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Effects of fire on rare *Ericameria fasciculata* (Asteraceae)

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EFFECTS OF FIRE ON RARE *ERICAMERIA FASCICULATA* (ASTERACEAE)

A Thesis

Presented to

The Faculty of the Department of Biological Sciences

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Jon Detka

December 2007

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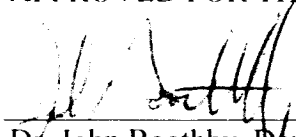
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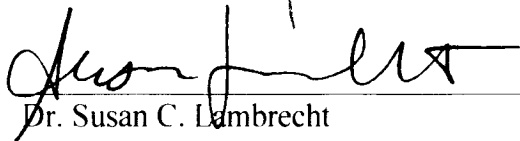
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ABSTRACT

EFFECTS OF FIRE ON RARE *ERICAMERIA FASCICULATA* (ASTERACEAE)

by Jon Detka

Eastwood's Golden Fleece (*Ericameria fasciculata*, Asteraceae) is a rare shrub endemic to the maritime chaparral plant community of the central California coast and a listed species of concern. No study has investigated the fire life history of *E. fasciculata*. A field study elucidated the effect of prescribed burning on *E. fasciculata*. Mature plant resprout was negatively affected by burn intensity, neighboring-plant density, and plant size. Larger mature plants were less likely to survive higher burn intensities. Immature plant survival was negatively effected by higher burn intensity. Post-burn seedling emergence was dependent on neighboring mature plant densities. A greenhouse study examined the potential for fire-related germination cues. A large percentage of seed were empty or inviable. Heating and charate had negative effects on seed germination. Results suggest that resprouting *E. fasciculata* is dependent on low burn intensity fire regimes with fire-return intervals that allow reproductive establishment between fire events.

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INTRODUCTION

Eastwood's Golden Fleece (*Ericameria fasciculata*, Eastw.) is a stout (< 5 dm tall) shrub in the *Asteraceae* (Hickman 1993), previously classified as *Haplopappus eastwoodiae*. *Ericameria fasciculata* is listed as a species of concern (List 1B) by the California Native Plant Society (Skinner 1994), and is proposed for listing as an endangered species on the Federal Endangered Species List (CNDDDB 2002). The most distinguishing features of *E. fasciculata* are its aromatic resinous cylindrical leaves arranged in fasciculate bundles and wide radiate flower heads containing pale yellow inflorescences that bloom in July, forming a single achene fruit attached to a dense golden-white pappus by October (Matthews 1997, Figure 1.1).

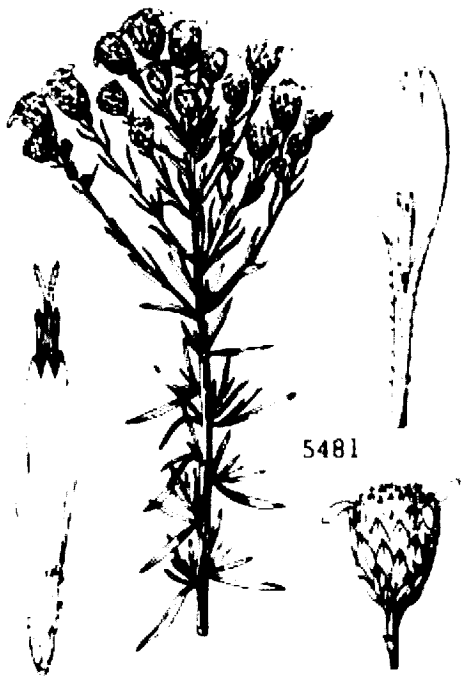


Figure 1.1. Eastwood's Golden Fleece, *Ericameria fasciculata* (Asteraceae) (Eastw.) Macbr. (*H. eastwoodiae* Hall). Illustration from Matthews (1997).

The geographic range of *E. fasciculata* is estimated at less than 4,000 hectares (CNDDDB 2002). Scattered individuals occur in coastal dune, central maritime chaparral, and coastal closed cone pine forest from 30 - 270 meters (MSL) elevation in Monterey County, California, but have historically been most abundant in the central maritime chaparral plant community (Griffin 1976, 1978; Van Dyke and Holl 2003). This central maritime chaparral plant community consists of a diverse array of fire-adapted endemic sclerophyllous shrubs, residing in predominately sandy soils and blanketed by the summer fog of the coastal regions (Griffin 1978).

It has been proposed that the decreased abundance and distribution of *E. fasciculata* may be associated with fire suppression (Griffin 1978). The former Fort Ord (11,330 ha, Figure 1.2) comprises the largest contiguous portion of maritime chaparral (5,059 ha) in the Monterey Bay region (Van Dyke and Holl 2003). It has been proposed that the eastern inland tracts of central maritime chaparral on the former Fort Ord may have been the primary habitat suitable for *E. fasciculata* (Griffin 1976). Recent field surveys have indicated relatively low abundance of *E. fasciculata* with little or no encounters of individual plants outside of known localities as reported in historical voucher records (Van Dyke and Holl 2003).

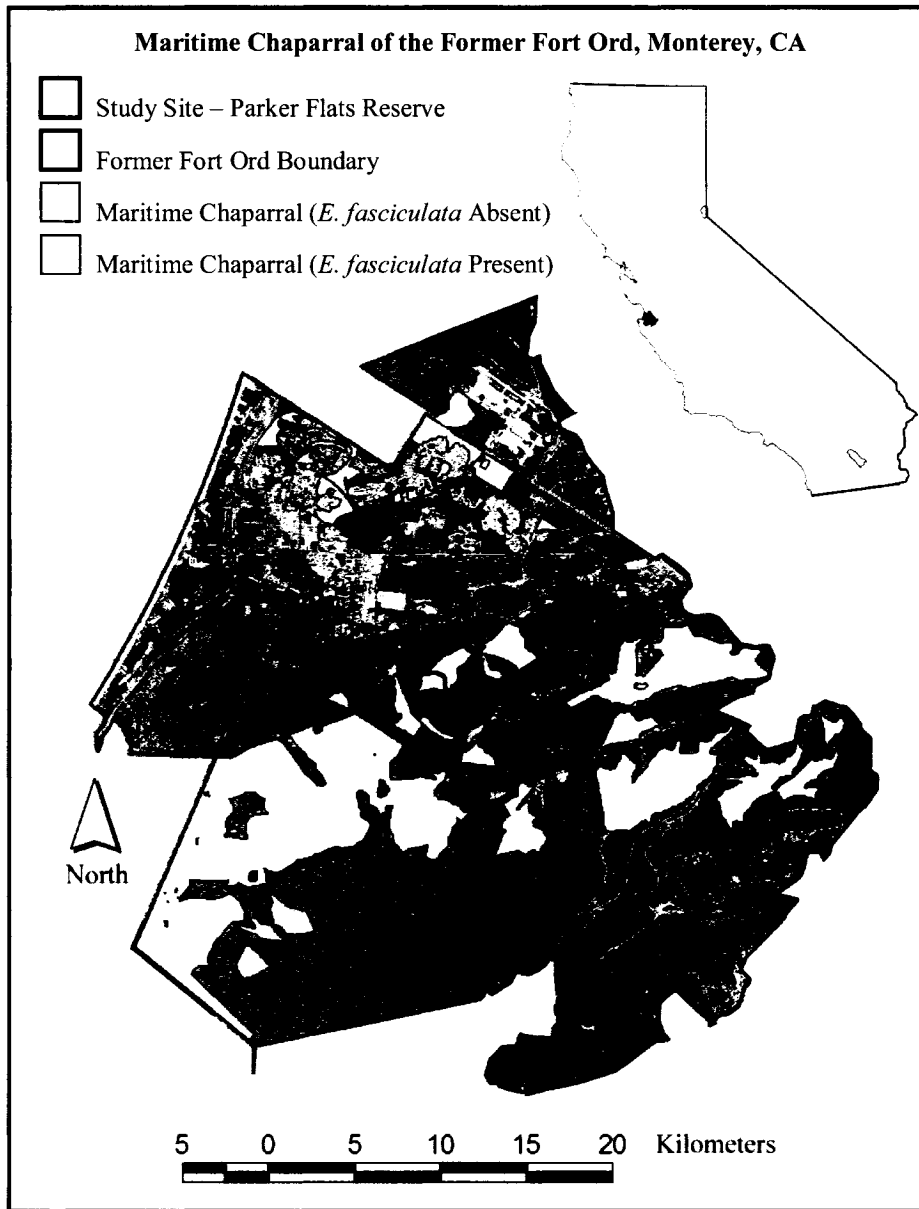


Figure 1.2. Maritime chaparral plant community of the former Fort Ord, Monterey, CA. Polygons indicate *E. fasciculata* presence (yellow) or absence (orange) within maritime chaparral. Based on GIS data from USACE / Jones & Stokes Associates (1992) surveys.

Restoration and conservation of rare endemic plant species requires that we understand the life history of these species and identify the factors that restrict their establishment and growth (Maschinski *et al.* 2004). It is also essential that our knowledge

extends beyond the habitat affinities of common endemics and seeks to understand the forces leading to current distributions and the management regimes needed to preserve these unique taxa in the future (Kruckeberg and Rabinowitz 1985). In particular, studies have demonstrated that fire regimes can differentially affect recovery and establishment of woody shrub species during different life history stages (Bellingham 2000, Schwilk and Ackerly 2005). Fire can affect chaparral taxa differently; by inhibiting or promoting floral production, eliminating or cueing seed germination, reducing or encouraging seedling abundance, and gleaning or preserving mature plant stands (Bond and Wilgen 1996).

Post-fire responses, or fire life histories, can be broadly described in terms of trade-offs between two fire survival strategies, as obligate resprouting or obligate seeding (Keeley and Zedler 1978, Bellingham 2000, Boyd 2007). These fire life histories can have the greatest impact on a population's resilience to pyric disturbance (Bond and Wilgen 1996, Keeley 2006, Boyd 2007). In addition, conditions associated with a fire regime can adversely affect those species with a particular fire life history while simultaneously promoting another species' success (Keeley and Zedler 1978, Bond and Wilgen 1996).

Several studies have demonstrated the dependence of chaparral vegetative and reproductive systems on fire (Went *et al.* 1952, Sweeny 1956; Christensen and Muller 1975a, 1975b; Keeley *et al.* 1981, Keeley and Keeley 1984, Keeley 1987, 2006; Tyler 1995, 1996; Odion and Tyler 2002). Some studies have also concluded that fire intensity can affect seedling production in chaparral (Moreno and Oechel 1989, 1991; Odion and Davis 2000). However, the majority of these studies investigated the role of fire in Southern California inland chaparral dominated by *Adenostoma* (Christensen and Muller

1975; Keeley 1981; Moreno and Oechel 1991; Swank and Oechel 1991; Odion and Davis 2000). Greenlee and Langenheim (1990) determined that a long fire-return interval has played a vital role in the formation of vegetative patterns in the Monterey Bay region. Furthermore, most studies have investigated the role of fire on resprouting and seed germination of common woody shrubs (Keeley and Zedler 1978, Keeley and Keeley 1984, Keeley 1987, 2006; Tyler 1995; Holl *et al.* 2000).

While there are some data on the fire life history of related taxa, it is difficult to hypothesize the potential fire life history of *E. fasciculata* based on current understanding of these taxa. Inferring a shared fire life history in closely related shrubs may not be a safe assumption given that closely related species can have radically different fire life histories (Schwilk and Ackerly 2005). For example, *Chrysothamnus nauseosus* is often referred to generally as a resprouting species capable of post-fire recovery from epicormic stems (Tueller and Payne 1987). However, differences in fire responses do exist between subspecies of *Chrysothamnus*. *Chrysothamnus nauseosus* ssp. *hololeucus* and *C. n.* ssp. *albicaulis* are both more susceptible to burning because of a reduced occurrence of resprouting. This can be contrasted with *Chrysothamnus nauseosus* ssp. *consimilis* and *Chrysothamnus nauseosus* subsp. *graveolens*, which rapidly resprout following burning (Neuenschwander [n.d.]). Holl *et al.* (2000) found that seeds from the common coastal scrub species *Ericameria ericoides* experience high rates of germination following burning treatments. Phylogenetically, *E. ericoides* is closely related to *E. fasciculata* (Roberts and Urbatsh 2003) and the two have been observed coexisting in the field (pers. obs. Jon Detka). The common chaparral shrub *Haplopappus squarrosus* responds as an obligate

resprouting shrub following fire (Keeley and Keeley 1984). In addition, the seeds of *H. squarrosus* respond negatively to fire-related heat treatments but are not affected by presence of light or charate (Keeley 1987). However, it could be misleading to assume that seed of *E. fasciculata* may perform similarly to *H. squarrosus* given their differences in rarity, habitat affinities, physical characteristics, and recent taxonomic reclassification. It is difficult to ascertain the role of fire on *E. fasciculata* plant recovery, seed germination, and seedling establishment from these studies.

The primary goal of this project was to conduct a species-specific study that identified the potential affect of prescribed burning on *E. fasciculata*. A combination of pre- and post-burn field sampling and greenhouse studies were employed to answer the following questions:

- (1) Do *E. fasciculata* plants survive fire? If so, what fire life histories does the species utilize?
- (2) Does burn intensity affect survival of immature (non-flowering) and mature (flowering) *E. fasciculata* plants differently?
- (3) What are the most important demographic features in post-fire recovery of *E. fasciculata*?
- (4) Does burning inhibit or promote seed germination and establishment of seedling?

Chapter 1 describes my field investigation designed to examine the first-year response of *E. fasciculata* to prescribed burning. This research aimed to establish whether *E. fasciculata* demonstrated any of the responses associated with obligate resprouting or obligate seeding. Chapter 2 tests specifically for associations between seed germination

and fire-related germination cues. This laboratory component was prompted on the preliminary observations that seedling emergence may be extremely rare in the field (Chapter 1) and fire-related cues are typically interrelated and difficult to control for in field designs.

CHAPTER 1 FIELD STUDY

1.1 BACKGROUND

The prescribed reintroduction of fire into plant communities is based on the supposition that fires historically occurred in a region and that the plant species in a community have specialized fire life histories that allow them to recover (Johnson and Miyanishi 1995). Prescribed fire can have dramatically different effects on the extent of regeneration in populations, communities and ecosystems depending on the assemblage of vegetation and fire regime (Johnson and Miyanishi 1995, Schmalbach *et al.* 2007).

Chaparral species have developed adaptations to pyric disturbance and are capable of regenerating via resprouting and/or seeding (Keeley and Zedler 1978). Vegetation response to fire can be viewed as a continuum with obligate resprouting and obligate seeding at the polar extremes (Ackerly 2004). For example, some specialized chaparral species regenerate entirely from the more derived obligate seedling fire life history strategy and require that seeds experience fire-related germination cues (Ackerly 2004). Yet, often closely related taxa can utilize degrees of both regenerative strategies ranging from facultative to obligate (Boyd 2007). The diverse array of vegetation responses in chaparral shrubs can make the implementation of fire management programs challenging. In addition, these objectives often require careful consideration when rare species with unknown fire life histories are a component of the plant community (Pendergrass *et al.* 1999, Boyd 2007).

Fire management of maritime chaparral on the former Fort Ord is implemented with the intent of reducing wildfire risks, clearing dense vegetation to assist in the removal of unexploded munitions and explosives, while simultaneously meeting plant community needs for fire as a natural regenerative process (U.S. Army Corp of Engineers 1997).

