on seed removal (Table 12).

Significant treatment effects were captured in the following trials: Trial 1: 27 July-1 August 2004, Trial 2: 13-20 July 2005, and Trial 3: 2-7 September 2005 (Fig. 18). The results of Trial 1 and Trial 3 were the same; even though each trial was conducted during a different month and time of year. Significantly more seeds were removed from treatments that either excluded rodents or had no exclusion while fewer seeds were removed from the treatments that excluded either ants or both ants and rodents. Excluding rodents in both trails significantly increased the number of seeds removed ($\text{mean}_{\text{Trial 1}} = 2.0 \pm 0.5$ seeds, $\text{mean}_{\text{Trial 2}} = 3.0 \pm 0.9$ seeds) compared to the treatment that excluded ants ($\text{mean}_{\text{Trial 1}} = 0.4 \pm 0.4$ seeds, $\text{mean}_{\text{Trial 2}} = 0$ seeds), which suggests that seed removal by ants was likely. Unlike the preceding trials, excluding rodents did not significantly impact seed removal in Trial 2. Instead, significantly more seeds were removed from the treatment that had no exclusion compared to the other treatments that excluded either ants, rodents or both ants and rodents. Therefore, the results of Trial 2 indicate that seed removal may be the result of ants or a combination of both ants and rodents because both species had access to the control (no exclusion) treatment.

All fixed effects including the interaction of site*treatment were significant in Trial 4 (20-25 July 2004) and Trial 5 (28 August-2 September 2005; Table 12). In Trial 4, significantly more seeds were removed from treatments that either excluded rodents or had no exclusion than treatments that excluded ants or both ants and rodents at Sites 2, 3 and 4 (Fig. 19). Site 1 had significantly more seeds removed from the control treatment and fewer seeds removed from the treatment that excluded ants with no significant impact on seed removal detected in either of the treatments that excluded rodents or both ants and rodents. In the subsequent year (2005), the results of Trial 5 suggested that excluding rodents significantly increased seed removal while excluding ants significantly decreased seed removal at Sites 1, 2 and 3. No significant differences were detected between any of the four treatments at Site 4 (Fig. 19).

Elaiosome

The results of the *A. californica* elaiosome survey revealed that the white elaiosome located along the hilum edge of the seeds was observed across five different populations over two years. Sites 1-4 were sampled in 2004 and out of 13,653 *A. californica* seeds examined, only 15 seeds lacked an elaiosome. In 2005, a total of 4,800 seeds were analyzed across Sites 1-4 with an additional 4,800 seeds from the North Las Vegas Airport, Nevada population. Out of a total of 9,600 seeds only 8 seeds lacked elaiosomes. Therefore, over 99% of the total number of *A. californica* seeds examined (23,253 seeds) possessed elaiosomes (Table 13).

In the first elaiosome experiment, no effect of time ($F_{1,48} = 3.742$, $P = 0.059$) was observed so data were combined. I observed a significant treatment effect ($F_{1,48} = 15.502$, $P = < 0.0001$), where seeds without elaiosomes (mean = 2.4 $\pm$ .47 seeds) were removed more than seeds with elaiosomes (mean = .78 $\pm$ .35 seeds; Fig. 20). No other fixed effects were significant (Table 14).

The second experiment yielded a significant effect of time ($F_{3,128} = 66.983$, $P = < 0.001$) therefore, Trial 1 and Trial 2 were analyzed separately. There was no significant treatment effect in either Trial 1: 28 August-2 September 2005 ($F_{1,16} = 4.146$) or Trial 2: 2-7 September 2005 ($F_{1,16} = 1.691$, $P = 0.212$; Fig. 21). However, in both trials, the treatments with nicked seeds with elaiosomes ($\text{mean}_{\text{Trial 1}} = 7 \pm 0.84$, $\text{mean}_{\text{Trial 2}} = 6 \pm 1.02$) had more seeds removed than the treatments with nicked seeds without elaiosomes ($\text{mean}_{\text{Trial 1}} = 5 \pm 0.80$, $\text{mean}_{\text{Trial 2}} = 5 \pm 0.94$). These results indicate a trend in ant preference for seeds with elaiosomes compared to seeds without elaiosomes when nicking was held constant. There was a significant site effect ($F_{3,16} = 8.001$, $P < 0.002$) in Trial 1 but no site effect was detected in Trial 2: 2-7 September 2005 ($F_{3,16} = 0.921$,

$P = 0.453$; Table 15). In Trial 1, Sites 2 and 3 had significantly higher seed removal compared to Site 4. There was no interaction captured in either Trial 1 or 2 (Fig. 22).

In the third experiment (23-28 September 2005), a significant treatment ($F_{2,70} = 28.714$, $P = < 0.0001$) and site effect ($F_{3,35} = 4.511$, $P = 0.009$) was observed. The treatment with nicked seeds and elaiosomes experienced twice the removal in the number of seeds compared to the treatments that had un-nicked seeds with elaiosomes and seeds without elaiosomes (Fig. 23). These results suggest that nicking the seed coat tends to attract ants. Site 2 had the highest number of seeds removed (mean = 9.0 ± 0.3 seeds) but was only significantly different from Site 3 (mean = 3.0 ± 0.2 seeds; Fig. 24). There was no site*treatment interaction captured in this experiment ($F_{6,70} = 1.591$, $P = 0.163$; Table 16).

A review of seed removal by replication within sites revealed that in Experiment 3 (23 August-8 September 2005), Site 1 had two instances where all the seeds from the three treatments were removed, Site 2 had five instances, Site 3 had none and Site 4 had only one instance where all the seeds were removed. To determine if Site 2 may have biased the results, I re-ran the mixed-model ANOVA without Site 2 ($F_{2,54} = 28.029$, $P < 0.0001$). The results were the same as when Site 2 was included ($F_{2,70} = 28.714$, $P = < 0.0001$), indicating removal of all seeds from the treatments did not bias the outcome of Experiment 3 by minimizing treatment effects. Therefore, even with 50% of the replications at Site 2 experiencing removal of all seeds from the three treatments, there was still evidence for strong selection by ants.

Alternatively, lack of removal could bias the results as well by inflating treatment effects. Site 3 was the only site to experience no seed removal from all 3 treatments in 2 of the 10 replications. Omitting the undetected replications from the analysis did not change the conclusions nor did removing both potential bias factors. Therefore, the evidence indicates ants selectively chose nicked seeds with elaiosomes over the other treatments.

Seed Bank

Overall, I found 2, 973 *A. californica* seeds out of a total of 1,004 soil cores (4,016 soil samples) from 5 sites which translates into 116 seeds m^{-2} in a 400 m^2 area. On average, 10.5 % of the seeds found were viable. Most seeds tended to be found either close to the surface or deep within the seeds bank. Seed distribution between soil depth increments were 0-2 cm 34%, 2-4 cm 21.9%, 4-6 cm 17.7% and 6-15 cm 26.4%. There were no significant differences between the proportion of viable seeds and depth however, a slight increase was seen within the 6-15 cm depth increment suggesting *A. californica* seeds may be long-lived.

Using the ground surface area associated with each core, the number of seeds was estimated at 116 ± 12.4 seeds/m^2 per sampling area (400 m^2) and an estimated 2.32×10^5 seeds per site (2,000 m^2). Seed bank sampling within the five sites revealed Site 5 had the average lowest number of seeds per m^2 (65 ± 19.78 seeds) compared to Site 1 (108 ± 9.83 seeds), Site 2 (167 ± 16.20 seeds), Site 3 (127 ± 31.47 seeds) and Site 4 (116 ± 36.32 seeds). The vertical distribution of seeds by depth per m^2 was: 0-2 cm (158 ± 25.99 seeds), 2-4 cm (102 ± 18.19 seeds), 4-6 cm (83 ± 15.90 seeds) and 6-15 cm (123 ± 37.59 seeds).

Seed density was affected by depth within the soil column ($P < 0.0001$; Table 17). This depth effect varied with site, as was indicated by the significant interaction between site and depth (P = 0.0350). An obvious trend within sites indicated that seed density tended to decrease with increased depth within the seed bank (Fig. 25). On average, about 10.5% (311 viable ÷ 2,973 total seeds) of the seeds found were viable. The proportion of viable seeds per depth, pooled across sites, is shown in Figure 26. The percent distribution of seeds according to their assigned category based on condition (fragment, filled but non-viable, or viable) by site and depth are illustrated in Figure 27. The lowest percentage of seeds within each site and depth was composed of viable seeds, which did not exceed > 20% at any one site or depth. As expected, the highest concentration of seed fragments, 47.4% were found in the upper portion of the soil column out of 1,010 seeds at that depth. There was a negative trend across sites, where the percentage of seed fragments decreased with increased depth within the seed bank down to 31.9%. Compared to other sites, site 4 had the lowest percentage of seed fragments among depths with zero fragments represented in the 4-6 cm and 6-15 cm increments. Overall across sites and depths, seeds within the seed bank were distributed among the following seed categories: 10.5% (viable seeds), 35.6% (seed fragments), and 53.9% (filled but non-viable seeds).

Seed Fate Model

Seeds are the future progeny of most plant species and the processes, both abiotic and biotic, that act on those seeds influences the patterns of plant species in both time and space (Harper et al. 1970, Harper and White 1974). Seed fate pathways include seed production, dispersal, and incorporation within the seed bank with losses along the way through predispersal loss, seed predation, decay and germination (Harper 1977). Figure 28 illustrates the fate of *A. californica* seeds at various ecological stages and the processes that influence them. The percentages in the model are the average of both years of data. On average, approximately 40% of the adult plants suffered mortality among sites. Before dispersal, 18% of all seeds produced suffered predispersal loss therefore, 82% of the seeds remained on the plant. As a fraction of the initial total seed production, 1% of the seeds was dispersed within the plants (fell into the plant and were trapped), 17% was dispersed away from the parent plants (average of plant-based and plot-based dispersal) while 64% was subjected to an unknown fate. Again, of the original 82% of the seeds left on the plant after pre-dispersal loss, 17% of the seeds reached the surface whereby 7% of the seeds were secondarily removed by ants and rodents (average removal from granivory trials). The fate of the other 10% of the seeds on the surface was unknown.

I assumed that the seed bank started over at 100% therefore, the total number of seeds found within the seed bank pooled across sites was broken down into the following categories: 10.5% were viable, 53.9% were filled but non-viable and the rest of the seeds, 35.6%, consisted of seed fragments. On average, 209 seedlings germinated from a 2000 m^2 area with approximately 72% suffering mortality which left 150 seedlings to progress on toward adulthood. Anywhere along the seed fate pathway, seeds maybe subjected to mortality, predation, incorporation within the seed bank, loss, germination or suffer an unknown fate.

CHAPTER 4

DISCUSSION

Seed Production

There is often large variation in seed production among plant populations (Leverich and Levin 1979, Schaal 1980, Campbell and Clarke 2006), and *A. californica* is no exception. During the 2-year study period (2004 and 2005), *A. californica* experienced a five-fold increase in the number of flowers and capsules per plant and seven-fold increase in seed production. Also, an 85% average increase in plant size occurred among plants that survived over the two-year study. During July 2004-April 2005, the Mojave Desert experienced 259 mm of precipitation, more than twice the annual average of 114 mm (National Weather Service 2006). Year-to-year variation in seed output is partially due to weather conditions (Nathan and Muller-Landau 2000) and typically explains the seed output differences in tropical trees (Wright 1999). Also, years with above-average rainfall during winter/spring months which are typical germination periods for the species, have coincided with prior *A. californica* recruitment episodes during the past (Meyers 1987, Mistretta et al. 1996). Therefore, the combined increases in reproductive structures, vegetative size and year-to-year variation in seed production among populations are probably the result of wetter than normal conditions during the 2004-2005 winter seasons.

The variation in seed production among capsules that can be explained by the plant size, plant diameter, the number of flowers or stalks per plant is minimal compared to the number of capsules a plant produces. The objective of the seed production model was to determine a realistic estimate of *A. californica* population production and provide a tool for conservation managers. However, there are several limitations associated with the seed production equation: No. seeds = $(\text{No. cap/plant})^{1.232} * 41.07$. First, the equation is based on data limited to the range of the observed values during this study for the number of mature capsules per plant in the sites studied and may not provide a useful estimate outside of these data bounds. Sub-sampling is recommended if the seed production equation is to be used for populations other than those ones in the study to help account for variation among *A. californica* populations. This tool provides an approximate idea of seed production per plant therefore, it is at best a rough estimate. Last, the equation is based on data gathered on a per plant basis, if used incorrectly there is the potential for an artificial inflation of estimated seed production. This can occur if the total number of mature capsules per area or population is inputted rather than on a per plant basis.

As expected, the number of seeds per plant was correlated with the number of flowers per plant and the number of capsules per plant each year (Table 2 and 3). However, seed production was significantly correlated to plant diameter ($r = 0.682$, $P = 0.002$) and plant size ($r = 0.695$, $P = 0.001$) only in the second year (2005). Plant size ($\text{mean}_{2004} = 339.3 \pm 121.9$, variance = 237,784.6; $\text{mean}_{2005} = 412.8 \pm 45.0$, variance = 36,467.6) and plant diameter ($\text{mean}_{2004} = 18.29 \pm 2.56$, variance = 104.54; $\text{mean}_{2005} = 22 \pm 1.11$, variance = 22.353) differences across years were not due to lower variance in 2004. The correlation between seed output per plant and plant size or plant diameter may change due to the availability of resources. Such plastic responses are generally influenced by environmental conditions which likely explains the correlation between seed output per plant with plant size and plant diameter during the wetter second season. Meyer (1987) found similar reproductive output results suggesting widely plastic expressions within and between five *A. californica* populations.

In 2004, all capsule attributes were highly significant ($P < 0.0001$) with the number of seeds per capsule but none were even remotely significant in the second year (Table 3). The lack of significance in the second year may have partially been attributed the eight-fold increase in sample size that occurred between years. Also, plants are extremely plastic in their responses to environmental conditions and strategies for surviving versus reproducing (Bloom et al. 1985). As a result, it would be expected that the number of seeds per capsule and even the size of the capsule would be plastic in time and place- based on resources. Therefore, these results suggest that the *A. californica* capsule attributes may not maintain a reliable relationship with seeds per capsule across years of varying environmental conditions therefore, they may not be reliable predictors of seed output per plant.

Meyer (1987) also found the volume of a capsule (cone) to be correlated with *A. californica* seed output with a sample size of $n = 100$ capsules, $r = 0.766$. In this study, when the sample size increased from $n_{2004} = 79$ capsules to $n_{2005} = 634$ capsules the relationship between the number of seeds per capsules and capsule volume fell apart ($P = 0.656$). The significant increase in sample size likely allowed for the partitioning of the strength of the effect of each predictor, which could not be done in the prior year due to the small sample size. These results suggest that capsule volume was not a good predictor of seed output.

Seed Dispersal

At the site level, the seed dispersal curve for *A. californica* was leptokurtic with a high peak and long right-tail. There was an obvious trend of seed deposition away from the parent plant rather than the immediate surrounding area. On a smaller spatial scale, plant-based dispersal studies indicated a similar seed dispersal trend.

The general seed dispersal pattern for this species tends to be an accumulation of seeds away from the parent plant in a northerly direction. I found that *A. californica* seeds can be found up to 800 cm from the closest reproducing adult plant, suggesting that *A. californica* seeds disperse further than previously believed (Meyer 1987, Sheldon 1994). Such dispersal distances may be a combination of wind and/or dispersal vectors.

Typically, seeds move only a short distance from the source (Levin 1981), however, this does not seem to be the case with *A. californica* seeds. Dispersal of seeds away from the parent plant appears to avoid processes that tend to increase density-dependent mortality resulting from close proximity to the parent plant (Janzen 1970, Howe and Smallwood 1982). Janzen (1970) found that seed predators tend to search for food within the immediate area of the source and generally ignore seeds a short distance away. If rodents in this study did the same, ants, wind and other abiotic vectors may be moving seeds to safe sites. Another possibility is the "Directed Dispersal Hypothesis" which assumes selection favors adaptations and/or dispersal agents that allow seeds to reach suitable locations for germination (Hanzawa et al. 1988, Willson and Traveset 2000). Van de Pijl (1982) found that the jacitation capsule is triggered by wind and results in seeds being broadcast further from the source than gravity in the family Papaveraceae, which appears to occur with *A. californica* capsules. This is considered primary dispersal, the movement of seeds from the parent to the surface (Chambers and MacMahon 1994). The presence of elaiosomes suggests that seeds are moved away from the parent plant once they reach the soil surface by ants to potential sites suitable for germination (Culver and Beattie 1980, Beattie and Culver 1981). Because *A. californica* seeds have elaiosomes and *A. Merriam*, a sister species does as well and the function appears to be dispersal by ants I assume the same is true for this species.

According to Vander Wall and Longland (2004), dispersal that includes two or more dispersal agents, may have become a favored adaptation because of the dual benefit of dispersal and the potential for reduced seed mortality. Plant species with this type of multiple dispersal agents are called diplochory species (Vander Wall and Longland 2004). Each dispersal syndrome by itself does not provide the 'ideal dispersal system' (see Howe and Smallwood 1982). For example, wind dispersal provides the opportunity for colonization of new areas; however, seeds tend to be disseminated across the ground randomly with regard to establishment sites less than 5 m from the parent plant (Vander Wall and Longland 2004). Myrmecochory, dispersal by ants, tends to provide escape and relocation of seeds to favorable microsites (Hanzawa et al. 1988). However, colonization of new areas is unlikely because ants generally do not transport seeds farther than an additional 0.5-3.5 m from initial dissemination (Vander Wall and Longland 2004). However, I have observed removal of *A. californica* seeds by ants within Site 2 which proceeded to move seeds to their ant nests 30-100 m away from the original seed location on the surface. Obviously, more research is required before it can be determined if seed dispersal of *A. californica* results in a net benefit or loss to the species.

