FLOWERING, FRUIT SET, AND SEED PREDATION IN ARCTOSTAPHYLOS MORROENSIS, A RARE OBLIGATE-SEEDING SHRUB

Authors: Tyler, Claudia M., Meade, Daniel E., and Odion, Dennis C.

Source: Madroño, 70(4) : 197-209

Published By: California Botanical Society

URL: https://doi.org/10.3120/0024-9637-70.4.197

MADROÑO, Vol. 70, No. 4, pp. 197–209, 2023

FLOWERING, FRUIT SET, AND SEED PREDATION IN *ARCTOSTAPHYLOS MORROENSIS*, A RARE OBLIGATE-SEEDING SHRUB

CLAUDIA M. TYLER
Earth Research Institute, University of California Santa Barbara, CA 93106
tyler@ucsb.edu

DANIEL E. MEADE
Althouse and Meade, Inc., 1602 Spring Street, Paso Robles, CA 93446

DENNIS C. ODION
Earth Research Institute, University of California Santa Barbara, CA 93106

ABSTRACT

Obligate seeding plants—those that are killed by fire and whose persistence depends on soil-stored seedbanks—may be particularly susceptible to indirect effects of habitat loss and fragmentation. Especially for rare species, fragmentation can create conditions that reduce the likelihood of achieving sufficient seed bank stores due to changes in the interactions of the remaining plants with their pollinators or their natural enemies such as herbivores or seed predators. *Arctostaphylos morroensis* (Morro Manzanita) is an endemic obligate seeder whose distribution has been reduced greatly to a small portion of coastal California in habitat that is fragmented by development. We examined the reproductive ecology of *A. morroensis* to determine the factors that affect seed input to the soil seed bank. In stands of different ages and percent cover of Morro Manzanita, we observed insect pollinators, and measured flower and fruit production, and rates of fruit predation over two years, hypothesizing that, based on previous literature on obligate-seeders, fruit set should be relatively high across all stands, fruit set should be resource-limited, and seed input should be relatively high. Our observations suggest that *A. morroensis* reproduction is dependent on pollinators, which were primarily bees. Contrary to our predictions, we found that fruit set was relatively low (averaging 10–18% over both years) at all stands and appears to be pollinator-limited. Fruit predation rates were high, with the majority of fruits in experimental trays removed in a matter of weeks. We suspect that seed input in this rare species is strongly limited by low fruit set and high seed predation.

Key Words: chaparral, flower production, fruit predation, habitat fragmentation, Manzanita, plant reproduction, pollination biology, pollinator-dependent.

When plant populations decline due to habitat loss, frequently both the remaining habitat and the associated populations are fragmented. Consequences of such fragmentation may include changes in the interactions of the remaining plants with their pollinators or with their natural enemies such as herbivores or seed predators, which may become either concentrated or scarce (Rathcke and Jules 1993; Jules 1998; Cunningham 2000; Aizen and Feinsinger 2003; Aguilar et al. 2006). If these “islands” of remaining habitat are in fire prone systems, such as those common to Mediterranean climates, the process of fragmentation can also alter the fire regime, leading to changes in the structure and composition of the plant communities in these patches (Zedler et al. 1983; Keeley and Fotheringham 2003; Regan et al. 2010).

Plant species native to fire prone systems have evolved traits that allow them to persist with and even depend upon fire. Some woody or shrub species have the ability to resprout following fire, while others are non-sprouters that rely on postfire establishment of seedlings from a long-lived dormant seed bank (Wells 1969; Keeley 1991; Whelan 1995). The latter are “obligate seeders”, a relatively uncommon life history type found mostly among shrubs in semiarid areas in California, Australia, and South Africa (Bond and van Wilgen 1996). Because the timing of death and reproduction of obligate seeders is associated with fire, their life history is considered to be an evolutionary response to fire (Wells 1969). Since the adults are consumed by fire, the persistence of populations of obligate seeders is dependent on the sufficient accumulation of viable seed in the soil seed bank in the interval between fires. In contrast, populations of shrub species that sprout from underground burls (i.e., resprouters or “facultative seeders”) primarily persist through periodic fire because adults generally survive, resprouting vigorously, while seedlings germinate and establish at low densities, especially in comparison to obligate-seeder congeners (Jepson 1916, Keeley 1977, Keeley and Zedler 1978).

