

POST-FIRE ECOPHYSIOLOGY OF ENDEMIC CHAPARRAL SHRUB SEEDLINGS  
FROM SANTA CATALINA ISLAND, SOUTHERN CALIFORNIA

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ABSTRACT

Island systems are generally more sensitive to the introduction of non-native species than comparable mainland systems and are particularly vulnerable to disturbances that create opportunities for invasion. We examined the impact of browsing by introduced deer on seedling establishment and physiology in three obligate seeding (i.e., non-resprouting) species on Santa Catalina Island for two years following a large fire in 2007: *Arctostaphylos catalinae* P. Wells (Ericaceae), *Ceanothus arboreus* E. Greene (Rhamnaceae), and *Ceanothus megacarpus* Nutt. var. *megacarpus* (Rhamnaceae). Four post-fire sites were established, with each site containing 12–20 plots exposed to browsing and 12–20 control plots protected from deer browsing. Browsing did not significantly affect seedling survival or physiology in *C. arboreus*, the only species to experience significant browsing; browsing did, however, significantly reduce seedling height. Predawn and midday water potentials, stomatal conductance, and growth differed among species during their first post-fire dry season. *Arctostaphylos catalinae* experienced the lowest dry season predawn water potentials (−3.3 MPa compared to −1.7 MPa for *C. arboreus* and −2.2 MPa for *C. megacarpus*). *Ceanothus arboreus* and *C. megacarpus* exhibited relatively high seedling survival (56% and 69%, respectively) and high resistance to xylem cavitation of stems ( $P_{50} = -6.0$  and  $-6.7$  MPa, respectively), compared to *A. catalinae* which had lower seedling survival (30%) and was less resistant to cavitation ( $P_{50} = -4.2$  MPa). Browsing significantly impacted seedling height, which could impact stand structure. Differential browsing pressure and seedling resistance to water limitation may have important consequences for long-term distribution and abundance of these island endemics on Santa Catalina Island.

Key Words: Drought, introduced species, life history type, mediterranean-type ecosystem, mediterranean-type climate region, vulnerability to cavitation.

Crown fires are a recurrent disturbance in the chaparral shrublands of southern California. Following a fire, chaparral shrubs persist through vigorous resprouting and fire-stimulated seed germination and seedling establishment. Woody shrub species are typically classified as falling into one of four different life history types in response to fire: obligate seeders, which persist only through the germination of fire-cued seeds; facultative seeders, which persist through a combination of resprouting from underground structures, as well as germination of fire-cued seeds; obligate resprouters, whose seeds are killed by fire and persist through resprouting; and opportunistic species, the adults and seeds of which are killed by fire but readily disperse seeds into burned sites from adjacent unburned areas. Under many conditions, mediterranean-type shrublands rapidly recover following fire and maintain their pre-fire composition (Hanes 1971).

Post-fire regeneration of chaparral stands may fail when the fire regime changes or if additional disturbances occur in tandem with fire. For instance, a change in the fire regime that reduces the time interval between successive fires (i.e., short fire return

intervals) may alter chaparral shrub community compositions or convert shrublands to alien grass-dominated savannahs or sage scrub communities (Zedler et al. 1983; Haidinger and Keeley 1993; Jacobsen et al. 2004; Lippitt et al. 2013). The occurrence of additional disturbances, including the addition of browsing by mammals (Howe 1981; Mills 1983; Quinn 1986; Moreno and Oechel 1991; Tyler 1995; Ramirez et al. 2012), drought (Pratt et al. 2014), or pathogens (Jacobsen et al. 2012), during the post-fire recovery period may also impact shrub community composition.

Many of these interactions and their subsequent impacts on chaparral shrub communities may be greater for island chaparral systems compared to mainland systems, particularly in the case of fire and herbivore interactions. This may be due to an increase in the vulnerability of island plants to being browsed (Bowen and van Vuren 1997; Vourc'h et al. 2001), to the population dynamics and behavior of introduced mammalian herbivores on islands that do not have natural predators (Knapp 2005; Stapp et al. 2006; Laundré et al. 2010), or to intense herbivory of post-fire areas, particularly when fires are small

TABLE 1. THE GPS LOCATIONS, ELEVATION, AND NUMBER OF PLOTS FOR FOUR SITES THAT WERE ESTABLISHED IN AN AREA THAT BURNED IN MAY 2007 ON SANTA CATALINA ISLAND, SOUTHERN CALIFORNIA. Within each site, multiple  $1 \times 1 \text{ m}^2$  plots were established in areas that were protected from large mammal browsing by tall fences (Fenced plots) or were established in areas not protected by fences and that were open to being browsed (Browsed plots).

| Site | Dominant obligate seeding shrub species            | GPS location (°)   | Elevation (m) | Browsed plots (#) | Fenced plots (#) |
|------|--|--------------------|---------------|-------------------|------------------|
| 1    | <i>Arctostaphylos catalinae</i>                    | 33.3539, -118.3584 | 420           | 20                | 20               |
| 2    | <i>Ceanothus arboreus</i>                          | 33.3568, -118.3471 | 315           | 15                | 12               |
| 3    | <i>Ceanothus arboreus</i>                          | 33.3501, -118.3430 | 280           | 12                | 12               |
| 4    | <i>Ceanothus megacarpus</i> var. <i>megacarpus</i> | 33.3491, -118.3656 | 430           | 20                | 20               |

(Quinn 1986; Knapp 2005). Additionally, for the location of the present study, the fire history on Santa Catalina Island is unknown and the fire return interval is assumed to be longer than the mainland, which may affect the ability of the vegetation to recover. The fire-regime in mainland southern California is a late summer-fall regime with fire return intervals of 30-100 years (Keeley et al. 1999; Keeley and Fotheringham 2001), but the fire regime on the island may be characterized by longer intervals between fires due to the rarity of lightning ignitions (Carroll et al. 1993).

Fire and browse may impact both the recovery of resprouting species and the recruitment of seedlings. For Santa Catalina Island in southern California, the negative impact of fire combined with large mammal browsing on post-fire recovery of chaparral community structure has already been demonstrated for resprouting species. A recent study of post-fire chaparral species with resprouting ability found that browsing by introduced mule deer (*Odocoileus hemionus* Rafinesque) lead to high mortality of resprouting shrubs (Ramirez et al. 2012). Browse-related reductions in plant crowns for three dominant species of resprouting shrubs at this site resulted in a more than 93% reduction in the canopy coverage (Ramirez et al. 2012). The period of this study also coincided with an extremely dry year, with only 130 mm of rain falling during the 2006-2007 rain-year compared to an 80-year average of 323 mm (Ramirez et al. 2012). Post-fire browsing by mammalian herbivores has also been shown to impact the post-fire vegetation recovery patterns of seedlings in mainland chaparral communities (Mills 1983; Mills 1986; Quinn 1986; Frazer and Davis 1988; Thomas and Davis 1989; Tyler 1995), but has rarely been studied on southern California islands, in part because of infrequent fires (Carroll et al. 1993; Duncan and King 2009). Following a small fire on Santa Catalina Island in 1999, two seeding species were reported to be sensitive to browse, although detailed data were not reported (Knapp 2005).

