

RESEARCH ARTICLE

SEED VIABILITY AND FIRE-RELATED TEMPERATURE TREATMENTS IN SEROTINOUS CALIFORNIA NATIVE *HESPEROCYPARIS* SPECIES

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ABSTRACT

Fire-prone serotinous California *Hesperocyparis* L. (cypress) have been experiencing low seedling recruitment, underscoring our need to better understand these species' responses to fire. We investigated the specific heating conditions required to break cone serotiny and to promote seed dispersal by focusing on five *Hesperocyparis* species of interior California: *Hesperocyparis nevadensis* (Abrams) Bartel, Paiute cypress; *H. bakeri* (Jeps.) Bartel, Baker cypress (also known as Modoc cypress); *H. forbesii* Jeps. Bartel, tecate cypress; *H. macnabiana* (A. Murray bis) Bartel, McNab's cypress; and *H. sargentii* (Jeps.) Bartel (Sargent's cypress). A muffle furnace was used to conduct eight temperature treatments of 250 °C to 700 °C, ranging in duration from 30 seconds to 5 minutes of exposure. The heat-released seeds were tested for viability using a tetrazolium red stain. Logistic regression analysis of seed viability indicated that duration of heating alone was highly significant ($P < 0.005$) for all species, regardless of temperature, with durations of 1 min or less resulting in the greatest viability. *Hesperocyparis forbesii* and *H. nevadensis* were capable of tolerating temperatures as high as 700 °C. Models predicting seed viability reflected interspecific differences, with *H. macnabiana* and *H. sargentii* having higher seed viability than *H. nevadensis* and *H. forbesii*, which had higher seed viability than *H. bakeri*. Lab results coupled with field observations following fire suggest that fire can trigger a massive release of seeds, overwhelming the inherently low viability and allowing for greater potential for adequate seedling establishment.

Keywords: cone heating, cone serotiny, cypress, fire temperatures, *Hesperocyparis*, seed germination

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INTRODUCTION

Woody plants have developed specific and elaborate reproductive and recruitment adaptations in areas where fire is a consistent ecological process. Cone serotiny, the retention of a canopy seed bank in protective structures for more than one year, is often common in such habitats, along with other traits such as resprouting and flammable foliage (Agee 1993, Bond and Keeley 2005). While prevalent among angiosperms in Australia and elsewhere in the southern hemisphere (Lamont *et al.* 1991), serotiny is mainly confined to the conifer genera *Pinus* (pine) and *Hesperocyparis* (cypress) in North America (Zedler 1977, McMaster and Zedler 1981, Barbour 2007). Some evidence implies that the presence of serotiny among other fire-adapted traits indicates a close relationship with stand-replacing fires that occur at intervals long enough for trees to reach reproductive maturity (McMaster and Zedler 1981, Agee 1993, Pausas *et al.* 2004). The primary advantage of cone serotiny is that seeds are released when conditions, such as growing space or light availability, are favorable for regeneration (Lamont *et al.* 1991, Keeley and Zedler 1998). For many serotinous species, heat is required for the cones to open and release seeds (Beaufait 1960, Vogl *et al.* 1977, Bradstock and Myerscough 1981, Zedler 1986, Enright and Lamont 1989, Lamont 1991, Clarke *et al.* 2010), although the degree and mechanism of serotiny varies by species (Vogl 1973, Harvey *et al.* 1980), and sometimes by population (McMaster and Zedler 1981, Mallek 2009). The degree and mechanisms of cone serotiny, and linkages between heating regime and seed release, while well documented in angiosperms of Australia, is largely unknown for many North American conifer species, an obvious disadvantage to their restoration and management.

Among species noted for cone serotiny, but for which little information is known, are the *Hesperocyparis* species of southwest North

America (Vogl *et al.* 1977; Mallek 2009). Californian *Hesperocyparis* have restricted native ranges (McMillan 1956, Vogl *et al.* 1977, Zedler 1977) and are usually dependent on fire for regeneration, as reflected by the dominance of serotiny in the genus (Wolf 1948, Bartel 1993). *Hesperocyparis* species are limited to isolated populations and are often associated with harsh, dry sites subject to extreme temperature fluctuations, and grow on serpentine, volcanic, or granitic substrates at elevations ranging from 300 m to 2100 m (Stuart and Sawyer 2001). *Hesperocyparis* species are facing a variety of possible threats to their perpetuation, and some populations are experiencing fire regimes and fire behavior altered from historic norms, with some being negatively affected by long-term fire exclusion (K.E. Merriam, USDA Forest Service, Quincy, California, personal communication). Other *Hesperocyparis* populations are threatened by extirpation from too frequent stand-replacing fires as a result of anthropogenic ignitions (de Gouveain and Ansary 2006). The many-faceted threats faced by *Hesperocyparis* populations require a more thorough understanding of the conditions leading to successful seedling recruitment following stand-replacing fires.

Of the ten species native to California, this study examined the five *Hesperocyparis* species most susceptible to fire due to their location and habitat: *Hesperocyparis nevadensis* (Paiute cypress), *H. bakeri* (Baker cypress), *H. forbesii* (tecate cypress), *H. macnabiana* (McNab's cypress), and *H. sargentii* (Sargent's cypress). After decades of fire exclusion, some interior California *Hesperocyparis* species face the paradox of wildfire threatening their perpetuation and, at the same time, fire being necessary to open serotinous cone scales and to prepare receptive seed beds. When high intensity fires occur too frequently, fire-dependent species become susceptible to an "immaturity risk," by which young trees are killed before reaching reproductive age (Zedler 1977, Keeley and Fotheringham 2000), which is esti-

mated to be between 10 yr and 15 yr in *Hesperocyparis* (Bartel 1993). *Hesperocyparis forbesii* populations have been shown to require fire return intervals longer than 40 years in order to develop an adequate canopy seed bank, and are vulnerable to extirpation from fire return intervals that are substantially less than 40 years (Zedler 1995, de Gouvenain and Ansary 2006).