The stalks of *A. californica* are on average 22 ± 0.74 cm in height and are slender. These characteristics seem to facilitate movement by wind which promotes dispersal of seeds away from the parent plant and partially explains the seed deposition patterns of the species. The directionality effect of *A. californica* seeds was also found by Sheldon-Thompson and Smith (1997). Northerly deposition in my study was most likely a result of wind blowing from the south due to the north–south oriented U-shaped valley sandwiched between two ridges at Sites 1-3 (Longwell et al. 1965, Meyer 1986). At Site 4, the winds tended to blow from the south up along the coast of Overton Arm of Lake Mead (The Virgin River Valley) of Lake Mead National Recreational Area.

Wind is likely the most important agent for primary dispersal of *A. californica* seeds away from the plant and may account for seeds found up to distances of 800 cm away from a source plant. However, secondary dispersal, the redistribution of seeds across the surface after initial dispersal (Chambers and MacMahon 1994) by wind may account for the distribution of *A. californica* seeds across the landscape as well. Even though minimal numbers of seeds were trapped in the plot-based studies, extrapolation out to the site-level suggests high numbers of *A. californica* seeds may be available for redistribution across the surface.

The minimal number of seeds trapped during plot-based studies may be the result of not enough sticky traps placed within each site to adequately capture dispersal by wind across the surface. Also, the desert is a highly heterogeneous environment created by sparse and clumped patches of vegetation cover (Reichman 1984, Aguiar and Sala 1997).

The interspaces between the mosaic vegetation patterns are characterized by numerous patches of bare ground (Aguiar and Sala 1999). The low percent cover causes wind velocities to be up to four times greater in the interspaces than shrubs. The interspaces provide pathways for "seed transport" which increase the chance seeds will be retained in soil cracks, crevices, litter and under shrubs (Nelson and Chew 1977, Reichman 1984, Eckert et al. 1986, Johnson and Fryer 1992). The high percentage of surface rock cover characteristic of *A. californica* habitat provides numerous microsites (Saxena 2005). The small size of *A. californica* seeds, approximately 2 mm in size, suggests these seeds would be easily ensnared in the highly heterogeneous environment typical of deserts. Chambers et al. (1991) found a strong relationship between seed size and soil particle size suggesting that small seeds tended to be trapped at small particle sizes ranging from 0.5-1.0 and 1.0-2.0 mm. Saxena (2005) found *A. californica* plants tended to reside on sites characterized as either loam or sandy loam soil which falls into Chambers et al. (1991) categories of small particle size.

I suggest that wind facilitates entrapment of *A. californica* seeds within the surface upon initial arrival or shortly after seeds reach the surface due to the spatially heterogeneous nature of the desert and removal by ants partially explains the lack of seeds trapped during plot-level studies. The implication of this study suggests that seeds may be retained on-site. *A. californica* seeds probably do not move off-sites where they have occurred in the past and are highly likely to reappear on those sites or near those sites because most seeds tend to be dispersed within 200 cm of reproducing plants. Additional research using radio-active labeling of seeds has provided the ability to track seeds during secondary dispersal in other studies which 'maps' possible seed fate pathways (Vander Wall 1994). The use of this technique may be able to further define the seed dispersal distribution for this species and seed fate pathways especially whether long-distance dispersal of the seeds between preferred habitat areas is possible or not.

Meyer (1987) suggested that many of the seeds fall within the parent plant which may prevent further dispersal of the seeds. I found that seed traps placed close to or slightly under the rosettes of the plants were unlikely to trap seeds from previous years that were lodged within the plants. On average, 35 ± 10.7 seeds were trapped within each study plant (n = 20 plants) ranging in viability from 33-96%. There is the possibility that seed removal did occur from within the plants by ants because numerous visual observations found ants crawling on the rosettes. Crist (1990) and Crist and MacMahon (1992) have found that foraging ants remove approximately 5% of the seeds produced from the actual plant itself in a shrub-steppe ecosystem. Further research is necessary before we can determine any potential impact ants may have on *A. californica* seeds, seedling recruitment and dispersal potential.

Granivory

In arid environments, granivores can impact seed survivorship and seedling recruitment (Crist and MacMahon 1992) by consuming considerable proportions of seeds from some plant species (Reichman 1979, Crist and MacMahon 1992). Several studies have reported varying percentages of post-dispersal seed predation by ants, rodents, and mammals ranging from 0% to 100% (Chew and Chew 1970, Soholt 1973, Hay and Fuller 1981, Boyd and Brum 1983; for a complete list refer to Crawley in Fenner 1992). The impact on rare plants can be quite severe if most of the seed crop is lost to predators. Exclusion trials can aid in identifying secondary seed dispersers and predators by excluding some species and allowing others (Bohning-Gaese et al. 1999). Powell (2003) proposed that *A. californica* seeds may be consumed and/or dispersed by ants and rodents. My intent was to identify possible secondary dispersers so future work could tease out the relationship between seed dispersers and seed predators.

In general, I observed strong treatment effects in the exclusion trials and heterogeneity among sites, which was probably a result of spatial heterogeneity in ant populations. Powell (2003; see also Figure 29) observed removal of *A. californica* seeds by ants. She found piles of seeds next to an ant mound at Stewart's Point. I discovered an *A. californica* seed in the top 2 cm of a *Myrmecocystus pyramicus* (honey pot ant) mound. Both of these observations suggest that ants collect, move and deposit *A. californica* seeds to new locales.

The occasional lack of significant differences between treatments that excluded rodents compared to those treatments that excluded ants may indicate potential removal by rodents. It is also possible that rodents were actively deterred by the Tangelfoot® treatment meant to exclude only ants. In this case, rodents could be more important dispersal agents or predators on *A. californica* seeds than indicated by these tests. However, there were no obvious signs of rodent activity detected around the exclusion trials or any of the other experiments, i.e. tracks, feces, up-turned exclosures, soil disturbance or visual observations. Possible explanations for this apparent lack of rodent activity may be due to (1) the time period during which these experiments occurred which was after natural dispersal of the species; (2) seasonality of rodent foraging patterns which are determined by a combination of temperature, light (time of day), humidity, food availability and competition (Whitford 1978, Kotler and Brown 1988); (3)

the small size of seeds (2 mm) may not meet the caloric requirements needed to overcome foraging efforts by rodents as suggested by Reichman (1979); or (4) the elaiosomes on A. californica seeds may serve a dual- purpose, attractant for ants and repellent of rodents, as did the elaiosomes of *Corydalis aurea* suggested by Hanzawa et al. (1985). Further research studying the potential interaction between rodents and *A. californica* seeds is required before their impact on *A. californica* populations and structure are understood. Nonetheless, a clear pattern across exclusion trials and visual observations provides a strong suggestion that ants remove *A. californica* seeds and are probably important in secondary dispersal, the redistribution of seeds across the surface.

Elaiosome

My results show that elaiosomes are a typical structure of *A. californica* seeds. Within the family of *Papaveraceae* alone, an unusually high percentage of the genera possess elaiosomes on their seeds including species in the genera of: *Arctomecon, Bocconia, Cathcartia, Chelidonium, Corydalis, Dendromecon, Dicentra, Fumaria, Hylomecon, Meconopsis, Sanguinaria and Stylophorum* (Fedde 1936 as cited in Berg 1966). The association of the genus *Arctomecon* with elaiosomes seems to have been either overlooked or downplayed in recent studies. Harper and Van Buren (2004) mention briefly that *Arctomecon humilis* possesses an elongated aril of white tissue near the hilum which appears to attract ants as the primary dispersal agent. However, no mention could be found regarding any type of elaiosome or aril associated with *Arctomecon merriamii*, the third member of the genus *Arctomecon.* Nevertheless, the mounting evidence suggests that this typical structure of *A. californica* is an elaiosome and not simply an attachment structure.

Myrmecochory, or seed dispersal by ants, has been shown to impact future recruitment and plant community structure in several ways. Generally, seeds are transported away from the parent plant to ant nests which potentially decrease seed predator mortality (Culver and Beattie 1978, Vander Wall and Longland 2004). Once seeds reach the ant nest, the elaiosomes, food bodies, are removed and the seeds are discarded unharmed into either underground “old galleries” (Fenner 1985) and waste midden piles (Culver and Beattie 1978, 1980) or surface midden piles outside ant nests (Fig. 29). Seeds discarded in underground waste midden piles tend to have higher germination rates and greater chances of reaching the seedling stage and flowering the next year (Culver and Beattie 1978, 1980) but see O’Dowd and Hay (1980) and Horvitz and Schemske (1986). The increased germination rates may be due to higher levels of nitrogen and phosphorous, increased aeration and water holding capacity in the soil than the surrounding areas (Culver and Beattie 1978, O’Dowd and Hay 1980, Hanzawa et al. 1988) plus the relative protection against seed predators (Vander Wall and Longland 2004). The seeds discarded outside ant nests in surface midden piles are likely subject to different environmental influences than those discarded under ground. Out in the open, the seeds are subjected to abiotic processes such as wind and water which can redistribute the seeds across the surface and biotic influences such as rodents which can consume the seeds or cache them (Reichman 1984, Chambers and MacMahon 1994). Both seed disposal scenarios potentially increase the chances for colonization of habitat patches away from parent plants (Vander Wall and Longland 2004).

Before any of the above impacts of ant dispersal on *A. californica* recruitment and population structure can be studied, one has to determine whether or not the elaiosome on

A. californica seeds promotes dispersal by ants. Figure 29 clearly shows *A. californica* seeds discarded in a surface midden pile, which suggests that ants collected the seeds and removed the elaiosomes. The motivation behind ant collection likely had to do with the elaiosome attached to *A. californica* seeds. However, the results of the elaiosome experiments elicited varied responses from the ants.

The results of the first elaiosome experiment clearly indicated that ants were more attracted to seeds without elaiosomes than with elaiosomes. However, when controlling for the 'nick effect' as in elaiosome Experiment 2, there was an obvious trend of ant selection for nicked seeds with elaiosomes compared to nicked seeds without elaiosomes. Therefore, the differing results suggest that the outcome of Experiment 1 may be attributed to: (1) the storage time of seeds after maturity (several days) may alter compounds normally discharged from the elaiosomes upon dispersal (Berg 1966, Mesler and Lu 1983, Kjellsson 1985); (2) when I removed the elaiosome, the seed coat was inadvertently nicked causing ants to be abnormally attracted to the seed; (3) complete removal of the elaiosome did not occur which thereby released the behavior enticing compounds (Mesler and Lu 1983), or (4) placement of the treatments in separate covered dishes may have biased removal by either causing disproportionately more seeds removed due to detection of the treatment or the lack of detection resulted in no removal.

To address potential bias, all treatments were pooled into a single covered dish in Experiment 3. The significant selection of nicked seeds with elaiosomes over un-nicked seeds with elaiosomes or seeds without elaiosomes suggests that nicking the seed coat somehow attracted the ants. Possible explanations may include: (1) the diminished capacity of the elaiosomes behavior altering compounds (Brew et al. 1989; (2) the temporal pressures of limited food availability due to the onset of winter may have forced the ants to be less selective in food sources (Brew et al. 1989); (3) seasonality may have affected the foraging behavior of ants (Whitford 1978); (4) ants exploited the discovered replications within each site or a combination of 1 and 2; or (5) a significant number of replications remained undetected by the ants and skewed the analysis.

The selection of less than ideal food sources resulting from temporal pressures or exploiting chance discovery of the replications may explain why several replications had all the seeds removed from the treatments. However, further analysis indicated that the treatments where all seeds were removed and those where no seeds were removed did not influence the overall conclusion, which was that ants preferentially selected nicked seeds with elaiosomes.

Due to the variable responses of the ants to the three different elaiosome experiments, I recommend further studies investigating elaiosome removal experiments using fresh seeds. Also, seasonality may affect foraging behavior of ants. Therefore, experiments should be conducted during natural dispersal of *A. californica* to minimize potential bias. Additionally, the chemical analysis of the elaiosome would conclusively categorize the appendage, determine its chemical make-up and allow comparison to other seed bearing elaiosomes and may elucidate links to foraging behavior of granivores.

Seed Bank

A soil seed bank is defined as a reserve of seeds within the soil column that remain dormant and viable until the right conditions occur to initiate germination (Fenner 1985). The survival of many desert plants relies on seed banks to buffer years of no or sparse recruitment due to dry environmental conditions that can last up to several years (Kemp

1989, Cabin and Marshall 2000). Without long-lived, persistent, and viable seed banks, plant species typical of these unpredictable environments would likely be at a higher risk for extinction (Parker et al. 1989).

I found that *A. californica* maintains a highly spatially heterogeneous seed bank, which is typical of seed distributions in the Mojave Desert (Nelson and Chew 1977, Reichman 1984, Rundel and Gibson 1996). This was evident by the numerous 0-2 cm soil samples ranging from 101-163 samples per site that had no seeds found within them. Out of 4,016 soil samples, I found seeds in 906 samples which roughly equates to 23% or a slightly better than a 1 in 5 chance of finding a seed within a soil sample.

Whether the seed bank is transient or persistent was not addressed in this study. However, there are at least four lines of evidence to support the suggestion that the seed bank persists in nature. First, the proportion of viable seeds was higher deep within the soil column (6-15 cm), suggesting that *A. californica* seeds may retain viability for a long time. Generally, small seeds like *A. californica* are indicative of species with persistent seed banks that occupy unpredictable environments (Thompson and Grime 1979, Fenner 1985). Second, *A. californica* has been observed to re-colonize previously occupied sites after the disappearance of plants for up to 15 years (Powell and Walker 1993, Meyer 1996). Preliminary seed retrieval studies by Meyer (1996) indicate long-term viability is likely as well, which Fenner (1985) suggests is an important feature of persistent seed bank. Third, several other studies have found evidence suggesting that deeply buried seeds tend to be older than those seeds closer to the surface because seed movement in soil tends to be slow (Bekker et al. 1998, Grandin and Rydin 1998, Bekker et al. 1999, Thompson 2000). Last, Harper and Van Buren (2004) noted that *A. californica* seeds exhibit immature embryos upon seed dispersal. This is a dormancy mechanism used to delay germination until more favorable conditions occur which is a typical feature of seeds in a persistent seed bank (Fenner 1985).

Arctomecon californica appears to disperse non-dormant seeds which may require several years within the seed bank for dormancy to break (Meyer 1996). However, seeds used in viability testing from 2005 seed production were store at room temperature in plastic bags for 6 months. Several capsules suffered from a fungus infection but the sample of seeds tested ranged in viability from 87.5 - 100%. These results suggest cold stratification may not be a requirement for dormancy release in a laboratory setting. Additionally, there were a high percentage of filled seeds that were deemed not viable due to their lack of tetrazolium staining. However, there is the possibility that these seeds may have been in a deep dormant state which may not stain at all due to low respiration levels thereby creating a False negative result (ASOA 2000). If this was the case, then the proportion of viable seeds within the seed bank would increase to 64.4% compared to 10.5%.

Most *Arctomecon californica* seeds within the seed bank were found either close to the surface or deep within the seed bank. These results are contrary to other studies that have demonstrated that 80-90% of most desert seeds are found in the upper 2 cm of the soil (Reichman 1979, Kemp 1989; but see Guo et al. 1998). The high amounts of clast cover likely provide numerous microsites available for entrapment of seeds as they are dispersed by wind (Saxena 2005), overland flows (Reichman 1984), or down-slope in steep terrain (Westelaken and Maun 1985). Additionally, large particle size soils regardless of seed size act as sieves trapping seeds within the soil column as well

(Chambers et al. 1991). Plus, small seeds have a higher probability of being entrapped in the soil surface after initial contact than large seeds (Chambers et al. 1991) suggesting that seed size in itself may secure incorporation within the soil seed bank (Harper et al. 1970, Bekker et al. 1998).

The penetration of *A. californica* seeds deeper into the soil column may be the result of microtopography trapping seeds and over land flows causing rapid burial of the seeds (Meyer 1987). Also Chambers et al. (1991) found that large particle sizes and rocks in the upper 2 cm of the soil creating large pore spaces may increase infiltration and downward movement of small seeds and soil fines deep within the seed bank. Saxena (2005) and Megill et al. (2007) tended to find similar soil structure at most of the *A. californica* sites that fit the description discussed by Chambers et al. (1991) above. Other processes that influence the rate of seed burial are precipitation (van Tooren 1988, Chambers and MacMahon 1994), animal and ant activity including digging, burrowing, disposal and re-caching of seeds(Parker et al. 1989), over land flows (Meyer 1987), gravity and seed size (Bekker et al. 1998). Additionally, several studies by Chambers (1991) and Chambers and MacMahon (1994) found that as small seeds travel deeper within the soil column and soil particle size decreases, high numbers of small seeds reach depths > 5 cm. This conceptual model for vertical seed movement provides several explanations for the likely distribution of *A. californica* seeds deep within the soil column.

The implications of the distribution pattern of seeds throughout the differing depths are speculative. First, the small size of the *A. californica* seeds may increase the chance of predator avoidance as Janzen (1971) hypothesizes for small seeds in general.

Reichman (1979) showed that seed predators do not forage below 7 cm, which suggests that any further within the seed bank may provide a safe-haven for seeds. However, Freas and Kemp (1983) found that desert annuals are unable to germinate from depths greater than 1 cm while desert shrub seeds are limited to 4cm and above (Williams et al. 1974). Cabin and Marshall (2000) state most species are unable to emerge from below 2 cm in the soil column. Because germination of plants is limited to the upper 4 cm of the soil column, Guo et al. (1998) suggested any seeds deeper than 7 cm can be considered lost to the seed bank because germination was unlikely to occur. However, *A. californica* seeds persist at depths greater than 7 cm within the soil column and tend show higher rates of viability deeper within the soil column versus closer to the surface (Fig. 25). It is possible that the deeper depths in the seed bank may be an advantage for the persistent nature of this species by providing protection against predators and a safe-haven until disturbance redistributes the seeds closer to the surface where the right conditions may prevail and germination takes place.