A large fire, which occurred in May 2007 and burned about 10% of the land area on Santa Catalina Island, provided us with the opportunity to examine how browse by introduced large mammalian herbivores may impact post-fire recovery of obligate seeding species. We were interested in examining whether obligate seeding species of chaparral shrubs in island ecosystems would success-

fully recover following this fire, particularly in the context of potential co-disturbance with browsing from introduced mule deer. Having already observed the severe effect browsing could have on the survival of large obligate resprouting species (Ramirez et al. 2012), we hypothesized that seedlings, being small and more delicate than an established resprout, would be more vulnerable to deer browsing and associated disturbance (trampling). We examined post-fire recovery of three shrub species by following seedling survivorship and several physiological and hydraulic parameters in plots not protected from deer browse and sites that were protected from deer, the only large mammalian browser currently present on the island.

## METHODS

Santa Catalina Island lies 22 miles (35 km) off the coast of southern California and contains several vegetation types, including stands of maritime chaparral (Westman 1983). A large fire occurred in May 2007, which burned about 10% of the land area on Santa Catalina Island. Within the burned area, we established 4 sites (Table 1), each of which was dominated by one of four island endemic chaparral shrub species or subspecies: *Arctostaphylos catalinae* P. Wells (Ericaceae) (site 1), *Ceanothus arboreus* E. Greene (Rhamnaceae) (sites 2 and 3), and *Ceanothus megacarpus* Nutt. var. *megacarpus* (Rhamnaceae) (site 4). All of these species are evergreens that are obligate seeding and non-resprouting after fire. Sites were selected based on the presence of these species as identified in adjacent unburned areas and from burnt stumps within the burned areas. Sites were surveyed to estimate the pre-fire density of these species within each site by surveying and recording the burnt stumps and root crowns within each site. Although these sites were largely dominated by our focal obligate seeding species, there were also resprouting evergreen shrub species present in low densities, including *Adenostoma fasciculatum* Hook. & Arn. (Rosaceae), *Crossosoma californicum* Nutt., *Heteromeles arbutifolia* (Lindl.) M. Roem. (Rosaceae), *Malosma laurina* (Nutt.) Abrams (Anacardiaceae), *Quercus pacifica* Nixon & C.H. Mull. (Fagaceae), *Rhamnus pirifolia* Greene (Rhamnaceae), and *Rhus integrifolia* (Nutt.) Rothr. (Anacardiaceae).

At each site we established 12-20,  $1 \times 1 \text{ m}$  randomly distributed permanent plots in an approx-

imately 500 m<sup>2</sup> area exposed to browsing and 12-20 randomly distributed permanent plots in an approximately 500 m<sup>2</sup> area protected from browsing by a tall plastic deer-proof fence with metal reinforcement along the lower few feet. The fences restricted access by large animals (deer and bison are both present on the island and in the study areas), whereas small terrestrial animals and birds were not restricted. Since bison are grazers and do not regularly browse woody vegetation (although we have observed some browsing by bison), these fences were primarily to limit deer access to shrubs, but also limited trampling by deer and bison.

Fenced plots were contained within or near larger fenced areas within the burned areas that were installed shortly after the fire by the Catalina Island Conservancy to protect sensitive and rare species from the intense deer browse that had previously been observed within a smaller burned area (Ramirez et al. 2012). For our sites, the two *C. arboreus* sites (sites 2 and 3) and the *A. catalinae* site (site 1) were located within larger fenced plots that were established by the Catalina Island Conservancy. To decrease the likelihood of fence breaches, in two of these sites, particularly where bison activity was high, we isolated our study areas using additional fencing to completely enclose only our study area within its own layer of fencing. We selected our sample areas to occur at fenced area margins where we could also sample an immediately adjacent unfenced area of similar aspect and pre-fire species composition. For *C. megacarpus*, we installed a fence specifically for the present study and this fenced area was not part of a larger fenced plot. All sites were located fairly close to one another, with the two most distant sites being 2.7 km apart and the other sites occurring in between.

Sites were established in February-March 2008 and plots were monitored through fall 2009. When plots were established, some seedlings had already germinated, but others were still germinating following the post-fire winter wet period. Monitoring occurred approximately monthly the first year and every three months during the second year of sampling. The 2007-2008 rainfall year, during which seeds would have been germinating, was similar to average (332 mm compared to an 80-year average of 323 mm from a nearby weather station; Ramirez et al. 2012). The second year of the study, 2008-2009, was drier than the first year, with only 196 mm of rainfall. Rainfall totals were obtained from a weather station located within 200 m of site 1 ([www.wrcc.dri.edu](http://www.wrcc.dri.edu)).

At each sampling visit, growth and survival were monitored. Each 1 × 1 m plot was divided into 10 cm × 10 cm cells using grids and all of the surviving seedlings in each cell were recorded for every plot during each sampling date. We subdivided the 1 m by 1 m plots into these smaller grids so that we could more easily track individual seedlings. We also recorded whether each seedling was browsed or

not. The heights of 10 randomly selected seedlings were measured within each plot at each visit. A different set of seedlings were randomly selected for these measures at each sampling time.