Ericameria fasciculata is a rare shrub that inhabits the fire managed maritime chaparral plant community of the former Fort Ord and its conservation is dependent on determining the regenerative potential of the species following prescribed burning. Often uncertainty regarding the potential impacts to a rare plant species can inhibit management action and in turn impact plant community composition and the fate of species of concern with known fire life histories (Boyd 2007). Conversely, executing a fire regime based exclusively on species with known fire life histories may result in a gambit for rare species with unknown fire life histories (Boyd 1987).

Fire management generally operates under the assumption that fire performance can be carefully controlled and measured as a method for assessing the potential range of impacts to vegetation (Johnson and Miyanishi 1995). The intended performance of a prescribed fire regime is generally described in terms of frequency and intensity. When fires are implemented, measures of fire intensity can serve as valuable tools for evaluating the potential impacts to a rare species of concern (Pendergrass *et al.* 1999). Burn intensity is one of the principal factors that influences the extent of disturbance associated with fire (Moreno and Oechel 1989, 1991). Studies have demonstrated that fire intensity can directly impact chaparral shrub resprout recovery (Bellingham 2000, Keeley 2006) and seedling establishment (Tyler 1996, Zammit and Zedler 1988). Fire ecologists have

developed pre-post burn field methods for inferring fire intensity as a function of ash color (Ulery and Graham 1993) and direct effects on aboveground shrub biomass (Moreno and Oechel 1989). Although assessment methods such as these do not directly measure fire intensity they can provide an adequate surrogate to burn intensity measurements (Keeley 2006) and help managers easily define burn prescription criteria for species conservation efforts.

This field study investigated the role of fire on the regenerative potential of *E. fasciculata* during the first year following fire. I conducted pre-burn and post-burn assessments to evaluate population resprout response, both immature (non-flowering) and mature (flowering), as well as the emergence and establishment of new seedlings. During post-burn surveys I also measured physical variables (*e.g.* air temperature, soil moisture) to elucidate potential differences in abiotic conditions in the burn and control areas.

1.2 FIELD MATERIALS AND METHODS

1.2.1 Study Site

All plants were located within the 61-ha Parker Flats Reserve, Fort Ord, CA (Latitude 36°38'4.60"N, Longitude 121°46'38.78"W) (Figure 1.2-1.3) Prescribed burning occurred on the reserve in September and October 2005 in accordance with the Fort Ord Habitat Management Plan (HMP) (USACE 1997, Pierce 2005). Prior to the burn, I delineated those areas in which *E. fasciculata* occurred as either burned (treatment) or unburned (control) areas, based on the intended burning plans (Figure 1.3).

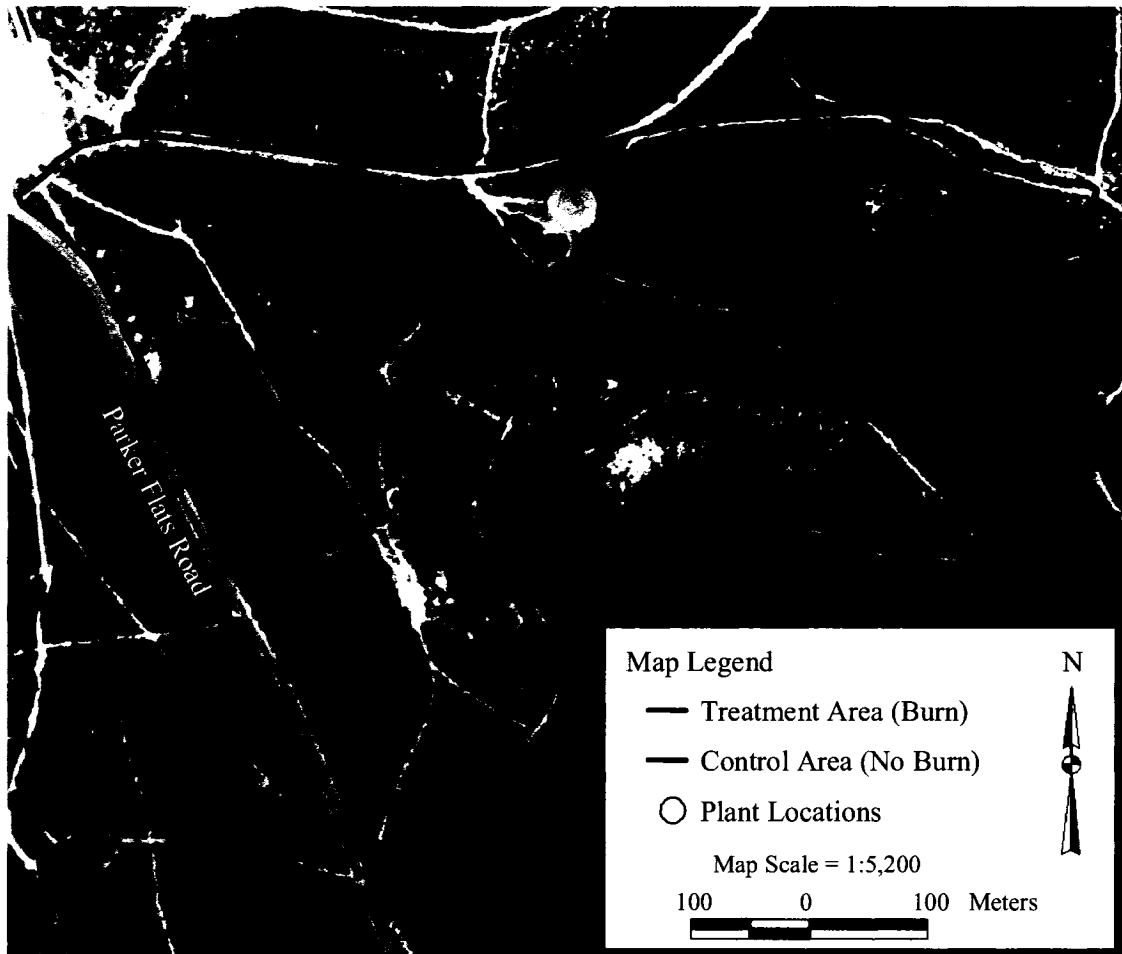


Figure 1.3. Location of burn treatment and control areas. Fort Ord, Parker Flats Reserve, Monterey, CA. (LAT 36°38'4.60"N, LONG 121°46'38.78"W)

1.2.2 Pre-Burn Field Survey

Prior to burning, I conducted site surveys in both the burned and unburned areas to tag a total of 300 *E. fasciculata* immature and mature individuals with heat resistant aluminum tags (Figure 1.3). I designated plants as mature if capitula were present. Plants without developed capitula were identified as immature. I catalogued the distance and heading between each tagged plant and used distance measurements to identify neighboring plants for estimates of mature plant density. OmegaLiq temperature-sensitive

lacquers (Omega Scientific, Stamford, CT) were placed on site and were used as indicators of burn intensity (Pierce 2005).

For each mature plant, I recorded plant height, number of branches, and total number of capitula for those plants with fewer than 200 capitula. An allometric relationship was used to predict total capitula for those plants with copious amounts of capitula ($n > 200$). I developed a linear regression using basal crown branch number and total capitula per basal crown branch to predict total number of capitula per plant ($\log(\text{total capitula}) = 0.988 \times \log(\text{capitula per branch} \times \text{branch number})$, $n=120$, $R^2 = 0.928$, $P < 0.0001$). Five ripe capitula were collected from each of 23 plants located outside of designated study sites during September 2005 to count seeds per capitula.

1.2.3 Post-Burn Field Surveys

Following the burns, I recorded ash color, surface soil condition, and condition of each plant to develop a burn intensity index. In addition, temperature-sensitive lacquer melt-point data was used to estimate burn intensity. Post-burn ash color patterns and the presence or absence of ash were used as indicators of fire severity (Ulery and Graham 1993). Munsell (X-Rite, Inc., Grand Rapids, MI) soil color charts were used to classify dominant ash color surrounding the base of burned plants. Condition of mature plants was assessed using the minimum branch diameter methodology of Moreno and Oechel (1989). I measured the diameter of the smallest remaining branch using calipers. In addition to this measurement I estimated the percent foliage burned, browned, and green for each tagged plant. A combination of ash color, soil condition and color, litter condition, plant

condition, and melting point of lacquers were used to establish five heat categories (Table 1.1).

Table 1.1. Burn intensity categories based on temperature-sensitive lacquers' melt points and post-burn site conditions.

Burn Category	Burn Intensity	Temp C°	Foliage Burned (%)	Mean Minimum Branch Not Burned (mm)	Ground (Surface) Condition
0	Unburned	<100	0%	-	No Ash, Singed Litter
1	Low	100-300	<50%	-	Singed to Black Ash
2	Medium	300-600	50-100%	0.5 mm - 1.0 mm	Black Ash
3	High	600-800	100%	> 1.0 mm	Black-Grey Ash
4	Very High	800-1000	100%	Completely Burned	Grey-White Ash

Every two weeks following the burns, I monitored the onset and progression of resprouting and flowering for all burned plants ($n=166$). In mid-October 2006, I measured height of resprouted plants and counted number of capitula. I selected 59 mature plants (30 from the burn area and 29 from the control) to monitor post-fire *E. fasciculata* seedling emergence. Plants were selected to form distinct non-overlapping 12.6 m² circular sites based on a 2-meter radius. Seedling surveys were done in each 12.6 m² area. This 2-m search radius adequately encompassed the majority of observed seed dispersal (< 2 dm from mature plant) (pers. obs. Jon Detka). Seedlings were marked once they had produced identifiable leaves. Distance and heading to the nearest mature plant was recorded for each seedling. Spatial data was used to estimate parent plant densities and available seed relative to each seedling. Survival was tracked for each individual until the end of October 2006.

Table 1.2. Post-burn survey counts of immature and mature *E. fasciculata* in burn and control areas. Total recovered counts are based on successful recovery of plant tags post-burn. Unburned plants were excluded from total burned plants. Burn intensity categories corresponded to the four categories described in Table 1.1.

Mature Plants (Burn)				
Unburned	Low	Medium	High	Very High
27	29	9	45	19
TOTAL (Mature Plants Recovered)			129	
TOTAL (Mature Plants Burned)			102	

Immature Plants (Burn)				
Unburned	Low	Medium	High	Very High
43	29	14	15	6
TOTAL (Immature Plants Recovered)			107	
TOTAL (Immature Plants Burned)			64	

Mature & Immature Plants (Burn)				
Unburned	Low	Medium	High	Very High
70	58	23	60	25
TOTAL (Immature & Mature Plants Recovered)			236	
TOTAL (Immature & Mature Plants Burned)			166	

Mature & Immature (Control)	
TOTAL (Mature Plants)	29
TOTAL (Immature Plants)	12
TOTAL (Mature & Immature Plants)	41

I monitored air temperature and soil moisture at each site. Air temperature was recorded hourly from May - October 2006 using ten LogTag TRIX-8 data loggers (LogTag Recorders Ltd., Kowloon, Hong Kong). Air temperature sensors were housed in 1000 cm³ Stevenson meteorological screens ~20 cm above ground. I measured soil

moisture every two weeks from mid-April – mid-July 2006 using an AQUATERR 200 (Aquaterr Instruments Inc., Costa Mesa, CA) soil moisture meter. Five soil moisture measurements were taken at each of the 59 tagged plants; four were 2-m from the plant in each of the cardinal directions and the fifth was ~10 cm from the base of each plant.

1.2.4 Data Analysis

I used paired t-test to analyze potential differences in percentage soil moisture from burn treatment and control areas. I used mean soil moisture values calculated from 5 measurements taken twice monthly in the 30 burn treatment sites and 29 control sites. Mean percentage soil moisture observations for each of the six sampling dates were compared between treatments using repeated-measures ANOVA (RMANOVA) with sampling date and treatment (burn vs. control) as the fixed factor.

I used paired t-test to analyze monthly near-surface air temperature from control and treatment areas to determine if a significant difference was evident. I examined minimum, maximum, and mean monthly near-surface air temperature for burn ($n=154$) and control ($n=154$) from mid-May to October 2006. Minimum, Maximum, and Mean near-surface air temperature for the six sampling dates were also analyzed using repeated-measures ANOVA (RMANOVA) with sampling date and treatment (burn vs. control) as the fixed factor.

I used arcsine-square root transformed proportions of surviving pre-burn immature plants (October 2006) and one-way ANOVA to determine whether burn intensity had an effect on proportions of survival of pre-burn immature plants.

I used logistic regression to examine the probability of resprout in mature *E. fasciculata* during the first year following burning given its pre-burn height, number of basal crown branches, neighboring mature plant-densities per 12.6m², burn intensity, and mean percent soil moisture. Of the 129 tagged mature plants in the treatment 102 were used for analysis. The 27 mature plants were excluded because they did not show any evidence of experiencing the burn treatment.

In order to select the best model for prediction of mature plant resprout I established coefficient estimates (β) using the quasi-maximum likelihood method to optimize the probability that the predicted values would match the observed data (Hosmer and Lemeshow 2000). Backward stepwise elimination of explanatory variables was used. For this elimination process, the variable with the smallest Wald statistic term was first selected and tested for significance (Hosmer and Lemeshow 2000). The Wald test uses Z-statistics computed by dividing the coefficients by their standard error. Squaring of the Z-statistic yields the Wald Statistics which fit a χ^2 distribution with 1 degree of freedom. Each variable with $P > 0.05$ was removed and a reduced model was fit to the data using the remaining explanatory variables. Prior to removal, I also examined the upper and lower 95% confidence intervals around each odds ratio. If the 95% confidence interval around the odds ratio includes the value of 1.0, then a change in value of the explanatory variable was not associated with a change in the odds of resprout. This suggested that the explanatory variable was not a useful predictor in the model and resulted in its removal. I also systematically removed each variable to determine if its use or absence deteriorated the overall model fit. The likelihood ratio test was used to examine overall model

performance by taking the differences in deviancies without any predictors in the model (intercept-only model) minus the deviance with all predictors in the model. A model was considered a better fit to the data if it demonstrated improvements from the intercept-only model.

I used Akaike's Information Criterion (AIC) to evaluate the final candidate sets of mature plant resprout models. The models were ranked using AIC and were adjusted for small sample size biases (AIC_c) (Burnham and Anderson 2002). The AIC_c approach penalized for the addition of parameters, thereby objectively selecting the most parsimonious model with a minimum number of parameters. AIC_c values were used to compute the ΔAIC_c , a measure of each model relative to the best model (i.e., lowest AIC_c) and Akaike weight (w_i), which provide a measure of the strength of evidence for each model by representing the ratio of AIC_c . Final candidate models were selected according to a confidence set, which is analogous to a confidence interval for a mean estimate, and included those models with Akaike weights (w_i) that were within 10% of the highest, comparable with the minimum cutoff point suggested by Royall (1997) as a general rule for evaluating the strength of AIC_c evidence. Model selection uncertainty and coefficient estimates (β) were determined by examining the standard error of candidate models. Large coefficient standard errors ($S.E. > 2\beta$) indicated that a coefficient was unreliable for predicting the observed resprout response and was eliminated from plausible models.

I used repeated-measure ANOVA (RMANOVA) to test whether the timing of mature plant resprout covaried with respect to burn intensity and height categories. Mature plants were grouped by height into two categories; short < 3dm and tall > 3dm.

Mean monthly proportions of mature plant resprout were arcsine-root transformed.

I used presence/absence data and seedling counts in the development of a two part conditional model to explain the presence and abundance of *E. fasciculata* seedlings in terms of a set of possible explanatory variables. I examined the potential explanatory role of pre-post mature plant density, pre-burn available seed, pre-post immature plant density, and soil moisture. Available seed per plant was based on the product of the total number of pre-burn capitula on a plant by the mean number of seeds per capitula ($\bar{X} = 22$). There was little variation in mean number of seeds per capitula ($F_{22,92} = 0.983$, $P = 0.493$). Mean soil moisture value during peak seedling emergence were used as model inputs for moisture. The two-part conditional modeling approach allowed for the separate fitting and interpretations of the presence/absence component and, given presence, the abundance component (Cunningham 2005). I used logistic regression to develop the presence/absence component of the model and Poisson regression to model the relationship between natural log transformed peak *E. fasciculata* seedling abundance during the first year following burning. The AIC approach was not required for the logistic regression procedures because a single possible explanatory variable provided the only plausible model.