Seed Fates Model

An overview of *A. californica* seed fate pathways provided as percentages based on initial seed production and seed bank estimates is shown in Figure 28. This is a simple model to aid understanding in the different ecological fates of *A. californica* seeds. The model was based on the average of two years of data collected for seed production, dispersal, and granivory except for the seed bank estimates. There are several gaps that exist within the model. For example, out of the 82% of seeds left on the plants, I captured 17% during plant-based dispersal and could not account for the other 64%. It is possible that the unaccounted for seeds (64%) were dispersed between the traps, the seeds dispersed further than 100 cm from the source, the outer limit of my dispersal design or seeds were removed directly from the plant by seed predators/dispersal vectors. Once the seeds reached the surface (17%), I was unable to account for 10% of the seeds while removal of the other 7% was attributed to granivory. Those seeds may have been aborted, lost to herbivory, dispersed by ants or incorporated within the seed bank. I suggest that many seeds entered the seed bank because of the heterogeneous environment that facilitated entrapment of the seeds. Future research is required before these gaps in the model can be addressed.

Management Recommendations

Natural migration of many rare species seems unlikely due to limited source populations to draw from, specific habitat requirements, possible dispersal limitations, low fecundity or a combination of the above factors (Rabinowitz and Rapp 1981, Rabinowitz et al. 1986). Restrictive geographic distribution of the species presents further obstacles for seed dispersal (Clark 1998, Higgins and Richardson 1999, Pakeman 2001). For such reasons, if a species is unable to migrate because the current locale is unsuitable (Peters and Darling 1985, McDonald and Brown 1992), then rare plants are extremely vulnerable to extinction.

The preservation of previous and current occupied areas and potential habitat is paramount for the future survival of this species especially when plants “disappear” from sites during the lull in their demographic pattern. Hickerson and Wolf (1998) found evidence of reduced genetic diversity in *A. californica* fragmented populations in the Las Vegas Valley coupled with significant reductions in the diversity and abundance of pollinators. Over time, lack of genetic variation may impact population fitness and impair the species ability to deal with climate changes or other environmental pressures. Also, Meyer (1987) suggested that *A. californica* plants are dispersal-limited mostly due to the island-like gypsum habitats this species tends to occupy. This may not be the case because Drohan and Buck (2006) have shown that *A. californica* plants can establish on soils other than gypsum. I have found *A. californica* seeds can disperse up to distances of 8 m from the closet reproducing adult however, this appears to be the exception rather than the norm. Regardless, it only takes one seed to survive, germinate, reproduce and set seed to promote the future regeneration and persistence of the species. Additionally, ant dispersal may or may not limit dispersal of the species given its unique habitat niche. Therefore, I suggest *A. californica* seeds tend to remain on-site but are patchy in time and space.

The reservoir of viable seeds deep within the seed bank suggests *A. californica* seeds may be long-lived. However, habitat disturbance caused by off-road vehicle traffic, mining, and feral burros disrupt the seed bank resulting in buried seeds being brought close to the surface where they can germinate (E. Powell, pers. comm.) thereby eliminating the persistent seed bank that would have buffered the species during unfavorable or natural disturbance events. The continued loss of habitat resulting from growth and other stressors are causing a decline in the number of *A. californica* populations in the Las Vegas Valley and the ecological impact of this decline on the environment may be great. Already, there are reduced numbers of pollinators found in the fragmented populations in Las Vegas Valley (Hickerson and Wolf 1993) which may partially explain the lack of reproductive success in these *A. californica* populations.

My management and future research recommendations for *A. californica* consist of (1) Preserve intact, undisturbed habitat, both currently occupied and potential habitat; by use of fencing, closures, grazing limitation, reduction of mining and exploration of the areas and/or signing; (2) Preserve dispersal vectors and pollinators; (3) Perform radio-active labeling to track the fate of *A. californica* seeds through dispersal to germination to determine the influences on the temporal and spatial patterns of the specie; (4) Examine the chemical makeup of the elaiosome and its role in dispersal; (5) Investigate the impact granivores have on *A. californica* seedling recruitment and population structure and (6) Conduct i*n situ* seed bank monitoring of *A. californica* seeds to determine average length of time seeds remain viable in the natural environment; (7) Resource allocation studies will provide a deeper understanding of the life history of the species; and (8) A model incorporating the demography of the species.

I recommend the following mitigation measures should be implemented if *A. californica* habitat should be disturbed: (1) Collect all mature capsules from the current site prior to disturbance, so that seeds can be sown on a new site. My results indicated that on average, 92.5% of the seeds collected from plants were viable; (2) Salvage soil up to 2 cm in depth in highly populated *A. californica* areas that have shown previous reproduction in the past year or years. This may maximize the chance of locating the seed bank; and (3) Salvage dead plants and remnants. The dead plants may provide additional sources of viable seeds trapped within the multitude of rosettes.

APPENDIX I

FIGURES

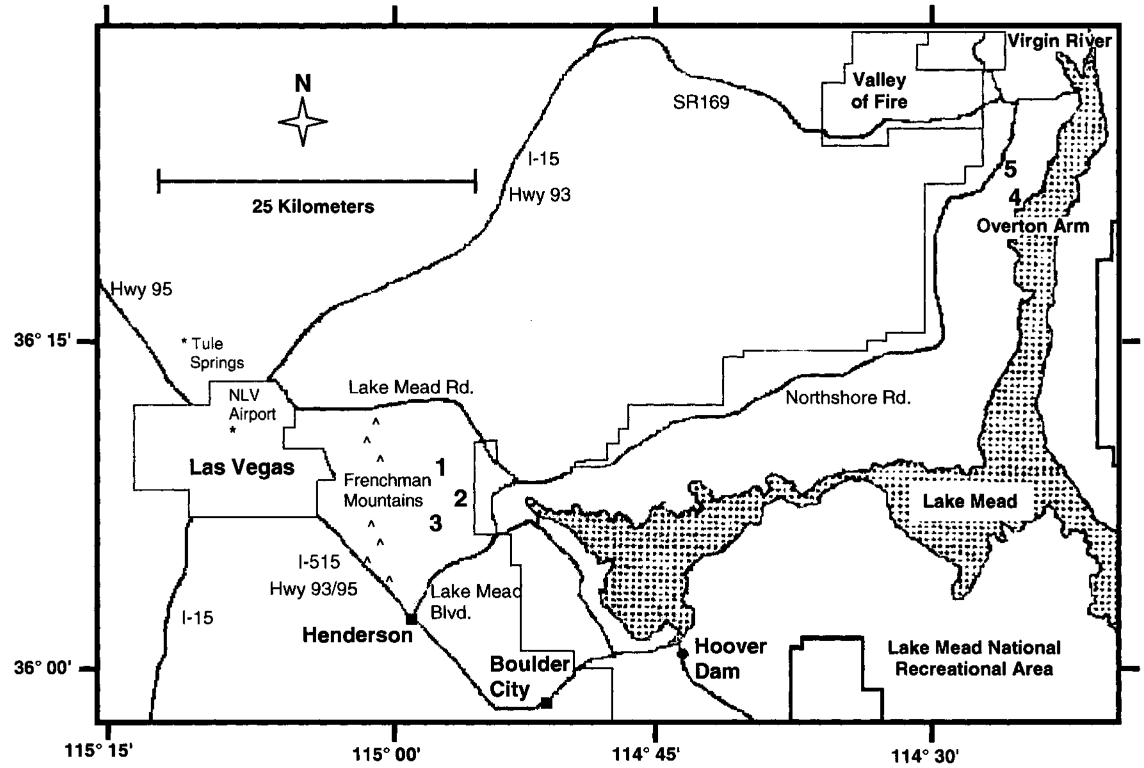

Figure 1. Map of the Las Vegas, Nevada, area depicting locations of the five study sites. Rainbow Gardens (Sites 1-3) and Stewarts Point (Sites 4-5). Adopted from Meyer (1986).

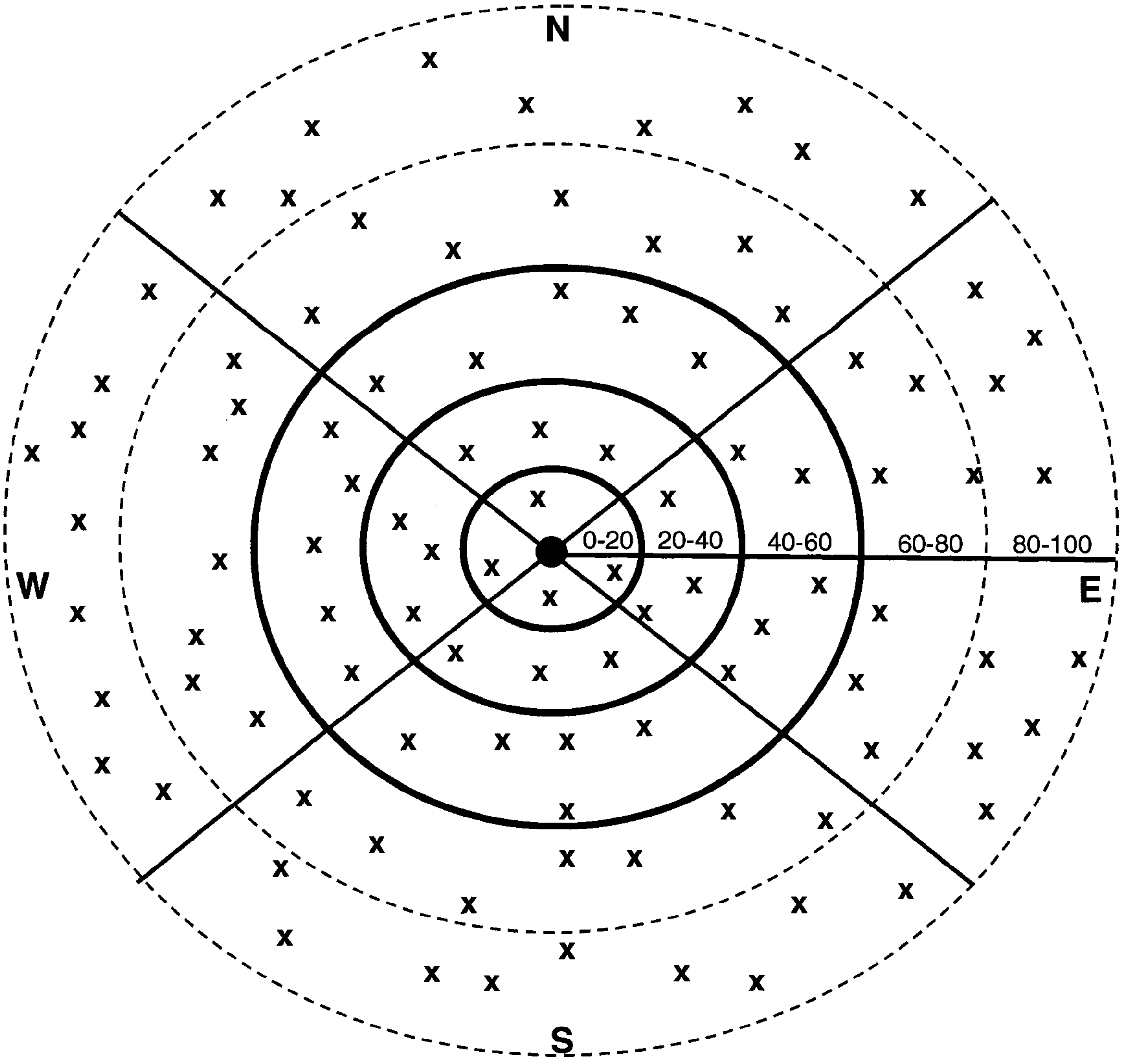

Figure 2. Schematic diagram of the plant-based seed dispersal design. Solid rings = 2004 design with 3 rings with a radius of 60 cm and combination of solid and dashed = 2005 design that consisted of 5 rings with radius of 100 cm.
(● = *A. californica* plant and **x** = sticky trap).

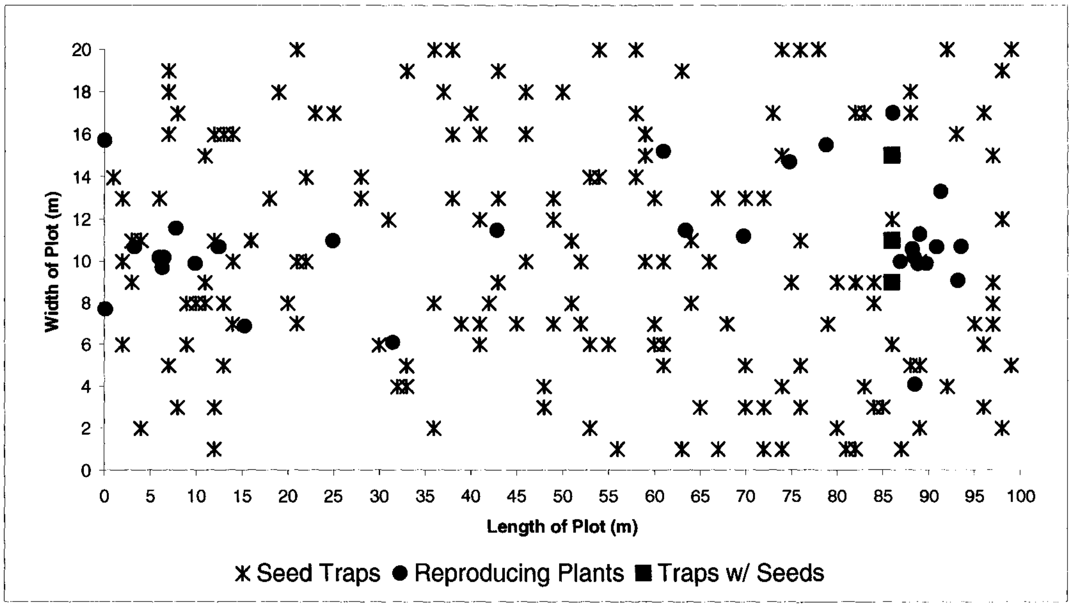

Figure 3. Typical schematic diagram of the secondary seed dispersal design with 180 randomly placed seed traps within the plot at Site 3 located in Rainbow Gardens near Las Vegas, Nevada. * Not to scale.

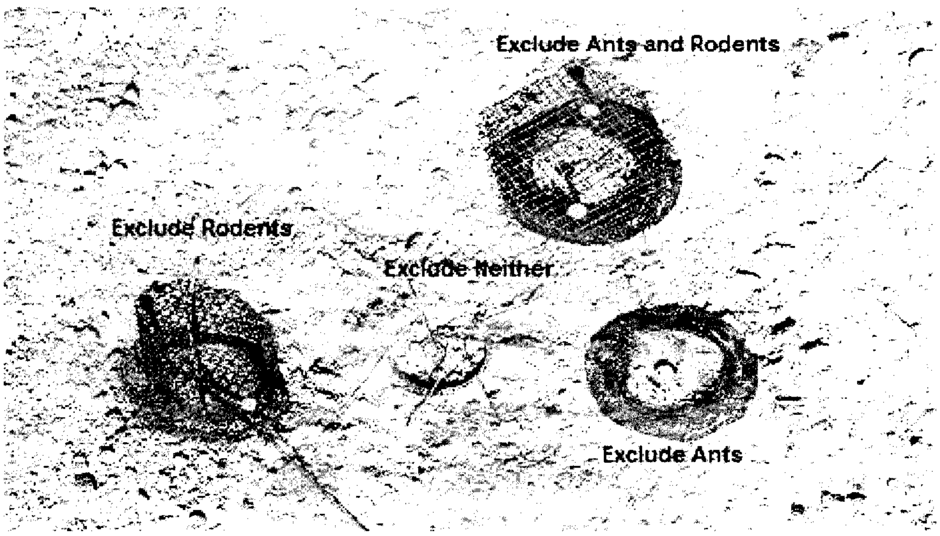

Figure 4. Pictorial of the exclusion design depicting all four treatments.

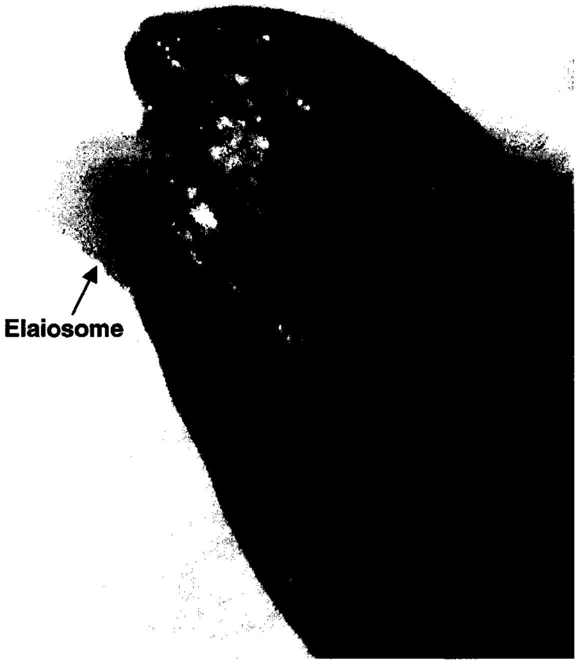

Figure 5. Pictorial of an elaiosome attached to the hilum edge of an *A. californica* seed. Photo courtesy of Elizabeth Powell.