During each sampling period, a series of physiological measurements were also conducted. Some of measurements involved the destructive harvesting of plant material (e.g., water potentials) and they were therefore conducted on plants that were not within our permanent plots. Instead, plants occurring within fenced and non-fenced areas adjacent to our plots were randomly selected, with different seedlings selected for each measurement period. Only one site was included for each species, with measurements conducted at sites 1, 3, and 4. During each sampling date, both predawn and midday water potentials were measured on 6-12 individuals each from within fenced and non-fenced areas of sites (Pressure chamber, Model 2000, PMS Instruments, Albany, OR, USA). Dark-adapted chlorophyll fluorescence ( $F_v/F_m$ ) was also measured in the morning, with cuvettes attached to one leaf each of 6-12 individuals from within fenced and non-fenced areas for each species. This parameter measures the intrinsic quantum efficiency of PSII and is a sensitive indicator of dehydration stress (Maxwell and Johnson 2000). Values between 0.8 – 0.86 indicate optimum quantum use efficiency and values below 0.8 indicate photoinhibition or reduced quantum efficiency, which is a sign that plants are under strain. Leaves were dark-adapted for 20 min before  $F_v/F_m$  was measured using a pulse-modulated fluorometer (OS1-FL, Opti-Sciences, Tyngsboro, MA, USA). Stomatal conductance was measured on 6-12 individuals from within the fenced and non-fenced areas for each species mid- to late-morning (10:00 to 12:30). Fully illuminated leaves were selected for measurements (SC-1 Leaf Porometer, Decagon Devices, Pullman, WA, USA). We found that this device overestimates stomatal conductance by a factor of two when compared to matched leaves using a Li-Cor 6400 (Li-Cor, Lincoln, NE, USA), thus we divided all values by two.

On October 18, 2009, samples were collected for the determination of vulnerability to water stress-induced cavitation from the same three sites used for physiological measurements. Entire seedling shoots were collected at predawn, wrapped in moist paper towels, and placed in plastic bags on ice in a cooler. For all three species, six samples were collected for each species from non-browsed plants near, but not within, our permanent plots. For *C. arboreus*, an additional 6 samples were collected from browsed plants. Browsed samples were not collected from the other two species, because they were not generally browsed and so browsed plants were not available. Samples were kept on ice during transport from the island to California State University, Bakersfield and then refrigerated once in the laboratory. Vulnerability to cavitation curves were then measured over the next three days using the standard centrifuge method

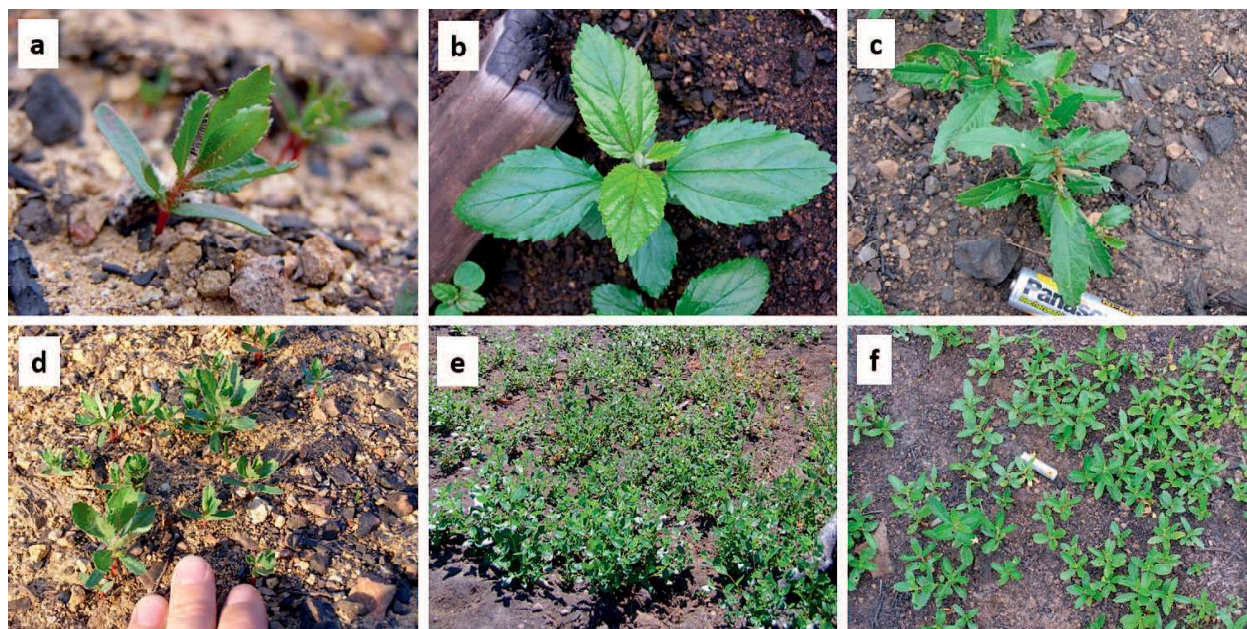


FIG. 1. Post-fire seedlings from three obligate seeding chaparral species on Catalina Island, southern California in April-May 2008: *Arctostaphylos catalinae* (a, d), *Ceanothus arboreus* (b, e), and *C. megacarpus* (c, f). Seedlings were easily identifiable during early seedling emergence (a, b, c) and occurred in near mono-specific stands at relatively high densities (see Table 2 for seedling density measures from the same initial measurement period as shown in panels d, e, f).

(Alder et al. 1997). Samples were flushed for 1 h at 100 kPa with an ultra-filtered (0.1  $\mu\text{m}$  filter) 20 mM KCl degassed solution before being subjected to increasing negative xylem tensions by being spun in a custom centrifuge rotor. Hydraulic conductivity was measured following each spin and these were used to calculate the percentage loss in conductivity at each imposed water potential relative to the initial flushed value. Vulnerability curves were plotted for each sample as the percentage loss in conductivity with declining water potential and were fit using a Weibull curve (Microsoft Excel 2010, Microsoft, Redmond, WA, USA) to calculate the water potential at 50% loss in hydraulic conductivity ( $P_{50}$ ). Curves were fatigue-corrected (Hacke et al. 2001) using an initial pressure of -0.5 MPa and  $P_{50}$  values were calculated using these fatigue corrected curves.

Comparisons of browsed and non-browsed (fenced) plots within a species were only conducted for *C. arboreus*, which was the only species among the three with individuals that were browsed throughout the study. These comparisons were conducted using t-tests when data could be transformed to meet statistical assumptions or using a Mann-Whitney rank sum test if data could not be transformed to meet normality assumptions. Comparisons across species focused specifically on traits measured during the dry season sampling periods during 2008 and 2009. These comparisons were conducted using ANOVAs with Tukey pairwise comparisons, including comparisons of survival among species following the summer dry seasons in 2008 and 2009, predawn and midday dry season water potentials, and  $P_{50}$ . Data were tested for

normality and transformed when required or, when transformations were not able to meet the assumption of normality, species were compared using a Kruskal-Wallis ANOVA on ranks with Dunn's pairwise comparisons. All statistics were run using SigmaPlot (11.1.0.102, Systat Software, Inc., Germany).