All analyses, except Poisson regression, were conducted using SYSTAT v. 10.0 (SYSTAT, San Jose, CA). The Poisson regression component of the two part conditional model was developed using GLM procedures in R v. 2.4.1 (Free Software Foundation, Inc., Boston, MA). In all analyses I used $\alpha = 0.05$ level of significance. For all parametric tests, Levene's test was used to test for the assumed homogeneity of variances for all

parametric tests and the assumption of normality was examined with probability plots of the residuals. The one sample Kolmogorov-Smirnov goodness of fit test was used to compare seedling abundance data with an expected Poisson distribution.

1.3 FIELD RESULTS

1.3.1 Soil Moisture

Soil moisture was slightly higher at the burn site earlier in the year but the burn and control sites had a similar decreasing trend in soil moisture through time (Figure 1.4).

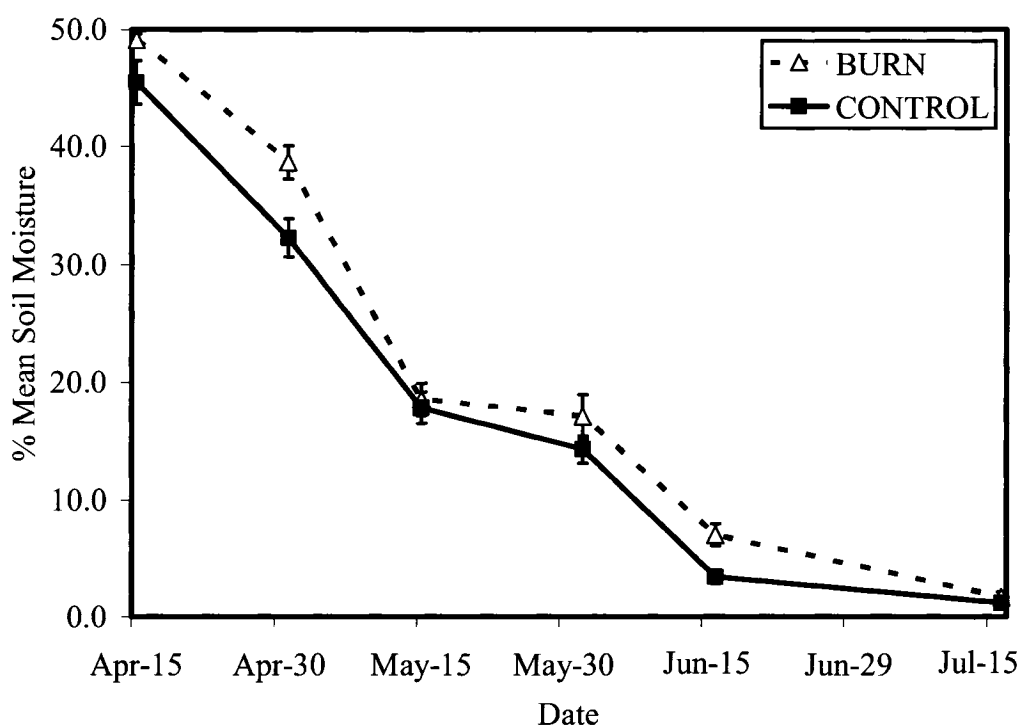


Figure 1.4. Mean percentage soil moisture for burn treatment area and control area. April to June Soil Moisture. Error bars indicate SEM.

Results of paired t-test suggest a significant difference between mean soil moisture at burn and control sites ($t = 3.73$, $d.f. = 5$, $P = 0.014$). Results of RMANOVA confirmed a significant difference in mean percentage soil moisture between burn and control areas ($P = 0.008$) and suggest no significant differences between area soil moisture changes through time ($P = 0.085$) (Table 1.3).

Table 1.3. Repeated-measures ANOVA results – mean percentage soil moisture.

Percentage Soil Moisture					
Source of Variation Between	SS	d.f.	MS	F	P
TREATMENT	811.751	1	811.751	7.572	0.008
Error	6110.39	57	107.2		
Source of Variation Within	SS	d.f.	MS	F	P
DATE	44346.7	5	8869.34	275.723	< 0.001
DATE x TREATMENT	315.375	5	63.075	1.961	0.085
Error	9167.77	285	32.168		

1.3.2 Near-Surface Air Temperature

The burn area experienced slightly higher temperatures than the control area until July after which it experienced slightly lower temperatures through the Fall (Figure 1.5). Results of paired t-test suggest a significant difference in mean monthly ($t = 3.85$, $d.f. = 153$, $P < 0.0002$), min monthly ($t = -9.66$, $d.f. = 153$, $P < 0.0001$), and max monthly ($t = 24.82$, $d.f. = 153$, $P < 0.0002$) near-surface air temperatures at burn and control sites.

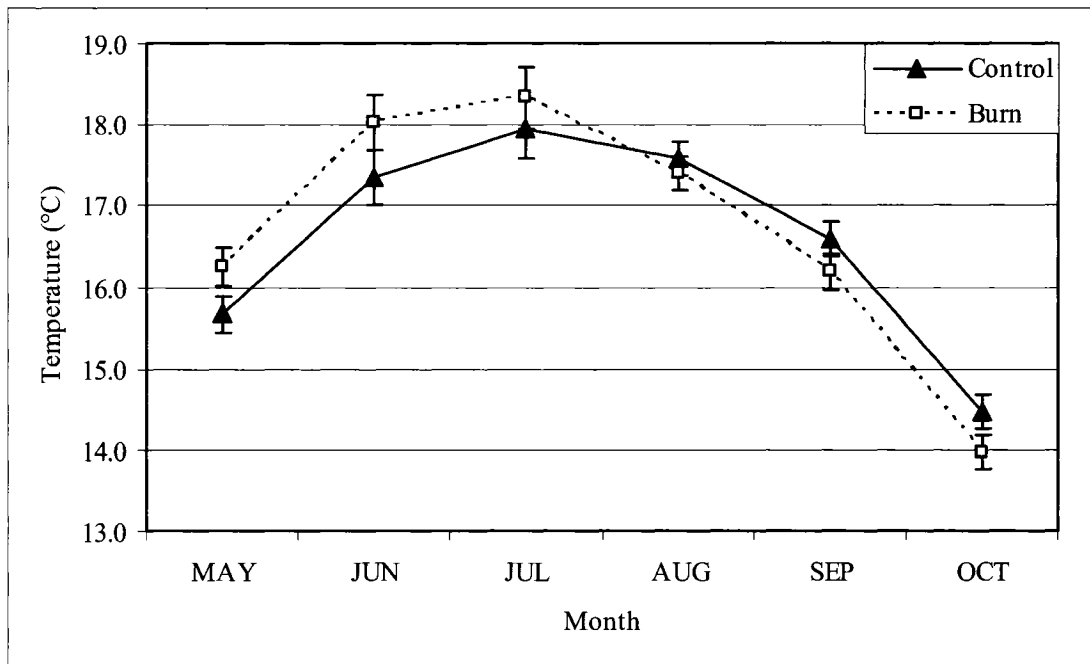


Figure 1.5. Mean monthly near-surface air temperature at burn treatment and control areas. Error bars indicate SEM.

However, RMANOVA suggest no significant difference in temperature between burn and control site, although there were significant date \times treatment interactions. (Table 1.4). Results of RMANOVA suggest no significant difference in minimum near-surface air temperature between burn and control site ($P = 0.096$) and no significant date \times treatment interaction indicating no difference in minimum temperature in the treatments through time ($P = 0.087$) (Table 1.4). While the differences were not significant, the burn treatment maintained slightly lower minimum temperatures (Figure 1.6).

Results of RMANOVA suggest no significant difference in maximum near-surface air temperature between the burn and control site ($P = 0.846$) (Table 1.4). However, there was a significant date \times treatment interaction indicating a difference in maximum temperature through time ($P = 0.009$) (Table 1.4). The burn area experienced higher

maximum temperatures than the control area until August, after which the control area experienced higher maximum temperatures (Table 1.4, Figure 1.7).

Table 1.4. Results of repeated-measures ANOVA (RMANOVA) for near-surface air temperature. Monthly mean, minimum, and maximum between control and treatment (Burn) areas.

Mean Near-Surface Air Temperature					
Source of Variation Between	SS	d.f.	MS	F	P
TREATMENT	0.12	1	0.12	0.046	0.836
Error	21.016	8	2.627		
Source of Variation Within	SS	df	MS	F	P
Date	35.266	5	7.053	54.497	< 0.001
Date*TREATMENT	3.171	5	0.634	4.9	0.001
Error	5.177	40	0.129		
Minimum Near-Surface Air Temperature					
Source of Variation Between	SS	df	MS	F	P
TREATMENT	24.198	1	24.198	3.563	0.096
Error	54.327	8	6.791		
Source of Variation Within	SS	df	MS	F	P
Date	35.457	5	7.091	11.955	< 0.001
Date*TREATMENT	6.182	5	1.236	2.085	0.087
Error	23.726	40	0.593		
Maximum Near-Surface Air Temperature					
Source of Variation Between	SS	df	MS	F	P
TREATMENT	0.51	1	0.51	0.04	0.846
Error	101.834	8	12.729		
Source of Variation Within	SS	df	MS	F	P
Date	450.548	5	90.11	19.767	< 0.001
Date*TREATMENT	82.1	5	16.42	3.602	0.009
Error	182.347	40	4.559		

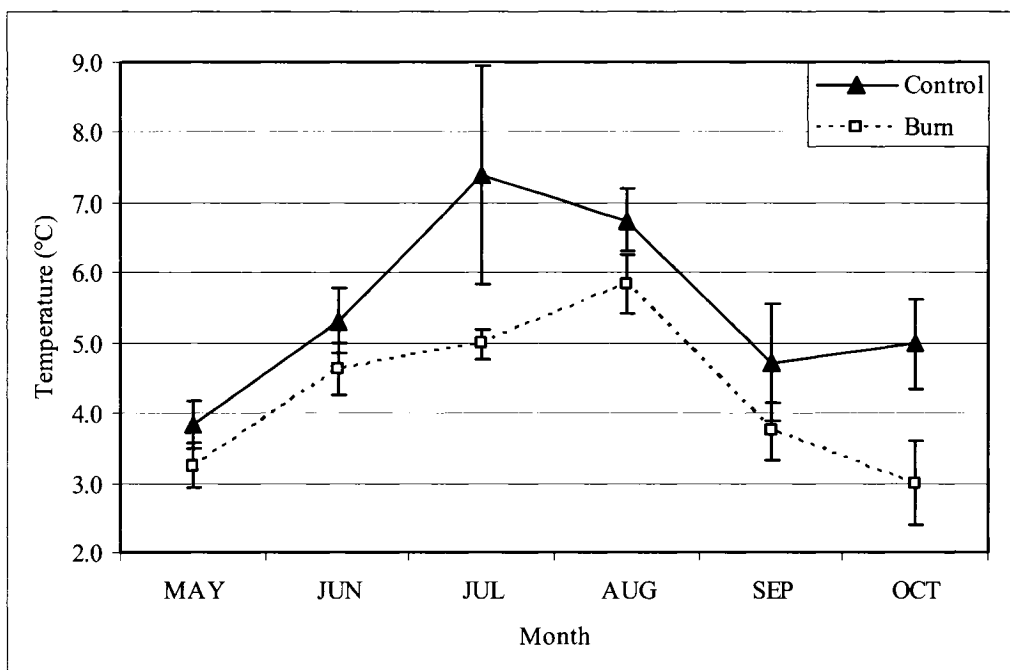


Figure 1.6. Minimum monthly near-surface air temperature at burn treatment and control areas. Error bars indicate SEM.

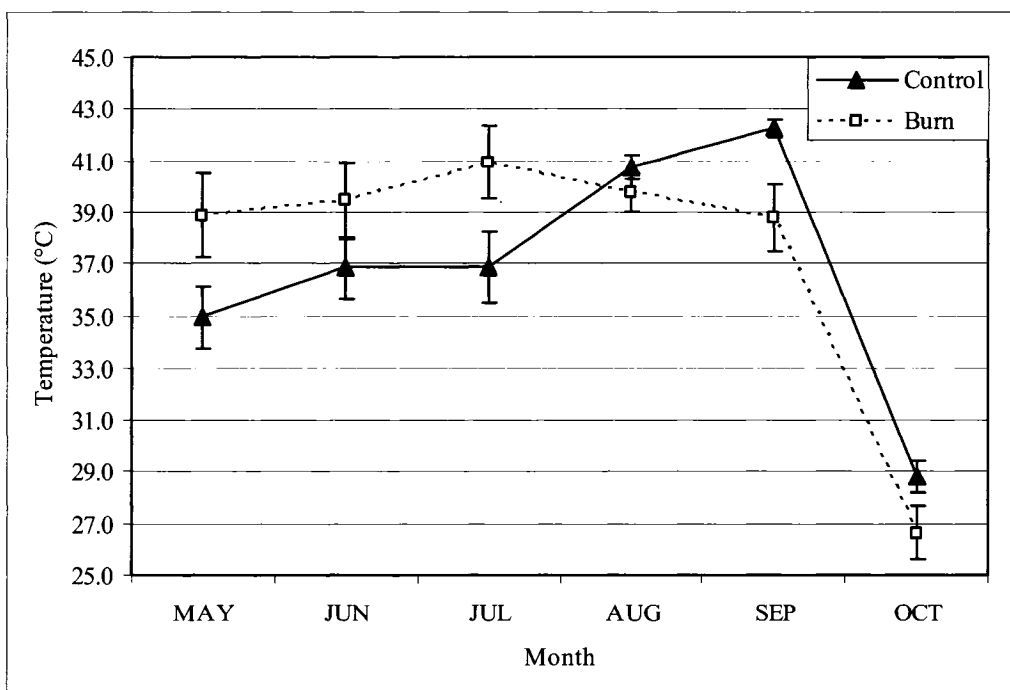


Figure 1.7. Maximum monthly near-surface air temperature at burn treatment and control areas. Error bars indicate SEM.

1.3.3 Immature Plant Burn Survival

One-Way ANOVA suggests that there was no significant difference in the proportion of surviving immature plants between the different burn intensities ($F_{3,67} = 1.510$, $P = 0.220$). A plot of mean percentage immature plant survival visually suggested that percent survival may have varied significantly between lower and higher burn intensities (Figure 1.8). So, I performed an additional one-way ANOVA of immature plant survival proportions grouped by two burn categories (Low $<600^{\circ}\text{C}$, High $>600^{\circ}\text{C}$). There was a significant difference in immature percent survival, with a higher proportion surviving under lower intensity burn conditions ($F_{1,69} = 4.236$, $P = 0.043$).