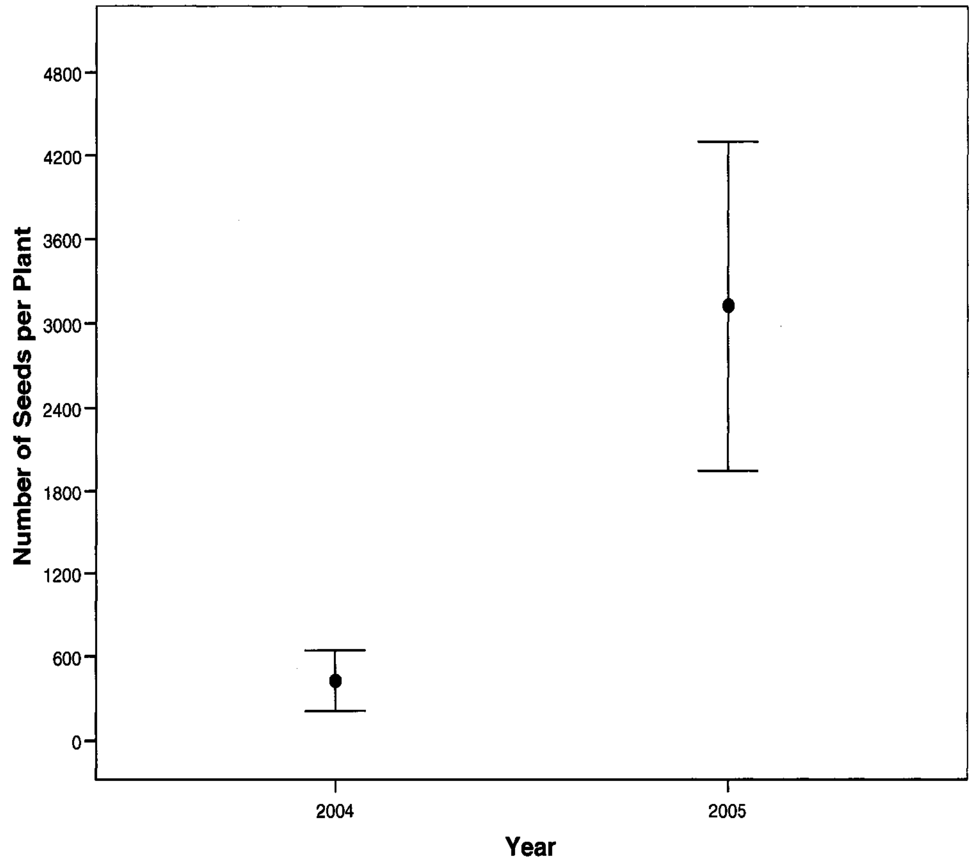

Figure 6. The number of seeds per plant pooled across sites with 95% confidence interval (n_{2004} = 16 plants and n_{2005} = 20 plants). Black dot = average number of seeds per plant.

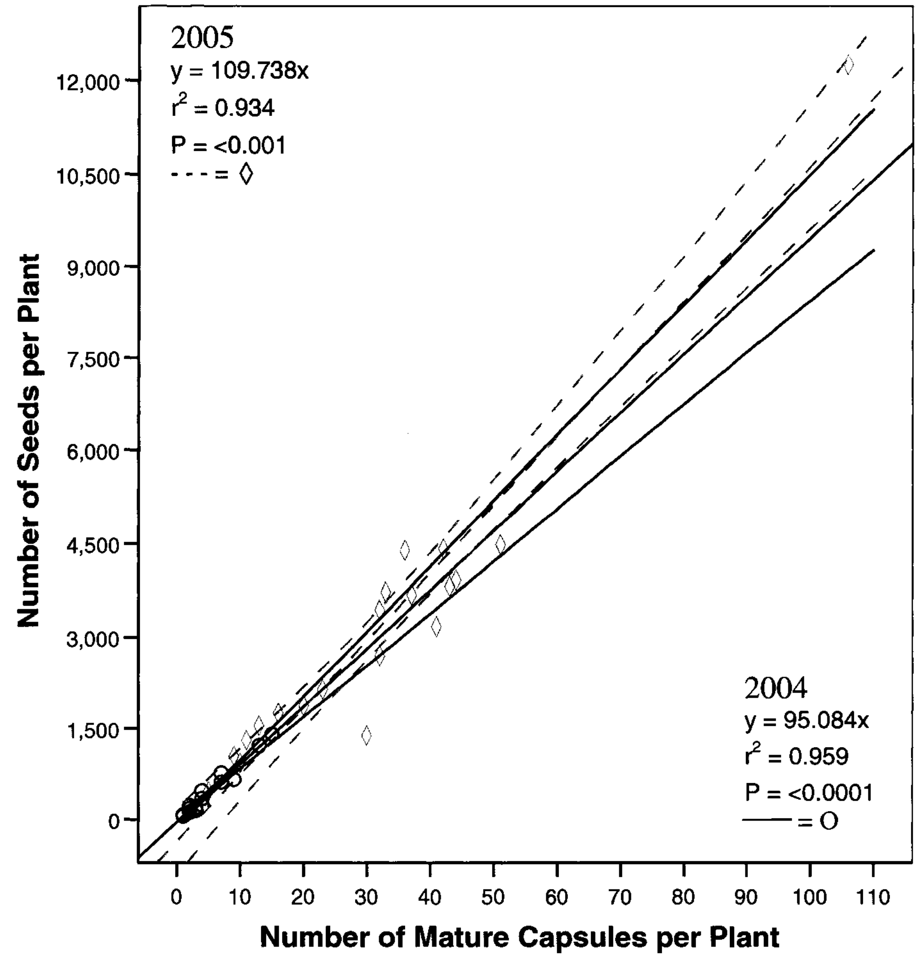

Figure 7. The relationship between the number of mature capsules per plant and the number of seeds per plant in 2004 and 2005, pooled across sites. The linear equations and r^2 values are shown along with the 95% confidence interval (n = 36 plants).

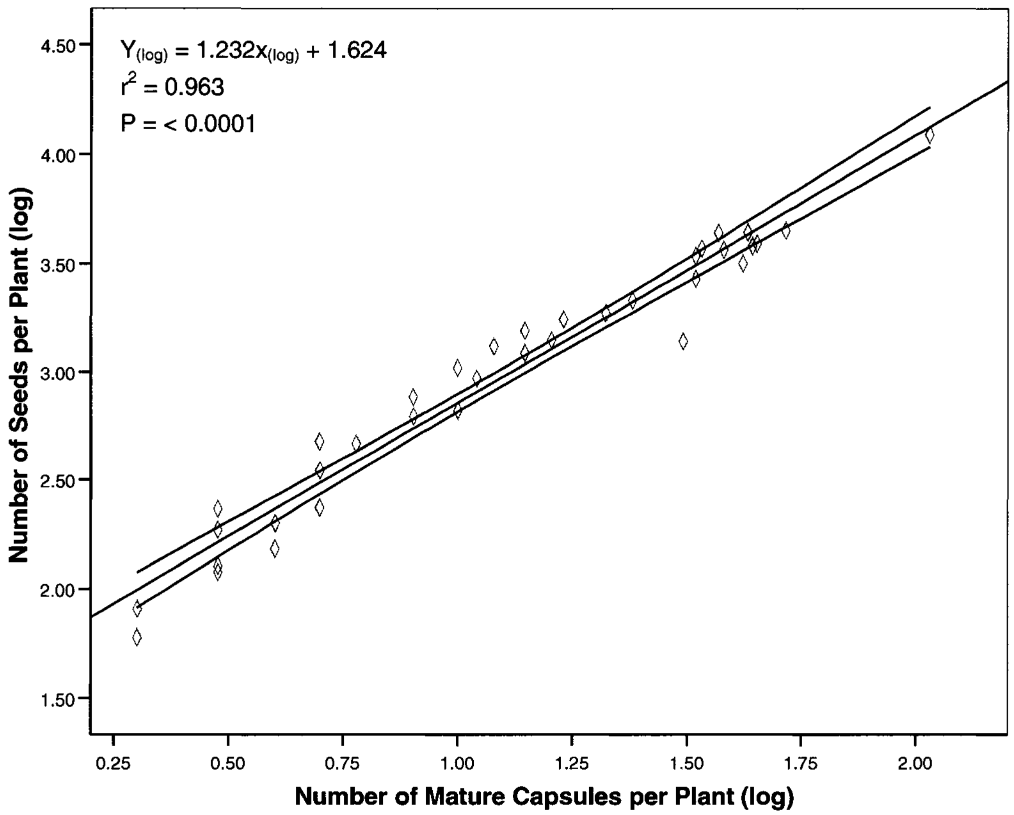

Figure 8. The relationship between the number of mature capsules and the number of seeds per plant pooled across sites and years. The linear equation and r^2 value along with the 95% confidence interval (n = 36 plants).

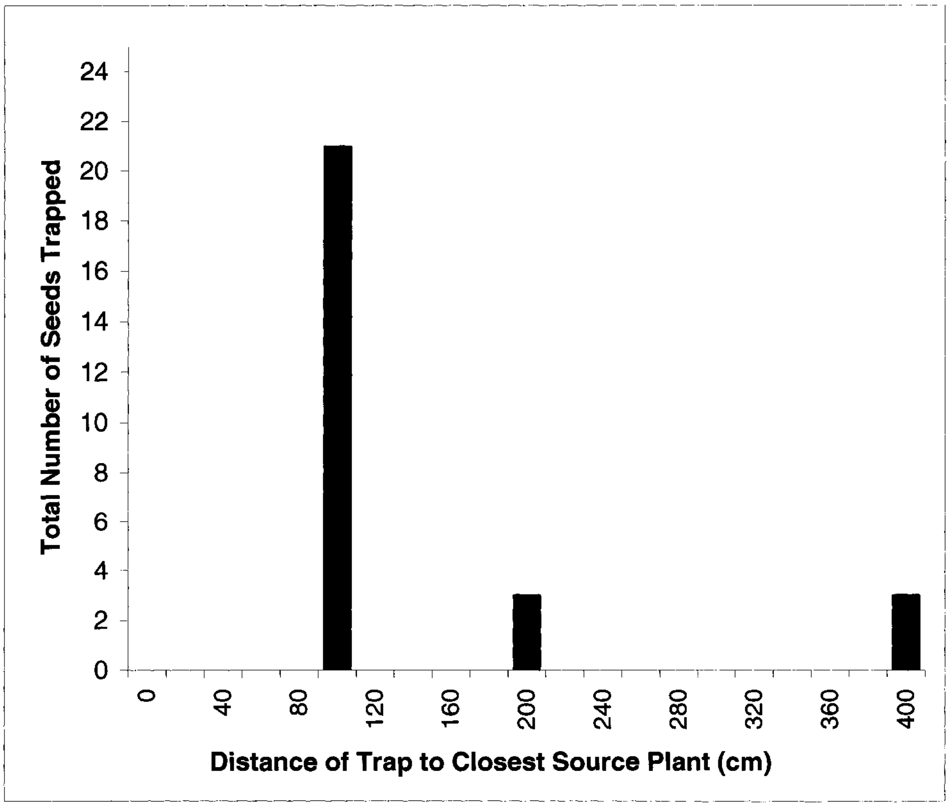

Figure 9. The distribution of the number of seeds trapped in relation to the nearest potential source plant, pooled across sites, in 2004 plot-based seed dispersal experiments (n = 8 seed traps).

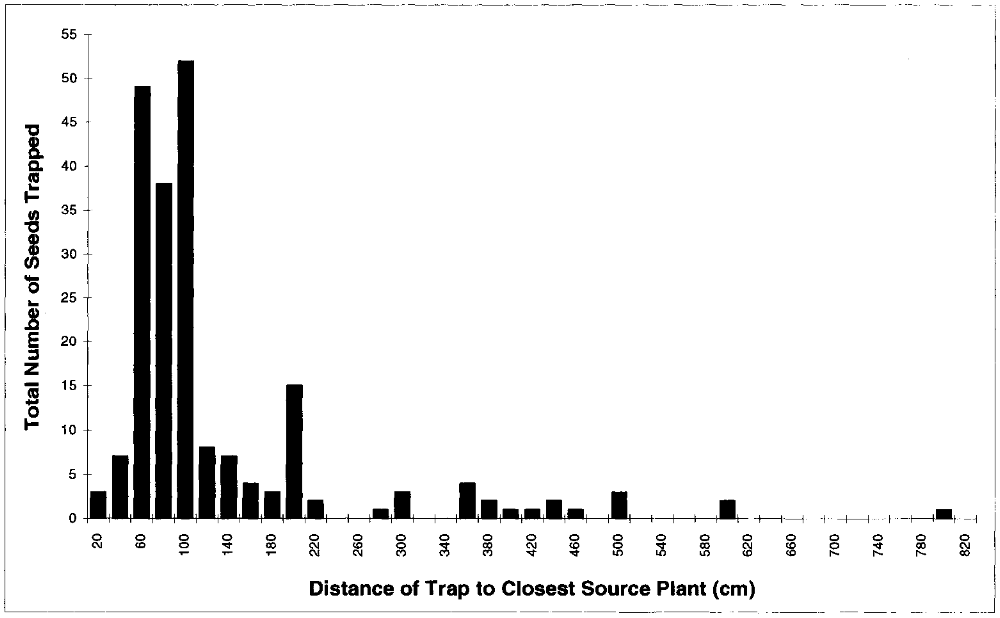

Figure 10. The distribution of seeds trapped in relation to the distance closest to the potential source plant, pooled across sites, in 2005 plot-based seed dispersal experiments (n = 51 seed traps).

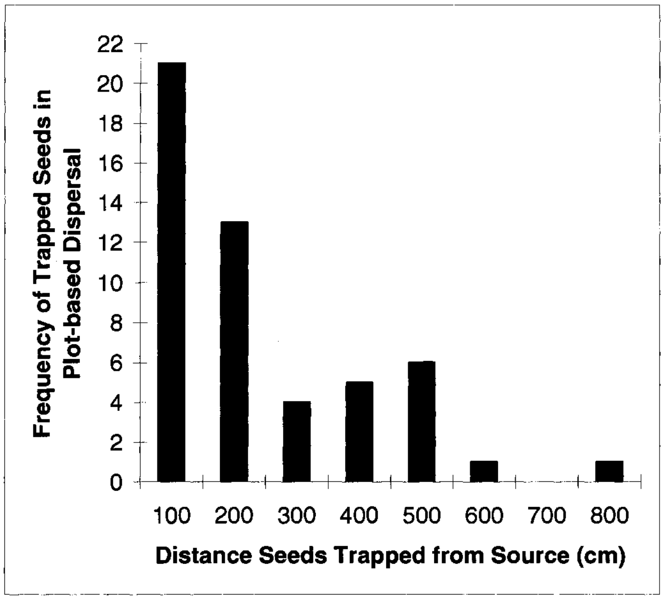

Figure 11. Frequency distribution for 2005 plot-based seed dispersal for the number of traps that caught seeds in relation to the distance to the closest reproducing adult plant (n = 51 traps).

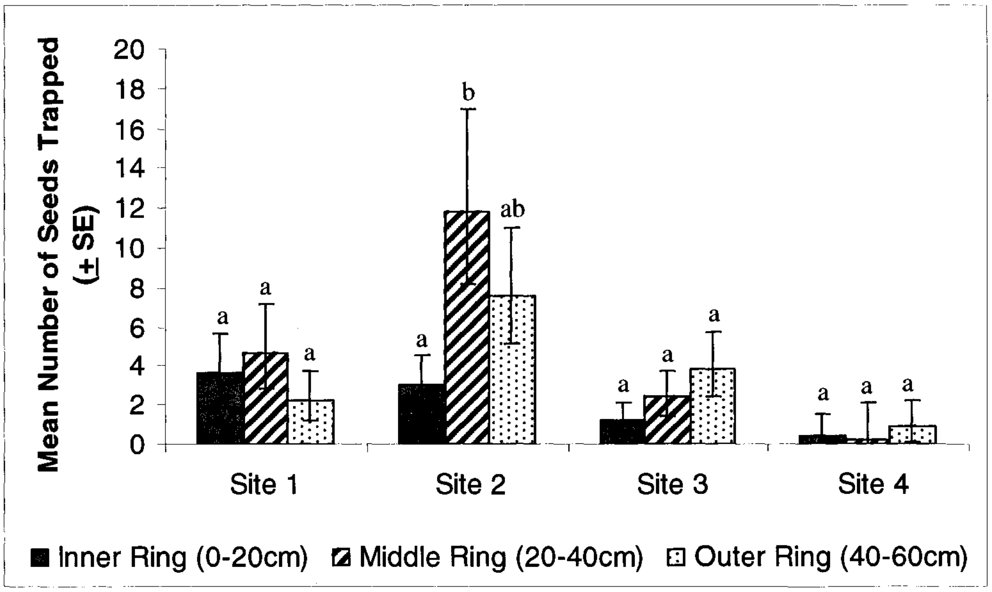

Figure 12. Least-squares means and SE for the number of seeds trapped by ring*site in 2004 for plant-based seed dispersal experiments (n = 16 plants). Columns with the same letters are not significantly different within sites (P > 0.05).