## RESULTS

Plots were established early during and following seedling emergence and seedlings of our target species were recorded in nearly all plots established within our sites (Fig. 1; only six of >120 plots did not have any seedlings of our target species emerge within the plot). Within our established plots, seedlings of our target species were present in high densities, with few other species present (Fig. 1, Table 2). Pre-fire shrub densities were generally very low (Table 2), and even after considerable seedling mortality during the first two dry seasons following seedling emergence (Fig. 2), seedling densities for all three species remained higher than pre-fire adult densities.

Browsing levels varied among species (Fig. 2). We observed only a single deer-browsed *A. catalinae* seedling over the course of this study and very limited browsing of *C. megacarpus* until our final sampling in October 2009, when there was a small increase in browse activity. These low levels of browse were not due to inactivity of deer in the area, because signs of deer activity (prints and scat) were observed across all sites and deer browse (identifiable by browse height and bite patterns) on other co-occurring

TABLE 2. THE PRE-FIRE DENSITY OF DOMINANT SHRUB SPECIES WITHIN EACH SITE AND THE DENSITY OF SEEDLINGS WHEN PLOTS WERE ESTABLISHED DURING THE ONSET OF SEEDLING EMERGENCE (APRIL 2008) AND FOLLOWING THE FIRST (SEPTEMBER 2008) AND SECOND (OCTOBER 2009) DRY SEASONS AFTER SEEDLING EMERGENCE (ACROSS PLOT MEAN  $\pm$  1 SE FROM WITHIN EACH SITE).

| Site | Species              | Pre-fire adult density (# m <sup>-2</sup> ) | Post-fire seedling density (# m <sup>-2</sup> ) | Post-fire seedling density (# m <sup>-2</sup> ) | Post-fire seedling density (# m <sup>-2</sup> ) |
|------|----------------------|---|---|---|---|
|      |                      |   | Apr-08  | Sep-08  | Oct-09  |
| 1    | <i>A. catalinae</i>  | 0.1335                                      | 42.9 $\pm$ 8.9                                  | 9.2 $\pm$ 2.2                                   | 4.6 $\pm$ 1.3                                   |
| 2    | <i>C. arboreus</i>   | 0.0084                                      | 50.5 $\pm$ 11.1                                 | 26.2 $\pm$ 5.4                                  | 21.8 $\pm$ 4.2                                  |
| 3    | <i>C. arboreus</i>   | 0.0081                                      | 158.9 $\pm$ 28.8                                | 66.1 $\pm$ 10.0                                 | 36.9 $\pm$ 4.5                                  |
| 4    | <i>C. megacarpus</i> | 0.0055                                      | 28.7 $\pm$ 5.2                                  | 17.4 $\pm$ 2.9                                  | 13.7 $\pm$ 2.4                                  |

resprouting species was also observed at all sites. For *C. arboreus*, we observed significant levels of browse in the non-fenced plots, with nearly all unprotected seedlings browsed during some sampling dates. Site 3 experienced two minor fence breaches by deer that resulted in some browse of fenced seedlings, but these breaks were quickly repaired.

Browse drastically reduced the height of unprotected *C. arboreus* seedlings (Fig. 2; final mean height of >60 cm for fenced seedlings and <20 cm for unprotected plants); however, browsing did not affect the survival of seedlings during the period of the present study (Table 3). There was no difference in seedling survival between browsed and non-