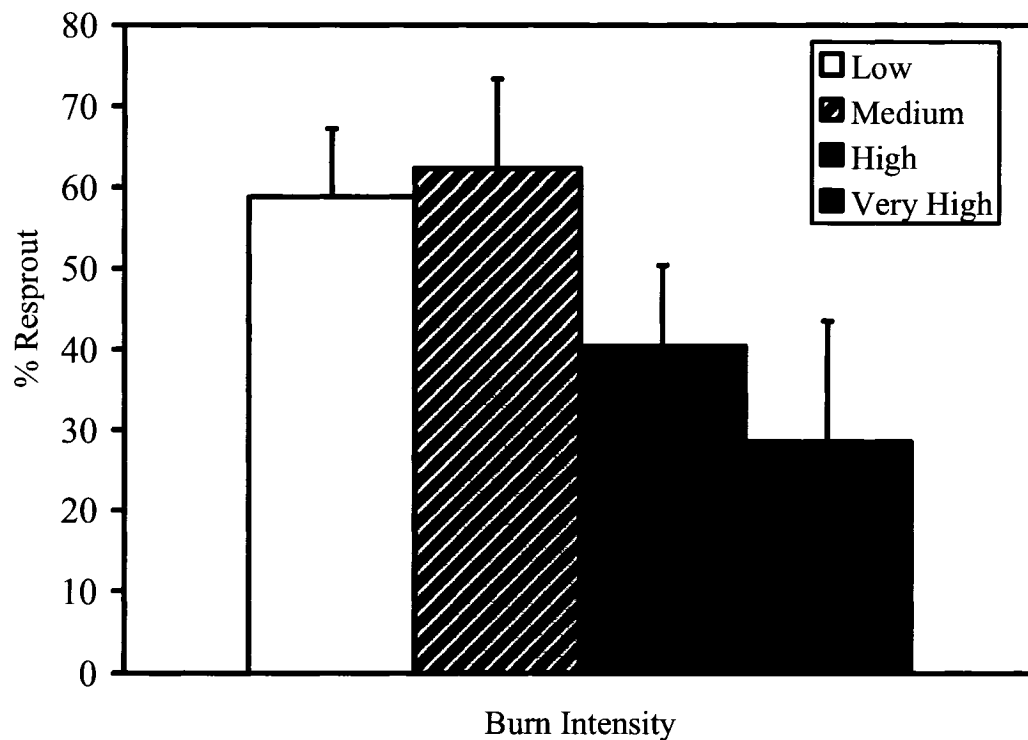


Figure 1.8. Percentage of immature plants surviving between four burn intensities. Error bars indicate SEM.

1.3.4 Mature Plant Post-Burn Resprout

Using a backwards stepwise procedure and AIC approach, I was able to successfully build a logistic regression model for resprout potential in mature *E. fasciculata* using burn intensity, pre-burn mature neighbor density, mature plant height, and number of basal crown branches. I found that the probability of a mature *E. fasciculata* resprouting in the first year was significantly related to burn intensity, pre-burn mature neighboring-plant densities, and the interaction of pre-burn mature plant height with number of basal crown branches (*i.e.* branches emanating from root crown). This model had good support ($w_i = 0.41$) for being the best model relative to other candidate models (Table 1.5 and 1.6).

Probability of Mature Plant Resprout =

$$(6.445 \times \text{Intercept}) - (1.65 \times \text{Burn Intensity}) - (2.71 \times (\text{Mature Plants}/12.6 \text{ m}^2)) \\ - (0.091 \times (\text{Number of Basal Crown Branches} \times \text{Plant Height}))$$

Eq. 1

Table 1.5. Ranking and comparison of peak (June 2006) mature plant resprout models for *Ericameria fasciculata* during the first year following prescribed burn.

MODEL	$\log L$	K	AIC_c	ΔAIC_c	w_i
BURN + PLNT+HT*MB	-44.15	4	96.7	0.0	0.41
BURN+PLNT+MB+HT	-43.60	5	97.8	1.1	0.24
BURN+PLNT+MB	-44.94	4	98.3	1.6	0.19
BURN+PLNT+MB+HT+MOIST	-42.84	6	98.6	1.9	0.16
NULL	-60.89	1	123.8	27.1	0.00

^a Number of parameters (K) in each model includes the intercept and all independent explanatory variables. The model with the lowest ΔAIC_c and greater w_i had the most support for being the better model (Burnham and Anderson 2002). BURN = Burn Intensity, PLNT = Number of Mature Plants / 12.6 m², HT = Mature Plant Height, MB = Number of Basal Crown Branches.

Table 1.6. Peak (June 2006) mature plant resprout models for *Ericameria fasciculata* during the first year following prescribed burning. Binary logistic regression model parameter estimates are reported with their coefficient (β) and corresponding standard error in parenthesis.

	Intercept	Burn Intensity (BURN)	Plants / 12m ² (PLNT)	Crown Branch Count (MB)	Height (HT)	Crown Branch- Height Interaction (MB*HT)	Soil Moisture (MOIST)
BURN + PLNT+HT*MB	6.445 (1.323)	-1.165 (0.312)	-0.271 (0.119)			-0.091 (0.028)	
BURN+PLNT+MB+HT	7.648 (1.634)	-1.171 (0.338)	-0.286 (0.129)	-0.336 (0.163)	-0.338 (0.213)		
BURN+PLNT+MB	7.084 (1.565)	-1.226 (0.335)	-0.274 (0.126)	-0.453 (0.153)			
BURN+PLNT+MB+HT+MOIST	8.954 (2.096)	-1.074 (0.301)	-0.287 (0.129)	-0.350 (0.152)	-0.210 (0.205)		-0.080 (0.061)
NULL	0.923 (0.220)						

^a Where models are in the form: $P = [1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)]]^{-1}$ and P, probability of resprout in a mature (pre-burn flower producing) plant, and β_i are the regression coefficients with X_i as the independent explanatory variables. BURN = Burn Intensity, PLNT = Number of Mature Plants / 12.6 m², HT = Mature Plant Height, MB = Number of Basal Crown Branches, MOIST = Mean % Soil Moisture.

Of the 73 cases of observed mature plant resprout, the model correctly predicted 58.6 cases (80%) and incorrectly predicted 14.4 cases (20%). The model performed poorly in terms of accurately predicting no resprout response. Of the 29 cases of observed lack of resprout response, the model correctly predicted only 50% of the cases. The combined influence of model sensitivity, correctly predicting resprout (80%), and specificity, correctly predicting no resprout (50%), led to an overall predictive capability of 72%. In other words, the model is capable of correctly predicting resprout 72% of the time. The relatively high occurrence of false positive predictions greatly reduced the predictive capabilities of the model.

All of the observed explanatory variables in this model had a negative impact on the probability of mature plant resprout. According to the model, the probability of a mature plant resprouting is decreased by increases in pre-burn neighboring mature plant

density, the interaction of number of basal crown branches with plant height, and burn intensity (Figures 1.9-1.11). The interaction between mature plant height and number of basal crown branches was most influential in reducing resprouting. For each decimeter increase in height or each addition of crown branches, the odds of resprouting decreased by a factor of 0.913. The next most influential factor was neighboring plant density, indicating that for every additional neighbor, the odds of resprouting decreased by a factor of 0.762. Lastly, burn intensity had the least amount of influence on resprout as each categorical increase resulted in a decreased odds factor of 0.312.

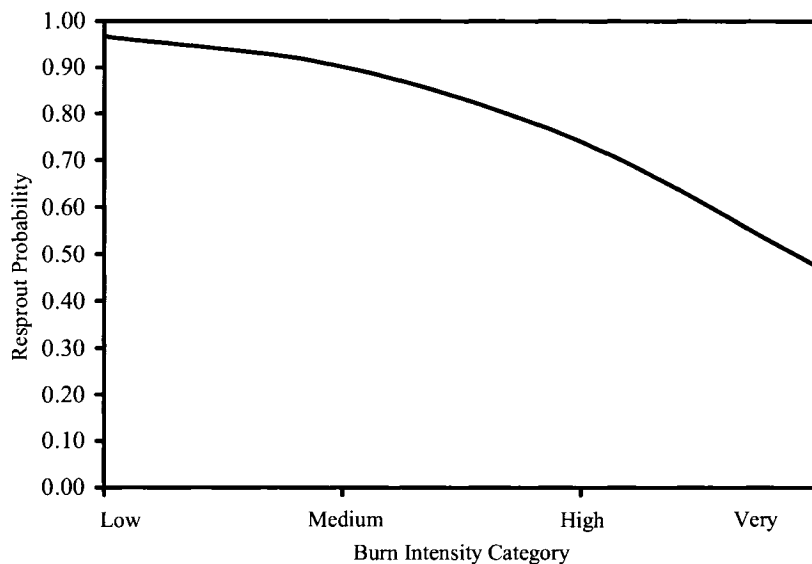


Figure 1.9. Probability of mature plant resprout one-year following fire based on burn intensity as an explanatory variable. The four burn intensity categories correspond to Low, Medium, High, and Very High described in Table 1.1. Model estimated resprout probability is based on burn intensity as a single explanatory variable with all other explanatory variables in the logistic model held constant. Figure is based on the model described in Eq. 1.

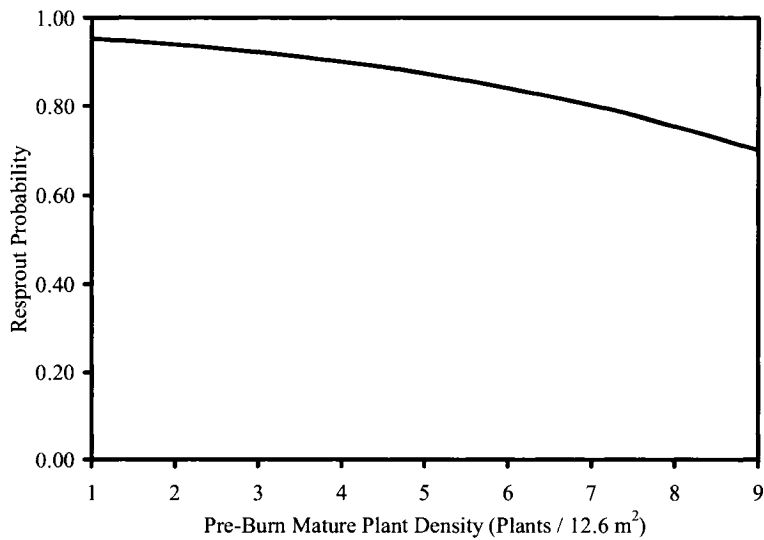


Figure 1.10. Probability of mature plant resprout one-year following fire based on neighboring mature plant densities (plants/12m²) as an explanatory variable. Logistic regression model estimate of probability is based on mature plant densities as a single explanatory variable with all other explanatory variables in the model held constant. Figure is based on the model described in Eq. 1.

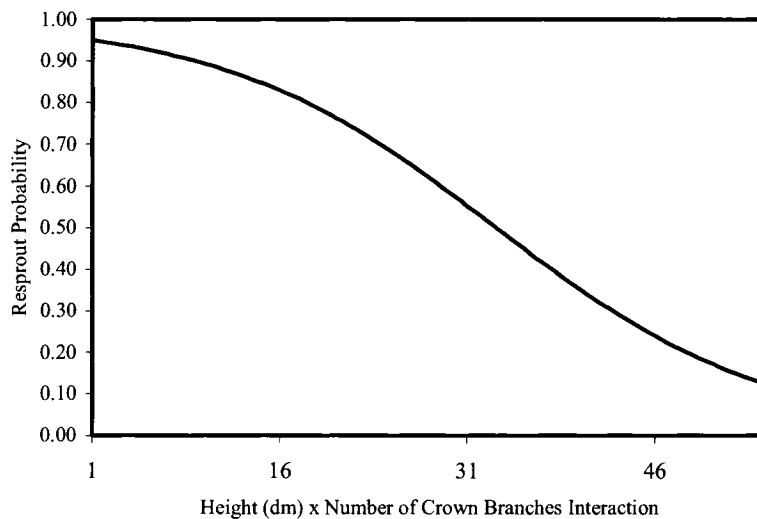


Figure 1.11. Probability of mature plant resprout based on plant height and number of crown branches interaction one-year following fire as an explanatory variable. Logistic regression model estimate of probability is based on mature plant densities as a single explanatory variable with all other explanatory variables in the model held constant. Figure is based on the model described in Eq. 1.

Results of RMANOVA indicated a significant difference in proportion of resprout between the four burn categories ($P = 0.007$) and between short and tall plants ($P = 0.010$) (Table 1.7). Overall, shorter plants (< 3 dm) tended to have the higher percentage of resprout following burning compared to taller plants (> 3 dm) (Figures 1.12 -1.14). Resprout response within the height categories was not significantly different over time ($F_{9,27} = 103.386$, $P = 0.575$). Plants that had experienced lower burn intensities tended to have higher rates of resprout compared to the highest burn intensity ($800^{\circ}\text{C} - 1000^{\circ}\text{C}$) (Figure 1.12 – 1.14). RMANOVA suggests that over time no significant difference in resprout response was evident within the four burn intensities ($P = 0.061$) (Table 1.7). Surviving mature plants vigorously resprout from numerous crown branches when exposed to higher burn intensities ($>600^{\circ}\text{C}$) ($t = -5.38$, $d.f. = 39$, $P < 0.0001$) (Figure 1.15).

Table 1.7. Results of repeated-measures ANOVA (RMANOVA) for monthly mean arcsine-root transformed proportions of mature plant resprout. Mature plant height (HT) consisted of two discrete height categories; short ($< 3\text{dm}$) and tall ($> 3\text{dm}$). Burn intensity categories corresponded to the four categories described in Table 1.1.

Proportion of Mature Plant Resprout					
Source of Variation Between	SS	df	MS	F	P
BURN	16393.8	3	5464.61	37.382	0.007
HT	4842.83	1	4842.83	33.128	0.010
Error	438.552	3	146.184		
Source of Variation Within	SS	df	MS	F	P
Date	7977.84	9	886.427	7.322	< 0.001
Date*BURN	5979.92	27	221.478	1.829	0.061
Date*HT	930.476	9	103.386	0.854	0.575
Error	3268.85	27	121.068		

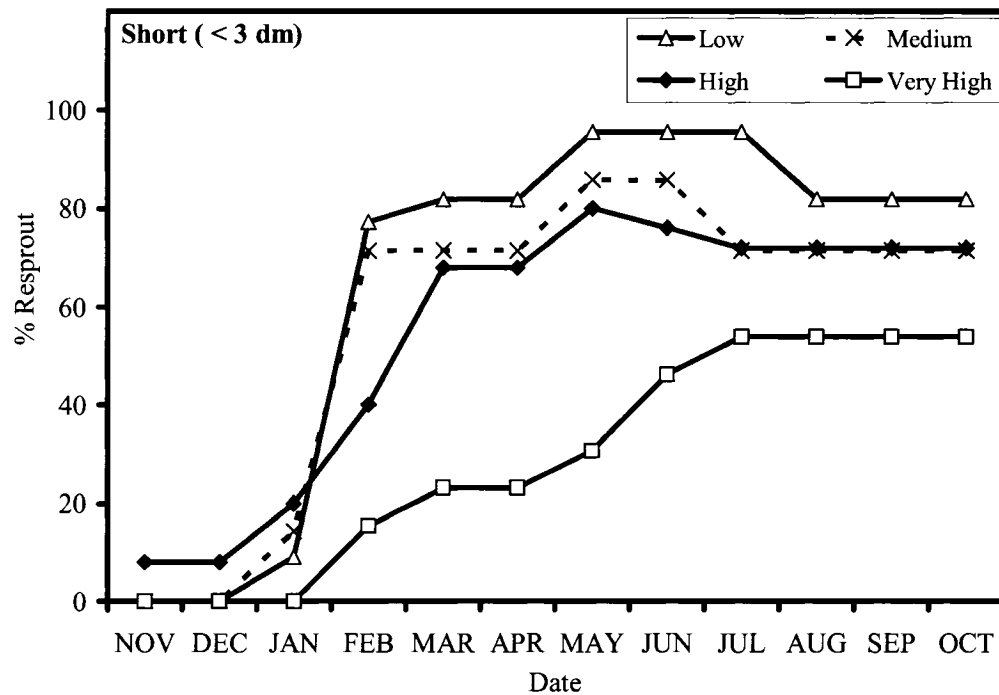


Figure 1.12. Percentage of post-burn mature plant resprout for plants with height less than 3 dm. Error bars indicate SEM.

