



# High resistance to managed and natural forest fire in a rare rock-outcrop specialist herb (*Boechea constancei*, Brassicaceae)



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## ABSTRACT

Fire may increase the abundance of many understory plants in forested ecosystems, such as gap-dependent herbs that respond quickly to increased light availability. Fire may or may not benefit some rarer understory herbs, such as stress-tolerant species specializing on rock outcrops. The latter species may benefit less from post-fire increases in light, and their slow-growing life histories might impair their abilities to survive, recover, and/or increase their rates of growth and reproduction following fires.

We examined the impacts of prescribed and natural fire on *Boechea constancei* (Brassicaceae), a rare herb growing on and around outcrops of infertile serpentine rock in upper montane conifer forests of the northern Sierra Nevada, California. We analyzed demographic transition rates of marked plants in response to experimental burns in winter 2012 and a subsequent lightning-caused fire in summer 2012. We measured leaf litter as a covariate, expecting that fire effects on *B. constancei* demography might be stronger in sites with more litter.

Prescribed fire marginally decreased the fecundity of large individuals, but elasticity analyses found these rates to have no effect on estimated population growth, while the naturally occurring fire had no significant effects on demography. Leaf litter was not significant as a covariate in any analyses. Estimated population growth rates were thus unaffected by either prescribed or natural fire.

Our results are consistent with the hypothesis that rock outcrop specialists are relatively insensitive to disturbance, and we suggest that such species may often have little bearing on the ecological costs and benefits of fire in forested systems.

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## 1. Introduction

Restoring appropriate fire regimes is of critical importance to the management of forested ecosystems, including the maintenance of biodiversity, the control of invasive species, and the reduction of risk to human communities. Among the consequences of 20th-century fire suppression have been losses of herb diversity in forest understories (Baker, 1994; Hawkes and Menges, 1995; Schemske et al., 1994) often reflecting the closure of sunny gaps (Sahara et al., 2015). In turn, managed fires have often been successful in restoring understory diversity and/or increasing the abundances of focal herb species (e.g., Gillespie and Allen, 2004; Hawkes and Menges, 1995; Liu et al., 2005). In demographic analyses, fire may increase germination (Baker et al., 2005; Maret and Wilson, 2005; Stevens and Latimer, 2015), seedling establishment (Barker and Williamson, 1988), growth and seed production (McConnell and Menges, 2002), and/or clonal growth (Menges

and Root, 2004). Impacts of fire on plant demography are not always positive, however. Fire may increase the mortality of seeds, seedlings, and/or adult plants (e.g., Agee, 1993; Auld and Denham, 2006; Stevens and Latimer, 2015), potentially leading to stasis or even decrease in population growth rates (Harrod and Halpern, 2009; Wall et al., 2012). The net impacts of fire on plant demography may vary among sites across species' ranges (Kaye et al., 2001; Pendergrass et al., 1999; Warton and Wardle, 2003), among vegetation types dominated by different woody species (Menges and Hawkes, 1998), and among species with different life history traits (Silvertown et al., 1993; Silvertown and Franco, 1993).

Net positive effects of fire on demographic rates are likeliest, all else being equal, for species with life history traits that enable them both to resist fire and to take advantage of resource-rich postfire conditions. Traits such as fire-induced germination, fire-resistant above- and belowground structures, and the ability to quickly resprout after fire, which are characteristic of many species inhabiting historically fire-prone environments (Keeley et al., 2011), contribute to net positive demographic effects of fire. In addition, net positive demographic effects of fire or other

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space-opening disturbances are expected to be strongest in species with fast-growing, resource-acquisitive functional strategies, which tend to be associated with fertile soils and benign climates, and which are capable of increasing their rates of reproduction and/or somatic growth in response to pulses of increased resource availability such as the light- and nutrient-rich conditions following fires (Grime, 1977; Gremer et al., 2013). For herbs, in addition, positive fire effects are likeliest in settings where dense overstory cover and/or litter layers are present before fire, since increased light availability is an important proximate cause of positive fire effects (Xiong and Nilsson, 1999; McConnell and Menges, 2002; Cavender-Bares and Reich, 2012).