The most northern *Hesperocyparis* species, *H. bakeri* and *H. macnabiana*, face a different challenge of altered stand conditions, possibly due to fire exclusion. Increases in shade-tolerant species and changes in stand density have put some populations of *H. bakeri* at risk of being out-competed (Keeler-Wolf 2004a). *Hesperocyparis bakeri* has been experiencing increased interspecific competition and greater stand density in areas that have experienced prolonged fire exclusion. Evidence of poor seedling regeneration and competition from shade-tolerant *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir) were observed on the Plumas and Lassen national forests by both Wolf (1948) and Stone (1965), and later by Keeler-Wolf (2004a). A long history of fire exclusion has left some *Hesperocyparis* populations facing a risk of cone senescence before fire can prepare the seedbed, resulting in little or no regeneration when fires do occur (Keeley and Fotheringham 2000). As prescribed fire may be an essential tool in restoring fire regimes in these historically fire-dependent ecosystems, determining the temperature regimes required to break cone serotiny and to allow subsequent seed germination for *Hesperocyparis* species is necessary.

Experiments with *Pinus* species (Saracino et al. 1997, Schwilk and Ackerly 2001) and with *Hesperocyparis* species (Ne'eman et al. 1999, de Gouvenain and Ansary 2006) have shown that traits such as highly flammable foliage, dead branch retention, and cone serotiny are strongly correlated with high-severity fire regimes. But little information exists on the specific environmental conditions necessary

for cone opening and regeneration (Vogl et al. 1977, Mallek 2009). Very high temperatures have been shown to reduce the germination ability of *Pinus* seeds (Torres et al. 2006, Moya et al. 2008), but are required in strongly serotinous species to open cones and release seeds (Vogl 1973, Habrouk et al. 1999, Reyes and Casal 2002). The primary focus of this study was to determine the specific heating conditions required to break cone serotiny of inland California *Hesperocyparis* species and to promote seed dispersal, while minimizing seed injury. In particular, specific study objectives were to determine: 1) the minimum heat load (i.e., temperature and duration) required for *Hesperocyparis* cones to break serotiny; 2) the effect of cone heat load on seed viability; and 3) whether individual species respond differently to heat loads. Study results provide a better understanding of how *Hesperocyparis* regeneration is affected by fire, allowing wildland fire managers to better manage and restore extant *Hesperocyparis* stands.

METHODS

Field Data Collection

We sampled five interior California *Hesperocyparis* species over a three month period from June to August, 2008. We located the study sites from the northern to southern end of California (Figure 1). Cones were collected from 18 trees at each of five sites, for a total of 90 trees sampled. A branch with at least ten cones was cut from each tree at 2 m above the ground. To avoid moisture loss, live branches were collected rather than individual cones. Cut branches were kept moist with wet paper towels in plastic bags and stored in a cooler containing ice for a maximum of 72 hours, in transit to the lab. Samples were refrigerated at 3°C to 5°C until the heat treatments commenced, usually within 48 hours. Cones from the 18 trees (for each species) were systematically mixed together so that each treatment

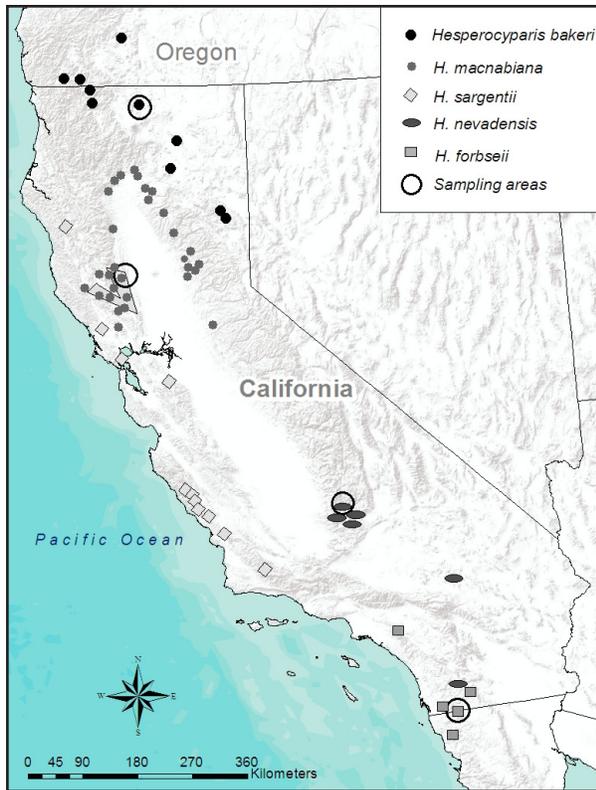


Figure 1. Range of all five native California *Hesperocyparis* used in the study. Circles indicate the sampling locations; *H. macnabiana* and *H. sargentii* were collected at the same site in Lake County, California, USA.

cell had cones from different trees. Cones selected for heat treatments were located near the ends of branches, avoiding those on the tips of branches that were brown, indicating immaturity (first- to second-year cones). Cones that were gray in color with a peduncle (indicating the cones were at least 3 yr to 5 yr old) on each branch were used for the treatments (Figure 2). Cones closer to the tree than the outer 0.5 m to 0.8 m of the branches were avoided as these were usually older than 5 years and invaded by burrowing insects, leading to premature desiccation.

Additionally, we collected seeds from the *H. macnabiana* collection site in Lake County, California, following the 2008 Walker Fire that occurred in the same population three weeks after live cone collection. The goal was to see



Figure 2. *Hesperocyparis nevadensis* (Paiute cypress) branch showing the typical sequence of cones, 3 years and older (note the gray scale color) that was collected from each tree. Sequoia National Forest, Tulare County, California, USA.

if the seed viability from the post-fire plots matched the seed viability measured for any specific heat treatment. The seeds were collected from five ground plots and five canopy plots in August, two months after the fire. Plots were 0.5 m × 0.5 m and at least 150 seeds were collected from each plot. The seeds from canopy plots were obtained by gently tapping branches with open cones over 0.5 m × 0.5 m trays. Seed density was estimated at 600 m⁻² to 800 m⁻² from the five ground plots. All collected seeds were transported to the laboratory in closed containers and tested for seed viability.