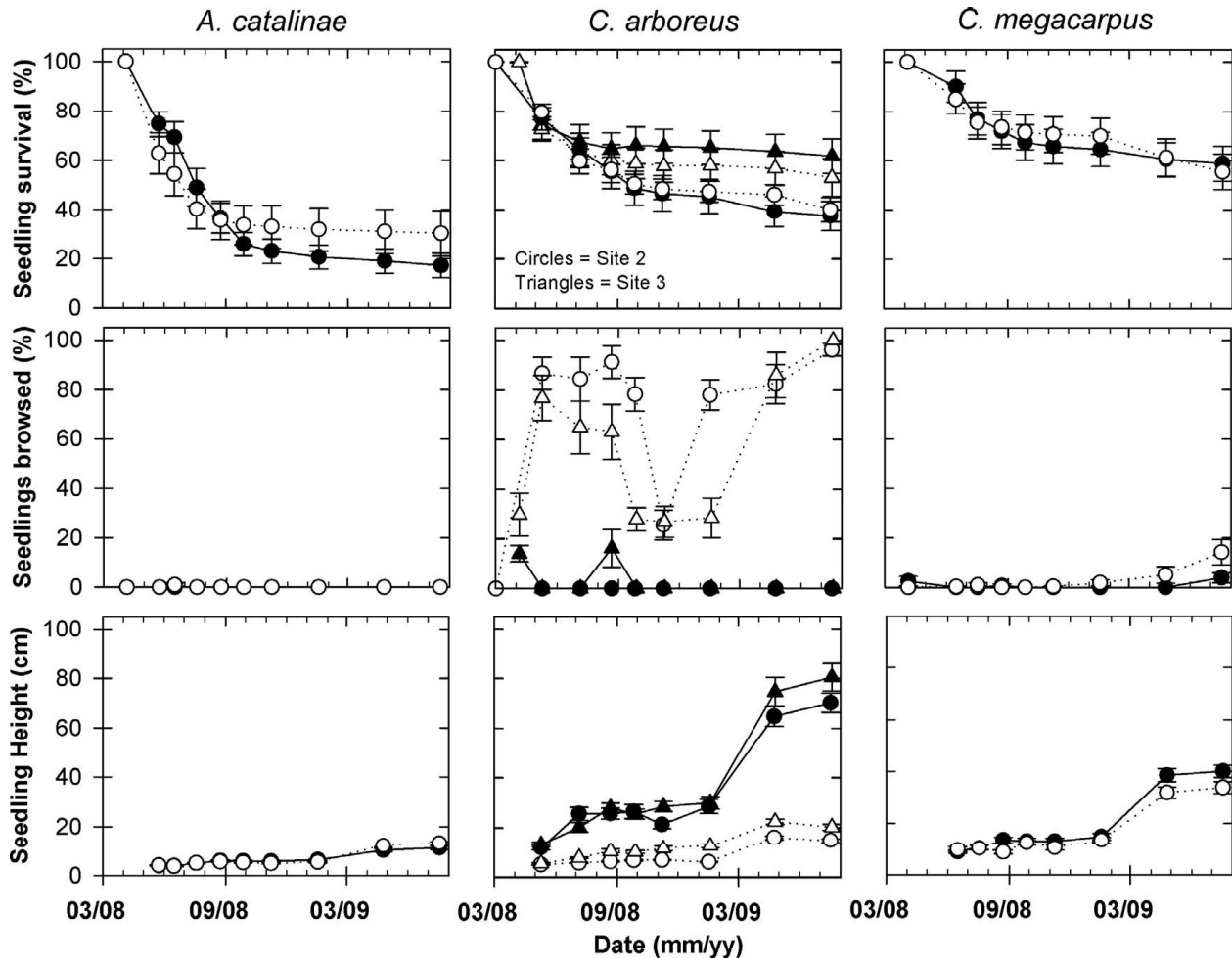


FIG. 2. Seedling survival, the percentage of seedlings browsed by deer, and seedling height of three island endemic chaparral species or subspecies during the first two years post-fire during seedling establishment. Open symbols are from plots that were non-fenced and therefore open to potential browse activity and closed symbols are from plots that were protected from browse by tall fences. Symbols represent means  $\pm$  1 SE. Sites are described in Table 1. There were three minor fence breakages during the course of the study (as seen by the low amount of browse activity for closed symbol data), but these were caught early and quickly repaired, resulting in minimal browse to protected plants.

TABLE 3. DRY SEASON SURVIVAL AND PHYSIOLOGICAL PARAMETERS FOR SEEDLINGS OF THREE SPECIES FROM SANTA CATALINA ISLAND ONE YEAR (2008) AND TWO YEARS (2009) POST-FIRE. Parameters include seedling survival (%), dark-adapted fluorescence ( $F_v/F_m$ ), predawn and midday water potential (MPa). Maximum stomatal conductance ( $g_{smax}$ ) for each year is also shown, with the month during the year corresponding to that maximum value included. Values are means with 1 SE indicated below the mean in parentheses. Different capital letters within a column indicate significant differences between species for the parameter in the column to the left and "ns" indicates that species were not significantly different ( $\alpha = 0.05$ ). An \* next to the "fenced" plot parameter for *C. arboreus* indicates that browsed and non-browsed plants were significantly different for that variable and an "ns" indicates that browsed and non-browsed plot did not differ significantly ( $\alpha = 0.05$ ).

| Species                          | Treatment  | Survival (%)  |               |                  | $F_v/F_m$        |                |                 | 2008 water potential (MPa) |                 |                 | 2009 water potential (MPa) |                 |                 | $g_{smax}$ (mmol m <sup>-2</sup> s <sup>-1</sup> ) |  |
|----------------------------------|------------|---------------|---------------|------------------|------------------|----------------|-----------------|----------------------------|-----------------|-----------------|----------------------------|-----------------|-----------------|--|--|
|                                  |            | 2008          | 2009          | 2008             | 2008             | 2009           | 2008            | Predawn                    | Midday          | 2008            | Predawn                    | Midday          | 2008            | 2009   |  |
| <i>A. catalinae</i>              | non-fenced | 33.6 (8.1)    | 26.7 (8.8)    | 0.762 (0.014)    | 0.782 (0.006)    | -3.62 (0.11)   | -4.14 (0.69)    | -3.75 (0.18)               | -2.90 (0.24)    | -3.89 (0.26)    | -3.97 (0.18)               | 97.1 (19.5)     | 197.5 (16.6)    |  |  |
|                                  | fenced     | 25.8 (4.8)    | 11.2 (3.1)    | 0.721 (0.059)    | 0.720 (0.028)    | -3.04 (0.76)   | -3.39 (0.64)    | -5.43 (0.43)               | -4.32 (0.63)    | -4.87 (0.64) *  | -5.03 (0.34) *             | 98.4 (25.1)     | 185.6 (33.0)    |  |  |
|                                  | combined   | 29.6 (4.5) A  | 18.8 (4.6) A  | 0.772 (0.030) A  | 0.751 (0.016) A  | -3.31 (0.62) A | -3.77 (0.46) A  | -4.59 (0.31) ns            | -3.66 (0.39) ns | -4.59 (0.31) ns | -4.50 (0.22) ns            | 97.8 (15.2) A   | 191.5 (17.7) AB |  |  |
| <i>C. arboreus</i> (site 3 only) | non-fenced | 58.8 (6.1)    | 51.6 (7.6)    | 0.818 (0.003)    | 0.777 (0.011)    | -1.39 (0.11)   | -2.29 (0.14)    | -3.97 (0.18)               | -3.89 (0.26)    | -3.97 (0.18)    | -3.97 (0.18)               | 411.5 (41.1)    | 190.7 (15.6)    |  |  |
|                                  | fenced     | 66.0 (7.3) ns | 60.1 (6.6) ns | 0.793 (0.007) *  | 0.806 (0.003) *  | -1.94 (0.16) * | -2.50 (0.16) ns | -5.03 (0.34) *             | -4.87 (0.64) *  | -5.03 (0.34) *  | -5.03 (0.34) *             | 501.3 (15.4) ns | 223.9 (22.8) ns |  |  |
|                                  | combined   | 62.5 (3.7) B  | 56.0 (4.6) B  | 0.811 (0.004) B  | 0.792 (0.006) B  | -1.68 (0.11) B | -2.40 (0.11) B  | -4.50 (0.22) ns            | -4.36 (0.23) ns | -4.50 (0.22) ns | -4.50 (0.22) ns            | 460.4 (27.5) B  | 207.3 (14.0) B  |  |  |
| <i>C. megacarpus</i>             | non-fenced | 71.5 (7.0)    | 52.0 (7.0)    | 0.792 (0.015)    | 0.749 (0.026)    | -2.74 (0.25)   | -3.30 (0.74)    | -5.01 (0.56)               | -5.13 (0.70)    | -5.01 (0.56)    | -5.01 (0.56)               | 63.6 (28.7)     | 147.8 (18.8)    |  |  |
|                                  | fenced     | 67.3 (7.1)    | 55.7 (6.9)    | 0.732 (0.011)    | 0.800 (0.008)    | -1.67 (0.15)   | -2.56 (0.34)    | -3.31 (0.28)               | -2.91 (0.22)    | -3.31 (0.28)    | -3.31 (0.28)               | 42.8 (9.8)      | 157.3 (9.8)     |  |  |
|                                  | combined   | 69.3 (4.7) B  | 53.9 (4.6) B  | 0.770 (0.013) AB | 0.774 (0.015) AB | -2.21 (0.20) B | -2.90 (0.24) B  | -4.22 (0.39) ns            | -4.02 (0.46) ns | -4.22 (0.39) ns | -4.22 (0.39) ns            | 53.2 (14.8) A   | 152.6 (10.3) A  |  |  |

browsed plots of *C. arboreus* when compared at the end of the summer 2008 dry season (Table 3 and Fig. 2; t-test, for site 2  $t = -0.233$ ,  $df = 25$ ,  $P = 0.826$ ; for site 3,  $t = 0.744$ ,  $df = 21$ ,  $P = 0.465$ ) nor when compared at the end of the summer 2009 dry season (t-test, for site 2,  $t = -0.532$ ,  $df = 25$ ,  $P = 0.599$ ; for site 3,  $t = 0.855$ ,  $df = 21$ ,  $P = 0.402$ ). Although there were significant differences between browsed and non-browsed plots of *C. arboreus* in some physiological traits, these differences were not greater than differences that were present between fenced and non-fenced plots for the other two species where browsing was not occurring (Table 3). Thus, these potential browse differences are difficult to separate from differences due to site heterogeneity. For cross-species comparisons, data from fenced and non-fenced plots have been pooled for most of the remaining results.

