EFFECTS OF FIRE ON GERMINATION OF *ERICAMERIA FASCICULATA* (ASTERACEAE), A RARE MARITIME CHAPARRAL SHRUB

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Abstract

Knowledge gaps regarding the greenhouse propagation of rare, fire-adapted plant species can impede community level conservation efforts that require fire and active revegetation as management tools. *Ericameria fasciculata* is a rare shrub endemic to the maritime chaparral community of the central California coast and a listed species of concern. Prescribed burning is actively used in maritime chaparral to maintain community composition and conserve several species of concern with known affinities for fire-related conditions. No study has investigated the seed viability and germination requirements for *E. fasciculata*. The goal of this study was to ascertain the (1) greenhouse propagation potential of *E. fasciculata* for planned restoration efforts and (2) to determine if fire-related conditions inhibit or promote *E. fasciculata* germination. Seed dissection and viability testing indicated that a large percentage of seed were empty or inviable. A greenhouse study examined the potential for fire-related germination cues from heating, light, and charate. Heating and charate had negative effects on seed germination. The combination of heating and charate treatments were particularly lethal. Exposure to light or the addition of GA_3 had no influence on germination rates. Results suggest that seed germination of *E. fasciculata* is inhibited by fire and, therefore, this species is dependent on seedling establishment between fire events.

Key Words: Asteraceae, *Ericameria fasciculata*, fire, germination, maritime chaparral.

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 climate change 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 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 and Mistretta 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 (Went et al. 1952; 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, the majority of these studies investigated the role of fire in Southern California inland chaparral dominated by *Adenostoma fasciculatum* Hook. & Arn. (Christensen and Muller 1975a, b; Keeley et al. 1981; Moreno and Oechel 1991; Swank and Oechel 1991; Odion and Davis 2000). There are no clear trends in the degree or trend of seed germination responses among closely related taxa in the maritime chaparral plant community (Davis et al. 1989). Furthermore, most studies have investigated the role of fire on germination of common chaparral shrub species (Keeley and Zedler 1978; Keeley and Keeley 1984; Keeley 1987, 2006; Tyler 1995; Holl et al. 2000).

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 and Mistretta 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 2001)

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 2001).

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 more seed residing near the surface of soils and are more dependent on light signaling than are larger seeded species (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 within families exhibited no consistent trend in light-related germination responses.

Previous studies have demonstrated a wide variety of effects of charred wood on germination of individual species (McPherson and Muller 1969;

Keeley and Pizzorno 1986; Keeley 1987; Thanos and Rundel 1995; Tyler 1996). 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).

Ericameria fasciculata (Eastw.) J. F. Macbr. is a stout (<5 dm tall) shrub in the Asteraceae (Hickman 1993), previously classified as *Haplopappus eastwoodiae* H. M. Hall. *E. fasciculata* is listed as a species of concern (List 1B) by the California Native Plant Society (Skinner and Pavlik 1994), and is proposed for listing as an endangered species on the Federal Endangered Species List (CNDDB 2002). The most distinguishing features of *E. fasciculata* are its aromatic, resinous, cylindrical leaves arranged in fasciculate bundles, its pale yellow radiate flower heads that bloom in July and its achenes that are attached to a dense golden-white pappus (Matthews 1997).

The geographic range of *E. fasciculata* is estimated at less than 4,000 hectares (CNDDB 2002). Scattered individuals occur in coastal dune, central maritime chaparral, and coastal closed cone pine forest from 30–270 meters (MSL) elevation in Monterey Co., 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).

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; Holl et al. 2000). Prior to this study, 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 prescribed burning (Detka 2007). In addition, initial attempts to propagate the species without fire-related stimuli in greenhouses yielded mediocre results (Detka personal observation).

MATERIALS AND METHODS

Seed Collection and Storage

Mature capitula were collected from 29 plants located on the Fort Ord, Parker Flats Reserve,

Monterey, CA (36°38′4.60″N, 121°46′38.78″W) during September 2005 and 2006. A voucher specimen was collected, pressed, and mounted for deposit at the Carl W. Sharsmith Herbarium, San Jose State University, CA. 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 5C–10C.

Seed Viability Testing

Prior to propagation trials, three random samples of 300 seeds each were acquired from 2005 and 2006 seed stocks. Seeds were visually inspected under 10× 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 1 mM $CaCl_2$ solution at lab temperature for 1 hr 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.