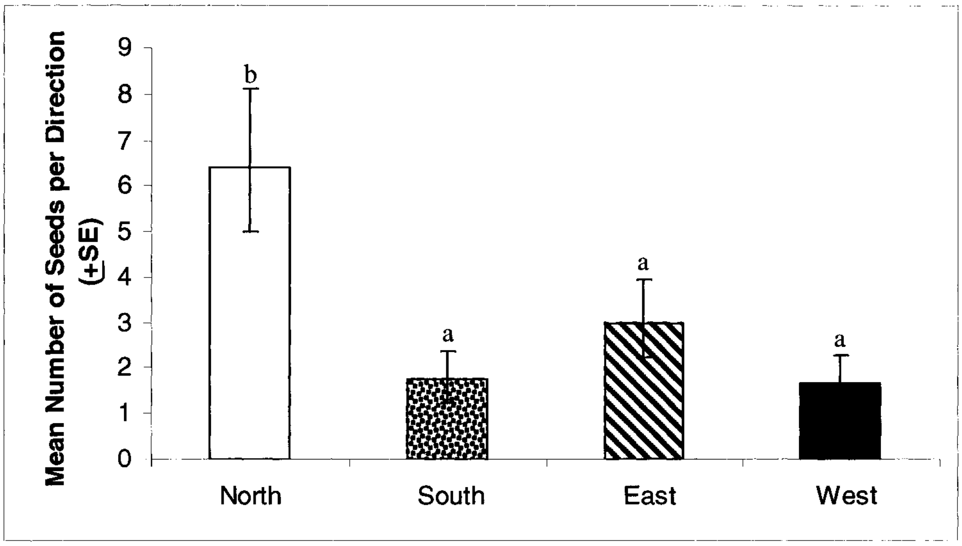

Figure 13. The mean and SE for the number of seeds trapped per cardinal direction during 2004 seed dispersal experiments (n = 16 plants). Columns with the same letters are not significantly different (P > 0.05).

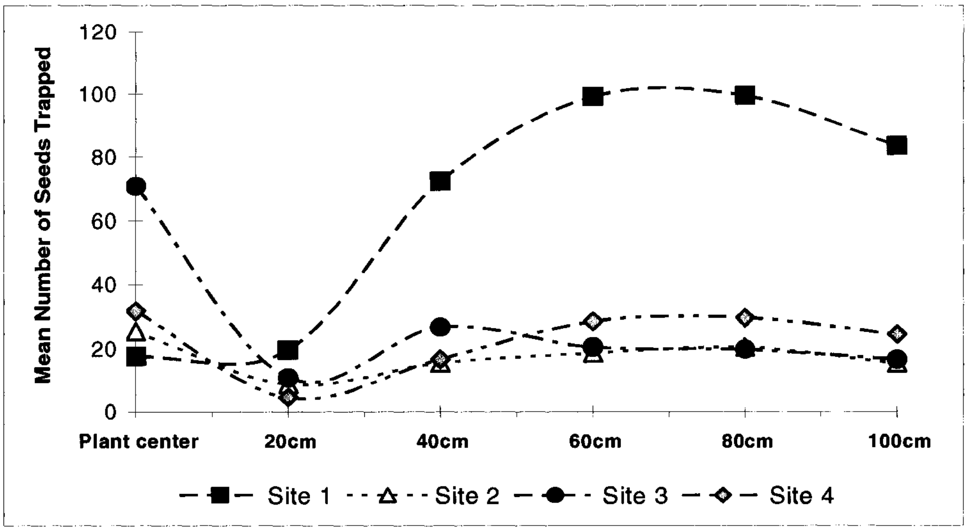

Figure 14. The mean number of seeds trapped per distance category for 2005 plant-based dispersal experiments illustrating the seed dispersal curve up to 100 cm from the plant. Dotted lines indicate categorical data (n = 15 plants).

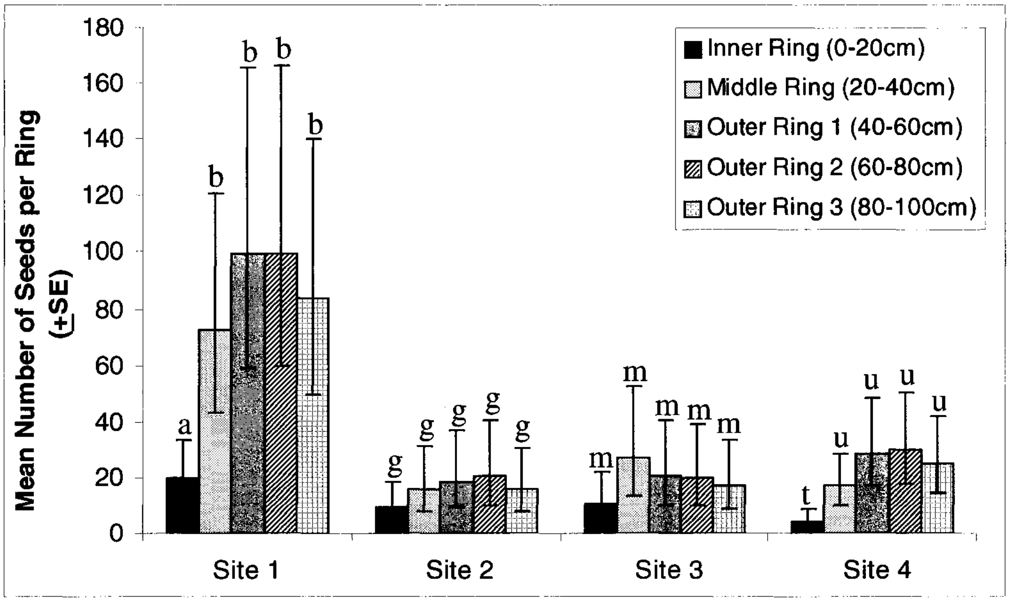

Figure 15. The mean and SE for the number of seeds trapped per *A. californica* plant per ring within sites during 2005 plant-based seed dispersal experiments. Columns with the same letters are not significantly different within sites ($P > 0.05$; n = 15 plants).

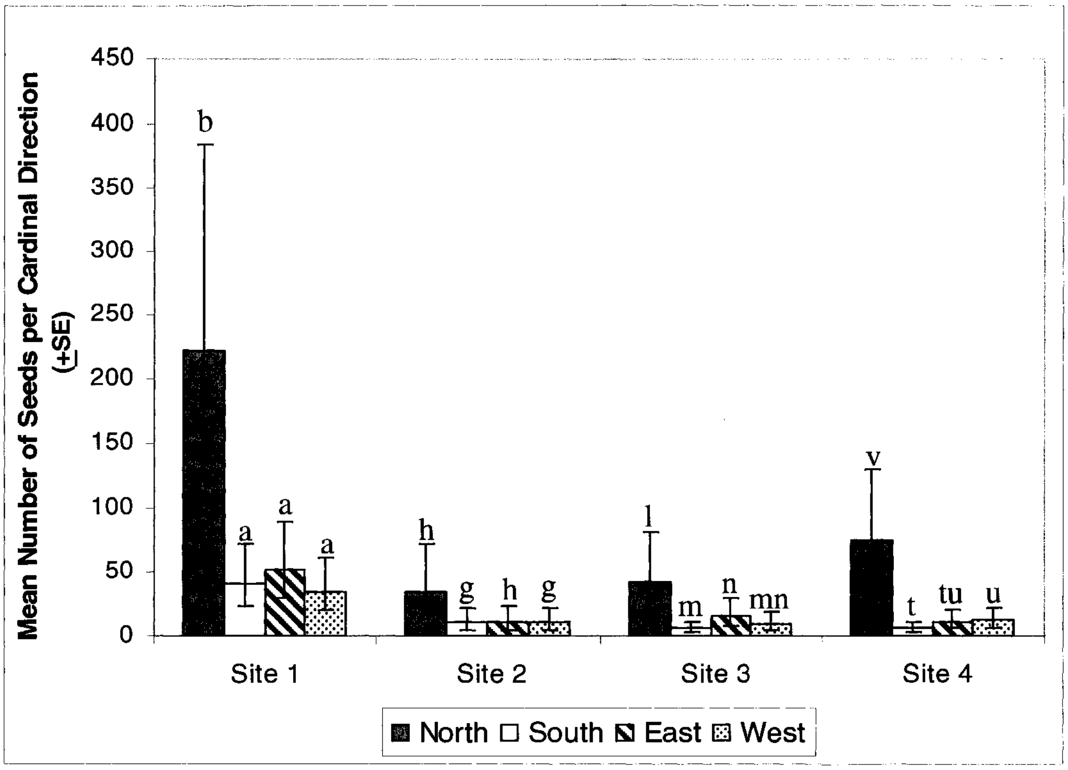

Figure 16. The mean and SE for the number of seeds trapped per *A. californica* plant per cardinal direction in 2005 across sites for plant-based seed dispersal experiments. Columns with the same letters are not significantly different within sites (P > 0.05, n = 15 plants).

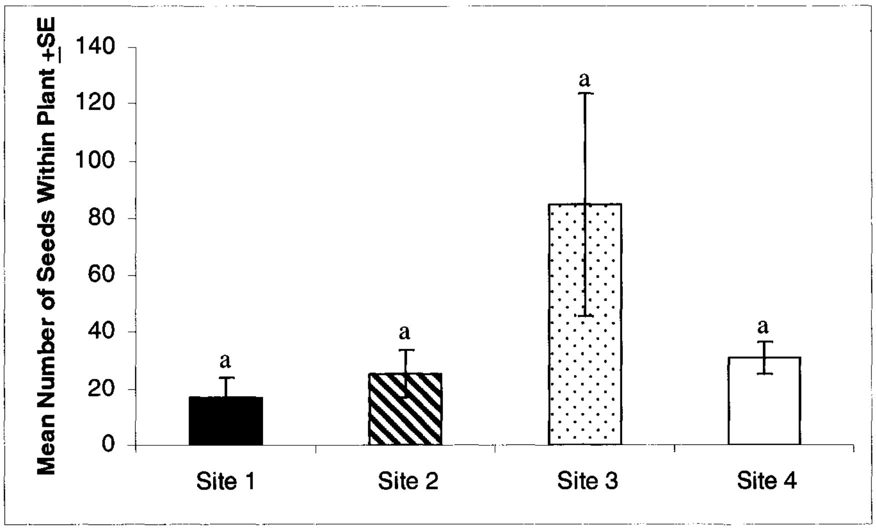

Figure 17. The mean and SE for the number of seeds that were found within plants in 2005 between sites (n = 20 plants). Columns with the same letters are not significantly different (P > 0.05).

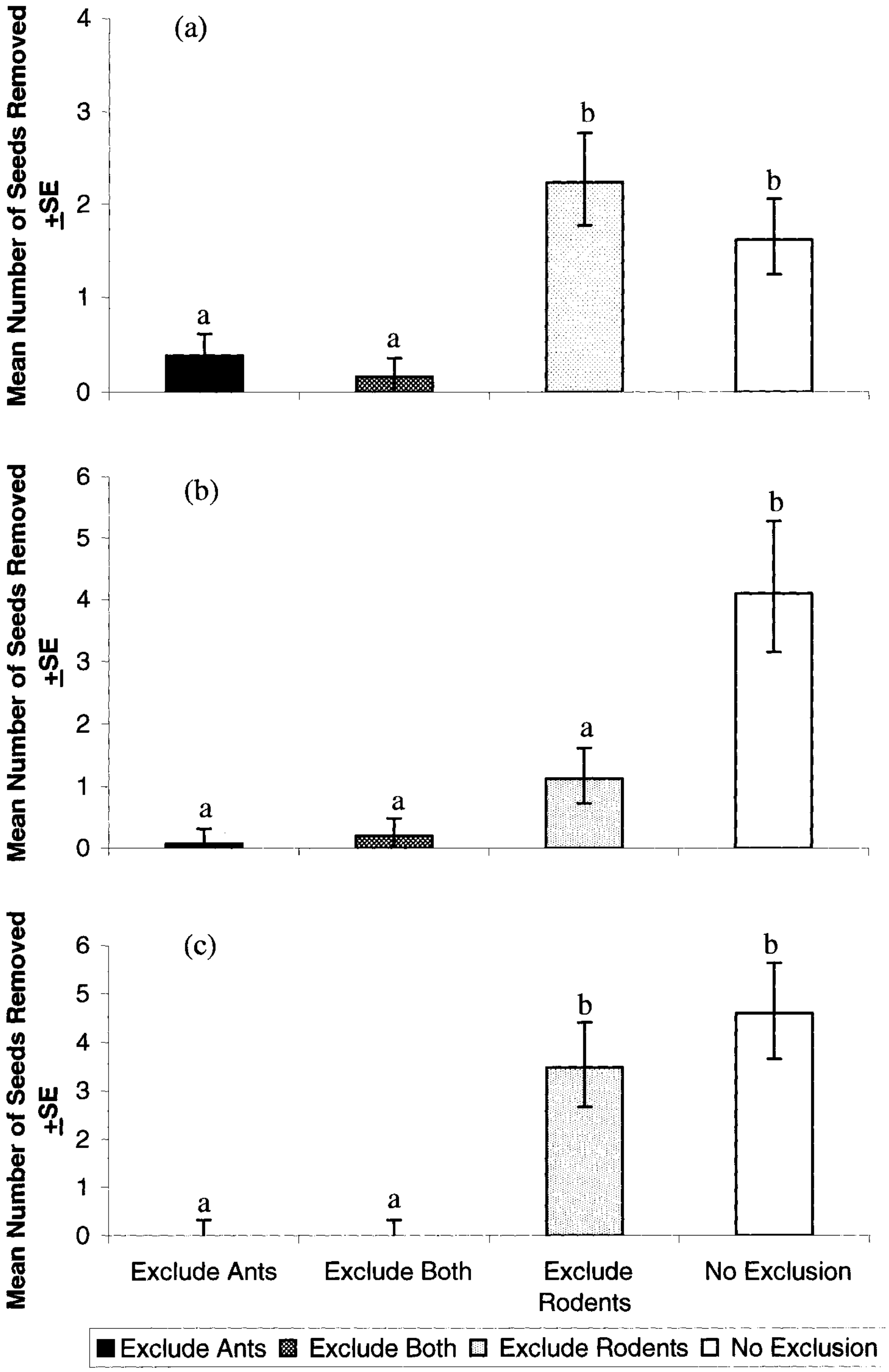

Figure 18. The mean and SE for the number of seeds removed per treatment in exclusion experiments (a) Trial 1: 27 July-1 August 2004; (b) Trial 2: 13 July-20 July 2005; and (c) Trial 3: 2 September-7 September 2005. Columns with the same letter are not significantly different within trials (P > 0.05, n = 4 sites).

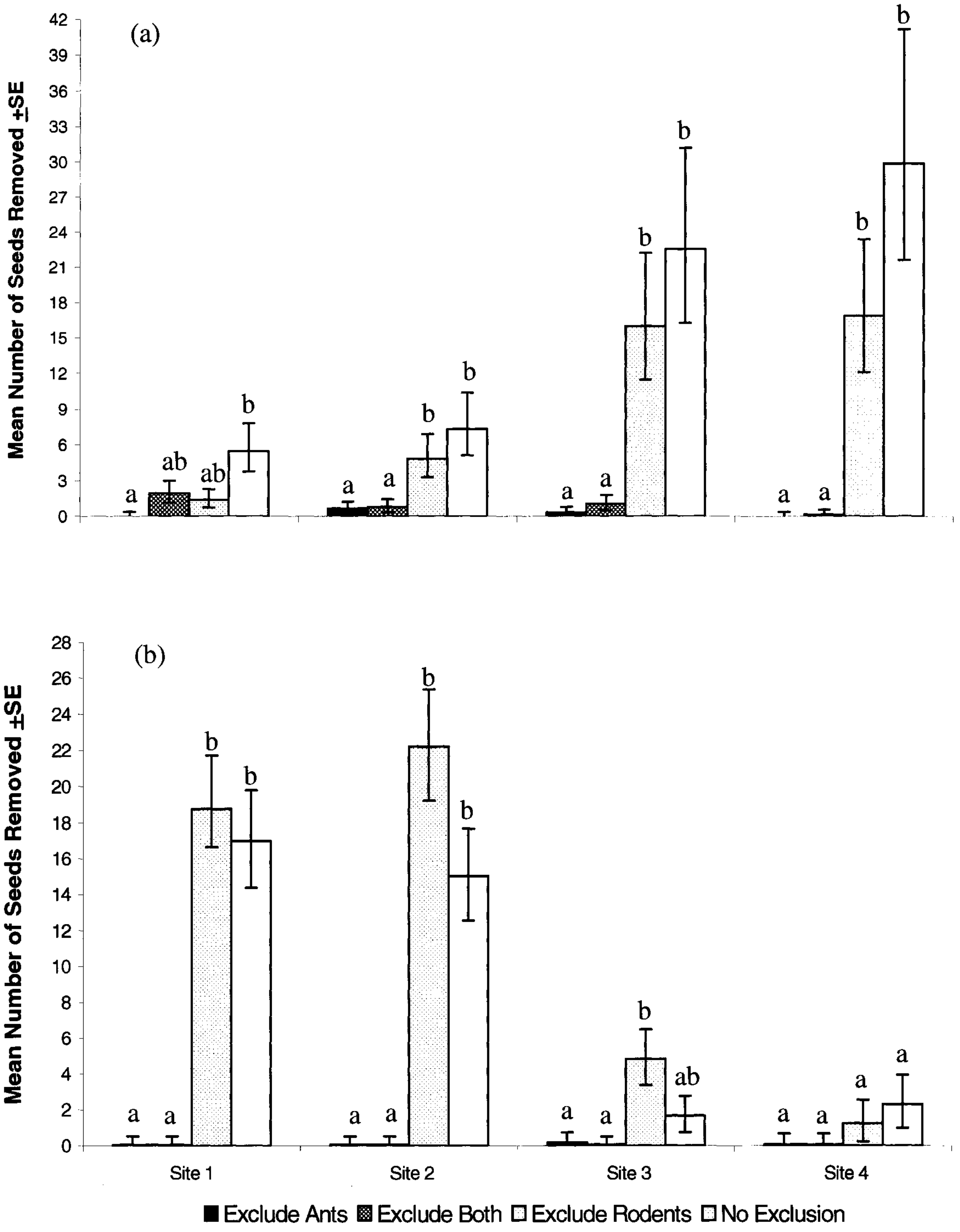

Figure 19. The mean and SE for the number of seeds removed per treatment within sites for exclusion experiments (a) Trial 4: 20 July-25 July 2004 and (b) Trial 5: 28 August-2 September 2005. Columns with the same letter are not significantly different within sites ($P > 0.05$, $n = 4$ sites).