Heat Treatments

A pilot study conducted with *H. macnabiana* found, through a combination of branch burning and oven treatments, that cones began to open at cone surface temperatures $\geq 250^{\circ}\text{C}$. The branches were burned under laboratory conditions to measure temperature duration, using insulated iron-constantan (Type K, 2 mm diameter) thermocouples wrapped around the branch and set next to the cones, and connected to a CR1000 datalogger (Campbell Scientific, Logan, Utah, USA). The branches were secured to a metal rod a few centimeters above

the source of flaming heat (a fuelbed of the same species' dry litter and foliage) on a laboratory burn platform beneath a 3 m × 3 m exhaust hood. This technique was later repeated with *H. sargentii*, *H. nevadensis*, and *H. forbesii*, but not with *H. bakeri*.

Based on the results of the pilot study, heat treatments of 250, 300, 350, 400, 500, 600, 650, and 700 °C were used. The time exposure treatments consisted of 0.5, 1, 2, 3, 4, and 5 minutes. Not all combinations of temperature and time were tested due to the pattern of shorter durations of heat exposure at increased temperatures found in a pilot study conducted before the actual experiment, so there was a total of 36 time × temperature treatments on 900 cones. At the time of treatment, cones were cut from the branches and then randomly selected, using five cones per treatment combination. A control for each species (no heat treatment) was maintained at room temperature on the same starting day as the other treatments and monitored the same length of time as the treated cones (35 days). A muffle furnace (Thermolyne Sybron Corporation, Dubuque, Iowa, USA; Model No. F-A1730) with a temperature range of 0 °C to 1000 °C was used for all of the heat treatments. For each heat treatment, the cones were set in a crucible and placed in the muffle furnace. The heating of the crucible was accounted for by measuring the surface temperature while in the muffle furnace with a thermocouple and adjusting the set temperature.

Seed Viability Tests

The amount of scale opening (mm) following heat treatment each day was measured with a set of calipers, and the number of seeds released was recorded for a minimum of 35 days. A cone was considered open when the scales had opened at least 4 mm because only then could the seeds fit through the opening. Cypress cone scales tend to separate at the same time and in a uniform pattern. All seeds re-

leased from cones were tested 60 days later for germination. Lots of 25 seeds for each treatment of each species plus the control were prechilled at 3 °C to 5 °C for 21 days on moist filter paper in Petri dishes, and then placed in a germination chamber (Stults Scientific Engineering Corporation, Springfield, Illinois, USA). The seeds were subjected to an alternating temperature regime of 16 hours at 20 °C, and 8 hours at 30 °C each day for at least 30 days, following the guidelines for *Hesperocyparis* species set forth by the Association of Official Seed Analysts (2008). Germinated seeds were counted each day to quantify total percent germination for each treatment and species.

After conducting two germination trials (50 total seeds tested per treatment), all *H. macnabiana* and *H. sargentii* seeds failed to germinate. To get a more complete picture of seed viability in these and the other *Hesperocyparis* species, live staining was applied to new, untested seeds following the conclusion of germination tests. The seeds were tested with a 1% tetrazolium red solution at 30 °C to 32 °C, for 12 hr to 18 hr, following the tetrazolium testing procedures outlined by the Association of Official Seed Analysts (2001). The stained seeds were cut and analyzed visually for viability based on the staining extent and the condition of the embryo (Figure 3), with only a completely stained embryo considered viable (Association of Official Seed Analysts 2001).

Statistical Analysis

Logistic regression (Hosmer and Lemeshow 2000) was used to assess the effect of the heating duration and temperature on the probability of seed viability following heat treatment, and to determine if these differed between the five species (after Escudero *et al.* 1999; Nuñez *et al.* 2003). The temperature and time of exposure of treatments were selected as the predictor variables (main effects terms). The entire model, which included tem-

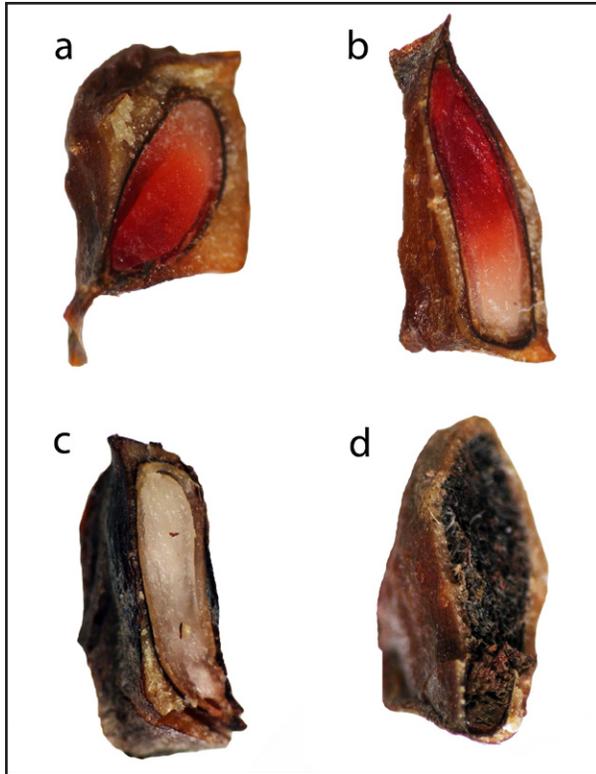


Figure 3. *Hesperocyparis sargentii* (Sargent's cypress) seeds cut longitudinally, showing the four categories of observation: (a) full stain of embryo; (b) incomplete stain of embryo; (c) unstained embryo; and (d) embryo absent. For all species studied, only (a) was considered viable.

perature, time, the interaction of the two, and independent terms, was tested along with all reduced (i.e., additive) models. A species effect term (representing the seed viability data of both species combined to test for significant differences) was included for all models that tested for differences between species.