Obligate seeders, especially those that are rare or in decline, may be especially susceptible to indirect effects of habitat loss and fragmentation. Seed input is critical to their persistence, yet fragmentation can create conditions that reduce the likelihood of achieving seed bank stores sufficient to replenish the population following fire. These conditions include reduced fruit and seed production due to reduced pollen flow/transfer or inbreeding depression (Thomson and Thomson 1989; Glemin et al. 2001; Willi et al. 2005; Scobie and Wilcock 2009), increased herbivory or seed predation due to concentration of natural enemies (Klinger and Rejmanek 2009), and greatly altered fire frequencies—either reduced or increased. In fire prone systems, such as the chaparral shrublands in California, habitat fragmentation caused by roads and residential development can potentially increase fire frequency because of greater chances of accidental or intentional anthropogenic ignitions (Keeley and Fotheringham 2003; Syphard et al. 2007), or increased abundance of weedy annuals that supply fine fuels (Mack and D'Antonio 1998), or active management to burn in order to reduce biomass of woody vegetation in wildlands adjacent to residences (Dunn 1989; Baeza et al. 2002). Greatly increased fire frequencies could negatively affect obligate seeding populations, even causing local extinctions, by reducing the period necessary for adequate seed accumulation (Keeley et al. 1999; Odion and Tyler 2002; Regan et al. 2010). At the same time, it is possible for fragmentation to lead to decreased fire frequency, particularly in small patches embedded in residential development, due to stringent fire suppression policies, even restricting prescribed burns, for fear of wildfire spread to developed parcels. If fire frequencies decreased greatly, stands could become senescent, and though the seeds are long-lived, viable seed densities in the soil seedbank could decline over time, reducing the potential for mass postfire seedling recruitment (Keeley 1992; but see Franklin et al. 2005).

The genus *Arctostaphylos*, or Manzanita, includes approximately 62 species, or including subspecies ~104 taxa worldwide, and the majority of these are obligate seeders (Parker et al. 2012). Over 90% of Manzanita species are endemic to California or adjacent areas. While they are major components of fire-prone vegetation such as chaparral (as overstory), and montane coniferous forest (as understory), many *Arctostaphylos* species are rare, narrow endemics with localized distributions (Stebbins and Major 1965; Parker 2007). One example is *Arctostaphylos morroensis* Wiesl. & B.Schreib (Morro Manzanita), an obligate seeder that is the dominant shrub species where it occurs, but whose highly localized distribution has been further reduced to a small portion of coastal California in habitat that is fragmented by development. Although relatively little is known about its ecology or reproductive biology (but see Mullany 1990; Odion and Tyler 2002; Tyler and Odion 2020), other *Arctostaphylos* species have been well-studied in California, providing useful comparative information with which to assess reproductive output and possible signs of reproductive stress due to habitat fragmentation. For example, given their dependence on a persistent and large seed bank for post-fire establishment, it is not surprising that, compared to resprouting congeners, obligate seeding *Arctostaphylos* species have been found to allocate more resources to flowering and seed production, and have higher fruit set, fruit production, and seed set overall (Keeley 1977; Keeley and Keeley 1977; Fulton and Carpenter 1979). Other *Arctostaphylos* species have been reported to depend on insects for pollination (Brum 1975, Fulton and Carpenter 1979)—a critical interaction that could be negatively affected by reduced patch size and isolation. However, dependence on external pollinators itself does not imply pollen or pollinator limitations to fruit production or fruit set for a species or individual populations. While there are potentially multiple limiting factors, studies of fruit production in *Arctostaphylos glauca* Lindl. and *A. glandulosa* Eastw. suggest that it might instead be resource-limited, as fruit production was positively related to rainfall in the preceding year (Keeley 1977) or level of available carbohydrates at time of fruit maturation (Keeley and Keeley 1988).

In this study we examined the reproductive behavior of the obligate-seeding *Arctostaphylos morroensis* to determine the factors that affect seed input to the soil seed bank. In stands of different ages and degrees of isolation, we observed insect pollinators, and measured flower and fruit production, and rates of fruit predation. Consistent with predictions about obligate seeders and previously published findings, we hypothesize that fruit set should be relatively high across all stands, fruit set should be resource-, rather than pollinator-limited, and seed input should be relatively high.

METHODS

Study Species

Arctostaphylos morroensis is an erect evergreen shrub in the heath family, Ericaceae (Fig. 1). It can be distinguished from other species of Manzanitas in the vicinity by its persistent shreddy gray bark, densely hairy lower leaf surfaces and leaf bases that are truncate to somewhat cordate (Kauffmann et al. 2021). Individuals, normally one to four meters in height, can become arborescent with old age. In *Arctostaphylos* nascent inflorescences are produced at the ends of new stems in late spring, and lie dormant for five to ten months (Weislander and Schreiber 1939; Wells 1999; Parker et al. 2012). In the following winter through early spring, these develop and produce dense clusters of urn-shaped flowers (Fig. 1). If fertilized, the flowers yield fruits (drupes), which ripen on the stem and drop in summer. The fruit, covered by a thin exocarp, contains a mealy mesocarp and a hard, bony endocarp enclosing multiple seeds (Meyer 2008; Parker et al. 2012).

Surveys of existing stands, dendrochronological evidence, and historical air photos indicate that

FIG. 1. *Arctostaphylos morroensis* at Dune and Hazard Canyon sites. A. Individual shrub within the maritime chaparral community. B. Inflorescence. C. *Apis mellifera* on *A. morroensis* flower. Photographs by Peter Slaughter, 2023.

present stands of *A. morroensis* are even-aged, dating back to the previous fire (Tyler and Odion 1996). Young individuals (seedlings or saplings) are rare in, or adjacent to, mature stands (Tyler and Odion 1996). These observations, in addition to *A. morroensis* being an obligate seeder, suggest that fire plays a crucial role in the establishment and persistence of this species.