Seedling survival declined throughout the dry season, with seedlings at site 4 (*A. catalinae*) exhibiting the steepest decline (Fig. 2). Sites significantly differed in seedling survival following the 2008 summer dry season (Table 3, Fig. 2; ANOVA  $F_{3, 121} = 16.063$ ,  $P < 0.001$ ). The highest survival occurred at site 4, which was dominated by *C. megacarpus* ( $69.3 \pm 4.7\%$ ), followed by *C. arboreus* ( $50.0 \pm 4.7\%$  at site 2 and  $62.5 \pm 3.7\%$  at site 3), with the lowest survival at site 1, which was dominated by *A. catalinae* ( $29.6 \pm 4.5\%$ ). The survival of *A. catalinae* at site 1 was significantly lower than for the other three sites that were dominated by the other two species. A similar pattern remained following the second dry season in summer 2009 (Table 3, Fig. 2; Kruskal-Wallis Analysis of Variance on ranks,  $df = 3$ ,  $H = 39.987$ ,  $P < 0.001$ ). In October 2009, both *C. megacarpus* and *C. arboreus* ( $32.3 \pm 4.2$  at site 2 and  $56.0 \pm 4.6\%$  at site 3) had relatively high survival, and the lowest survival was again at site 1 where *A. catalinae* occurred. The survival of site 1 *A. catalinae* in October 2009 was significantly lower than site 4 *C. megacarpus* and site 3 *C. arboreus*, but was not different from site 2 *C. arboreus*. Lower initial densities combined with lower survival resulted in low post-fire seedlings densities for *A. catalinae* two years post-fire when compared to the other two species (Table 2).

Predawn and midday water potentials, stomatal conductance, and fluorescence differed between species and with season during the first two years post-fire (Table 3, Fig. 3). Of the three species, only *A. catalinae* exhibited a mean dark adapted fluorescence of  $< 0.75$  indicating it was experiencing some photoinhibition. The timing of the photoinhibition coincided with the greatest decline in seedling survival during the 2008 dry season suggesting that stress during the dry period was linked to mortality. During this same time, *A. catalinae* seedlings also displayed the lowest predawn (Kruskal-Wallis Analysis of Variance on ranks,  $df = 2$ ,  $H = 13.533$ ,  $P = 0.001$ ) and midday water potentials (Kruskal-Wallis Analysis of Variance on ranks,  $df = 2$ ,  $H = 10.322$ ,  $P$