Logistic relationships are expressed as the following model:

$$P = \frac{1}{1 + e^{-z}} \quad (1)$$

where P is the probability of seed viability and z is a linear function containing the predictor variables included in the model ($z = b_0 + b_1 \times \text{temperature} + b_2 \times \text{time} + b_3 \times \text{temperature} \times$

time). The coefficients of the z function were estimated using the maximum likelihood function. The models were selected based on the significance of the variable (using the P -value of the coefficients) and the change in deviance, which is the value of the change in the -2 log likelihood between the model with and without predictor variables (Hosmer and Lemeshow 2000). A deviance value is meaningless unless compared to those of models with predictor variables added in one at a time, and a negative change in the value is considered a better fit. Testing of assumptions and residual diagnostics of the model were conducted using procedures described by Hosmer and Lemeshow (2000). This included assessing whether the variables were dichotomous, the outcomes were statistically independent, the model was correctly specified, and that the categories of viable or not viable were mutually exclusive and collectively exhaustive. Model fit was assessed by the calculation of percent correctly classified predicted values from the models, and plotting the residuals of the deviance values. All statistical analyses were carried out in R, an open source statistical program (R Development Core Team 2009).

RESULTS

All but one of the *Hesperocyparis* species had similar heat thresholds for breaking cone serotinity. Four of the *Hesperocyparis* (*H. nevadensis*, *H. bakeri*, *H. macnabiana*, *H. sargentii*) opened when heated at 500 °C for at least 2 minutes, resulting in substantial release of seed (>50% of total seed release) (Figures 4 and 5) compared to the control (Table 1). *Hesperocyparis forbesii* also had a threshold at 500 °C, but only for durations of four minutes and longer (Figure 5b). Even at 600 °C to 700 °C, the proportion of *H. forbesii* seeds released was low relative to the other species that appeared to be nearing complete release of seeds eight days after treatment, for a greater range of treatment combinations. For example, the

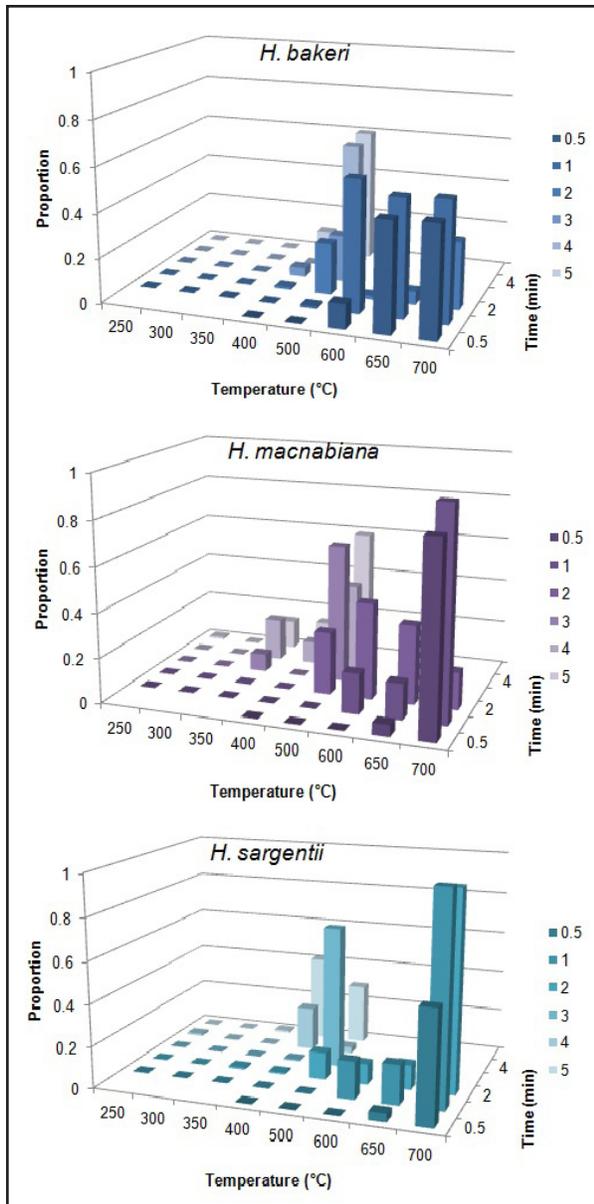


Figure 4. The cumulative proportion (compared to the total released at the end of the experiment period) of seeds released at four days following heat treatment for *Hesperocyparis bakeri* (Baker cypress), *H. macnabiana* (McNab's cypress), and *H. sargentii* (Sargent's cypress) respectively, showing all temperature and time combination treatments.

cones of *H. sargentii* and *H. macnabiana* exposed to 700°C released nearly 100% of their seeds after four days (Figure 4). *Hesperocyparis bakeri*, the most northerly species, released more of its seeds compared to *H. forbesii* (the most southerly species in California)

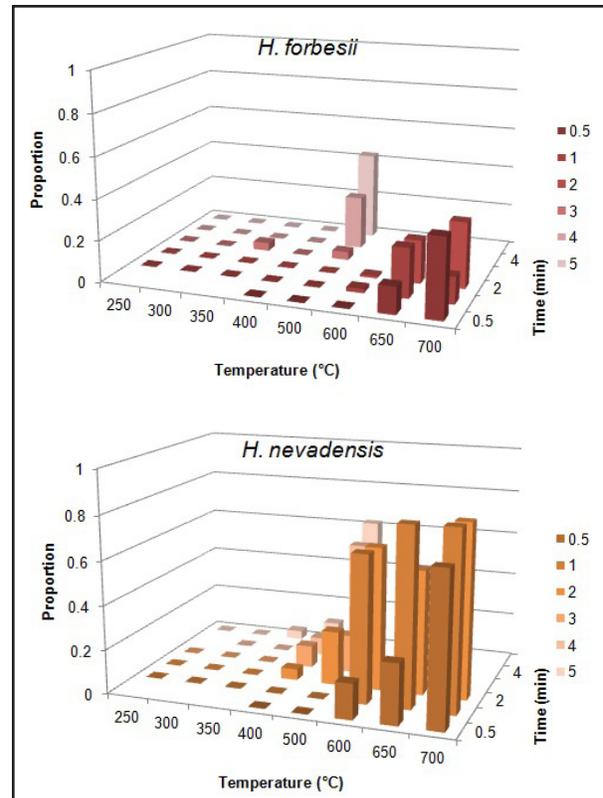


Figure 5. The cumulative proportion (compared to the total released at the end of the experiment period) of seeds released at four days following heat treatment for *Hesperocyparis nevadensis* (Paiute cypress) and *H. forbesii* (tecate cypress) respectively, showing all temperature and time combination treatments.