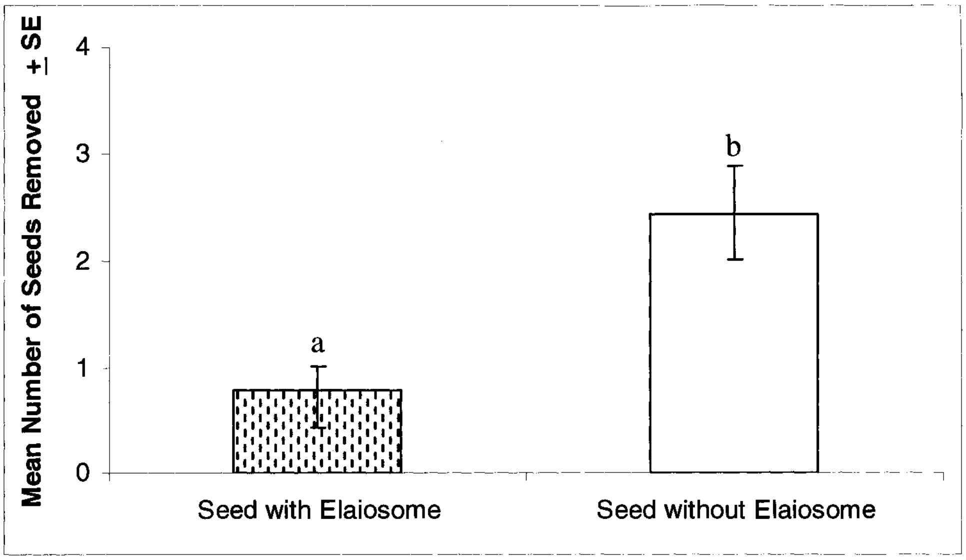

Figure 20. Means and SE for the number of seeds removed per treatment in Elaiosome Experiment 1 pooled across trials. Columns with different letters are significantly different ($P < 0.05$, $n = 4$ sites).

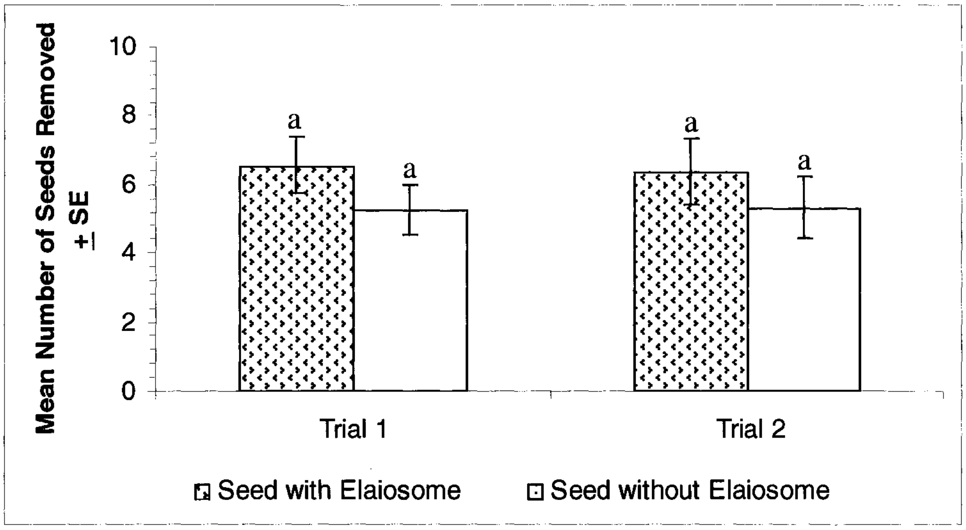

Figure 21. Means and SE for the number of seeds removed per nicked treatment in Elaiosome Experiment 2. Trial 1 = 28 August–2 September 2005 and Trial 2 = 2-7 September 2005. Columns with the same letter are not significantly different within sites ($P > 0.10$, n_1 and $n_2 = 4$ sites).

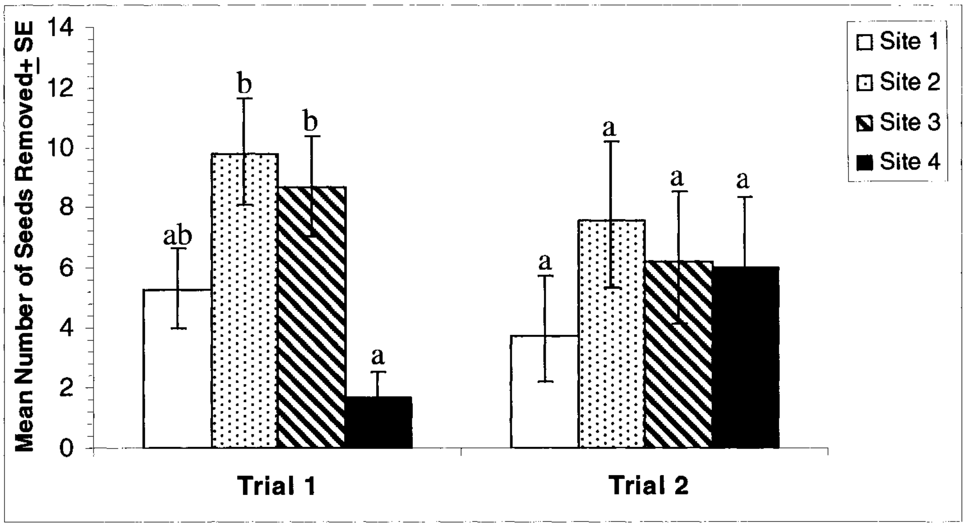

Figure 22. Means and SE for the number of seeds removed per site in Elaiosome Experiment 2. Trial 1 = 28 August– 2 September 2005 and Trial 2 = 2-7 September 2005. Columns with the same letter are not significantly different within sites ($P > 0.05$, n_1 and $n_2 = 4$ sites).

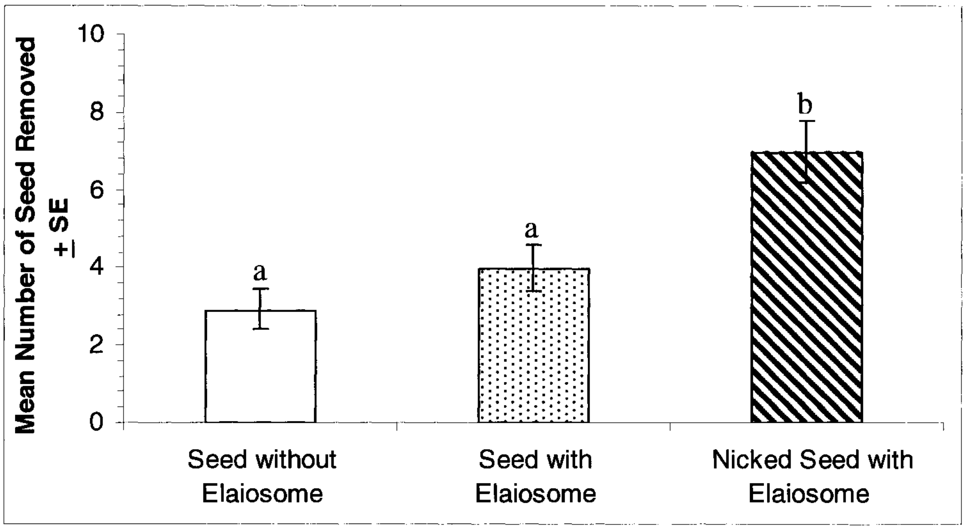

Figure 23. Means and SE for the number of seeds removed per treatment in 2005 Elaiosome Experiment 3. Columns with the same letter are not significantly different (P > 0.05, n = 4 sites).

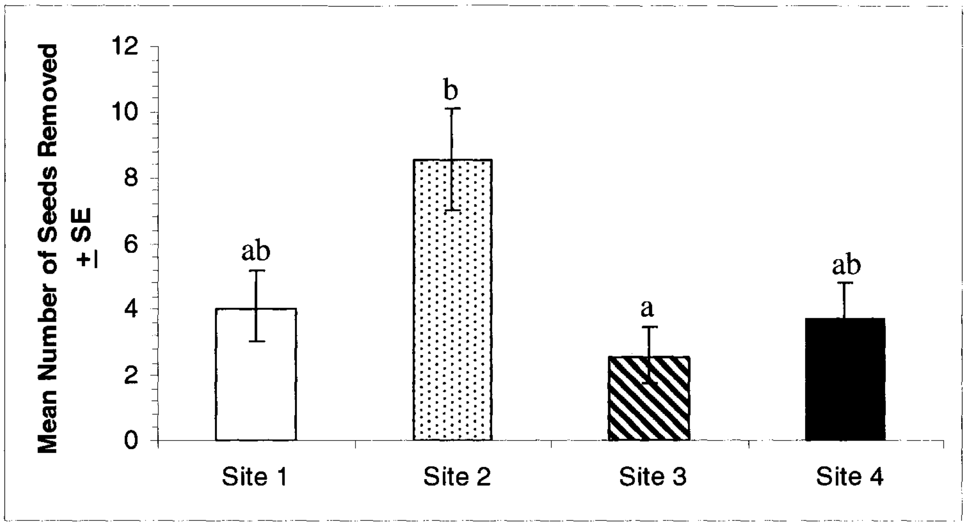

Figure 24. Means and SE for the number of seeds removed per site in 2005 Elaiosome Experiment 3. Columns with the same letter are not significantly different between sites (P > 0.05, n = 4 sites).

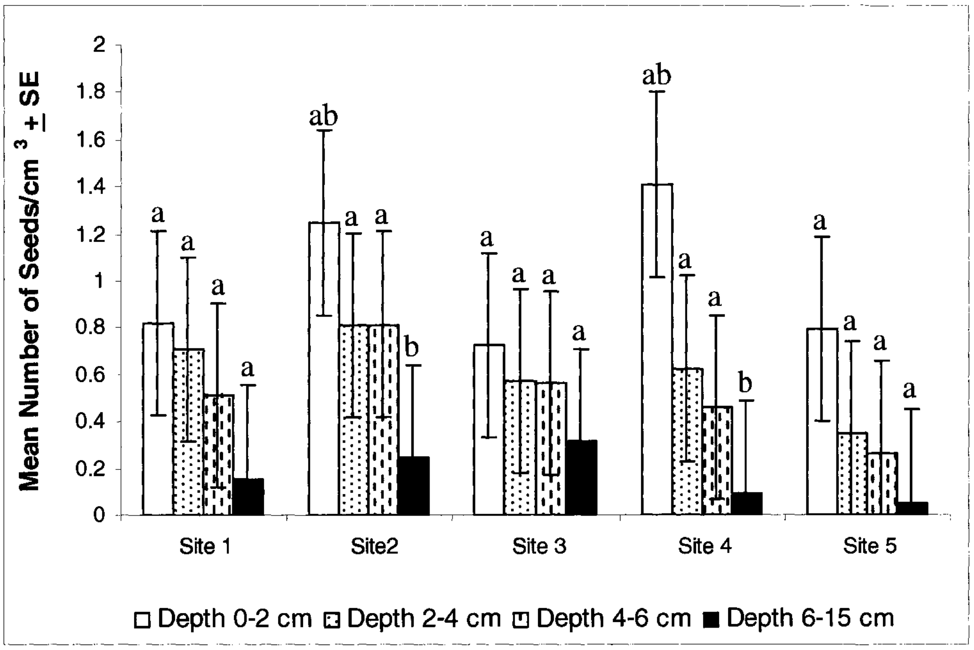

Figure 25. The mean and SE for the total number of *A. californica* seeds found within the seed bank by depth and site in 2005. Columns with the same letter are not significantly different within sites ($P > 0.05$, n = 5 sites).

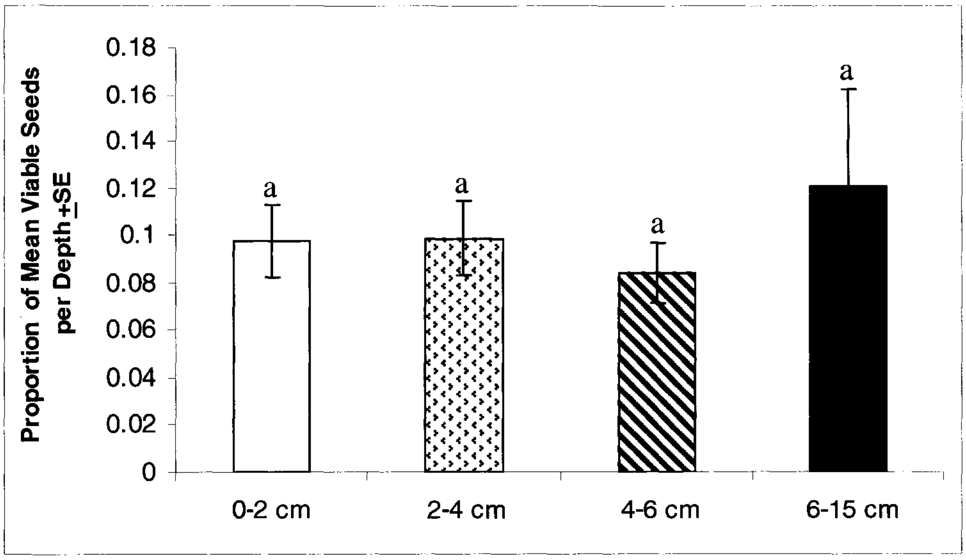

Figure 26. The proportion of viable seeds per depth pooled across sites for the 2005 seed bank study. Columns with the same letter are not significantly different between depths (P > 0.05, n = 5 sites).

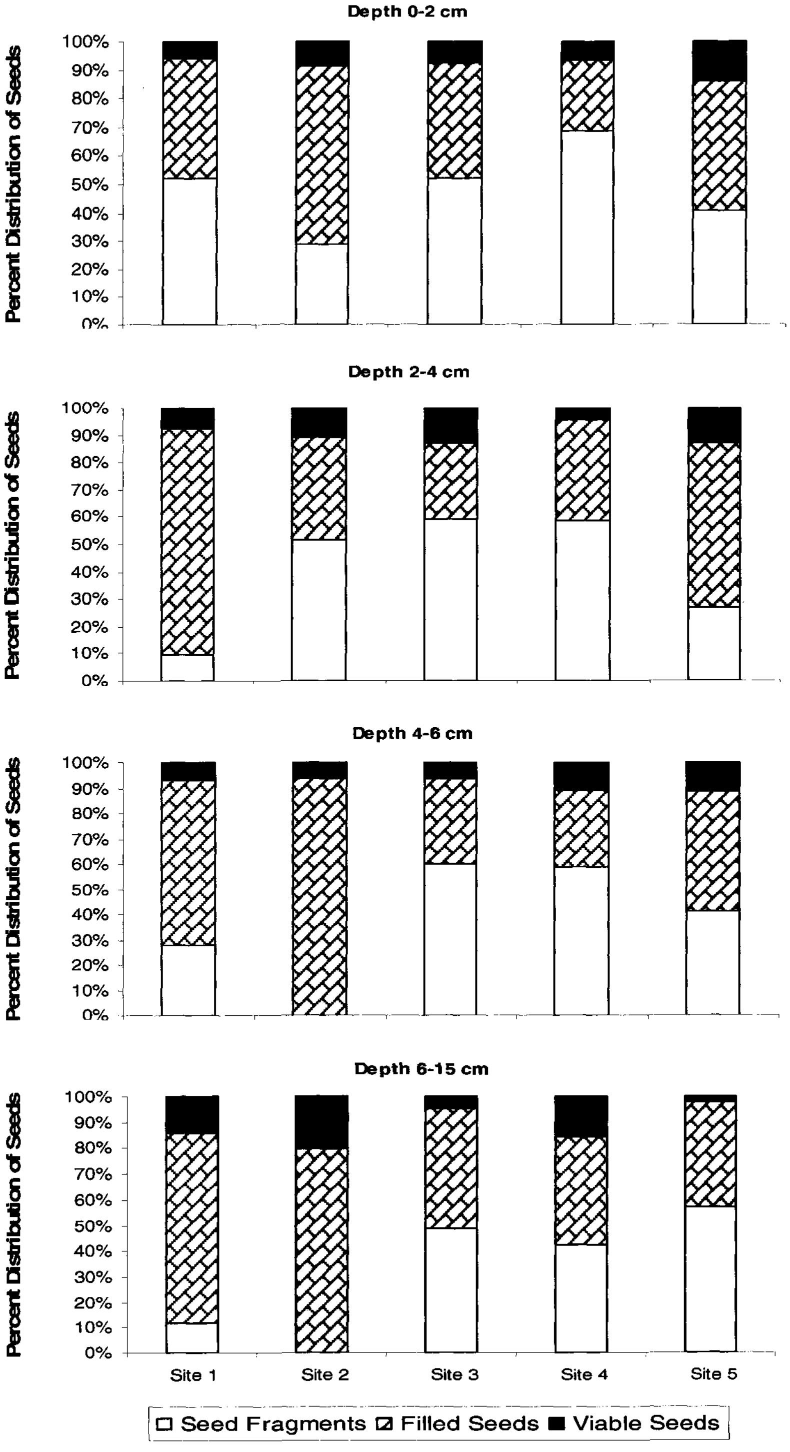

Figure 27. The percent distribution of each seed category (fragment, filled but non-viable or viable) for the total number of seeds found within sites and depths (0-2 cm, 2-4 cm, 4-6 cm and 6-15 cm) in 2005 seed bank study (n = 5 sites).