On infertile soils, there are several interrelated reasons to expect the demographic effects of fire to be weak or possibly even negative. First, since lower and patchier fuel loads may lead to less frequent and/or severe fires in plant communities on infertile soils, adaptations or preadaptations to fire may be less prevalent in members of these communities (Safford and Harrison, 2004; Anacker et al., 2012). Second, infertile soils have a higher prevalence of species with slow-growing, stress-tolerant functional strategies, which are less able to increase their growth rates in response to resource pulses than are species with fast-growing functional strategies (Grime, 1977; Gremer et al., 2013). Third, the sparse overstory cover and/or litter layer often associated with infertile soils may lead to a negligible postfire increase in light availability, and thus to less potential for postfire increases in rates of seed germination and/or somatic growth (Safford and Harrison, 2004).

Understory herbs specializing on rocky outcrops within a forested matrix are a little-studied group with respect to their demographic responses to fire. Throughout the world, bedrock outcrops of various types support distinctive floras, generally consisting of species with life-history traits that allow them to tolerate soil infertility and water scarcity but not low light availability (e.g., Baskin and Baskin, 2000; Ware, 2002; Anderson et al., 2007; Kruckeberg, 2005). In California, an endemic-rich herb flora is found on outcrops of infertile serpentinite (ultramafic) rock, embedded within forest, shrubland, or grassland depending on regional climate (Harrison et al., 2006). There is little evidence that the Californian serpentinite flora is adapted to frequent fires or depends on fire for the prevention of woody species encroachment (Safford and Harrison, 2004; Anacker et al., 2012). Since serpentinite rock outcrops are generally not light-limited environments in the absence of fire, and since the species that inhabit them generally have the low rates of resource uptake and growth typical of the stress-tolerant functional strategy, their endemic species may benefit little from fire or may even be harmed by it.

We examined the demographic effects of prescribed and naturally occurring fire on the demography of *Boechera constancei* (Brassicaceae), an endemic to serpentinite outcrops in the montane conifer forests of the Californian Sierra Nevada. As a State-listed rare plant (California Native Plant Society, 2015), *B. constancei* is one of a suite of species that forest managers must monitor while implementing stand structure restoration, risk reduction, and biodiversity maintenance objectives (Merriam et al., 2010; USDA Forest Service, 2013). *B. constancei* mainly occurs on open outcrops, but is also found sparsely in the nearby understory, offering the opportunity to ask whether demographic effects of fire on this species are modulated by variable litter levels.

## 2. Methods

### 2.1. Study system

Our experimental study took place in the Meadow Valley quadrant of Plumas National Forest in the northern Sierra Nevada

(39.98°N, 121.05°W). The Chips fire occurred approximately 13.4 miles to the NW in the Caribou quadrant (Supplemental Fig. 1; 39.98°N, 121.05°W). The experimental plots and natural fire occurred at elevations (experimental plot mean = 1382.4 m, natural fire site mean = 1382.2 m).

The vegetation at both sites is montane mixed conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), incense cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), sugar pine (*P. lambertiana*), and Ponderosa pine (*P. ponderosa*). Burn scars indicate a historic fire return interval of 8–22 years in the Plumas National Forest prior to 20th-century fire suppression (Moody, 2006). Between 2001 and 2016, however, four high-severity fires occurred in the forest (USDA Forest Service, 2013; Coppoletta et al., 2016), leading to the increased use of prescribed burns and mechanical thinning treatments to reduce fuel loads (Merriam et al., 2010; USDA Forest Service, 2013).

“Serpentine” or ultramafic rocks (peridotite and serpentinite), and soils weathered from these rocks, are widespread in the study region. Serpentine substrates are relatively infertile due to excess Mg and low Ca and N, and are home to many restricted (endemic) species tolerant of these soil conditions but intolerant of competition (Kruckeberg, 1984; Huenneke et al., 1990). Forests occur on the deeper serpentinite soils at our site, but they are substantially less productive than those on nearby nonserpentine soils (DeSiervo et al., 2015). Protruding from these forests are outcrops of serpentinite bedrock that support sparse woody vegetation and many endemic herbs including *B. constancei*.

Our target organism, *B. constancei*, is a perennial that is strictly endemic to serpentinite substrates (Safford et al., 2005) and is known from only 48 occurrences in Plumas and Sierra Counties, California (California Native Plant Society, 2015). While *B. constancei* is most common on bedrock outcrops, with low litter accumulation (median depth = 8.0 mm, interquartile range = 4.7–13.9 mm), it also occurs scattered in nearby forest understories on serpentinite soils where litter may be considerably deeper (up to 78 mm; E. J. Case, unpublished data).