four days following heat exposure (Figures 4 and 5). Heat treatments increased the chance and rate of cones opening and seeds released compared to the control. Across species, untreated cones did not begin to open until at least 21 days. Even though the control for *H. bakeri* had the shortest time (21 days) before the cone scales opened at least 1 mm, it was approximately five more days before seeds were released (when cones opened at least 4 mm). In contrast, all *H. forbesii* cones and most of *H. nevadensis* failed to open after 40 days (the end of the experiment period).

Germination results revealed three important overall trends related to duration and temperature, and timing of germination: (1) seeds exposed to higher temperatures (400°C and

Table 1. Comparison of time (days) until control cones opened, number of cones open, and seed release data for all five species studied.

Cypress species	Time for cones to open (days)	Cones open, out of 5 (n)	Total seeds released once cones opened (n)
<i>Hesperocyparis bakeri</i>	21	3	0
<i>Hesperocyparis macnabiana</i>	35	1	3
<i>Hesperocyparis sargentii</i>	35	3	15
<i>Hesperocyparis arizonica</i> ssp. <i>nevadensis</i>	>40	1	0
<i>Hesperocyparis forbesii</i>	>40	0	0

above) had higher germination rates for shorter exposure periods, and no germination in seeds exposed to heat for more than two minutes; (2) there was a higher percentage of seed germination for all species at the lower temperatures than at the higher temperatures for short exposure times; and (3) the timing of germination of seeds from the northern species was different than those of the southern species. For *Hesperocyparis forbesii* and *H. nevadensis* (the southern-most species), germination began to occur on day 7, while for *H. sargentii* and *H. bakeri* (more northern species), germination began later, on day 14. Within the first 30 days of the germination trial, the *H. forbesii* control had the highest germination capacity of 36%, compared to only 8% for the *H. bakeri* control, and no seeds germinated from the other species. *Hesperocyparis sargentii* had a slow germination response, with a few seeds germinating after 30 days of treatment. Because of very low germination rates for *H. macnabiana* and *H. sargentii*, the germination trials were complemented with a seed viability trial using tetrazolium red staining.

Hesperocyparis macnabiana seeds collected within the burned area of the Walker Fire had an average viability of 16.8% for the ground plots and 12.8% for the canopy plots, with viability ranges of 12% to 20% and 0% to 28%, respectively. Seed viability of the control (no heat treatment) for *H. macnabiana* was 16%, 20% for *H. bakeri*, and 8% for *H. sargentii*. The control for *H. nevadensis* had a seed viability of 12%, and 24% for *H. forbesii*.

The results obtained with the logistic regression models show that all species' probability of seed viability is negatively affected by increased exposure to heat. *Hesperocyparis macnabiana* had the greatest seed viability probability (20%) for low temperature exposures (up to 300°C), followed by *H. forbesii* (19%). For all species, heating time had a highly significant ($P < 0.005$) effect on the probability of seed viability for all species tested (Table 2). For exposure times longer than two minutes, the probability of seed viability was very low (0% to 3%) for *H. nevadensis*, *H. bakeri*, and *H. forbesii*. *Hesperocyparis macnabiana* and *H. sargentii* had predicted probabilities of 3% and 2%, respectively, but still had some predicted seed viability at five minutes of exposure.

The effect of temperature on probability of seed viability was significant for all species except for *H. nevadensis* (Table 2). Predicted *H. macnabiana* seed viability decreased from a maximum of 12% to 4% between 250°C and 400°C, respectively. *Hesperocyparis forbesii*, *H. nevadensis*, and *H. sargentii* all followed a similar declining pattern in probability of seed viability as temperature increased. *Hesperocyparis bakeri* was the most sensitive to temperature exposure and displayed a much lower probability of seed viability in general, with a maximum predicted viability of 5% at 0.5 min and then decreasing to 1% at 2 min. The model with the interaction of time and temperature was only significant for *H. forbesii* and *H. nevadensis* (Table 2).

Table 2. Logistic models fitted for all five *Hesperocyparis* species in the study, along with measures of deviance of the model terms and correct classification (%) of predicted model outputs. The best-fitting models are designated by the associated deviance, in bold. T = Temperature, t = time, model terms in bold are significant using a probability level of 0.05, model terms in italics indicate not significant, deviance values in bold indicate selected models, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant ($P > 0.05$). Where P -values of model terms have the same level of significance, only one sign is used (i.e., *** for both T and t), for simplicity.

Species	Model	Deviance (constant)	Deviance (model)	Correct classification (%)	P -values	Coefficients
<i>H. bakeri</i>	<i>T</i>		35.996	98.7	ns	-0.003
	t	38.116	22.781	98.7	**	-1.241
	T, t		11.175	98.7	**	-0.008, -1.923
	<i>T, t, T*t</i>		8.862	98.7	ns	
<i>H. macnabiana</i>	T		52.244	95.7	***	-0.008
	t	78.544	71.457	95.7	*	-0.308
	T, t		27.402	95.7	***	-0.01, -0.656
	T, t, T*t		25.654	95.7	*, ns	
<i>H. sargentii</i>	T		47.303	96.6	**	-0.004
	t	55.462	45.798	96.6	**	-0.421
	T, t		25.418	96.6	***	-0.007, -0.710
	T, t, T*t		24.998	96.6	*, ns	
<i>H. nevadensis</i>	<i>T</i>		45.754	97.6	ns	-0.002
	t	47.133	24.163	97.6	***	-1.019
	T, t		11.885	97.6	***	-0.006, -1.409
	T, t, T*t		8.027	97.6	ns	-0.0002, 0.887, -0.007
<i>H. forbesii</i>	T		70.197	96.5	**	-0.004
	t	78.375	58.209	96.5	***	-0.695
	T, t		32.213	96.5	***	-0.007, -1.076
	T, t, T*t		24.089	96.5	ns, *	-0.006, 1.469, -0.008

The results show three important differences amongst the species comparisons. First, there was no significant difference between *H. macnabiana* and *H. sargentii* seed viability responses to heat exposure (Table 3). Second, the situation was the same for *H. forbesii* and *H. nevadensis*. *Hesperocyparis bakeri* differed from the other species (Table 3), so the original model (T, t) was used (Table 2). Third, the predicted probability of viability of *H. bakeri* was low compared to the other four species across all durations and temperatures of exposure (Figure 6).