We used a 1% 2,3,5-triphenyl-tetrazolium Chloride (TZ) staining technique (Carolina Biological Supply Co., Burlington, NC) to evaluate collected intact seeds for embryo viability from each seed stock for 2005 and 2006 (Lakon 1949). Prior to TZ staining we soaked intact seeds in a 1 mM $CaCl_2$ solution at laboratory temperature for 1 hour to imbibe seeds to soften the seed coat for dissection. We 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.

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 *Ericameria fasciculata*. The fire-related treatments were: (1) pre-sowing heat, (2) powdered charate from *Adenostoma fasciculatum* wood, and (3) light. Initial germination trials had produced poor rates of germination so gibberellic acid (GA_3) treatment was applied.

Seeds were 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 (GA_3) or no gibberellic acid (GA_3).

Seeds were dry heated in the open steel tins using a forced convection oven set at 70°C for 1 hr, 100°C for 5 min, and 120°C for 5 min 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 we removed seeds from the tins and placed them in 50 ml centrifuge tubes (BD Biosciences, MA).

Sixteen of the 32 centrifuge tubes were designated for the GA_3 treatments. GA_3 treated seeds were imbibed with a mixture of 20 ml of 1 mM $CaCl_2$ solution and 20 ml of 100 ppm GA_3 solution. We designated a control treatment for the remaining 16 centrifuge tubes to receive 40 ml of $CaCl_2$ only. Seeds were soaked in solutions at laboratory temperature (22°C–25°C) for 3 hr. 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 premoistened 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 × 25 mm) containing two sheets of 150 mm #1 filter paper (Whatman International Ltd., Maidstone, England). Filter paper was pre-moistened with 1 mM $CaCl_2$ 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, 1 g 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 *A. fasciculatum* stems in a steel burn barrel with a propane torch. Once the stems appeared charred, but not completely reduced to ash, we 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 improved mean percent germination by 6% in *E. fasciculata* (t = 3.530, df = 4, P = 0.024) (Detka 2007). During preliminary trials, we 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 (Detka 2007). Therefore, we did not use 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. We 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 μmol s^{-1} m^{-2}) for a 13-h photoperiod, as recommended in Comstock et al. (1989).

We 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. We 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.

Data Analysis

We used two-way ANOVA to determine if differences were evident between the observed proportions of viable seed in 2005 and 2006 seed stock. We used multi-way ANOVA to compare the proportion of seedlings emerging within and between the different propagation treatments. We 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.

RESULTS

Seed Viability Testing

Results of seed dissection and TZ staining indicated that approximately 10% of *Ericameria fasciculata* seeds were viable. In both the 2005 and 2006 seed stock, empty and dead seeds were more prevalent than viable seed (Fig. 1). 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).

Greenhouse Germination Trials

The addition of GA$_3$ ($F_{1,64}$ = 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 1).

The use of charate had a deleterious effect on germination ($F_{1,64}$ = 48.963, P < 0.001) resulting in mean germination responses less than 1% in all cases (Table 1). The interaction of charate and higher temperature treatments (>70°C) had a particularly lethal effect on *E. fasciculata* seed germination ($F_{3,64}$ = 18.619, P < 0.001) (Table 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 resulting in the near elimination (99%) of germination response. The highest rates of germination occurred in seeds that received no heat treatments (control) and no charate (Table 1). Comparison of mean percent germination of seeds receiving no heating and 70°C heat treatment indicated a mean reduction in germination response of 35% with the addition of the 70°C heat treatment.