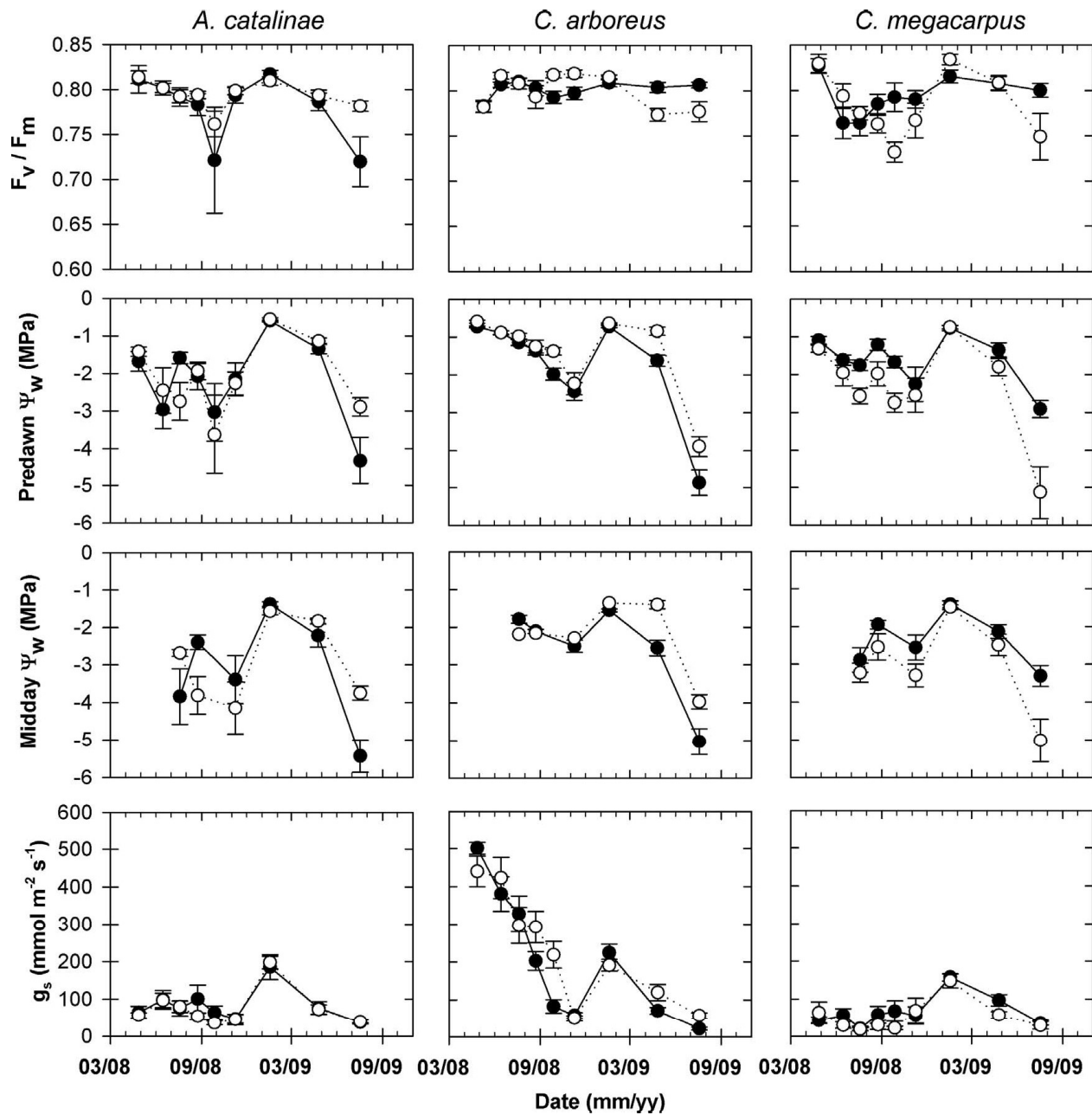


FIG. 3. Dark adapted fluorescence ( $F_v/F_m$ ), predawn and midday water potentials ( $\Psi_w$ ), and stomatal conductance of seedlings of three island endemic chaparral species or subspecies during the first two years post-fire during seedling establishment. Open symbols are from plots that were non-fenced and therefore open to potential browse activity and closed symbols are from plots that were protected from browse by tall fences. Symbols represent means  $\pm$  1 SE.

= 0.006). We also measured the lowest water potential value of the study in a very dry individual seedling of *A. catalinae* during summer 2008, including an individual with a water potential of -9.82 MPa predawn. Stomatal conductance was generally low for both *A. catalinae* and *C. megacarpus* seedlings and much higher in *C. arboreus* (Table 3, Fig. 3), which mirrored the differences in growth rates among these species (Fig. 2). *Arctostaphylos catalinae* was delayed the first year when compared to the other species, as indicated by a later peak in stomatal conductance, with a June peak in stomatal conductance (i.e.,

maximum seasonal  $g_s$ ) for *A. catalinae* compared to April for the other two species (Table 3, Fig. 3). Differences among species were less pronounced in the second year post fire for all physiological traits (Table 3, Fig. 3).

Vulnerability to cavitation varied among species, but did not vary with browsing in *C. arboreus*. The  $P_{50}$  of browsed versus non-browsed individuals of *C. arboreus* were not different (t-test,  $t = 0.738$ ,  $df = 10$ ,  $P = 0.478$ ); therefore, data from both browsed and non-browsed plants were pooled for comparisons among species. Vulnerability to water-stress induced

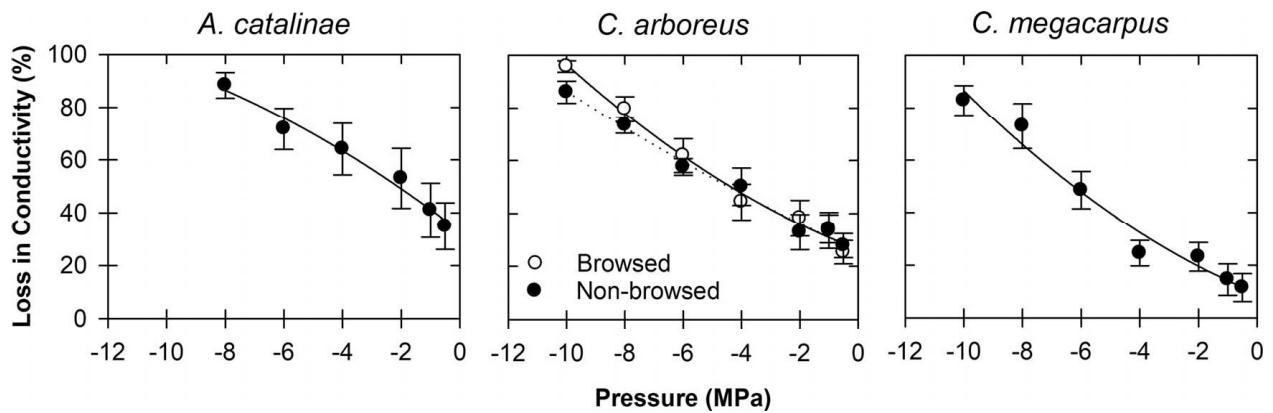


FIG. 4. Vulnerability to cavitation curves of seedlings of three island endemic chaparral species or subspecies. Open symbols are from seedlings that had been browsed and closed symbols are from seedlings that had not been browsed. Symbols represent means  $\pm$  1 SE. No browsed plants were measured from *A. catalinae* and *C. megacarpus*, because seedlings of these species were not being browsed at the time that samples were collected.

cavitation varied among species (Fig. 4; ANOVA,  $F_{2,21} = 4.787$ ,  $P = 0.016$ ). *Arctostaphylos catalinae* was significantly more vulnerable than *C. megacarpus* ( $P_{50} = -4.17 \pm 0.62$  compared to  $-6.74 \pm 0.60$  MPa,  $P < 0.05$ ) and *C. arboreus* was intermediate ( $P_{50} = -6.00 \pm 0.44$ ) and not different from the other two species ( $P > 0.05$ ).

#### DISCUSSION

Deer strongly favored *C. arboreus* seedlings and we observed very little browsing of the other two studied species, although deer were active at all sites and there was evidence of browse on co-occurring resprouting shrubs. Browsing activity on *C. arboreus* seedlings varied seasonally, with the greatest levels of browsing occurring during the summer dry season, presumably because of reduced browse options on the landscape. These high levels of deer browse are consistent with the nitrogen fixation capacity of this species and its high rates of growth (Herms and Mattson 1992).

Browsing did not significantly affect seedling mortality; however, browsing did significantly affect plant height, consistent with findings on post-fire seedlings of *Ceanothus* species on the mainland (Thomas and Davis 1989). The other physiological parameters that we measured, including water potential, stomatal conductance, fluorescence, and vulnerability to cavitation were not impacted by browsing. If browsing persists, seedlings will likely not be able to tolerate the high intensity of browsing that we observed in the long term (e.g., Ramirez et al. 2012); moreover, this browsing will dramatically impact stand structure and canopy coverage as stands mature. The effect of browse on carbon balance of plants, including the inability of the plants to develop a full photosynthetic canopy, may also make them more vulnerable to drought (Trifilò et al. 2017) and they will not be able to reproduce, thus no seed bank will form. Monitoring of these plots is ongoing as important plant/deer interactions are

occurring over long time scales. The large differences in canopy coverage between browsed and protected sites will likely affect island ecology (Ramirez et al. 2012), the flowering and fruiting of browsed populations (Dvorak and Catalano 2016), and plant physiological performance (Pittermann et al. 2014).