All of the models predicted probabilities of seed viability less than 30% for all species, as can be seen in Figure 6. The results of the classification tables, in which the percent cor-

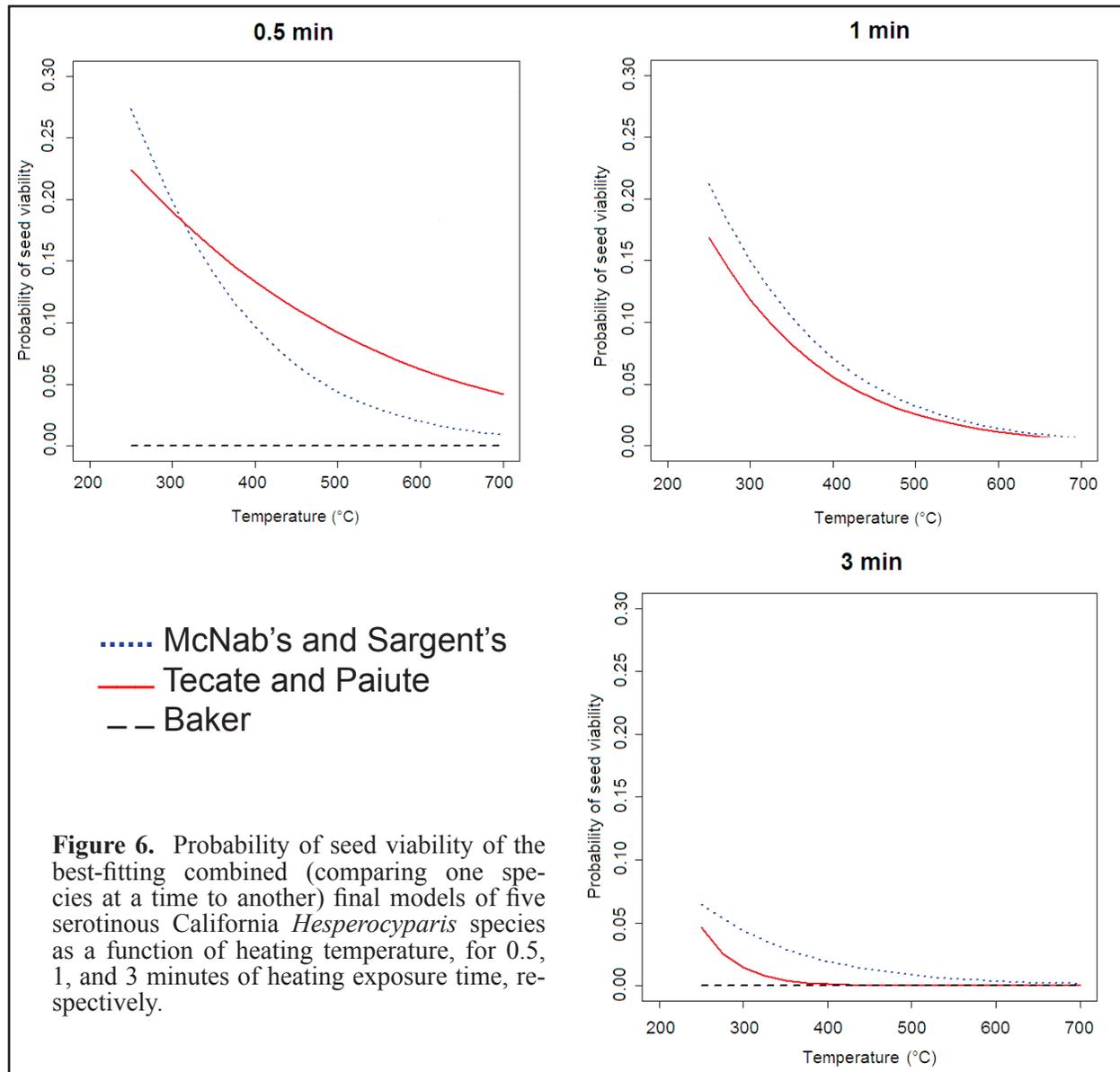
rectly classified probabilities of the predicted model was compared to the percent of the observations, were all greater than 95% (Tables 2 and 3). The coefficients of the selected models are also provided in Tables 2 and 3.

DISCUSSION

Our study found that, across *Hesperocyparis* species, seed germination ability is negatively impacted by prolonged exposure to high temperatures. There appears to be a trade-off between temperature and exposure time for stimulating seed release while simultaneously maintaining viable seed. High proportions of seed were more frequently released at higher temperatures (650 °C to 700 °C) and at greater

Table 3. Logistic models fitted for the species interactions of the five *Hesperocyparis* species in the study, along with measures of deviance of the model terms and correct classification (%) of predicted model outputs. The best-fitting models are designated by the associated deviance in bold. T = Temperature, t = time, S = species term, model terms in bold are significant using a probability level of 0.05, and model terms in italics indicate not significant, deviance values in bold indicate selected model, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ns = not significant ($P > 0.05$). Where P -values of model terms have the same level of significance, only one sign is used (i.e., *** for both T and t), for simplicity.