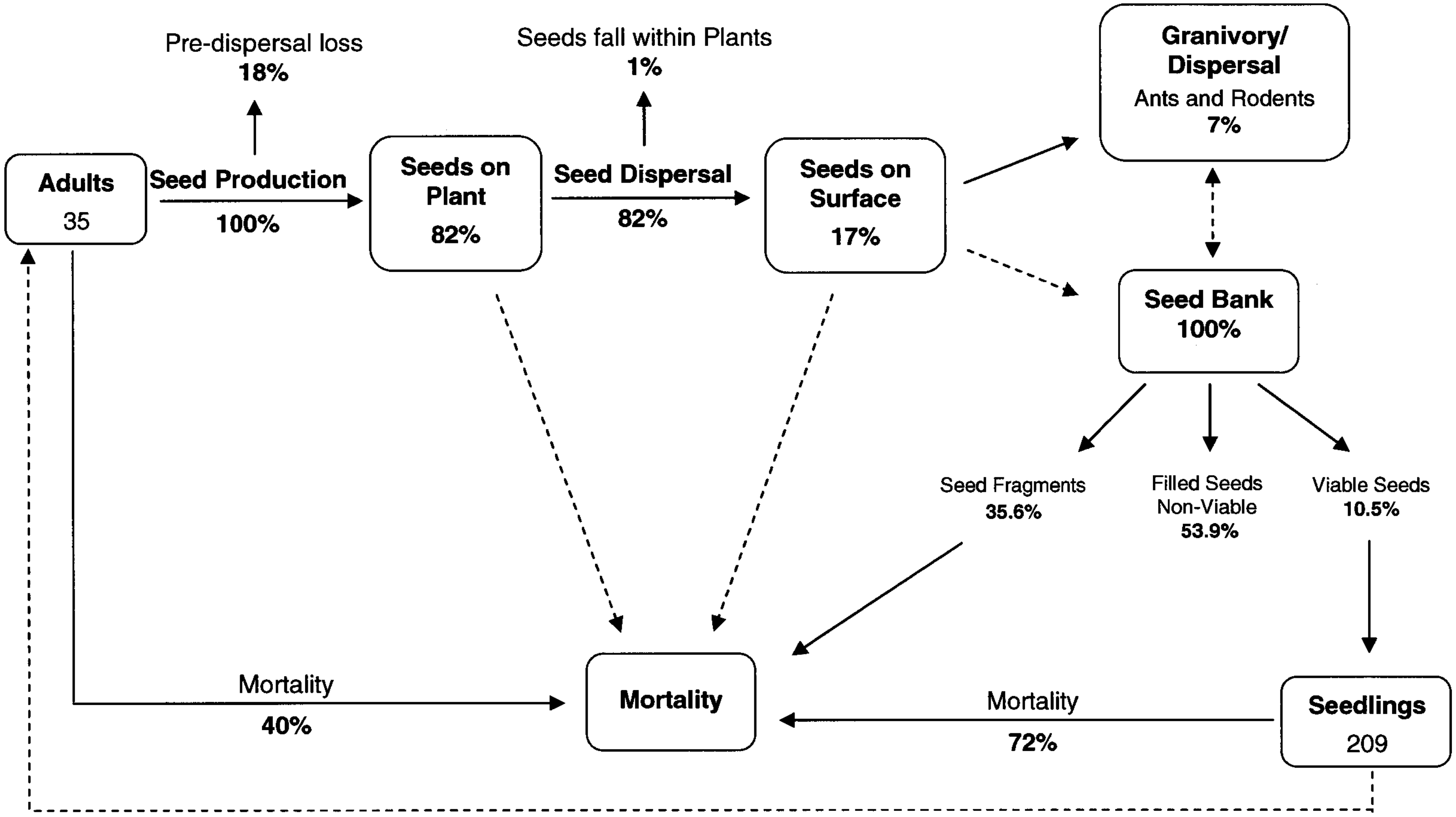

Figure 28. Schematic diagram tracing the major causes and consequences of *Arctomecon californica* seed fates over the two-year study. All percentages are based on the original 100% of seed production except at the seed bank stage which starts over at 100%. The solid arrows are based on actual measurements and represent processes that act on the seed as it travels through various ecological stages designated by rounded boxes. The broken arrows indicate seed fate processes not measured in the study. Adapted after Nathan and Muller-Landau (2000).

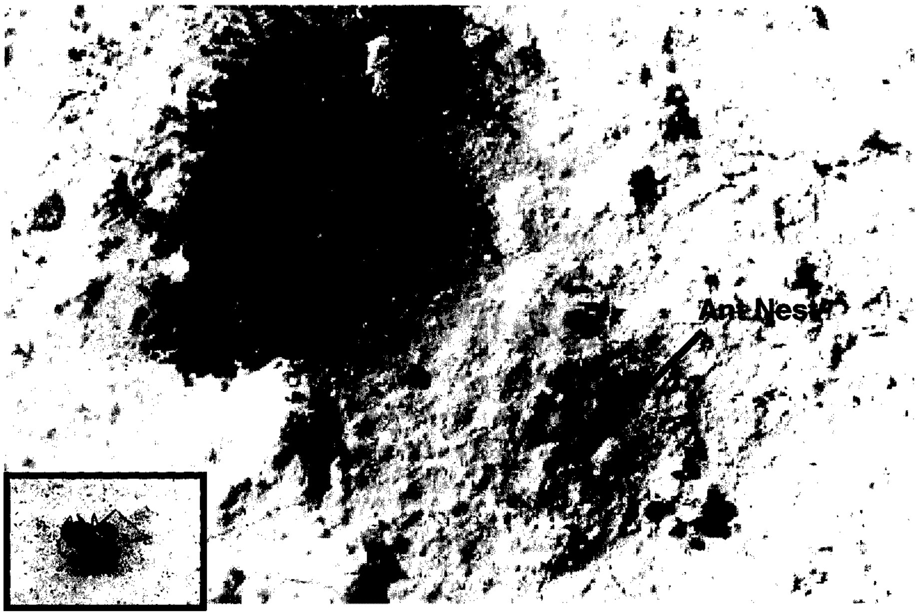

Figure 29. Ant midden pile of *Arctomecon californica* seeds outside of the ant nest at Stewarts Point, Lake Mead National Recreational Area. Inset picture illustrates an ant with an *Arctomecon californica* seed in its possession. Photos courtesy of Elizabeth Powell.

APPENDIX II

TABLES

Table 1. The percent viable seeds per plant based on a sample of pooled mature capsules per plant collected during 2005 seed production measurements (n = 19 plants).

Site	Plant	Total Seeds	Seeds Tested	Number of Viable Seeds	Percent Viable †
1	1	174	174	163	93.7
	2	85	85	84	98.8
	3	114	100	90	90.0
	4	40	40	35	87.5
	5	473	457	400	87.5
2	3	208	100	92	92.0
	4	517	140	132	94.3
	5	666	210	194	92.4
	9	149	100	91	91.0
3	1	28	28	27	96.4
	3	224	224	215	96.0
	4	116	100	97	97.0
	6	80	80	76	95.0
	9	1133	100	88	88.0
4	1	11	11	11	100.0
	2	232	100	214	92.0
	4	185	100	97	97.0
	9	331	331	308	93.1
	12	105	100	95	95.0

† Percent viable calculated as seeds tested ÷ number viable.

Table 2. The results of Pearson correlation analysis between the numbers of seeds per plant and plant characteristics for 2004 (n = 16 plants) and 2005 (n = 20 plants). All factors were affected by multicollinearity in the model.

Year	Variables	Coefficient	P-value
	Plant Size (cm^2)	0.151	0.5780
2004	Plant Diameter (cm)	0.151	0.5780
	Number of Flowers/plant	0.417	0.1080
	Number of Stalks/plant	0.233	0.3840
	Number of Rosettes/plant	0.332	0.2080
	Number of Mature Cap/plant	0.956	< 0.0001
	Plant Size (cm^2)	0.752	<0.0001
	Plant Diameter (cm)	0.735	<0.0001
2005	Number of Flowers/plant	0.507	0.0230
	Number of Stalks/plant	0.340	0.1430
	Number of Rosettes/plant	0.315	0.1760
	Number of Mature Cap/plant	0.945	< 0.0001

Table 3. Results of the ANCOVA modeling the fixed effect of year, the number of mature capsules as the covariate and the number of seeds per plant as the dependent variable for 2004 and 2005 seed production studies (n = 36 plants).

Source	df	MS	F	P-value
Year	1	315198.757	1.325	0.2580
Capsules	1	10887722.720	45.777	<0.0001
Year*Capsules	1	55731.551	0.234	0.6320

Table 4. The estimated number of seeds produced per site and average per *A. californica* plant over the two-year study period. Seed output per reproducing plant was derived using the seed production equation: No. seeds = 41.07* (No. mature capsules)$^{1.232}$ per plant.

Year	Site	No. of Plants per Site	Average Estimated Seeds per Plant +/- SE	Estimated Seeds per Site
2004	1	21	768 ± 240.3	16,122
2004	2	30	1,396 ± 351.4	41,894
2004	3	27	1,406 ± 387.8	37,972
2004	4	7	510 ± 225.9	3,572
2005	1	42	3,931 ± 706.4	161,157
2005	2	33	6,132 ± 1,094.7	202,373
2005	3	30	5,149 ± 915.7	154,455
2005	4	97	13,490 ± 2,130.5	1,254,609

Table 5. The results of the Spearman rank correlation analysis between the numbers of seeds per capsule and capsule attributes for 2004 (n = 79 capsules) and 2005 (n = 634 capsules). All factors were affected by multicollinearity in the model.

Year	Variables	Coefficient	P-value
	Capsule Radius $_{(cm)}$	0.474	< 0.0001
	Capsule Diameter $_{(cm)}$	0.474	< 0.0001
2004	Capsule Length $_{(cm)}$	0.548	< 0.0001
	Volume of Cone $_{(cm^3)}$	0.474	< 0.0001
	Volume of Sphere $_{(cm^3)}$	0.474	< 0.0001
	Volume of Cylinder $_{(cm^3)}$	0.474	< 0.0001
	Capsule Radius $_{(cm)}$	-0.042	0.293
	Capsule Diameter $_{(cm)}$	-0.042	0.293
2005	Capsule Length $_{(cm)}$	0.049	0.227
	Volume of Cone $_{(cm^3)}$	-0.018	0.656
	Volume of Sphere $_{(cm^3)}$	-0.042	0.293
	Volume of Cylinder $_{(cm^3)}$	-0.018	0.656

Table 6. Results of the mixed model ANOVA modeling the main effects of site, ring, direction and the random effect of plant(site) on the number of seeds trapped from the edge of the plant (dependent variable) in 2004 seed dispersal studies. The dependent variable was $\text{Log}_{10(x+1)}$ transformed (n = 16 plants).

Source	Numerator Df	Denominator Df	F	P-value
Site	3	12.010	3.460	0.113
Ring	2	132.021	6.788	0.002
Direction	3	132.062	12.705	0.000
Site*Ring	6	132.023	2.468	0.027
Site*Direction	9	132.075	1.216	0.290
Ring*Direction	6	132.061	0.749	0.611
Site*Ring*Direction	18	132.074	0.748	0.756

Table 7. Results for mean percent of seeds trapped during plant-based seed dispersal in 2004 (n = 16 plants; mean % ± SE).

Site	Plant	Est. Seeds Produced	No. of Seeds Trapped	% Seeds Trapped†	Site Mean Percent ‡
1	1	701	218	31	
1	2	615	68	11	18 ± 4.5
1	3	452	57	13	
1	5	452	72	16	
2	1	10,499	766	7	
2	2	968	189	20	15 ± 3.6
2	3	532	42	8	
2	4	1,061	279	26	
2	5	227	35	15	
3	1	2,824	42	1	
3	2	1,060	60	6	9 ± 5.4
3	3	227	69	30	
3	4	1,250	44	4	
3	5	701	29	4	
4	2	41	23	56	
4	3	373	15	4	30 ± 26.2

† Number of seeds trapped ÷ estimates of seeds produced

‡ Number of % seeds trapped per site ÷ number of plants per site

Table 8. Results of the mixed model ANOVA modeling the number of seeds trapped as the dependent variable and the main effects of site, ring, direction and the random effect of plant(site) for 2005 seed dispersal studies. The dependent variable was $\text{Log}_{10(x+1)}$ transformed (n = 15 plants).

Source	Numerator Df	Denominator Df	F	P-value
Site	3	12.010	1.643	0.2320
Ring	4	228.000	22.902	<0.0001
Direction	3	228.000	91.333	<0.0001
Site*Ring	12	228.000	1.798	0.0490
Site*Direction	9	228.000	3.340	0.0010
Ring*Direction	12	228.000	3.376	<0.0001
Site*Ring*Direction	36	228.000	1.153	0.2650

Table 9. Results for the mean percent of seeds trapped during plant-based seed dispersal in 2005 (n = 15 plants; mean % ± SE).

Site	Plant	Est. Seeds Produced	Number of Seeds Trapped	% Seeds Trapped †	Site Mean % ‡
1	1	12,546	2,727	22	
1	2	877	83	9	
1	3	12,695	2,206	17	22 ± 4.2
1	4	8,112	2,187	27	
1	5	7,839	2,646	34	
2	1	13,897	1,011	7	
2	2	14,505	2,828	19	18 ± 5.8
2	3	5,468	1,502	27	
3	3	10,787	374	3	
3	4	3,866	1,119	29	16 ± 7.5
3	5	13,293	2,144	16	
4	1	3,747	516	14	
4	2	5,981	1,198	20	20 ± 1.9
4	3	1,061	246	23	
4	4	17,777	3,650	21	

† Number of seeds trapped ÷ estimates of seeds produced

‡ Number of % seeds trapped per site ÷ number of plants per site

Table 10. Results of the mixed-model ANOVA modeling the main effects of site, treatment, time, all interactions and random effect of replicate(site) on the number of seeds removed in exclusion experiments as the dependent variable pooling Trials 1-5 (n = 4 sites).

Source	Num. Df	Denom. Df	F	P-value
Site	3	268.00	2.716	0.0450
Trt	3	268.00	132.018	<0.0001
Time	4	268.00	15.228	<0.0001
Site*Trt	9	268.00	2.037	0.0360
Site*Time	11	268.00	3.737	<0.0001
Time*Trt	12	268.00	4.006	<0.0001
Site*Trt*Time	33	268.00	2.231	<0.0001

Table 11. Results of the two factor non-parametric ANOVA adjusted for ties modeling the main effects of site, trt, site*trt with the number of seeds removed in exclusion experiments as the dependent variable. Trial 1: 27 July-1 August 2004 (n = 4 sites). Also shown are the results of the mixed model ANOVA modeling the main effects of site, treatment, site*treatment and the random effect of replicate(site) with the number of seeds removed in the exclusion experiments as the dependent variable. Trial 2: 13 July-20 July 2005 ($\mathrm{Log}_{10(x+1)}$) and Trial 3: 2 September-7 September 2005 (n = 4 sites).

Trial	Source	Df	SS	H_{adj}	P-value
	Site	2	14.66	0.075	0.25
1	Trt	3	4315.80	22.020	0.001
	Site*Trt	6	624.92	3.188	0.10

Trial	Source	Num. Df	Denom. Df	F	P-value
	Site	3	40.00	1.042	0.3840
2	Trt	3	40.00	11.953	<0.0001
	Site*Trt	9	40.00	0.974	0.4760
	Site	3	15.00	1.071	0.391
3	Trt	3	45.00	18.662	<0.001
	Site*Trt	9	45.00	0.939	0.501

Table 12. Results of the mixed model ANOVA modeling the main effects of site, treatment, site*treatment and the random effect of replicate(site) for the number of seeds removed in the exclusion experiments. Trial 4: 20 July-25 July 2004 ($\mathrm{Log}_{10(x+1)}$ and Trial 5: 28 August-2 September 2005 ($\mathrm{Sqrt}_{(x+.375)}$; n = 4 sites).

Trial	Source	Numerator Df	Denominator Df	F	P-value
4	Site	3	60.0	4.999	0.004
	Trt	3	60.0	65.435	<0.0001
	Site*Trt	9	60.0	4.528	<0.0001
5	Site	3	14.0	16.099	<0.0001
	Trt	3	42.0	101.910	<0.0001
	Site*Trt	9	42.0	10.029	<0.0001

Table 13. Elaiosome presence versus absence survey among five different *A. californica* populations over a two-year period.

Year	Site	Seeds w/o Elaiosomes	Seeds w/ Elaiosomes	Number of Seeds	Percent w/ Elaiosomes
2004	1	6	3,664	3,670	99
2004	2	5	3,660	3,665	99
2004	3	2	3,663	3,665	99
2004	4	2	2,651	2,653	99
2005	1	1	1,199	1,200	99
2005	2	0	1,200	1,200	100
2005	3	1	1,199	1,200	99
2005	4	1	1,199	1,200	99
2005	NLV Airport	5	4,795	4,800	99

Table 14. Results of the of the mixed model ANOVA modeling the main effects of site, trt, site*trt and replicate(site) as a random effect on the number of seeds removed in the elaiosome Experiment 1 pooled across sites. Trial 1: 14-25 July 2005 (n = 4 sites).

Source	Numerator Df	Denominator Df	F	P-value
Site	3	48.0	3.298	0.058
Trt	1	48.0	15.502	<0.0001
Time	1	48.0	3.742	0.059
Site*Trt	3	48.0	0.828	0.485
Site*Time	3	48.0	2.689	0.057
Trt*Time	1	48.0	0.217	0.644
Site*Trt*Time	3	48.0	0.099	0.960

Table 15. Results of the of the mixed model ANOVA modeling the main effects of site, trt, site*trt with replicate nested within site as a random factor for the number of seeds removed in the elaiosome Experiment 2. Trial 1: 28 August-2 September 2005 (n = 4 sites) and Trial 2: 2-7 September 2005 (n = 4 sites).