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 (>1 cm) may be able to endure exposure from low burn intensities and germinate without exposure to light, and (3) dispersal and subsequent coloniza-
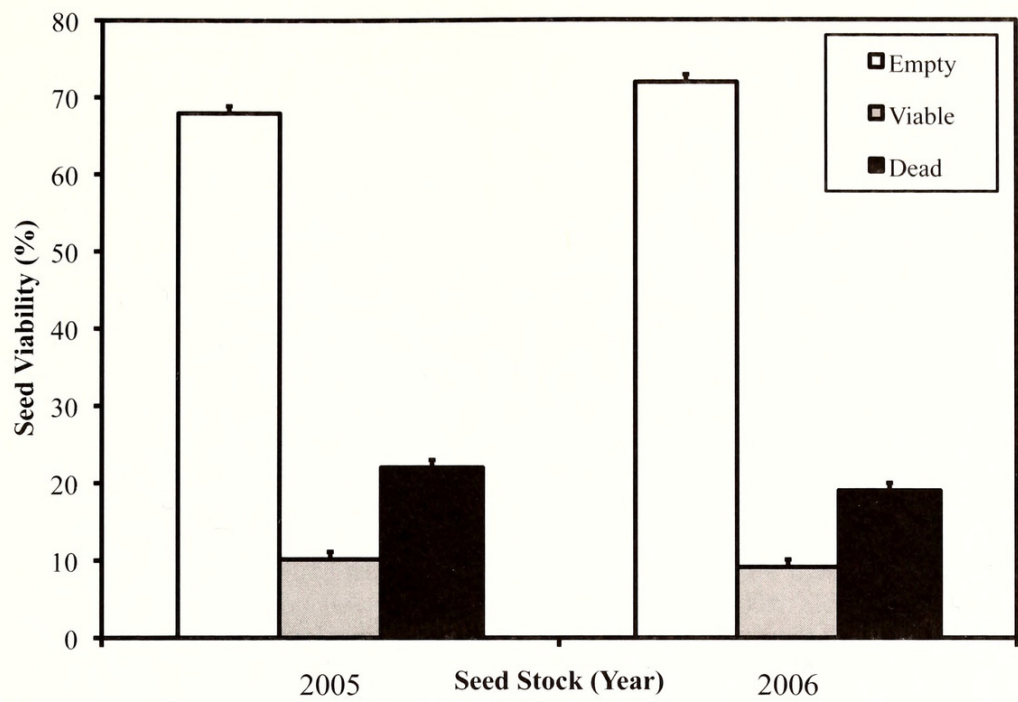
FIG. 1. Mean percent seed viability from 2005 and 2006 seed stocks. Viability percentage is based on results of seed dissection and 2,3,5-triphenyl-tetrazolium chloride (TZ) staining. Mean percentage is based on average of replicate trials (n = 3) for each seed stock. Error bars indicate SEM.

tion 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 2001; Boyd 2007). For example, Keeley (1987) found that the seeds of *Haplopappus squarrosus* (Hook. & Arn.) Greene 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. We 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* were more apt to vigorously crown resprout and flower (Detka 2007), increasing seed availability for dispersal into areas containing little charate and more intact vegetation cover.

Trends in post-burn germination of *Ericameria ericoides* (Less.) Jeps. may also support the observed fire-related germination responses of *E. fasciculata* seed. *Ericameria ericoides* is closely

TABLE 1. MEAN PERCENTAGE GERMINATION OF *E. FASCICULATA* IN RESPONSE TO ORTHOGONALLY GROUPED TREATMENTS OF GA$_3$, 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).

	Light				Dark			
	Control[a]	70°C 1 hr[a]	100°C 5 min[b]	120°C 5 min[b]	Control[a]	70°C 1 hr[a]	100°C 5 min[b]	120°C 5 min[b]
GA$_3$								
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$_3$)								
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)	—	—

related to *E. fasciculata* (Roberts and Urbatsch 2003) and resides in the same habitat range. 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 volatized as stems were reduced entirely to ash.

The extremely low germination rates are apparently due to the complete absence of embryonic tissues in a large proportion of achenes. The lack of embryonic tissue in otherwise intact achenes has been frequently observed in the Asteraceae (Keeley 1987; Padgett et al. 1999; Meyer and Carlson 2001; Alkio and Grimm 2003; Ransom Seed Laboratory 2006). Previous studies have proposed that the high frequency of empty achenes is the result of increased seed abortion due to self-pollination or pollination among closely related plants (Connor and Hall 1997) or the result of variation in resource availability (Sobrevila 1989). Padgett et al. (1999) has suggested that reduced seed set reflects an adaptive mechanism to deter herbivores by hiding viable achenes among empty ones (Connor and Hall 1997). In this study, we did not test specific mechanisms for the observed low seed, but the implications are significant for restoring this rare species.

Active restoration of *E. fasciculata* into areas of suitable habitat may be required to insure the conservation of the species. We 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 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).

Ericameria 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*.

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