Species	Model	Deviance (constant)	Deviance (model)	Correct classification (%)	P-values	Coefficients
<i>H. bakeri</i> and <i>H. macnabiana</i>	T		106.500	97.2	***	
	t		117.910	97.2	***	
	T, t		63.505	97.2	***	
	T, t, T*t		59.249	97.2	*, ns	
	T, t, S, T*t	134.37	42.979	97.2	*, ns, ***, ns	
	<i>T, t, S, T*t, T*S</i>		40.774	97.2	ns, *, ns	
	T, t, S, T*t, t*S		35.832	97.2	*, ns, *	-0.006, -0.878, -0.306, -0.003, 1.249
<i>T, t, S, T*t, t*S, T*S</i>		35.743	97.2	ns		
<i>H. sargentii</i> and <i>H. macnabiana</i>	T		102.700	96.0	***	
	t		118.560	96.0	***	
	T, t		56.059	96.0	***	-0.008, -0.676
	T, t, T*t	134.96	53.878	96.0	** , ns	
	T, t, S, T*t		52.868	96.0	** , ns	
	T, t, S, T*t, T*S		50.895	96.0	** , ns	
	T, t, S, T*t, t*S		52.459	96.0	** , ns	
T, t, S, T*t, t*S, T*S		50.885	96.0	** , ns		
<i>H. nevadensis</i> and <i>H. forbesii</i>	T		118.550	97.0	**	
	t		84.933	97.0	***	
	T, t		47.541	97.0	***	
	<i>T, t, T*t</i>	127.09	35.059	97.0	ns, **	-0.0002, 1.287, -0.008
	<i>T, t, S, T*t</i>		33.379	97.0	ns, **	
	<i>T, t, S, T*t, T*S</i>		32.460	97.0	ns, **, ns	
	<i>T, t, S, T*t, t*S</i>		32.454	97.0	ns, **, ns	
<i>T, t, S, T*t, t*S, T*S</i>		32.175	97.0	ns, **, ns		
<i>H. bakeri</i> and <i>H. forbesii</i>	T		115.230	97.5	**	
	t		91.495	97.5	***	
	T, t		54.864	97.5	***	
	<i>T, t, T*t</i>	125.389	44.123	97.5	ns, **	
	<i>T, t, S, T*t</i>		34.725	97.5	ns, **	-0.0005, 1.514, 1.024, -0.009
	<i>T, t, S, T*t, T*S</i>		34.621	97.5	ns, **, ns	
	<i>T, t, S, T*t, t*S</i>		33.223	97.5	ns, **, ns	
<i>T, t, S, T*t, t*S, T*S</i>		33.054	97.5	ns, **, ns		



exposure times, yet for nearly all species, no seed viability was found at these temperatures. While fire intensities (including temperature) vary tremendously within fires (Alexander 1982), these *Hesperocyparis* species will open their cones and release viable seeds under most of the temperatures tested, although seeds will not be viable under the most extreme temperatures. Similar results in studies found strongly serotinous *Banksia* shrub species released substantial seed amounts with high heat exposure (Bradstock and Myerscough 1981, Lamont and Barker 1988), and seed viability decreased

with high temperature exposure in *Pinus banksiana* Lamb. (jack pine) (Beaufait 1960).

Hesperocyparis species may be at a competitive disadvantage in re-colonizing a site following severe crown fires with long residence times, as has been observed in stands of *H. bakeri* (K.E. Merriam, personal communication). *Hesperocyparis* species seedlings are usually less competitive than other, more shade-tolerant species, so optimal *Hesperocyparis* seedling establishment occurs in the first year following fire (K.E. Merriam, personal communication). Serotinous *Banksia* shrubs

in Australian heathlands also have the best seedling establishment in the first year following fire (Enright and Lamont 1989). As angiosperms, the *Banksia* shrubs have adapted to a similar dry climate in shrub lands and rely on serotiny and resprouting for stand re-establishment (Zammit and Westoby 1987, Lamont 1988, Enright and Lamont 1989, Whelan et al. 1998). The coniferous *Hesperocyparis* species are obligate seeders and therefore must rely exclusively on serotiny in fire-prone ecosystems. *Hesperocyparis* species' successful ability to exploit a narrow ecological niche with little competition may also be their greatest weakness in terms of large, landscape-level threats such as altered fire frequencies, increased land development, and changing vegetation composition (K.E. Merriam, personal communication).

Cones were selected from trees in isolated populations, and their patterns of serotiny may differ from other sites, but these broad patterns found suggest that there are differences between the northern and southern species' cone responses to heat exposure, and the ability of seeds to germinate. *Hesperocyparis forbesii*

cones were more resistant to breaking serotiny, as has been found in previous studies (Garcilán 2010), but were more likely to germinate within one week of placement in the germinators. *Hesperocyparis bakeri* cone serotiny was easier to break at lower temperatures, but fewer seeds germinated within two weeks. *Hesperocyparis bakeri* was more heat sensitive than the other four *Hesperocyparis* species, with more seeds released sooner and with lower seed viability at higher temperatures or longer exposure to heat. *Hesperocyparis forbesii* was the most heat tolerant species, requiring a much longer time to open and release seeds, and its seed viability was less affected by high temperatures (Figure 6). These trends may reflect different geographic locations, climates (e.g., temperature regime and onset of precipitation), and habitats where these species occur (Table 4). However, since multiple cones were collected from individual trees, there is a possibility that samples may have been pseudo-replicates. Although not previously studied in *Hesperocyparis* species, variations in serotiny due to the influences of climate and fire regime have been found in studies of serotinous *Bank-*

Table 4. Fire regime requirements for each of the five species studied, by location, north to south. Fire regimes are taken from published literature, heat tolerance is based on original findings of seed viability.