Trial	Source	Numerator Df	Denominator Df	F	P-value
1	Site	3	16.0	8.001	0.002
	Trt	1	16.0	4.415	0.059
	Site*Trt	9	16.0	1.461	0.263
2	Site	3	16.0	0.921	0.453
	Trt	1	16.0	1.691	0.212
	Site*Trt	3	16.0	0.416	0.416

Table 16. Results of the mixed model ANOVA modeling the main effects of site, trt, site*trt with replicate nested within site as a random factor for the number of seeds removed in the elaiosome Experiment 3. Trial 1: 23-28 September 2005(n = 4 sites).

Source	Num. Df	Denominator Df	F	P-value
Site	3	35.0	4.511	0.009
Trt	2	70.0	28.714	<0.0001
Site*Trt	6	70.0	1.591	0.163

Table 17. Results of the mixed model ANOVA modeling the main effects of site, depth, site*depth with soil core as a random factor for the total number of seeds found bootstrapped in the seedbank study (n = 5 sites).

Source	Numerator Df	Denominator Df	F-value	P-value
Site	4	984	51.690	0.4610
Depth	3	2952	5.768	0.0001
Site*Depth	12	2952	1.898	0.0350

BIBLIOGRAPHY

Aguiar, M.R. and O.E. Sala. 1997. Seed distribution constrains the dynamics of Patagonian steppe. Ecology 78:93-100.

Aguiar, M.R. and O.E. Sala. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology and Evolution 14:273-277.

AOSA. 2000. Tetrazolium Testing Handbook. Jack Peters (ed.). Contribution No. 29. Association of Official Seed Analysts. New Mexico 88003.

Beattie, A.J. and D.C. Culver. 1981. The guild of myrmecochores in the herbaceous flora of West Virginia forests. Ecology 62:107-115.

Bekker, R.M., J.P. Bakker, U. Grandin, R. Kalamees, P. Milberg, P. Poschlod, K. Thompson, and J.H. Willems. 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. Functional Ecology 12:834-842.

____, ___, E.J. Lammerts, A. Schutter, and A.P. Grootjans. 1999. Vegetation development in dune slacks: The role of persistent seed banks. Journal of Vegetation Science 10:745-754.

Berg, R.Y. 1966. Seed dispersal of Dendromecon: Its ecologic, evolutionary, and taxonomic significance. American Journal of Botany 53:61-73.

Bloom, A.J., F.S. III. Chapin, H.A. Mooney. 1985. Resource limitation in plants--An economic analogy. Annual Review of Ecology and Systematics 16: 363-392.

Bohning-Gaese, K., B.H. Gaese, and S.B. Rabemanantsoa. 1999. Importance of primary and secondary see dispersal in the Malagasy tree *Commiphora guillaumini.* Ecology 80:821-832.

Boyd, R.S. and G.D. Brum. 1983. Post-dispersal reproductive biology of Mojave Desert population of *Larrea tridentata* (Zygophylaceae). American Midland Naturalist 110:25-36.

Brew, C.R., D.J. O'Dowd and I.D. Rae. 1989. Seed dispersal by ants: behavior-releasing compounds in elaiosomes. Oecologia 80:490-497.

Cabin, R.J. and D.L. Marshall. 2000. The demographic role of soil seed banks. I. Spatial and temporal comparisons of below-and above-ground populations of the desert mustard *Lesquerella fendleri*. Journal of Ecology 88:283-292.

Campbell, M.L. and P.J. Clarke. 2006. Seed dynamics of resprouting shrubs in grassy woodlands: Seed ran, predators and seed loss constrain recruitment potential. Austral Ecology 31:1016-1026.

Chambers, J.C., J.A. MacMahon and J.H. Haefner. 1991. Seed entrapment in alpine ecosystems: Effects of soil particle size and diaspore morphology. Ecology 72: 1668-1677.

Chambers, J.C. and J.A. MacMahon. 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25:263-292.

Chew, R.M. and A.E. Chew. 1970. Energy relationships of the mammals of a desert shrub (*Larrea tridentata*). Ecological Monographs 40:1-21.

Clark, J.S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. American Naturalist 152:204-224.

Crawley, M.J. 1992. Seed predators and plant population dynamics. Pages 157-191 In M. Fenner, (ed.). Seeds: The ecology of regeneration in plant communities. CAB International Wallingford, Oxon, United Kingdom.

Crist, T.O. 1990. Granivory in a shrub-steppe ecosystem: Interactions of harvester ant foraging and native seeds. Dissertation. Utah State University, Logan, Utah, USA.

____,____ and J.A. MacMahon. 1992. Harvester ant foraging and shrub-steppe seeds: Interactions of seed resources and seed use. Ecology 73:1768-1779.

Culver, D.C. and A.J. Beattie. 1978. Myrmecochory in *Viola*: Dynamics of seed-ant interactions in some West Virginia species. Journal of Ecology 66:53-72.

____,___ and ___. ______. 1980. The fate of viola seeds dispersed by ants. American Journal of Botany 67:710-714.

Drohan, P. and B. Buck. 2006. Soil physical, chemical, and mineralogical properties and their effects on *Eriogonum corymbosum* var. and *Arctomecon californica* in North Las Vegas. Report prepared for the Bureau of Land Management.

Eckert, R.E., Jr., F.F. Peterson, M.S. Meurisse, and J.L. Stephens. 1986. Effects of soil-surface morphology on emergence and survival of seedlings in big sagebrush communities. Journal of Range Management 39:414-420.

Fedde, F. 1936. Papaveraceae, Pages 5-145 In A. Engler and K. Prantl Die natürlichen pflanzenfamilien. 2 Ed., vol. 17b.

Fenner, M. 1985. Seed ecology. Chapman and Hall, New York, New York, USA.
_____,__. 1992. The ecology of regeneration in plant communities. C·A·B· International, Wallingford, Oxon, UK.

Freas, K.E. and P.R. Kemp. 1983. Some relationships between environmental reliability and seed dormancy in desert annual plants. Journal of Ecology 71:211-217.

Grandin, U. and H. Rydin. 1998. Attributes of the seed bank after a century of primary succession on islands in Lake Hjälmaren, Sweden. Journal of Ecology 86:293-303.

Guo, Q., P.W. Rundel, and D.W. Goodall. 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. Journal of Arid Environments 38:465-478.

Handel, S.N. and A.J. Beattie. 1990. Seed dispersal by ants. Scientific American 263:54-61.

Hanzawa, F.M., A.J. Beattie, and A. Holmes. 1985. Dual function of the elaiosome of *Corydalis aurea* (Fumariaceae): Attraction of dispersal agents and repulsion of *Peromyscus maniculatus*, a seed predator. American Journal of Botany 72:1707-1711.

______,____, A.J. Beattie, and D.C. Culver. 1988. Directed dispersal: Demographic analysis of an ant-seed mutualism. American Naturalist 131:1-13.

Harper, J.L. 1977. Population biology of plants. Academic Press, London, United Kingdom.

_____,___, P.H. Lovell, and K.G. Moore. 1970. The shapes and sizes of seeds. Annual Review of Ecology and Systematics 1:327-356.

_____, ___ & White, J. 1974. The demography of plants. Annual Review of Ecology and Systematics 5: 419–463.

Harper, K.T. and R. Van Buren. 2004. Dynamics of a dwarf bear-poppy (*Arctomecon humilis*) population over a sixteen-year period. *Western North American Naturalist* 64:482-491.

Hay, M.E. and P.J. Fuller. 1981. Seed escape from heteromyid rodents: The importance of microhabitat and seed preference. Ecology 62:1395-1399.

Hickerson, L.L. 1998. The reproductive ecology, demography, and population genetic structure of *Arctomecon californica* Torrey and Fremont (Papaveraceae) in fragmented and unfragmented habitat. Masters Thesis, Utah State University, Logan.

_______, ____. and P.G. Wolf. 1998. Population genetic structure of *Arctomecon californica* Torrey & Fremont (Papaveraceae) in fragmented and unfragmented habitat. Plant Species Biology 13:21-33.

Higgins, S.I. and D.M. Richardson. 1999. Predicting plant migration rates in a changing world: The role of long-distance dispersal. American Naturalist 153:464-475.

Horvitz, C.C. and D.W. Schemske. 1986. Ant-nest soil and seedling growth in a Neotropical ant-dispersed herb. Oecologia 70:318-320.

Howe, H.F. and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.

Hughes, L. and M. Westoby. 1992. Mark effect of diaspore characteristics on removal of seeds adapted for dispersal by ants. Ecology 73:1300-1312.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist 104:501-528.

_____,____. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465-492.

Johnson, E.A. and G.I. Fryer. 1992. Physical characterization of seed microsites – movement on the ground. The Journal of Ecology 80:823-836.

Kemp, P.R. 1989. Seed banks and vegetation processes in deserts. Pages 257-281 In M.A. Leck, V.T. Parker, and R.L. Simpson (eds.). Ecology of soil seed banks. Academic Press, San Diego, Californica, USA.

Kjellsson, G. 1985. Seed fate in a population of *Carex pilulifera* L. Oecologia 67: 416-423.

Kotler, B. P. and J.S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics 19:281-307.

Leverich, W.J. and D.A. Levin. 1979. Age-specific survivorship and fecundity in *Phlox drummondii* Hook. American Naturalist 113:881-903.

Levin, D. A. 1981. Dispersal versus gene flow in plants. Annuals of the Missouri Botanical Garden 68:233-253.

Longwell, C. R., E.H. Pampeyan, B. Bowyer, and R.J. Roberts. 1965. Geology and mineral deposits of Clark County, Nevada. Nevada Bureau of Mines Bull. 62:1-218.

MacMahon, J.A. 1985. The Audubon Society Nature Guides: Deserts. Pages 382-383. Alfred A. Knopf, Inc. New York, New York, USA.

Marshall, D.L., A.J. Beattie, and W.E. Bollenbacher. 1979. Evidence for diglycerides as attractants in an ant-seed interaction. Journal of Chemical Ecology 5:335-344.

McDonald, K.A. and J.H. Brown. 1992. Using montane mammals to model extinctions due to global change. Conservation Biology 6:409-415.

Megill, L.A., L.R. Walker, and D. Johnson. 2007. Seed bank study for *Arctomecon californica*. Final report to the Bureau of Land Management, Las Vegas, NV.

Mesler, M.R. and K.L. Lu. 1983. Seed dispersal of *Trillium ovatum* (Lilliaceae) in second-growth redwood forests. American Journal of Botany 70:1460-1467.

Meyer, S.E. 1986. The ecology of gypsophile endemism in the eastern Mojave Desert. Ecology 67:1303-1313.

______,___. 1987. Life history of *Arctomecon californica*, a Mohave Desert endemic perennial herb. Unpublished manuscript, available from author, Shrub Sciences Laboratory, U.S. Forest Service, Provo, UT.

______,___. 1996. Seed germination ecology and seed bank dynamics of *Arctomecon californica*. Interim report to the Nature Conservancy.

Mistretta, O., R. Pant, T. Ross, and M. Porter. 1996. Current knowledge and conservation status of *Arctomecon californica* Torrey & Fremont (Papaveraceae), the California bearpoppy. Report prepared for Nevada National Heritage Program and U.S. Fish and Wildlife Service.

Myerscough, P.J. and J.K. Marshall. 1973. Population dynamics of *Arabidopsis thaliana* (L.) Heynh. Strain "Estland" at different densities and nutrient levels. New Phytologist 72:595-617.

Nathan, R. and H.C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15:278-285.

National Weather Service. 2006. http://www.wrh.noaa.gov

Nelson, J.F. and R.M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. American Midland Naturalist 97:300-320.

O'Dowd, D.J. and M.E. Hay. 1980. Multalism between harvester ants and a desert ephemeral: Seed escape from rodents. Ecology 61:531-540.

Oostermeijer, J.G.B. 1989. Myrmecochory in *Polygata vulgaria* L., *Luzula campestris* (L.) DC. and *Viola curtisii* Forster in a Dutch dune area. Oecologia 78:302-311.

Pakeman, R.J. 2001. Plant migration rates and seed dispersal mechanisms. Journal of Biogeography 28:795-800.

Pantone, D. J., B. M. Pavlik, and R. B. Kelley. 1995. The reproductive attributes of an endangered plant as compared to a weedy congener. Biological Conservation 71: 305-311.

Parker, V.T., R.L. Simpson, and M.A. Leck. 1989. Pattern and process in the dynamics of seed banks. Pages 367-384 In M.A. Leck, V.T. Parker, and R.L. Simpson (eds.). Ecology of soil seed banks. Academic Press, San Diego, Californica, USA.

Peters, R. and D.S. Darling. 1985. The greenhouse effect and nature reserves. Bioscience 35:707-717.

Phillips, A.M. and B.G. Phillips. 1988. Status report for *Arctomecon californica* Torr. & Frem. U.S. Fish and Wildlife Service. Albuquerque, New Mexico.

Powell, E. 1999. Report on 1998 surveys for *Arctomecon californica*, Las Vegas bearpoppy, in Lake Mead National Recreation Area. Report prepared for the Lake Mead National Recreational Area.

______,__. 2003. Summary of Las Vegas bearpoppy transect monitoring data -Year 2003. Report prepared for the Lake Mead National Recreational Area.

______,__. 2005. Personal communication regarding *Arctomecon californica*, general knowledge.

______,___ and L. Walker. 2003. MSHCP Proposal on Factors affecting rarity of the LasVegas bearpoppy. Lake Mead National Recreation Area. Clark County, Nevada.

Rabinowitz, D. and J.K. Rapp. 1981. Dispersal abilities of seven sparse and common grasses from Missouri prairie. American Journal of Botany 68:596-604.

______,__, S. Cairns and T. Dillon. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. Pages 182-204 In M. Soule, editor. Conservation Biology. Sinauer Associates, Sunderland, Massachusetts.

Reichman, O.J. 1979. Desert granivore foraging and its impact on seed densities and distributions. Ecology 60:1085-1092.

______,___. 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. Journal of Biogeography 11:1-11.

Roth, I. 1977. Fruits of angiosperms. Encyclopedia of plant anatomy. Volume 10. Gebrüder Borntraeger, Berlin, West Germany.

Rundel, P.W. and A.C. Gibson. 1996. Ecological communities and processes in a Mojave Desert ecosystem. Cambridge, Cambridge University, USA.

Saxena, R. 2005. Differences in soil physical, chemical and mineralogical properties between inhabited and uninhabited *Arctomecon californica* habitats. Masters Thesis, University of Nevada, Las Vegas.

Schaal, B.A. 1980. Reproductive capacity and seed in *Lupinas texensis*. American Journal of Botany 67:703-709.

Science Applications International Corporation. 2001. Bearpoppy Hill restoration and seed bank study. Report prepared for Bureau of Land Management. Clark County, Nevada.

Sheldon, S. K. 1994. *Life history and soil characteristics of two species of Arctomecon (Papaveraceae).* Las Vegas: University of Nevada, unpublished M.S. thesis.

Sheldon-Thompson, S.K. and S.D. Smith. 1997. Ecology of *Arctomecon californica* and *A. merriamii* (Papaveraceae) in the Mojave Desert. Madroño 44:151-169.

Soholt, L.F. 1973. Consumption of primary production by a population of kangeroo rats (*Dipodomys merriami*) in the Mojave desert. Ecological Monographs 43:357-376.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. Second Edition, W.H. Freeman and Company, San Francisco, USA.

Swearingen, T.A. 1981. Unpublished manuscript. The vascular flora of the Muddy Mountains, Clark County, Nevada. University of Nevada, Las Vegas, Nevada.

Thompson, K. and J.P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. Journal of Ecology 67:893-921.

______,___. 2000. The functional ecology of soil seed banks. Pages 215-235 In M. Fenner (ed.). Seeds the ecology of regeneration on plant communities. C·A·B International, Wallingford, UK.

Thorne, R.F. 1976. The vascular plant communities of California. Pages 1-31 In J. Latting (ed.). Plant communities of southern California. California Native Plant Society, Special Publication 2, Sacramento, California, USA.

van Tooren, B.F. 1988. The fate of seeds after dispersal in chalk grassland: the role of the bryophyte layer. Oikos 53:41-48.

Van der Pijl, L. 1982. Principles of dispersal in higher plants. 2d Ed. Prentice-Hall, Inc., New York, New York, USA.

Vander Wall, S.B. 1994. Seed fate pathways of antelope bitterbrush: Dispersal by seed-caching yellow pine chipmunks. Ecology 75:1911-1926.

_______,_____. and W.S. Longland. 2004. Diplochory: Are two seed dispersers better than one? Trends in Ecology and Evolution 19:155-161.

Westelaken, I.L. and M.A. Maun. 1985. Spatial pattern and seed dispersal of *Lithospermum caroliniense* on Lake Huron sand dunes. Canadian Journal of Botany 63:125-132.

Whitford, W.G. 1978. Structure and seasonal activity of Chihuahua desert ant communities. Insectes Sociaux 25:79-88.

Williams, W.A., O.D. Cook, and B.L. Kay. 1974. Germination of native desert shrubs. Californica Agriculture 28:13.

Willson, M. and A. Traveset. 2000. The ecology of seed dispersal. Pages 85-110 In M. Fenner (ed.). Seeds: The ecology of regeneration in plant communities. CABI Publishing, New York, New York, USA.

Winkle, V.K. 2004. Rare plant research at the Springs Preserve. Springs Preserve, Las Vegas Valley Water District, Las Vegas, NV.

Wright, S.J. 1999. The El Niño southern oscillation, variable fruit production and famine in a tropical forest. Ecology 80:1632-1647.

Zar, J.H. 1984. Biostatistical Analysis. 2d ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, USA.

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