Demography of *B. constancei* has not been previously studied. We found that adult plants varied from 1 to 92 rosettes on branches that arise from a woody caudex. There is considerable size variation; for example, individuals with one rosette ranged from approximately 5 to 40 mm in diameter. Seed reproduction appears to be infrequent; we observed only 13% of our marked adult plants to produce fruits in any one year, and only 79 seedlings emerged from 1522 fruits. From our demographic data, we estimated the lifespan of adult *B. constancei* to be 5–11 years (E. J. Case, unpublished data).

Immediately following fire, the rosettes on adult *B. constancei* die back, but vegetation resprouts from the woody caudex the spring after fire (Coppoletta, 2010). A greenhouse study found that its germination was inhibited by light litter cover (20% reduction caused by 8 mm of litter; Olliff, 2012), suggesting the potential for *B. constancei* to benefit from fire-induced litter reduction.

### 2.2. Prescribed fire experiment

We began by identifying 59 *B. constancei* subpopulations, defined as a group of individuals separated from others by >50 m, and measured litter depth (distance between the soil surface and highest litter) at 5 points at each subpopulation. We then selected 5 subpopulations each from the 18th, 32nd, 57th, 59th, and 93rd percentiles of litter depth. At each of the 5 subpopulations, we haphazardly established 5 pairs of 1 × 1 m plots with similar litter depth, 1–30 m apart (mean 14.1 m ± 7.6 m SD), for a total of 25 pairs of plots. We marked plots with rebar, weighed litter at 5 locations per plot, and counted and permanently marked all *B. constancei* individuals. Estimated litter fuel loads were low

in all of these *B. constancei*-containing plots, ranging from 0.78 to 21.7 Mg ha<sup>-1</sup> (median), compared to a mean of 38 Mg ha<sup>-1</sup> in fire-suppressed mixed conifer forests elsewhere in the region (Chiono et al., 2012). For analysis, we binned litter depth into “high” and “low” categories (above and below median).

On January 10–11, 2012, we burned one randomly selected plot (plus a 0.25 m buffer) from each of the 25 pairs. Burns were conducted by a Plumas National Forest fire crew, and reflected the seasonal timing, weather conditions, and methodology under which prescribed burns are normally conducted (C. Rowe, personal communication, January 12, 2012). Fine fuel moisture (11% unshaded/13% shaded) and relative humidity (57%) were moderate. The edge of each plot buffer was drip-fueled with 2 parts unleaded gasoline to one part red dye diesel, and plots were allowed to burn (dry bulb temperature 250 °C) until all available fuels were consumed.

### 2.3. Naturally-occurring fire study

We evaluated the effects of a naturally occurring summer fire on *B. constancei* demography using observations of transitions of marked individuals before and after the 2012 Chips Fire, which occurred near to but not overlapping the area of our prescribed fire experiment. In July 2011, we had established 300, 1 × 1 m plots containing *B. constancei* to monitor populations within the perimeter of the 2001 Storrie Fire. We visited all known populations within the Storrie Fire perimeter, and permanently marked all individuals in 10 × 10 m grids in populations with at least 50 individuals. We did not collect data on litter depth in all plots, and therefore could not include it in analyses. However, litter depth was low in general, trees were sparse, and tree mortality was low, suggesting litter depth had returned to pre-fire levels at the time of study. From July 29 – August 31, 2012, the lightning-ignited Chips Fire burned through parts of the Storrie fire perimeter. The Chips Fire burned at high intensity due to high winds, dry fuels, high prevalence of snags, and steep topography (Fites et al., 2012). In June 2013, we re-examined the 300 plots described above, and classified 49 plots as burned and 251 as unburned by the Chips Fire, based on the presence or absence of charred plants and litter.

### 2.4. Demographic data collection

In the first summer of observation (July 2011 for controlled burn; July 2012 for natural fire), we marked every *B. constancei* individual in each plot with a unique metal tree tag and plastic-coated electrical wire. We defined an individual as all rosettes within five centimeters of one another because *B. constancei* reproduces through underground ramets and observation of individuals with cotyledons is rare. For each individual, we recorded the number of rosettes, bolts (inflorescences), fruits, and a visual estimate of area covered by the plant (range 0.1–85 cm<sup>2</sup>). We repeated these measurements on tagged individuals in subsequent summers (July 2013 and July 2014 for experimental burn and July 2013 for the natural fire). Untagged small individuals without cotyledons were assumed to be the vegetative progeny of the nearest established plant. No new individuals were >1 m from a parent plant.