Species	Climate ¹	Vegetation	Historic fire regime	Current fire regime	Heat tolerance	Source
<i>H. bakeri</i>	30 °C, -4 °C, 973 mm	mixed conifer	frequent, mixed severity	infrequent, high severity	low	Wolf (1948), Keeler-Wolf (2004a)
<i>H. macnabiana</i>	33 °C, 2 °C, 988 mm	inner coast chaparral	mixed, frequent high severity	infrequent, high severity	medium	Mallek (2009)
<i>H. sargentii</i>	33 °C, 2 °C, 988 mm	inner coast chaparral	infrequent, high severity	infrequent, high severity	medium	Ne'eman et al. (1999)
<i>H. nevadensis</i>	36 °C, 0 °C, 336 mm	foothill woodland	unknown frequency, high severity	unknown frequency, high severity	high	van Wagtenonk and Fites-Kaufman (2006)
<i>H. forbesii</i>	36 °C, 6 °C, 306 mm	southern California chaparral	infrequent, high severity	frequent, high severity	high	de Gouvenain and Ansary (2006)

¹The first value represents the average summer high temperature, the second value the average winter low, and the third value the average annual precipitation. All climate data was obtained from the nearest US Department of Commerce National Oceanic and Atmospheric Administration weather station for each population sampling site.

sia species in Australia (Cowling and Lamont 1985, Bellairs and Bell 1990).

A very low germination rate under laboratory conditions has been consistently found for both *H. macnabiana* and *H. sargentii* across different studies (McMillan 1956, Ceccherini et al. 1998) and was confirmed by our study. Our observations in burned *H. macnabiana* stands and unburned *H. sargentii* stands suggest that natural germination does occur in high numbers. Field observations made one year following the Walker Fire revealed 12 seedlings m⁻² to 20 seedlings m⁻² in the same location of the seed release measurements. Other locations of *H. macnabiana* stands burned within the last ten years reveal heavy local regeneration of this species. *Hesperocyparis macnabiana* released between 600 seeds m⁻² to 800 seeds m⁻² after the Walker Fire, suggesting that a mass seed release probably makes up for the low germination ability. The lack of seed germination response in *H. macnabiana* and *H. sargentii* also suggests that they may have different germination requirements from the other *Hesperocyparis* species studied, such as diurnal photoperiod, moisture exposure, or temperature related to their individual climate regime.

Across all *Hesperocyparis* species in this study, seed viability was negatively affected by greater duration of heating, and to a lesser extent, higher temperatures. During wildland fires, cones are heated for short periods at high temperatures and the seeds are protected from heat exposure by the insulation of the cone, but that protection has been found to lose effectiveness for longer heating durations (Habrouk et al. 1999, Moya et al. 2008) and with decreased cone scale thickness (Linhart 1978). Overall, the requirement of some heat to open cones and release seeds shown for all the species studied here strongly indicates that these species have adapted to fire as a regular occurrence for producing the right conditions for regeneration (Enright and Lamont 1989, Escudero et al. 1999, Habrouk et al. 1999, Goubitz

et al. 2003, Nuñez et al. 2003). The fact that there appear to be differential tolerances to heating among the species, and that not all respond the same to various “fire conditions,” suggests that a single fire management approach to all *Hesperocyparis* species would be detrimental to their perpetuation. As was observed in burned *H. bakeri* and *H. macnabiana* stands, seedling regeneration can occur from lightly scorched to completely consumed canopies, regardless of branch or tree death. This implies that not all species need a stand-replacing or even moderate severity surface fire to successfully reproduce. The main limiting factors for regeneration (once the cones are open) appear to be light and moisture. However, the cones must be open first and, as has been shown by our results, some species will open their cones by mechanical removal or desiccation (e.g., removal of branch, burrowing insects, advanced age), but some species like *H. forbesii* fail to ever open in the absence of substantial heat. This implies that creating canopy gaps around the cypress trees in the absence of fire may only be useful for certain species, such as *H. bakeri* in which interspecies competition is a significant factor. Factors that must be considered for all species are level of cone serotiny, associated vegetation and fuel, timing of cone maturation, location and extent of populations, local fire history, and historical versus current fire regime.

Previous studies of related serotinous species have investigated variation in the mechanisms of cone serotiny and their ecological and management implications. In previous studies of other cypress species, the heat from a fire is only one of many possible mechanisms for cones to open and spread seed (Lev-Yadun 1995), and although not explicitly measured in our study, some desiccation of older cones was observed and may warrant further study. Unlike the results of our study, Linhart (1978) found a decrease in heat tolerance of seeds of serotinous *Pinus* species in southern California (versus northern species), and cited seed pre-

dation to be a possible driver (along with fire frequency and intensity) of variation in cone serotiny. Similar to the *Hesperocyparis* species we studied, a lot of variation in cone serotiny occurs in *Pinus contorta* Douglas ex Loudon and its varieties, and appears to be somewhat related to the elevation and climate of occurrence, historic fire frequency and intensity, type of disturbance (stand-replacing fire versus not) and genetic variation (Lotan 1976, Perry and Lotan 1979, Muir and Lotan 1985, Schoennagel *et al.* 2003, Pierce and Taylor 2011).

Although a few studies have examined *Hesperocyparis* species, their life history traits, and regeneration responses to fire (Ne'eman *et al.* 1999, de Gouvenain and Ansary 2006, Mallek 2009), and others have made observations of botanical characteristics (Jepson 1923; Wolf 1948; Stone 1965; Keeler-Wolf 2004a, 2004b), none have studied the role of heat tolerance directly as was done in this study. As has been shown in previous studies with pines

(Despain *et al.* 1996, Escudero *et al.* 1999, Habrouk *et al.* 1999, Reyes and Casal 2002, Nuñez *et al.* 2003, Torres *et al.* 2006), *Hesperocyparis* species in this study responded negatively to high temperatures at longer durations and exhibited similar patterns in seed release, but what is of greater ecological interest and value to management are the differences in individual species' responses. This is the first study to compare *Hesperocyparis* species responses to different heat exposures, indicating that further research is needed in examining the role of a species' regeneration response to contrasting fire behavior, in the context of other competing species. As climate change, increased human activities, and land use practices continue to cumulatively affect fire regimes in landscapes where *Hesperocyparis* species occur (Westerling *et al.* 2006, Westerling and Bryant 2008), the need for greater knowledge of these fragmented species mounts.

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