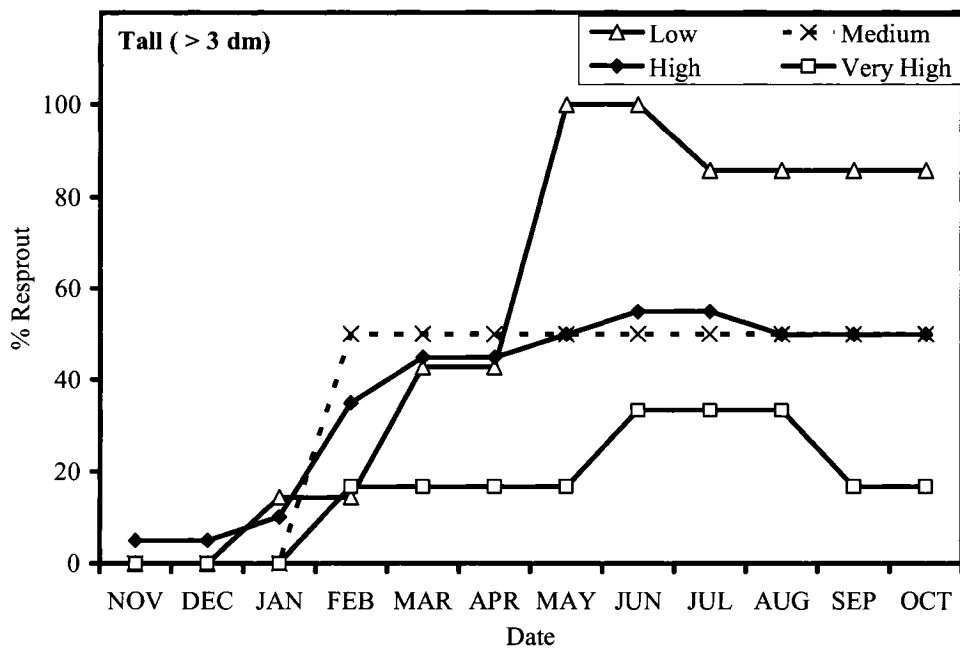


Figure 1.13. Percentage of post-burn mature plant resprout for plants with height greater than 3 dm. Error bars indicate SEM.

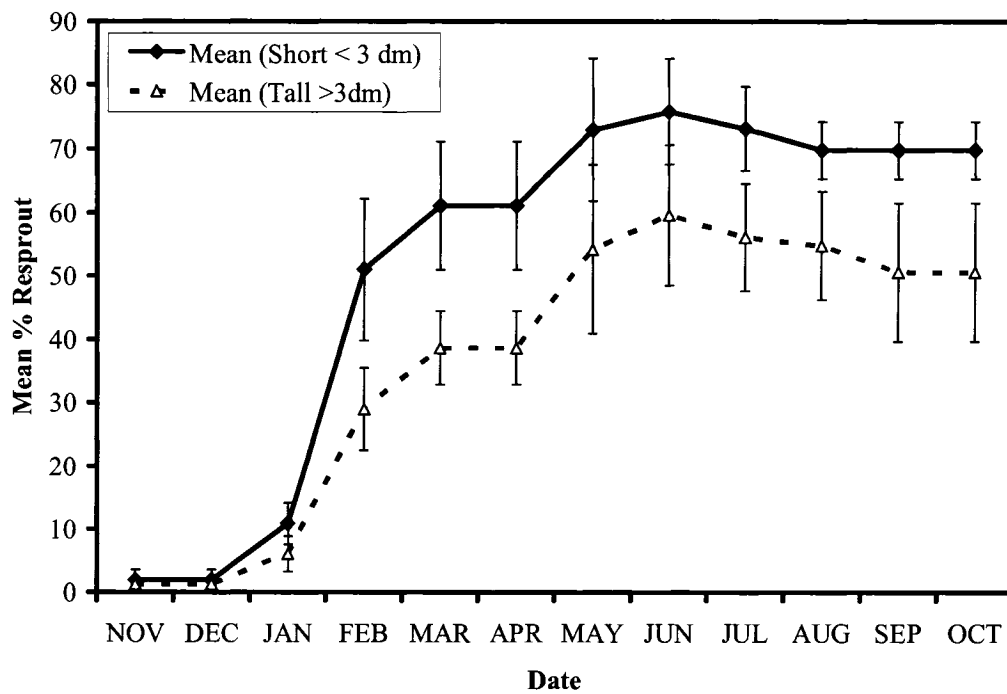


Figure 1.14. Mean percentage of post-burn mature plant resprout for plants with height greater than 3 dm and less than 3 dm. Error bars indicate SEM.

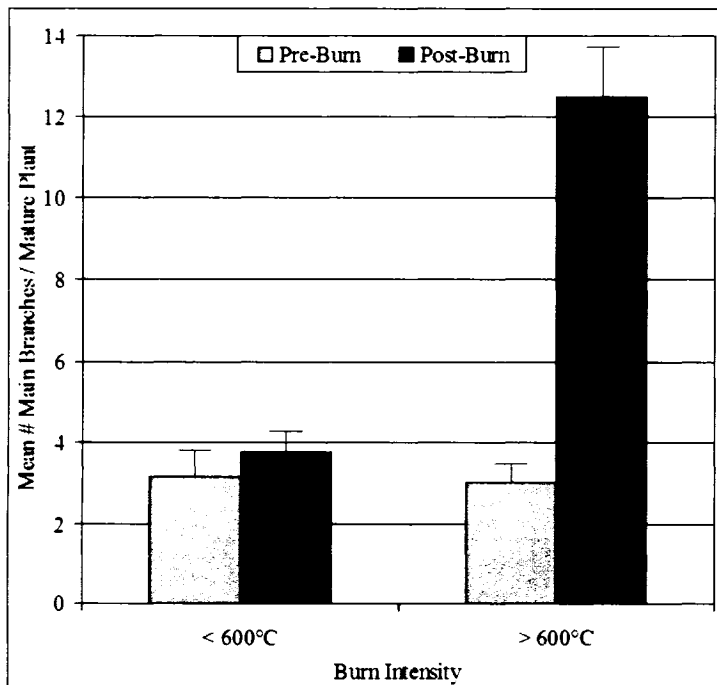


Figure 1.15. Mean number of pre-post burn crown branches per surviving mature plants. Error bars indicate SEM.

1.3.5 Post-Burn Flowering Response

No significant difference was observed between pre-post burn mean number capitula per plant in low ($<600^{\circ}\text{C}$) ($t = -0.602$, $d.f. = 88$, $P = 0.548$) or high ($>600^{\circ}\text{C}$) burn intensities ($t = -0.566$, $d.f. = 39$, $P = 0.574$) (Figure 1.16).

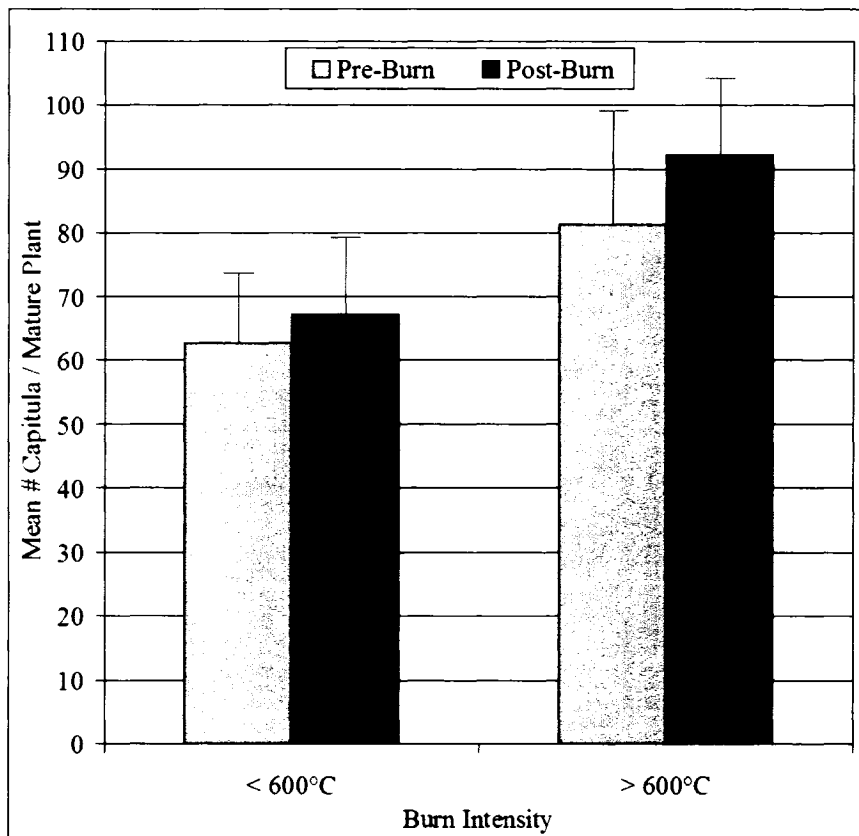


Figure 1.16. Mean number of pre-post burn capitula produced by surviving mature plants. Error bars indicate SEM.

1.3.6 Post-Burn Seedling Presence and Abundance

Observed seedling emergence was infrequent, occurring at only 6 burn monitoring sites (20%) and 7 control sites (24%). This resulted in presence/absence data and abundance counts with relatively large occurrences of zero observations (Figure 1.17).

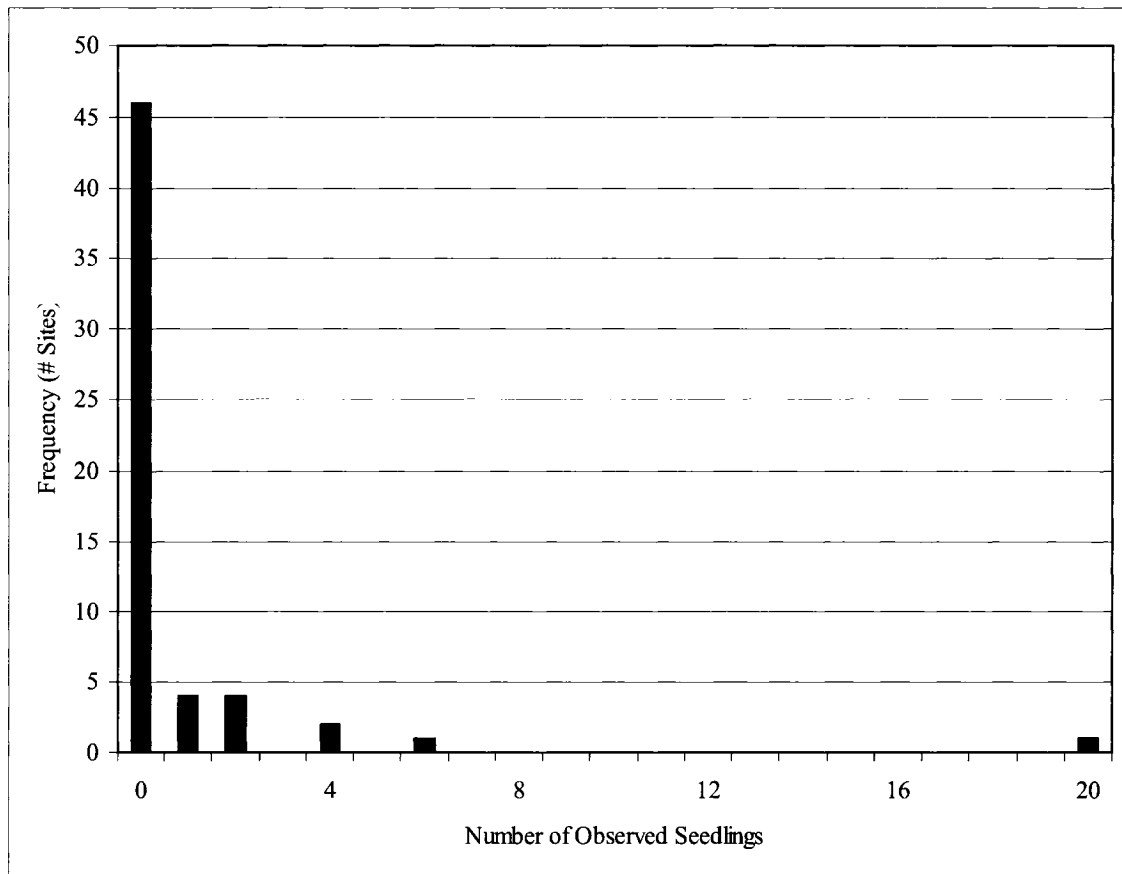


Figure 1.17. Frequency distribution of seedling abundance from 59 grouped monitoring sites (burn treatment = 30, control = 29). Each monitoring site encompassed a 12.6 m² area.

Seedling abundance in the burn treatment (32 seedlings total) was higher than in the control (14 seedlings total). Although seedling abundance was relatively higher in the burn area, it is critical to point out that mature plant densities, and thus potential seed source, were also significantly higher in the burn area ($\bar{X} = 3.00, SE = 0.39$) compared to the control area ($\bar{X} = 1.63, SE = 0.12$) ($t = 3.29, df = 3, P = 0.002$). The percentages of surviving seedlings 1-year following the burn were extremely low in both the burn (22%) and control (0%) areas.

Using a two-part conditional modeling approach, I was able to construct a model to explain *E. fasciculata* seedling presence and abundance as a function of pre-burn mature neighboring plant density. The resulting model components were:

Component #1:

$p = P \{ \text{at least one seedling present} \}$ and

$$\text{logit}(p) = (-2.264 \times \text{Intercept}) + (0.390 \times (\text{Pre-burn Mature Plants}/12.6 \text{ m}^2))$$

$$(\text{SE} = 0.179)$$

Component #2:

$$\log(\lambda) = (-0.036 \times \text{Intercept}) + (0.174 \times (\text{Pre-burn Mature Plants}/12.6 \text{ m}^2))$$

$$(\text{SE} \sim 0.039)$$

Where, λ = natural log transformed mean abundance of *E. fasciculata* seedlings (given presence).

Eq. 2

I found that the probability of *E. fasciculata* seedling presence and relative abundance (given presence) in the first year was significantly ($P < 0.05$) related to pre-burn mature neighboring-plant densities. The number of pre-burn mature plants in a 12.6 m² area had a positive influence on the probability of seedling presence (Figure 1.18) and seedling abundance (Figure 1.19) at a site. The presence component of the model suggested that the odds of observing at least one emerging *E. fasciculata* seedling in a 12.6 m² area is increased by approximately 0.39% for a 1% increase in the number of pre-burn mature plants per 12.6 m². The abundance component of the model suggested that

E. fasciculata seedling abundance increased by approximately 0.17% for a 1% increase in the number of pre-burn mature plants per 12.6 m² area.