Because seed production and seedling and survival were low, we estimated the production of new individuals through seed from fruit counts as [number of fruits on individual plot] × [a single estimate of average seeds per fruit] × [estimate of seedling survival]. Mean seeds/fruit was based on 589 fruits collected from 102 individual plants throughout the study region. For the controlled burn experiment, plot-specific seedling survival was obtained by planting 50 seeds in a marked grid in each experimental plot (2500 seeds total), just before the rains of October 2012, and resampling

in July 2013 and 2014. For the naturally occurring fire, we used the average of all planted seeds. Our planting experiment did not yield new individuals in the second year of germination, so we did not include a multiyear seedbank term in our model.

### 2.5. Statistical analysis – prescribed burn

We classified adult *B. constancei* individuals into three size stages: small (<2.5 cm<sup>2</sup>), medium (2.5–10 cm<sup>2</sup>), and large (>10 cm<sup>2</sup>). We then calculated probabilities of stasis (remaining in a stage), growth (transition to a larger stage), and shrinkage (transition to a smaller stage), with stages beginning at one round of annual sampling in July and ending at the next one; all nine possible transitions were observed. For the experimental burn, we calculated transition rates one (2012–2013) and two years (2013–2014) after the fire.

We tested the effects of burn status (burned/unburned) and litter depth (high/low), on the nine transition rates among the three size classes using log-linear models (Haberman, 1972). We analyzed each transition (one and two years post-fire) separately. Analyses were conducted using function “loglin” in the “MASS” package of R (Venables and Ripley, 2002). For each stage, we calculated three-way contingency tables and tested whether predictor × stage interaction term (Eq. (1): fate ~ stage \* Burn + pre-existing distribution of individuals among treatments \* litter; Eq. (2): fate ~ stage \* Litter + pre-existing distribution; Eq. (3): fate ~ stage \* Litter \* Burn + pre-existing distribution) increased goodness of fit (log-likelihood) beyond the null model (Eq.: fate ~ stage + pre-existing distribution of individuals among treatment levels) with a chi-square test on the log-likelihood ratio statistic ( $\Delta\chi^2$ ).

Because our sample sizes for some transitions were relatively small, and because total survival (=stasis + growth + shrinkage) may be of critical importance to the demography of perennial herbs (Silvertown et al., 1993), we also examined fire and litter effects on total survival of each of the three size classes in the prescribed burn experiment. We modeled survival (=stasis + growth + shrinkage) of each size class as a function of burn status, litter, and their interaction. We used a binomial model with a logit link function in “glm” in the base package of R.

We tested for treatment effects on fecundity (fruits per individual) using linear mixed models. For each plot we calculated the average number of fruits per large individual as the response variable. For the prescribed fire, burn category (burned/control) and litter category (high/low) were the predictors, and year and site were random effects. We evaluated the significance of our models with likelihood ratio tests and a null model which only included random effects (Caswell, 2001). Analyses were conducted using function “lmer” in the “lme4” package of R (Bates et al., 2015).

We calculated  $\lambda$  using the ‘popbio’ package of R and tested for significant differences in  $\lambda$  among all factorial combinations of litter categories and burn treatments with nonparametric randomizations (Angert, 2006; Caswell, 2001). For each main effect, we calculated treatment-specific null  $\lambda$  values from transition matrices of individuals pooled by treatment factor (litter, burn). For each stage, we randomly permuted fates and seed counts among individuals, generating a null expectation of lambda if individuals survived and reproduced independently of treatment. This method of stratified permutation maintained the observed distributions of stage 1, stage 2, and stage 3 individuals within treatments and the overall average transition rates for each stage. We calculated treatment-specific null  $\lambda$  values from the resampled stage by fate matrix, following the procedure as described above. We compared absolute differences in 1000 simulated  $\lambda$  values to our observed  $\lambda$  values to yield a two-tailed p-value.