*A. catalinae* seedlings were not browsed and *C. megacarpus* experienced only limited browse during late summer 2009. The lack of browse for these species was likely related to two factors. First, the slower growth rates of these species meant that they were much shorter than *C. arboreus* seedlings and most resprouting shrubs as well. These results are consistent with post-fire deer browse of *Ceanothus megacarpus* and *C. spinosus* seedlings on the mainland (Thomas and Davis 1989). Thomas and Davis (1989) found that deer did not browse post-fire seedlings until the seedlings achieved a certain height. The undesirability of some species, particularly of *A. catalinae*, to the deer is likely linked to the small stature of their seedlings. As these plants grew taller, and after the completion of the present study, they later became targets of intense browse (Jacobsen and Pratt, unpublished data). For *C. megacarpus*, browse only occurred toward the end of the second summer when plants had grown substantially ( $> 40$  cm in height). However, this does not fully explain the pattern, since there were some individuals that were above the apparent minimum browse height that were not browsed.

A second possibility may be that *A. catalinae* and *C. megacarpus* are less palatable and therefore are not as preferred as *C. arboreus*, especially during the post-fire period when there are also other abundant herbaceous browse options available. Indeed, preference for *C. arboreus* has been previously described, although this was from a prior period on the island when goats and pigs, as well as deer, were present and potentially impacted vegetation patterns and browse behavior (Knapp 2005). If differential browsing pressure is maintained, it may have important consequences for long-term species abundances and



distributions on Santa Catalina Island for these island endemics.

Seedling survival levels differed between the three species, with most seedling mortality occurring during the first dry season post-fire. This is consistent with what has been described for chaparral seedlings germinating post-fire at mainland sites (Kummerow et al. 1985; Frazer and Davis 1988; Thomas and Davis 1989; Moreno and Oechel 1992). However, the initial densities of post-fire seedlings were much higher than reported for mainland sites (Keeley and Zedler 1978; Frazer and Davis 1988; Thomas and Davis 1989; Moreno and Oechel 1992). Our density values were especially striking when compared as initial ratios of pre-fire adult to post-fire seedling densities. Our values for *Ceanothus* species ranged between 5,218 to 19,617 compared to two mainland studies that ranged between 4.3 to 10.0 (Frazer and Davis 1988; Thomas and Davis 1989). This may be due to the long inter-fire period preceding the fire, which allowed abundant and long-lived seeds to build up in the soil seed bank. It is also likely that seed bank predators are absent in some areas of the island or are at low population densities, which allows large seed banks to persist. Seedling densities remained quite high at the conclusion of the present study. Additional thinning has occurred at the sites and will presumably continue as the stand matures (Hanes 1971; Schlesinger and Gill 1978).

In contrast to the pattern we observed with respect to seedling densities, our sites on the island showed much lower densities of pre-fire adults than those previously reported on the mainland (Schlesinger and Gill 1978; Keeley and Zedler 1978; Mills 1986; Frazer and Davis 1988; Thomas and Davis 1989; Moreno and Oechel 1992). This may be because island plants do not live as long as mainland plants, although we are not aware of any prior data supporting this potential explanation. It may also be due to a long fire-free period on the island prior to the current fire, as low adult densities and relatively high seedling to parent ratios have been described for ancient mainland chaparral sites (Keeley et al. 2005). Alternatively, it may be due to impacts from introduced herbivores in the long fire-free period prior to the current study. Although mule deer and bison (*Bison bison* L.) are the only large introduced mammals currently on the island, the island has also hosted introduced cattle (*Bos taurus* L.), sheep (*Ovis aries* L.), goats (*Capra hircus* L.), and pigs (*Sus scrofa* L.) within the last century. Goats and pigs, in particular, were documented to have large impacts on the Santa Catalina Island vegetation, even in the absence of fire (Coblentz 1977; Schuyler et al. 2002; Knapp 2005). In the absence of these large mammalian herbivores, the predicted mature shrub densities for protected plots is thus difficult to estimate, although a range of 0.4 – 6 individuals per m<sup>2</sup> would be consistent with previous studies from the mainland. *Arctostaphylos catalinae* seedling densities already fall within this range, just two years post-fire.

Differential dry season survival appears to be related to differences in drought tolerance and physiology at the seedling stage when rooting depths are shallow causing seedlings to be especially prone to dehydration. The *A. catalinae* seedlings at site 1 exhibited the lowest survival through the first dry season as well as the second dry season. This species was also the most vulnerable to water-stress induced hydraulic failure and experienced the most negative water potentials. Consistent with these patterns,  $F_v/F_m$  values for *A. catalinae* were significantly lower than for the other two species suggesting that plants were experiencing greater stress (Venturas et al. 2016; Guadagno et al. 2017). Lower survival for this species is consistent with a previous study that found that  $P_{50}$  was a strong predictor of chaparral seedling dry season survival (Pratt et al. 2008), with the most vulnerable species displaying the highest mortality. This is also consistent with increased water stress of seedlings due to decreased rooting depth and extent compared to resprouts and mature plants (Frazer and Davis 1988; Thomas and Davis 1989; Clemente et al. 2005; Padilla and Pugnaire 2007). Additionally, *A. catalinae* seemed relatively vulnerable to dehydration-induced vascular damage while the *Ceanothus* spp. did not. The  $P_{50}$  for the two *Ceanothus* species were similar or only slightly more vulnerable than values reported for mainland adults and seedlings of *Ceanothus* (Jacobsen et al. 2007; Pratt et al. 2007; Pratt et al. 2008; Jacobsen et al. 2014), whereas the  $P_{50}$  for *A. catalinae* was more vulnerable than previously reported for 9 *Arctostaphylos* species (Jacobsen et al. 2007; Jacobsen and Pratt 2013). Thus, higher mortality for *A. catalinae* seedlings is consistent with its vulnerability. An important caveat to the present study is that different species were sampled at only one or two sites within the post-fire burn area and, especially for *A. catalinae* seedlings, it may be that they are able to survive in higher numbers in more favorable microsites.

In conclusion, although browsing by introduced mule deer has resulted in large reductions in the height of browsed seedlings, this has not yet resulted in impacts on seedling survival or physiology. Species differ in their physiology, and *A. catalinae*, appears to be the most sensitive to dehydration stress of the three examined species and may be particularly threatened by the occurrence of drought during the post-fire recovery period. This species also began with the lowest seedling densities and experienced the greatest seedling mortality, suggesting that it may be particularly at risk. Longer term monitoring will be required to determine whether browsing by introduced mule deer impacts stand composition during the typical thinning phase that occurs with the transition to stand maturity.

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