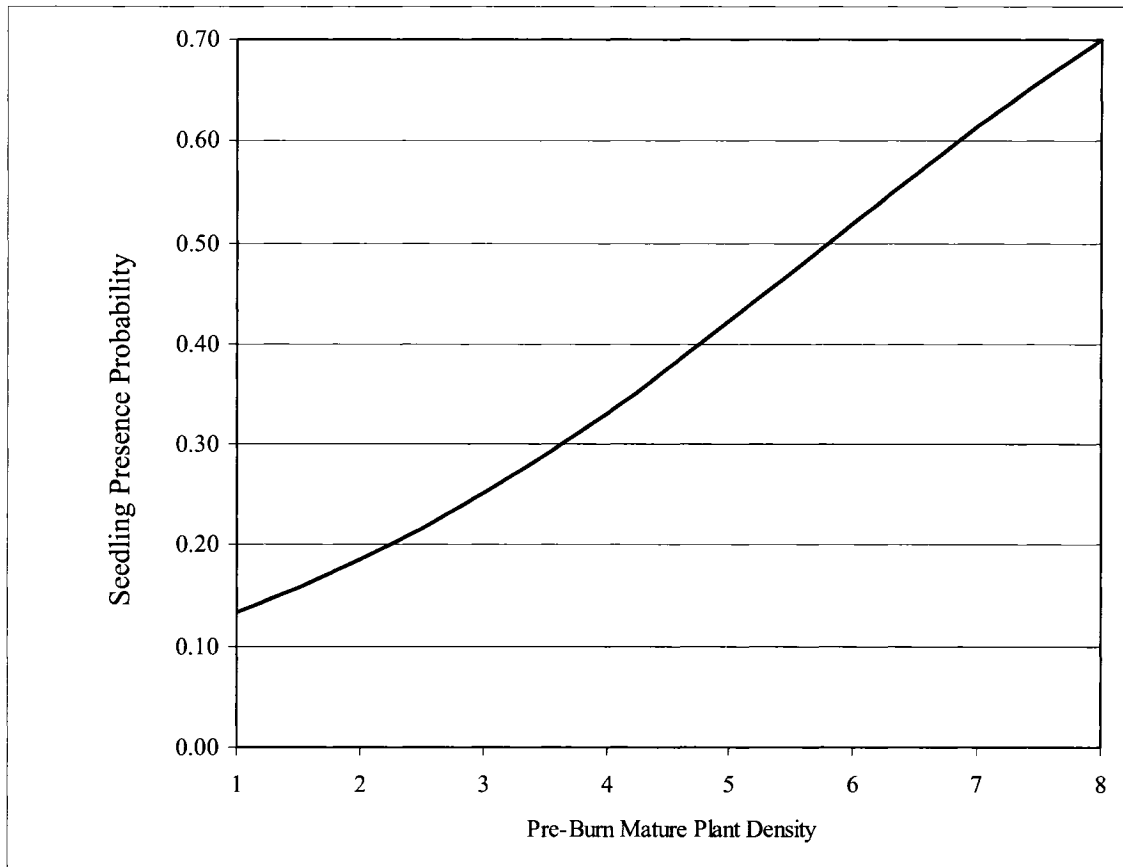


Figure 1.18. Effects of pre-burn mature plant densities (plants/12.6 m²) on the probability of seedling presence. Based on logistic regression (Component #1) of two part conditional model outlined in Eq. 2.

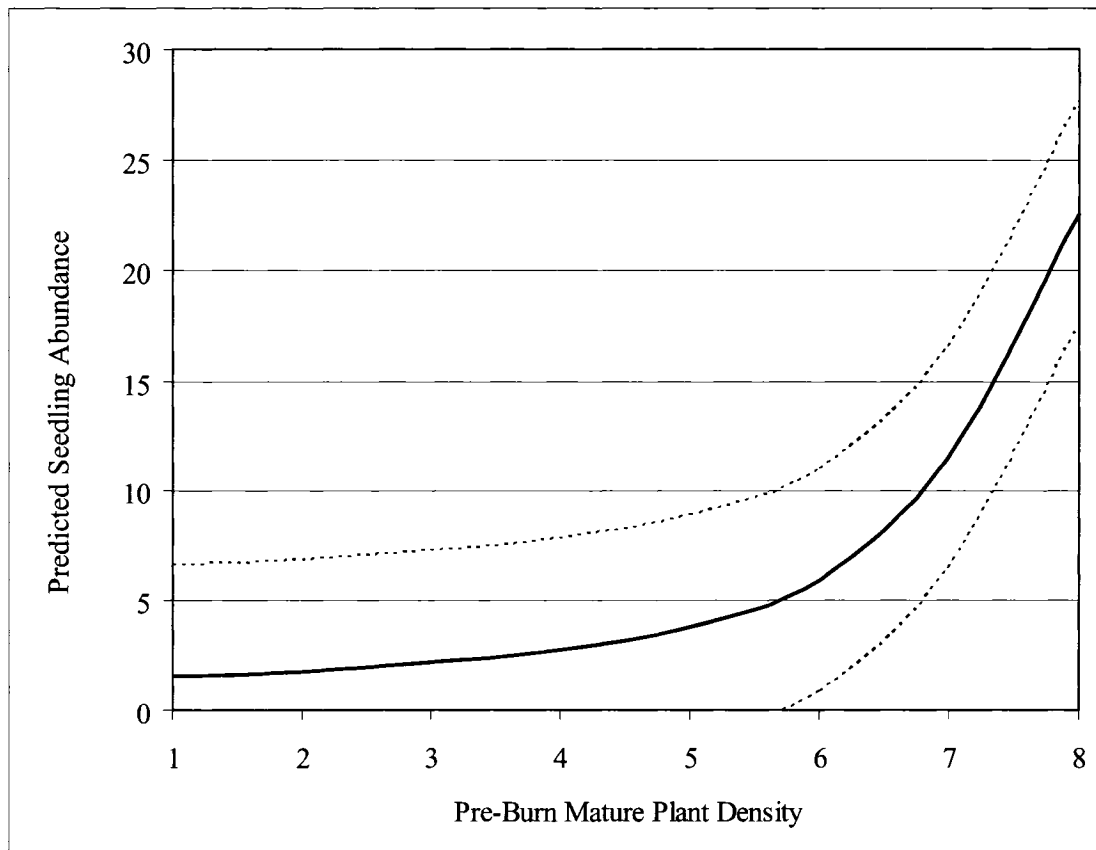


Figure 1.19. Predicted seedling abundance in the first year following prescribed burning, given pre-burn mature plant densities, together with 95% confidence intervals. Based on Poisson regression (Component #2) of two part conditional model and given seedling presence. Component #2 outlined in Eq. 2.

1.4 DISCUSSION

Immature and mature *E. fasciculata* plants are capable of surviving lower intensity fire events by resprouting vigorously from root crowns during the first wet winter season following fall burns. Results of 1-way ANOVA of immature plant resprout and logistic regression modeling of mature plant resprout collectively suggest that immature plants and large mature plants are most sensitive to increases in burn intensity. This trend concurs with studies showing that increased frequencies of low intensity disturbance tend to favor resprouting woody species over seeding species (Bellingham 2000). In addition, fire

events too short in succession or high in intensity can increase mortality for woody species (Zedler *et al.* 1983, Keeley 2006). In some studies, the largest and smallest sized individuals of a resprouting species may be the least likely to resprout following exposure to higher burn intensities (Moreno and Oechel 1993).

One possible explanation for the increased mortality following fire in immature and large mature *E. fasciculata* plants may be associated with the extent of developed woody tissue available to protect against cambium and epicormic bud damage (Bond and van Wilgen 1996). Immature *E. fasciculata* plants may have less protective woody tissue surrounding their root crowns and larger mature *E. fasciculata* plants may have more developed (*e.g.* thicker) woody tissues. The relatively low amount of woody tissue protecting immature plant root crowns may increase the degree of damage to adventitious buds and reduce resprout response. Conversely, the increased amount of woody tissue surrounding the root crowns of larger mature plants may reduce the potential for resprouting by covering adventitious buds under an impenetrable tissue layer (Keeley 2006).

Although this may be the case, inferring a size/age correlation should be interpreted with caution. *E. fasciculata* may exhibit facultative resprouting throughout its entire life-span, potentially resulting in a mixture of branch ages and heights on individuals. This “layering” phenomenon is a common strategy for many Mediterranean-type shrubs and may have a bearing on the interpretation of resprout potential of *E. fasciculata* (Keeley and Keeley 1984). Individual plants may have a disturbance threshold that limits the amount and extent of resprouting, and the degree of resprouting may be a function of

fire intensity, fire frequency, and obligate/facultative strategy. For example, burning large mature *E. fasciculata* plants at higher burn intensities reduces the likelihood of survival and this would reduce the occurrence of the “layering” phenomenon in *E. fasciculata* populations. However, consistently burning larger mature plants at lower burn intensities with a long fire-return interval could result in a higher occurrence of branch “layering”. A large portion of pre-burn branches survived on mature plants when exposed to low burn intensities and the addition of new post-burn resprouts would result in two different age branches on surviving individuals. In addition, if *E. fasciculata* exhibits a facultative resprout response and plants were exposed to low burn intensities with a fire frequency on the order of decades (Greenlee and Langenheim 1990), then under this regime more surviving plants might have several basal crown branches of differing age. A similar layering response might be observed if *E. fasciculata* utilizes an obligate resprout strategy and plants were exposed to a series of frequent but low intensity fires.

It is evident from this study that *E. fasciculata* is capable of resprouting after fire but additional study is required to determine if the degree of resprout potential is largely an obligate or facultative event. In 1999 the entire Parker Flats site was manually mowed for unexploded military ordnance clearance and later the area was designated as habitat preserve after it was determined that obligate seeding special status plant species were negatively impacted as a result of vegetation removal in the absence of fire (Zander Associates 2002).

It is apparent from the logistic regression model of mature plant resprout that burn intensity, mature plant density, and plant size (*e.g.* height and number of basal crown

branches) are important factors that can affect resprout potential. However, the relatively high occurrence of false positive resprout predictions in the model greatly reduced the predictive capabilities of the model. This modeling approach was useful in identifying variables that may explain mature plant resprout following prescribed burns. However, future predictive modeling efforts should focus on correcting the source of potential false positives, thereby enabling the model's use as a predictive tool for conservation efforts.

I suspect that *E. fasciculata* is capable of resprouting without fire events given the observed presence of several mature plants with cutting scars indicating post-mowing survival (pers. obs. Jon Detka). Field observations confirm that relatively shorter *E. fasciculata* were capable of bending under the weight of pre-burn mechanical vegetation removal (pers. comm. Lars Pierce). This resulted in largely intact above ground *E. fasciculata* biomass following brush mowing and chaining. Chaining is a method of removing brush from a site prior to burning by dragging a large chain between two tractors. Additional study will be required to ascertain if *E. fasciculata* is capable of facultative resprouting following pre-burn vegetation removal (e.g. cutting and chaining).

Conservation management efforts concerned with supporting immature and mature stands of *E. fasciculata* should consider methods that reduce burn intensity by manually reducing fuel loads surrounding mature and immature plants. This method will insure that other obligate seeding maritime chaparral species will still receive higher burn intensities necessary for their conservation (Boyd 2007, Bellingham 2000).

Season of fire regimes should also be considered when managing *E. fasciculata* as drought years and available soil moisture may significantly impact post-fire recovery. It

was evident from this study that the onset of resprout coincided with increased water availability from precipitation. During this study, the region experienced its second consecutive year of above normal precipitation. In 2005/06, precipitation was 62.9 cm, well above the average 49.8 cm (CDEC 2007). In addition, the majority of resprouting in mature *E. fasciculata* occurred prior to the seasonal decreases in soil moisture. These results suggest that the onset and observed losses in resprouting individuals may have been associated with available soil moisture. One of the proposed logistic regression models of mature plant resprout suggested that soil moisture played an important role in the occurrence of resprout. However, the addition of the moisture variable to the model significantly reduced the support as the better model. This discrepancy may be associated with the sampling method used to measure soil moisture. I measured near-surface soil moisture and this methodology may not adequately represent soil moisture at depths accessible by mature plants with more extensive root systems.

Flowering in mature *E. fasciculata* tended to originate exclusively from new crown branch resprouting during the late summer following fire (pers. obs. Jon Detka). Fire-stimulated flowering in woody resprouting shrubs is generally thought to be a facultative response associated with increased light, moisture, space, and nutrients (Platt *et al.* 1988, Bond and van Wilgen 1996). Ample rainfall in 2005-2006 may have decreased drought stress and provided additional moisture resources allowing flowering to occur during the following dry season.

Fire-stimulated resprouting and flowering of mature *E. fasciculata* in the first year following fire may lead to more lucrative reproduction in the fire-free years that follow.

Rapidly resprouting and flowering of mature *E. fasciculata* between fires could hypothetically allow for greater dispersal and establishment success into areas previously occupied by vegetation.

The rare occurrence of flowering by surviving immature plants (<10% occurrence) in the first year following burning may suggest that immature plants have yet to acquire the necessary below-ground resource stores to reproduce. Instead, immature plants may allocate available resources to growth and survival. This is a common phenomenon, as it is generally accepted in life-history theory that there are trade-offs between reproductive effort, growth, and survival (Cole 1954). While increased soil fertility following fire may lead to enhanced reproduction (Brewer 1995), I hypothesize that immature *E. fasciculata* may have lacked an extensive root network to take advantage of potential post-burn moisture and nutrient resources.

Given that *E. fasciculata* resprouts are capable of flowering in the first year following fire, conservation efforts need to consider the importance of burn timing and account for potential post-fire flowering. Early fall burns may promote flowering response and seed distribution by allowing ample time for burned plants to resprout and flower before the following dry season.

The emergence of *E. fasciculata* seedlings in the field during the first year following fire was rare. The two-part conditional model suggests that seedling presence and abundance is largely dependent on mature plant densities, not on burning conditions. It is likely that relatively higher mature plant densities in the burn area were responsible for the observed differences in abundance of seedlings between the burn and control areas.

Future conservation and restoration efforts should focus on maintaining patches containing several mature *E. fasciculata* as a means of increasing the probability of successful seedling establishment.

Soil moisture and air temperature differences between the burn and control may also account for the difference in seedling emergence and survival rates. Studies support that obligate resprouting species tend to produce seedlings that are more sensitive to water stress (Keeley and Zedler 1978, Frazer and Davis 1988). In general, the burn area experienced higher soil moisture levels and lower maximum air temperatures during the dry season compared to the control site; these conditions may have been more suited to supporting seedlings.

Therefore, it cannot be concluded that increased seedling abundance in the burn treatment is entirely the product of fire-related conditions. In addition, results of a seed viability study in the lab found that *E. fasciculata* seed germination was inhibited by exposure to increased fire-related heating and sowing in a charate substrate (Chapter 2).

The occurrence of seedlings in the first year following a burn should not be considered indicative of *E. fasciculata* reproductive potential. Chaparral shrubs initially tend to devote resources to post-fire resprouting. Markedly increased seedling abundance is generally observed in the third or fourth year following burns (Sweeney 1956, Schwilk and Ackerly 2005). It has been proposed that increased shrub seedling establishment several years after fire may be associated with competition from the post-fire flush of herbaceous annuals in the first year following a burn (Moreno and Oechel 1991). During seedling surveys, I had noted the presence of dense stands of non-native annual grasses

surrounding the understory of burned *E. fasciculata* and an absence of emerging seedlings. Invasion by non-native annual grasses may reduce the presence and abundance of *E. fasciculata* seedlings post-fire.

Mature plant survival did not appear to impact seedling survival, so conservation efforts should insure that a portion of mature plant stands receive low burn intensities and a fire-return interval that encourages resprout and flowering in the following season. Seedlings or immature plants will also likely be nearby. In all observed cases, seedlings were no more than 2.5 dm away from a mature plant and field crews only observed *E. fasciculata* seedlings in areas where existing plants resided (pers. comm. Lars Pierce).