We tested for interactive effects of burning and litter on  $\lambda$  with a stratified randomization test (Caswell, 2001). We permuted

individual fates across burn treatments to simulate fire-independent transitions, but restricted permutations within litter category to control for main effects (Levin et al., 1996). We also restricted permutations within stage to control for chance differences in pre-treatment stage distributions. We then calculated the standard deviation of  $(\lambda^{H,B} - \lambda^{H,U})$ ,  $(\lambda^{L,B} - \lambda^{L,U})$  to test whether the slope of burn-unburned response differed between high and low litter categories, and calculated two tailed p-values as for main effects. Finally, we tested the contribution of each stage to  $\lambda$  with the elasticity function of the popbio package (Stubben and Milligan, 2007).

### 2.6. Statistical analysis – naturally occurring fire

All calculations and analyses were the same for the naturally occurring fire as for the prescribed burn experiment, with the following differences. First, we had only one set of transition probabilities (2013–2014) rather than two. Second, we omitted the litter depth term because we lacked the necessary pre-fire data. Finally, because we found no effects of the natural fire on individual demographic rates, we did not estimate or analyze  $\lambda$  for the natural fire data.

## 3. Results

### 3.1. Prescribed fire experiment

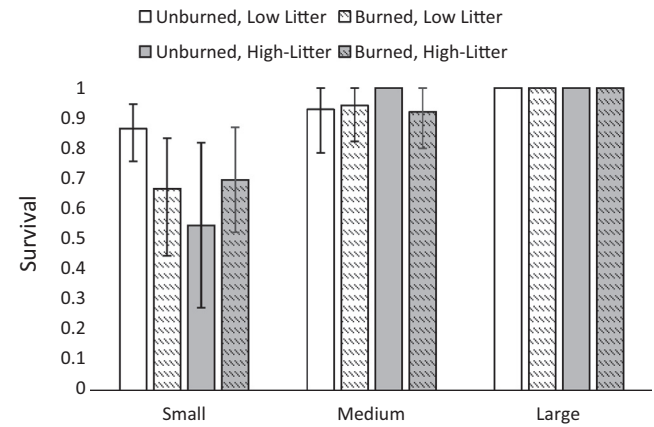
Burn treatments did not significantly affect any of the nine individual transition rates for adult plants (small individuals,  $\Delta G^2 = 2.0$ ,  $p = 0.51$ ; medium individuals  $\Delta G^2 = 1.1$ ,  $p = 0.78$ ; large individuals  $\Delta G^2 = 5.5$ ,  $p = 0.14$ ). Litter depth also did not affect transition rates in small ( $\Delta G^2 = 2.3$ ,  $p = 0.52$ ), medium ( $\Delta G^2 = 0.96$ ,  $p = 0.81$ ), or large ( $\Delta G^2 = 2.3$ ,  $p = 0.96$ ) individuals. The interaction between litter depth and burning was also non-significant for all stages (small,  $\Delta G^2 = 3.5$ ,  $p = 0.74$ ; medium  $\Delta G^2 = 2.1$ ,  $p = 0.91$ ; large  $\Delta G^2 = 2.3$ ; large  $\Delta G^2 = 6.4$ ,  $p = 0.48$ ; see Supplemental Table 1 for transition rates by treatment combination).

Similarly, fire did not affect the total survival (stasis + growth + shrinkage) of any of the three size classes (Fig. 1, small,  $F_{1,172} = 0.044$ ,  $p = 0.83$ ; medium  $F_{1,137} = 0.046$ ,  $p = 0.96$ ; large,  $F_{1,268} = -0.004$ ,  $p = 1.0$ ). Nor were survival probabilities affected by litter (small  $F_{1,172} = 0.018$ ,  $p = 0.89$ ; medium,  $F_{1,137} = 0.006$ ,  $p = 1.0$ ; large,  $F_{1,268} = -0.000$ ,  $p = 1.0$ ), or the fire-litter interaction (small  $F_{1,172} = 0.059$ ,  $p = 0.81$ ; medium  $F_{1,137} = -0.006$ ,  $p = 1.0$ ; large,  $F_{1,268} = 0.002$ ,  $p = 1.0$ ). Large *B. constancei* individuals survived at the greatest rate (99%), medium-sized individuals survived almost as well (97%), and small individuals survived much less well (58%) across all treatments.

Plants in burned plots produced an average of  $0.35 \pm 0.19$  fewer fruits per individual than plants in unburned plots, a difference that was marginally significant ( $X^2_1 = 3.2$ ,  $p = 0.070$ ) after accounting for the pre-fire distribution of reproductive-sized individuals. Litter did not explain variation in reproduction ( $X^2_1 = 0.22$ ,  $p = 0.63$ ), and the addition of a litter-burn interaction term did not increase explanatory power beyond that provided by burn treatment alone ( $X^2_2 = 0.70$ ,  $p = 0.70$ ). Seedling recruitment was quite low in both the burned and unburned treatments (53 new individuals in 2013, 20 new individuals in 2014).