Ericameria fasciculata has exhibited many of the characteristics indicative of coastal California sage scrub species rather than a maritime chaparral shrub. Coastal sage scrub species are typified by reduced stature, rapid growth rate following disturbance, relatively lighter wind-borne seeds, and low post-fire seedling emergence following burning events (Wells 1962, Keeley and Keeley 1984). *E. fasciculata* may function as more of a maritime chaparral invader capable of establishing in disturbed adjacent perimeters and internal gaps of dense maritime chaparral stands. It is plausible that *E. fasciculata* would be able to survive fire in these relatively lower fuel load gaps, quickly resprouting, flowering, and distributing seed into newly expanded nearby post-fire disturbance sites. Similar post-fire responses were observed in the closely related, and more common, southern California coastal scrub species *Haplopappus squarrosus* (Keeley and Keeley 1984).

Ericameria fasciculata exhibits post-fire responses that are indicative of resprouting fire life histories. Knowledge of differences in *E. fasciculata* fire life history responses can help managers determine the potential impacts that may be associated with a conservation action. The degree of plant maturity and relative size of individuals were determining factors affecting post-fire survival. *E. fasciculata* conservation efforts should focus on assessing reproductive maturity and stand densities of existing plants prior to prescribed burns. Pre-burn surveys should occur during the fall season when mature plants are flowering. Managers can anticipate that surviving post-burn resprouting plants will flower from numerous basal crown branches, producing copious amounts of seed in the first year following burns. In addition, monitoring for *E. fasciculata* seedlings should begin in the first year following burns and may need to extend several years after burns to insure that seedlings have established following the post-fire herbaceous flush.

Restoration activities that include active planting of *E. fasciculata* should consider installing plants during the late-fall rainy season in recently disturbed maritime chaparral gaps or edges containing some intact surviving vegetation to mimic low burn intensity post-fire conditions.

CHAPTER 2 GREENHOUSE GERMINATION STUDY

2.1 BACKGROUND

The ability to propagate rare endemic plant species has become increasingly important with the advent of conservation goals directed at revegetation and restoration of endemic plant communities (U.S. Army Corps of Engineers 1997, Padgett *et al.* 1999). The legal impetus for such actions in California stem from the ratification of the Endangered Species Act (ESA) and the California Endangered Species Act (CESA). In tandem with these legal requirements, a growing appreciation of native California flora and the intrinsic values associated with species diversity has prompted the need for additional information regarding the propagation of endemic plant species (Emery 1988). Much of this concern for the protection and conservation of rare species also stems from the knowledge that increased anthropogenic influences (*e.g.* global warming and habitat fragmentation) are moving at rates that exceed the ability of species with restricted distributions to accommodate (Davis 1989). In response to these biological crises, it has been recommended that urgency be placed on the development of conservation techniques that can be used to actively increase the size and distribution of rare plant populations (Primack and Miao 1992).

Active restoration of rare endemic plant populations by seed broadcasting typically fails to establish self-sustaining populations (Primack 1996). Several hypotheses have been proposed as explanations for the lack of success from introduced seed and general inability to establish self-sustaining regenerative populations. These include the need for (1)

suitable habitat/community composition, (2) potentially specialized germination responses and (3) improper seasonal timing of seed collection or distribution (Primack 1996, Willson and Traveset 2000). In addition, seed broadcasting challenges are compounded when working with rare species as the current plant distribution may not adequately represent the conditions required for germination, required germination conditions may be unknown, and wildland seed stock may be in short supply. Therefore, restorationists have shifted their efforts to propagating rare species in greenhouses for reintroduction into wildlands (Gordon-Reedy 1997, Padgett *et al.* 1999). Active outplanting of greenhouse-propagated plants into suitable unoccupied habitat may increase the dispersal potential of a species with limited seed dispersal capabilities (Primack and Miao 1992).

It is well established that many plant species in fire-prone Mediterranean-type plant communities have unique fire adapted seed life histories (Sweeney 1956, Keeley and Zedler 1978, Keeley 1987). In general, these germination adaptations are responses to the drastically altered environmental conditions that are present following fire events. However, there are no clear trends in the degree or trend of seed germination responses for closely related taxa in the maritime chaparral plant community (Davis *et al.* 1989).

Woody chaparral plant species with an obligate seeding fire life history are particularly challenging to propagate given that many are reliant on specific combinations of fire-related germination cues for their emergence (Keeley 1987, Emery 1988, Gordon-Reedy 1997, Padgett *et al.* 1999, Boyd 2007). Fire may impact seed germination by altering the microscale environmental conditions through heating, charate, and changes in available light (Keeley 1987, Davis *et al.* 1989, Baskin and Baskin 1998)

During a fire, temperatures at the surface of sandy soils can exceed 600°C (Sweeney 1956). However, heating from fire dramatically decreases (50-200°C) with small changes in depth (1- 2 cm) and duration (< 20 minutes) (Sweeney 1956, Davis *et al.* 1989). Germination responses of woody chaparral shrubs to dry heating at temperatures similar to near-surface burial (70-120°C) are extremely varied, ranging from increases, decreases, and no effect on germination rates (Baskin and Baskin 1998).

The increased availability of light often associated with the post-burn chaparral environment can have a significant impact on the emergence of seedlings (Sweeney 1956, Keeley 1987). Fire can dramatically reduce canopy vegetation cover and litter, increasing the amount of available light. There are few clear trends in light-facilitated germination response among plants, but it is generally accepted that smaller seeded species have seed residing near the surface of sandy soils are more dependent on light signaling (Pons 2000). Keeley (1987) noted 22 species from 15 families of woody California chaparral shrubs that exhibited a significant light-stimulated germination response. Interestingly, several species in related families exhibited no light-related germination responses.

Previous studies have demonstrated a wide variety of effects of charred wood on germination of individual species (Keeley 1987, Tyler 1996). In addition, debate continues about the influence of several active ingredients present in the charate of the common chaparral shrub *Adenostoma fasciculatum*. For example, Keeley and Pizzorno (1986) suggest that the active component of *Adenostoma fasciculatum* charred wood (charate) may be an oligosaccharin that stimulates germination. McPherson and Muller (1969) suggested that the volatilization of allelopathic inhibitors reduces the suppression

of seed germination. In contrast, Thanos and Rundel (1995) found that nitrogenous compounds in charate may be responsible for the herbaceous flush following burns and that the flush response is weaker in woody shrubs. Additionally, studies have elucidated that there are species-specific germination responses to different combinations of heat, light, and charate (Keeley and Keeley 1984, Keeley *et al.* 1985, Keeley 1987, Tyler 1996).

Several taxa related to *E. fasciculata* have demonstrated a range of post-fire responses making it difficult to infer the potential for fire stimulated seed germination (Keeley and Keeley 1984, Keeley 1987, Tueller and Payne 1987, Neuenschwander [n.d.], Holl *et al.* 2000). Prior to this work, the germination response of *E. fasciculata* seed was not known. This study was prompted primarily in response to the need for information regarding (1) greenhouse propagation potential of *E. fasciculata* for planned restoration efforts and (2) to determine if burning inhibits or promotes *E. fasciculata* seed germination. Field observations noted low occurrences of natural post-burn *E. fasciculata* seedling emergence coupled with a catastrophic mortality rate in the first year following burning (Chapter 1). In addition, initial attempts to propagate the species without fire-related stimuli in greenhouses yielded mediocre results (pers. obs. Jon Detka).

2.2 GREENHOUSE MATERIALS AND METHODS

2.2.1 Seed Collection and Storage

Ripe capitula were hand collected from 29 plants located outside of designated study sites (Fort Ord, Parker Flats Reserve, Monterey, CA. LAT 36°38'4.60"N, LONG

121°46'38.78"W) during September 2005 and 2006. All collected seed was grouped by year and no cleaning or sorting was conducted. Seeds were stored loosely in brown paper bags in unlit standard refrigeration at 5° -10°C.

2.2.2 Seed Viability Testing

Prior to propagation trials, 3 random samples of 300 seeds each were acquired from 2005 and 2006 seed stocks. Seeds were visually inspected under 10x hand lens magnification and sorted into three categories; intact, aborted, and dead. Seeds with obvious external structural deformations, such as being smaller than the mean seed length or width, were imbibed in 1mM CaCl₂ solution at lab temperature for 1 hour and dissected under a dissection microscope to determine if an embryo was present. Those seeds with no embryos present and no signs of physical damage, predation, or fungal attack were recorded as aborted. Seeds that appeared intact with no external deformations, physical damage, or fungus present were grouped as intact. Seeds with obvious physical damage from predation or fungal attack were recorded as dead.

I used a 1% 2,3,5-Triphenyl-tetrazolium Chloride (TZ) staining technique (Carolina Biological Supply Co., Burlington, North Carolina) to evaluate collected intact seeds for embryo viability from each seed stock for 2005 and 2006 (Lakon 1949). Prior to TZ staining I soaked intact seeds in a 1mM CaCl₂ solution at laboratory temperature for 1 hour to imbibe seeds to soften the seed coat for dissection. I removed the seed coats of intact seeds under a dissection microscope and inspected for intact embryo material. Seeds containing no embryo or the presence of decayed soft tissues were recorded and

pooled in the dead category. Those seeds containing intact embryos were soaked in TZ staining solution for 18 hours. Care was also taken to insure that embryos remained completely submerged in the solution with no contact to air or exposure to light. The presence of a pink to red coloration along portions of the embryo indicated viable seed.

2.2.3 Greenhouse Germination Trials

Greenhouse germination trials were conducted in the late fall following seed collection to examine the role of fire-related cues in the germination of *E. fasciculata*. The fire-related treatments were: (1) pre-sowing heat, (2) powdered charate from *Adenostoma* wood, and (3) light. Initial germination trials had produced poor rates of germination so gibberellic acid (GA₃) treatment was applied.

Seeds were initially sorted from remaining plant material and inspected for signs of physical damage (i.e. predation, fungal invasion) or obvious deformities. Thirty-two lots of 150 intact seeds were sorted into steel soil tins and were designated to receive orthogonally grouped treatments of heat (70°C - 120°C) or no heat, light or dark, charate or no charate, and gibberellic acid (GA₃) or no gibberellic acid (GA₃) (Figure 2.1).

	Light			
GA ₃	No Heat	100°C	No Heat	100°C
	70°C	120°C	70°C	120°C
No GA ₃	No Heat	100°C	No Heat	100°C
	70°C	120°C	70°C	120°C
	Charate		No Charate	

OR

	Dark			
GA ₃	No Heat	100°C	No Heat	100°C
	70°C	120°C	70°C	120°C
No GA ₃	No Heat	100°C	No Heat	100°C
	70°C	120°C	70°C	120°C
	Charate		No Charate	

Figure 2.1. Diagram of orthogonally grouped treatments of GA₃, light or dark, heat treatments, and charate. Each heat treatment cell represents a complete treatment grouping in a single Petri dish containing 150 seeds. For example, the grey cell (top left) received treatments of light, GA₃, charate, and no pre-sowing heat. Each replicate ($n = 3$) consisted of the 32 possible treatment groupings.

Seeds were dry heated in the open tins using a forced convection oven set at 70°C for 1 hour, 100°C for 5 minutes, and 120°C for 5 minutes to mimic fire conditions observed by Sweeney (1956) and recommended in Keeley (1987). A control treatment was also designated and received no heating. Immediately following heat treatment I removed seeds from the tins and placed them in 50ml centrifuge tubes (BD Biosciences, MA).

Sixteen of the 32 centrifuge tubes were designated for the GA₃ treatments. GA₃ treated seeds were imbibed with a mixture of 20ml of 1 mM CaCl₂ solution and 20ml of 100 ppm GA₃ solution. I designated a control treatment for the remaining 16 centrifuge tubes to receive 40ml of CaCl₂ only. Seeds were soaked in solutions at laboratory

temperature (22°C - 25°C) for 3 hours. Seeds that were designated for dark propagation treatment were housed in centrifuge tubes wrapped in aluminum foil to prevent light exposure.

Previous greenhouse trials using a sterile pre-moistened soil mixture (4 parts peat, 2 parts perlite, and 2 parts vermiculite) resulted in extremely poor seed germination response across all treatments and this prompted the adoption of Petri dish propagation techniques. Each group of 150 treated seeds were sown into 32 plastic Petri dishes (150 mm x 25 mm) containing two sheets of 150mm #1 filter paper (Whatman International Ltd., Maidstone, England). Filter paper was pre-moistened with 1mM CaCl₂ solution and any standing solution was removed. Petri dishes were covered with their lids and sealed in re-sealable plastic food storage bags to decrease moisture loss. All Petri dishes were cold stratified for 1 month in an unlit refrigerator at 5°C-10°C.

For seeds receiving charate treatment, 1g of powdered charred wood was applied evenly on top of Petri dish filter paper prior to pre-moistening. Charate was made by charring fresh cut *Adenostoma fasciculatum* stems in a steel burn barrel with a propane torch. Once the stems appeared charred, but not completely reduced to ash, I extinguished the fire by covering the barrel with a lid. Woody charred stems (5-10 mm diameter) were removed and pulverized in a SPEX mill (SPEX CertiPrep, Metuchen, NJ) to produce a fine charate powder.

Analysis of preliminary germination trials had determined that cold treatment significantly improved germination in *E. fasciculata* ($t = 3.530$, $d.f. = 4$, $P = 0.024$) (Table A-1). During preliminary trials, I had noted fungal invasion in both the cold

treatment and control. This prompted the testing of a potential pre-sowing disinfection treatment. Results of disinfection solution testing suggested that the solution was effective in reducing fungal invasion but at a significant cost to seed germination (Table B-1). Therefore, I refrained from using the Clorox seed disinfection treatments in any future germination trials.

Following cold stratification, Petri dishes were placed on an indoor Juliana grow rack (ACF Greenhouses, Buffalo Junction, VA) at laboratory temperature (22°C - 25°C) and out of direct sunlight. I incubated seeds receiving dark treatment on the grow rack shelves in cardboard boxes with removable lids. Ventilation holes were placed on the backside of the boxes to allow sufficient air flow. Seeds undergoing light treatment were placed under 40w fluorescent bulbs (GRO-LUX Wide spectrum, Sylvania LTD., Danvers, MA) under low light (approximately 70-100 $\mu\text{mol s}^{-1} \text{ m}^{-2}$) for a 13-h photoperiod as recommended in Comstock *et al.* (1989).

I surveyed Petri dishes every two days to count germinated seeds and remoisten filter paper with DI water if necessary. Germination was scored based on the first observation of radicle emergence. All dark treatment dishes were surveyed under indirect green light. Monitoring continued for 30 days. I based the monitoring time period on previous growth trial observations that suggested a peak in seedling emergence approximately 10-14 days following removal from cold stratification and a rapid decline in germination thereafter.

2.2.4 Data Analysis

I used two-way ANOVA to determine if differences were evident between the observed proportions of viable seed in 2005 and 2006 seed stock. I used multi-way ANOVA to compare the proportion of seedlings emerging within and between the different propagation treatments. I used SYSTAT v. 10.0 (SYSTAT, San Jose, CA) for all statistical analyses. Levene's test was used to test for homogeneity of variances and the assumption of normality was examined with probability plots of the residuals.

2.3 GREENHOUSE RESULTS

2.3.1 Seed Viability Testing

Results of seed dissection and TZ staining indicated that approximately 10% of *E. fasciculata* seeds were viable. In both the 2005 and 2006 seed stock, empty and dead seeds were more prevalent than viable seed (Figure 2.2). There was no significant difference in the proportion of empty, viable, and dead seed condition between the 2005 and 2006 seed stock ($F_{2,12}=0.514$, $P = 0.611$).

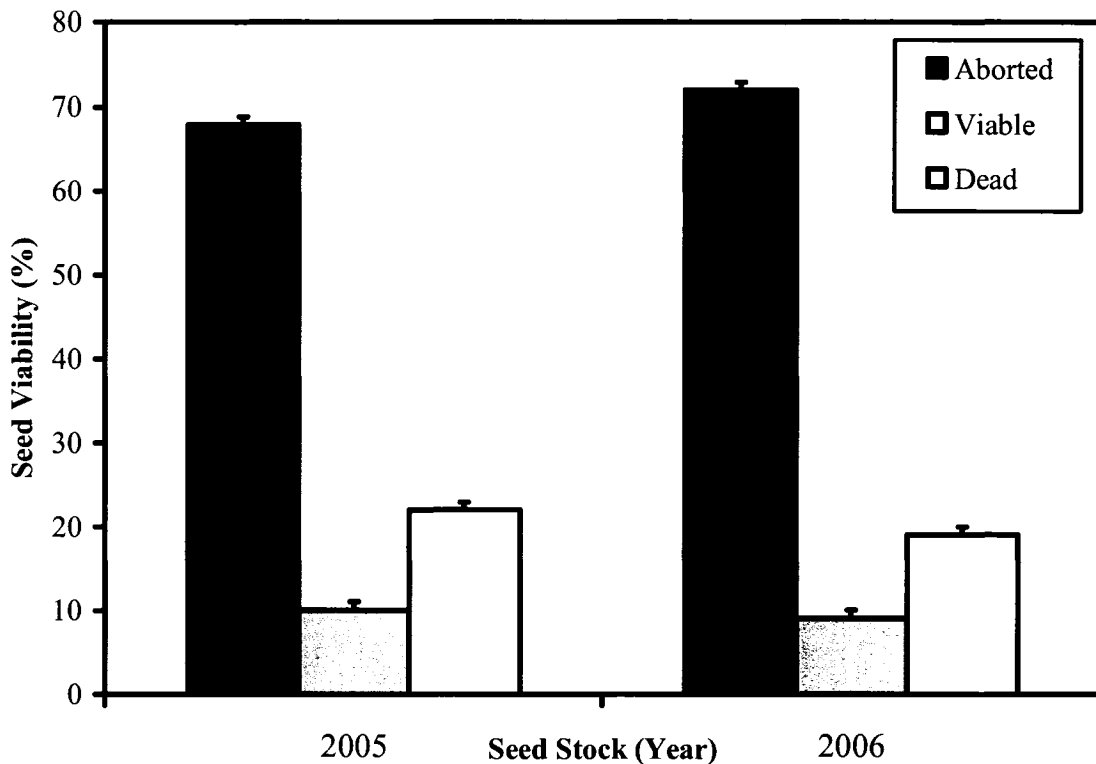


Figure 2.2. Mean percent seed viability from 2005 and 2006 seed stocks. Viability percentage is based on results of seed dissection and 2,3,5-triphenyltetrazolium chloride (TZ) staining. Mean percentage is based on average of replicate trials ($n=3$) for each seed stock. Error bars indicate SEM.

2.3.2 Greenhouse Germination Trials

The addition of GA₃ ($F_{1,64} = 0.269$, $P = 0.606$) and light stimulus ($F_{1,64} = 1.261$, $P = 0.266$) had no significant impact on *E. fasciculata* germination (Table 2.1). The use of charate had a deleterious effect on germination in all cases ($F_{1,64} = 48.963$, $P < 0.001$) (Table 2.1). The interaction of charate and higher temperature treatments ($>70^{\circ}\text{C}$) had a particularly lethal effect on *E. fasciculata* seed germination ($F_{3,64} = 18.619$, $P < 0.001$) (Table 2.1). No other significant interactions between main effects were evident. Heat treatments as a main effect had a significant effect on the germination of *E. fasciculata*

($F_{3,64} = 23.147$, $P < 0.001$). Post hoc tests suggested that there is a significant difference in percent germination between seed experiencing lower temperature heat treatments (Control and 70°C) compared to higher temperature (100°C and 120°C) heat treatments ($P < 0.001$). Higher temperature treatments (>70°C) had catastrophic effects. The highest rates of germination occurred in seeds that received no heat treatments (control) and no charate (Table 2.1).

Table 2.1. Mean percentage germination of *E. fasciculata* in response to orthogonally grouped treatments of GA₃, light or dark, heat treatments, and charate. Each mean value is based on ($n = 3$) Petri dishes each containing 150 seeds. Temperature treatments sharing the same superscript letter were not significantly different ($P > 0.05$ from Bonferroni post hoc test). Standard error (*SE*) values are reported in parentheses. In all cases charate and non-charate treatments were significantly different. Significance values for the remaining main effects in the multi-way ANOVA were not significant ($P > 0.05$).

	GA ₃							
	Light				Dark			
	Control ^a	70°C 1 h ^a	100°C 5 min ^b	120°C 5 min ^b	Control ^a	70°C 1 h ^a	100°C 5 min ^b	120°C 5 min ^b
Control	5.78(1.11)	2.89(0.59)	-	-	5.33(1.15)	3.78(0.44)	-	-
Charate	0.22(0.22)	0.44(0.44)	-	-	0.44(0.44)	0.22(0.22)	0.22(0.22)	-

	Control (No GA ₃)							
	Light				Dark			
	Control ^a	70°C 1 h ^a	100°C 5 min ^b	120°C 5 min ^b	Control ^a	70°C 1 h ^a	100°C 5 min ^b	120°C 5 min ^b
Control	4.44(1.18)	3.78(0.44)	-	-	8.22(4.26)	4.44(1.74)	-	-
Charate	0.22(0.22)	0.22(0.22)	-	-	0.67(0.01)	0.44(0.44)	-	-

2.4 DISCUSSION

Ericameria fasciculata is found in fire-prone plant communities (Griffin 1978) and yet fire-related germination cues appear to have predominantly negative effects on seed germination. Dry heating conditions similar in temperature to those associated with near-surface burial resulted in marked decreases in germination at temperatures greater than 70° C. In addition, the presence of charate had a particularly deleterious effect on germination. Interestingly, the presence of light had little or no impact on seed germination. This low tolerance for heating and charate and unresponsiveness to light suggests that *E. fasciculata* seed (1) existing prior to fall burning is largely destroyed during fall burns, (2) buried relatively deeper in the near soil surface (> 1cm) may be able to endure exposure from low burn intensities and germinate without exposure to light, and (3) dispersal and subsequent colonization may occur from adjacent unburned or low intensity burned sites.

The observed germination responses to fire-related conditions are not uncommon in chaparral species known to utilize an obligate resprouting post-fire strategy and may indicate preferences for niches in the mosaic of post-burn environmental conditions and trade-offs associated with resprouting (Keeley and Zedler 1978, Keeley 1987, Baskin and Baskin 1998, Boyd 2007). For example, Keeley (1987) found that the seeds of *Haplopappus squarrosus* responded negatively to heat treatments, but charate presence and available light had no associated effect on germination. Prior to this finding, Keeley and Keeley (1984) also found that *H. squarrosus* was capable of vigorously resprouting in the first-year following burns. I propose that seeds of *E. fasciculata* may demonstrate a

similar post-fire seedling establishment strategy to *H. squarrosus* by occupying a niche in the low burn intensity environment. In this environment, access to light and charate would be less available due to burial depth and the increased likelihood of unburned surviving aboveground vegetation cover. In low intensity burns, mature *E. fasciculata* are more apt to vigorously crown resprout and flower (Chapter 1), increasing seed availability for dispersal into areas containing little charate and more intact vegetation cover.

Trends in post-burn germination of *E. ericoides* may also support the observed fire-related germination responses of *E. fasciculata* seed. *E. ericoides* is closely related to *E. fasciculata* (Roberts and Urbatsh 2003) and has been observed residing in the same habitat range (pers. obs. Jon Detka). Further experimental comparisons between the common *E. ericoides* and the rare *E. fasciculata* may serve to elucidate differences in post-fire recovery performance leading to patterns of rarity in *E. fasciculata*. Holl *et al.* (2000) observed high rates of germination in *E. ericoides* following surface burn treatments using fresh *Adenostoma fasciculatum* stems, which may initially seem contrary to trends observed in *E. fasciculata*. Observed germination of *E. ericoides* seed following surface burn treatments may have been associated with burial depths that were deep enough to protect seed from high temperature exposure (e.g. > 70°C) (Holl *et al.* 2000). In addition, the proposed associated toxicity of allelopathic chemicals present in *A. fasciculatum* charate may have been volatilized as stems were reduced entirely to ash.

It is now apparent from seed dissection and tetrazolium viability analyses that the low rate of germination observed in propagation trials can be attributed principally to the complete absence of embryonic tissues in a large proportion of *E. fasciculata* achenes.

Extreme variation in seed mass (Sobrevila 1989, Meyer and Carlson 2001) and the complete absence of embryonic tissue in otherwise intact achenes (Keeley 1987, Padgett *et al.* 1999, Alkio and Grimm 2003) is a known to occur frequently in Asteraceae. More specifically, this trend has been observed in several woody Asteraceae shrub species endemic to California (Keeley 1987, Padgett *et al.* 1999, Meyer and Carlson 2001, unpublished data Ransom Seed Laboratories 2006).

Several studies have explored the occurrence of empty achenes and seed abortion in Asteraceae. Self-pollination within capitula of some species could lead to empty seeds, but rates of aborted achenes are also influenced by environmental gradients (*e.g.* elevation and climate) and resource availability (Sobrevila 1989). Restricted pollen distribution and seed dispersal can result in an increased occurrence of mating between close relatives. In the extreme case of self-compatible perennial species, there can also be a tendency to build up deleterious genetic material in the maternal genotype resulting in a higher rate of seed abortion (Connor and Hall 1997). Padgett *et al.* (1999) has proposed that this trend in reduced seed set may serve as an adaptive advantage by hiding viable achenes within capitula filled with empty achenes as a means of reducing insect predation. On rare occasions I observed mature seed bugs (Lygaeidae) and casings in seed stock. However, signs of seed predation were less frequent than the occurrence of predominantly intact, but empty, seed.

I hypothesize that the small population size and clumped distribution of mature *E. fasciculata* coupled with their limited ability to successfully establish seedlings far from mature plant stands (Chapter 1) has facilitated the increased occurrence of empty achenes.

Pollinator-exclusion studies are needed to determine if *E. fasciculata* seed viability is related to self-compatibility, position in capitula of individual plants, and localized distribution of mature plants. In addition, further study needs to investigate the role of resource availability and the occurrence of aborted seed development. Environmental stresses associated with fire and seasonal variability in available soil moisture may exacerbate this phenomenon.

Active restoration of *E. fasciculata* into areas of suitable habitat may be required to insure the conservation of the species. I recommend that active restoration efforts include wildland seed collection and viability testing in advance of prescribed burning events. Ripe capitula should be collected for site specific propagation from local wildland populations to increase the likelihood of preserving the genetic integrity of the species and insure that seed stock is representative of healthy individuals best adapted to localized conditions (Pavlik 1996). Wildland seed collection of rare species in this fashion should also set limits on the extent of seed collection from donor plants and adopt measures to reduce the risk of decimating available wildland seed stocks from established populations (Guerrant 1996).

E. fasciculata propagation should include preliminary tetrazolium staining assessments of seed stock viability. Tetrazolium staining techniques can be employed quickly and inexpensively as a means of estimating germination potential and the amount of seed needed to produce the projected number of seedlings for restoration efforts. In this study, estimates of germination potential using tetrazolium staining were slightly higher (9-10%) than the highest observed germination in Petri dish propagation trials (6-

8%). Two explanations can account for the overestimation of seed viability using this technique. First, seeds were not rejected if they had any indication of pink to red staining along portions of the embryo. This approach increased the speed of assessment but may have reduced the accuracy by not accounting for those seeds that were experiencing the late stages of gradual tissue die-off (Lakon 1949, Grooms 2006). Secondly, bacteria and fungi can result in a surface staining of seeds. All embryos were inspected by surface scraping and sectioning to insure that staining was complete, but it is still plausible that advanced fungal invasions could have yielded a false positive reading (Lakon 1949, Gutormson 2005).

Caution should be used in interpreting germination potential from Petri dish propagation as several dishes experienced fungal colonization that may have reduced germination. Keeley (1987) proposed that some of the fungal invasion that he observed in similar germination trials of woody chaparral shrubs may be attributed to the lack of fungal resistance by empty or inviable seed. Due to the large number of potentially empty *E. fasciculata* seed, special care should be exercised to visually evaluate and discard seeds that appear to have signs of fungal invasion or physical defects. In addition, further propagation research should be conducted to establish if conventional vermiculite sowing techniques yield higher rates of emergence in *E. fasciculata*.

Ericameria fasciculata can successfully be grown in a greenhouse environment with very few required propagation procedures. Seeds should be sown directly onto moistened filter paper in standard Petri dishes and placed into cold stratification for 1 month using conventional refrigeration (5°C-10°C). Following cold stratification, seeds

can be germinated in a greenhouse or laboratory with minimal lighting requirements (*e.g.* conventional fluorescent grow lights). Temperatures can remain at normal room temperature (22°C - 25°C) during incubation. Peak germination can be expected in the first 10-14 days of incubation. Seeds can be successfully transplanted into standard seedling flats containing a pasteurized growing media approximately 1-2 days following radicle emergence (pers. obs. Jon Detka).

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APPENDIX A COLD TREATMENT TRIALS

Three replicate dishes, each containing 100 seeds (2005 stock), were cold stratified for 1 month at 5°C – 10°C in unlit refrigeration. Control stratification (no cold) consisted of storage in unlit dry cool room temperature (~ 15-20°C) for 1 month. All seeds were sown into plastic Petri dishes (150 mm x 25 mm) containing two sheets of 150mm #1 qualitative filter paper pre-moistened to saturation point with 1mM CaCl₂ solution. Following stratification, seeds were incubated with a 13-h photoperiod at 70-100 ($\mu\text{mol s}^{-1} \text{m}^{-2}$) and scored daily for emergence of radical.

Table A-1. Results of cold stratification treatment on percent germination of *E. fasciculata* seed.

Treatment	
No Cold	Cold
4	10
1	6
-	7

APPENDIX B SEED DISINFECTION TRIALS

Three replicate dishes, each containing 100 seeds (2006 stock), were soaked in a disinfection solution containing 10% Clorox and 8 drops of Tween 20 (polyoxyethylene sorbitan monolaurate, Sigma Chemicals Company). Treatment seeds were initially imbibed in 1mM CaCl_2 for 30min, rinsed and soaked in disinfection solution for either 5 minutes or 10 minutes. Control seeds remained in CaCl_2 for 30 minutes and were not exposed to the disinfection treatment. All seeds were rinsed with sterile DI water and placed in plastic Petri dishes (150 mm x 25 mm) containing two sheets of 150mm #1 qualitative filter paper pre-moistened to saturation point with 1mM CaCl_2 solution. All seeds were cold stratified for 1 month at 5°C-10°C refrigeration. Following stratification, all seeds were incubated at lab temperature (22°C - 25°C) under grow lights with a 13-h photoperiod at 70-100 $\mu\text{mol s}^{-1} \text{m}^{-2}$.

Results of one-way ANOVA suggest a significant difference in percentage germination between the disinfection treatments ($F_{2,6}=13.811$, $P = 0.006$). Fisher's LSD post-hoc test further revealed that both the 5 minute soak time ($P = 0.023$) and the 10 minute soak time ($P = 0.002$) disinfection treatments significantly lowered seed germination rates compared to the control.

Table B-1. Results of seed disinfection solution soaking time on the percent germination of *E. fasciculata*.

	Control	Treatment (Soak Time)	
		5 min	10 min
	11	8	3
	9	5	1
	10	2	-
Mean	10	5	1
SD	1.0	3.0	1.5
SE	0.6	1.7	0.9