The slight decrease in fecundity associated with fire was not strong enough to impact population growth estimates. Estimates of  $\lambda$  did not differ significantly among burn treatments (2012,  $\lambda_{\text{burn}} = 0.98$ ,  $\lambda_{\text{control}} = 0.91$ ,  $p = 0.86$ ; 2013,  $\lambda_{\text{burn}} = 0.85$ ,  $\lambda_{\text{control}} = 0.91$ ,  $p = 0.34$ ), litter depths (2012,  $\lambda_{\text{low}} = 0.95$ ,  $\lambda_{\text{high}} = 0.98$ ,  $p = 0.64$ ; 2013,  $\lambda_{\text{low}} = 0.90$ ,  $\lambda_{\text{high}} = 0.88$ ,  $p = 0.70$ ), or burn  $\times$  litter

### (a) 2012–2013:



### (b) 2013–2014:

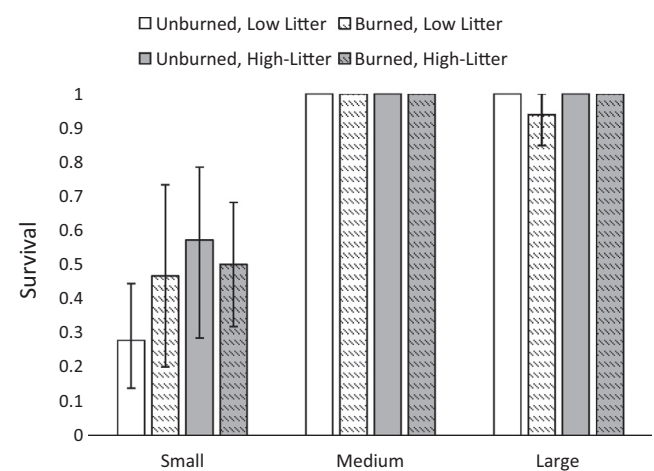


Fig. 1. Survival rates of large, medium, and small individuals by burn treatment (B = Burn/C = control) and litter category (H = High/L = Low) from the prescribed burn experiment. Survival = growth + stasis + shrinkage = one minus mortality. Error bars represent 95% confidence intervals from bootstrapped transitions.

combinations (2012,  $p = 0.25$ ; 2013,  $p = 0.33$ ). The transition from large individuals to large individuals had the greatest effect on  $\lambda$  in all treatment combinations except unburned, high litter, where the transition from medium individuals to medium individuals had the greatest effect (Supplemental Table 2).

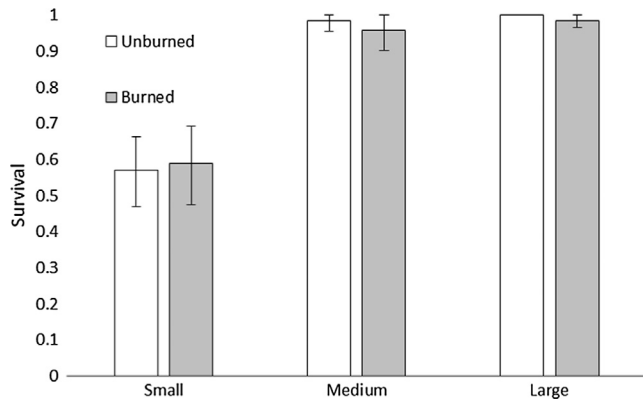
### 3.2. Naturally-occurring fire

The Chips Fire did not affect any of the nine transition rates among small ( $\Delta G^2 = 2.6$ ,  $p = 0.46$ ), medium ( $\Delta G^2 = 1.5$ ,  $p = 0.68$ ), or large ( $\Delta G^2 = 2.6$ ,  $p = 0.47$ ) adult individuals (Fig. 2). Nor did it affect fecundity of medium ( $X^2 = 0.93$ ,  $p = 0.33$ ) or large ( $X^2 = 1.2$ ,  $p = 0.28$ ) individuals (small individuals did not reproduce).

### 3.3. Population viability

Across all populations and treatment combinations, our demographic analysis indicated population decline in 2012–2013 ( $\lambda = 0.91$ , 95% CI = 0.88–0.96). In the Meadow Valley populations, the bootstrapped 95% CI for  $\lambda$  overlapped 1 in 2012–2013 ( $\lambda = 0.95$ , 95% CI = 0.90–1.02), but not in 2013–2014 ( $\lambda = 0.88$ , 95% CI = 0.83–0.93) or overall ( $\lambda = 0.91$ , 95% CI = 0.88–0.96). In the Caribou populations, for which we have only one year of





**Fig. 2.** Survival rates of large, medium, and small individuals by burn category (B = Burn/C = control) from the naturally occurring fire. Survival = growth + stasis + shrinkage = one minus mortality. Error bars represent 95% confidence intervals from bootstrapped transitions.

transition rates,  $\lambda$  values indicated a decline in 2012–2013 ( $\lambda = 0.93$ , 95% CI = 0.88–0.95).

#### 4. Discussion

We found no effects of either prescribed winter fire or lightning-caused summer fire on the demographic rates of *B. constancei*, except for a modest negative effect of prescribed fire on fecundity that did not affect estimated rates of population growth. Our results contrast with many published studies that document increased germination and seedling establishment after fire and/or litter removal (see Introduction). However, while many species rely on fire as a germination cue, this is clearly not the case in *B. constancei*. Indeed, there is no known case of a serpentine-endemic herb with fire-dependent germination, suggesting that in infertile environments where light is abundant and fire is infrequent, there is little selective pressure for fire dependency (Safford and Harrison, 2004). Moreover, seedling recruitment was very low in our study, and elasticity analysis indicated that variation in seedling recruitment in *B. constancei* causes very little variation in population growth rates, in agreement with general demographic theory for long-lived and slowly growing species in stable environments (Silvertown et al., 1993; Valverde and Silvertown, 1998). Our results therefore do not suggest prescribed fire as an effective tool for expanding population sizes of *B. constancei*.

In addition to not increasing recruitment, fire also did not diminish survival rates among established *B. constancei* individuals, even in high-litter environments. Our results contrast with Odion and Davis (2000) and Brooks (2002), who found that mortality of seeds and/or adult plants increased along gradients of fire severity caused by variation in dead aboveground biomass. We found that rates of survival for medium and large *B. constancei* in all treatments were very high (97–99%), and again in agreement with theory (Silvertown et al., 1993), our demographic analyses showed that these high rates of adult survival were critical to population stability. At the same time, fire did not cause increased rates of transition to larger size classes, consistent with the status of *B. constancei* as a “stress tolerator” *sensu* Grime (1977), with high resource use efficiency and low maximal rates of growth that constrain the ability to capitalize on resource-rich conditions such as the high light availability following fires.

Prescribed fires for forest management are typically conducted in seasons when moderate temperature, moisture, and wind conditions promote a low probability of fire escape; in California, this is

usually a rainless period in winter (Knapp et al., 2009). Natural fires, in contrast, tend to happen when dry fuels coincide with lightning storms, which is typically in mid- to late summer in the Sierra Nevada. This seasonal mismatch calls into question some of the potential benefits of prescribed fire for biodiversity; one particular concern is whether buried seeds and other belowground plant structures may be vulnerable to fire-induced mortality in winter when the ground is moist (Knapp et al., 2009). In this context, our results are robust, in that we found high consistency in the lack of demographic effects on *B. constancei* using both prescribed winter fire and a natural summer fire in the same year.

One factor potentially contributing to our results was the relatively low level of litter found around *B. constancei*, even in forest understory. It is possible that a long fire-free period could lead to higher levels of litter accumulation in forest understories than we observed, which could either suppress *B. constancei* recruitment between fires, or cause fires to burn at high severities that could kill *B. constancei* adults. However, if that were the case, the many *B. constancei* individuals found on bare rock outcrops would likely to be less affected than those inhabiting forest understories.

#### 5. Conclusions

Our study suggests that *B. constancei* – and perhaps by extension, other rare rock-outcrop specialist plants with similar life histories of slow recruitment and growth, lack of fire-dependency, and high survivorship – need not necessarily evoke a high level of concern from those responsible for managing fires in forested landscapes. Based on current evidence, prescribed fires need not be conducted specifically to restore *B. constancei*, nor do its populations need to be protected against the advance of a natural fire.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.10.058>.

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