This species of Manzanita is a narrow endemic restricted to a small portion of coastal area in San Luis

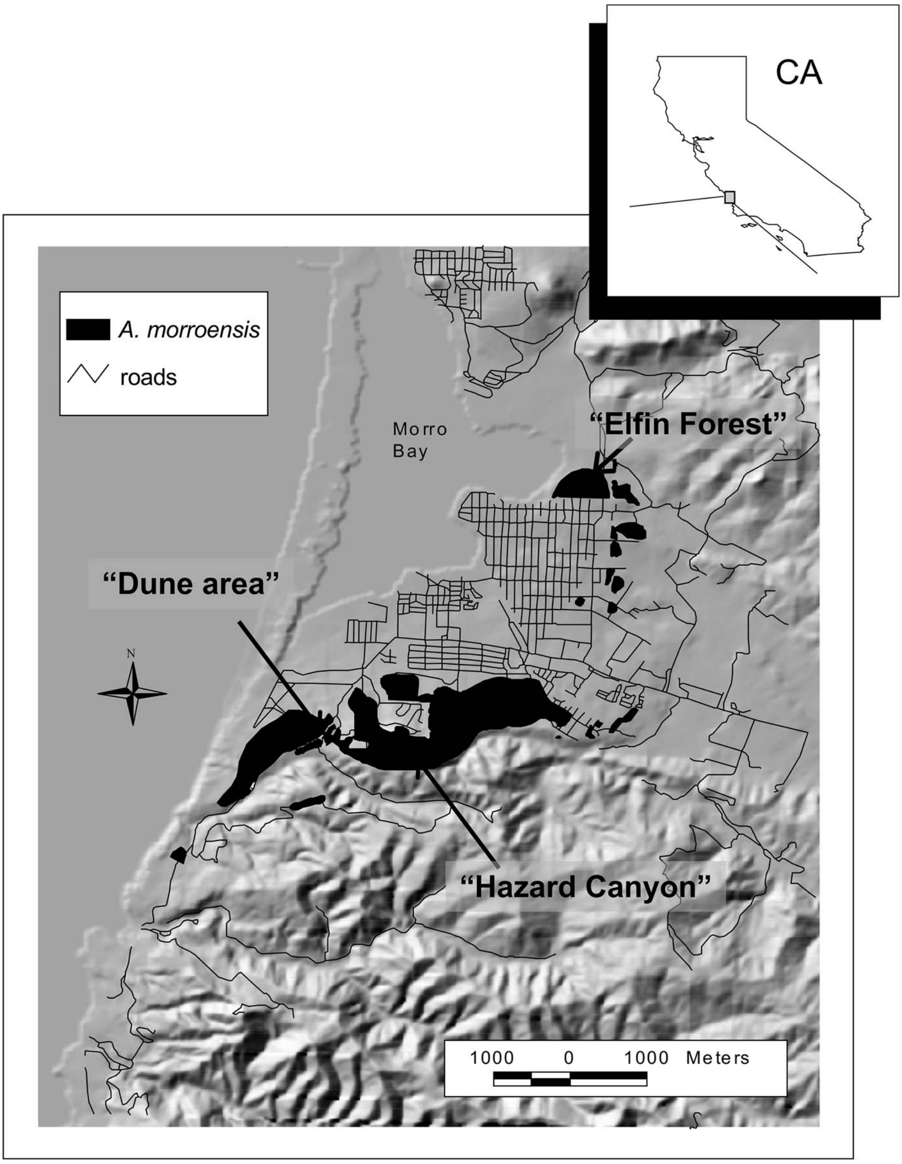

FIG. 2. Range map of *Arctostaphylos morroensis* (in black) and location of sites sampled. Center of range approximately 35.301, −120.844.

Obispo County, California. Here, an area totaling ~350 ha (865 acres) supports from 1–100% cover of the shrub amid maritime chaparral (Fig. 2). It was listed as a threatened species by the U. S. Federal government in 1994.

Site Descriptions

Studies were conducted in 1998–1999 near the southern portion of Morro Bay, San Luis Obispo County, California, USA (35.301, −120.844 Fig. 2). Substratum of the sites is Pleistocene eolian sand mapped as Baywood fine sandy loam (Tyler and Odion 1996). The climate is Mediterranean, with mild, dry summers and cool, moist winters. Fog is common. Mean annual rainfall (as recorded at the Morro Bay Fire Station) is 42.1 cm (Fig. 3), with 75% occurring between November and April.

We focused on three different sites that reflected a range of *A. morroensis* cover classes and stand age (Fig. 2). The first site was a dune area in Montaña de Oro State Park. This site was a mix of maritime chaparral and coastal sage scrub; co-dominants included *Ceanothus cuneatus* (Hook.) Nutt.and *Ericameria ericoides* (Less.) Nutt. ex Jeps. The percent cover of *A. morroensis* ranged from 25–50% to 75–100% (Mullany 1990).

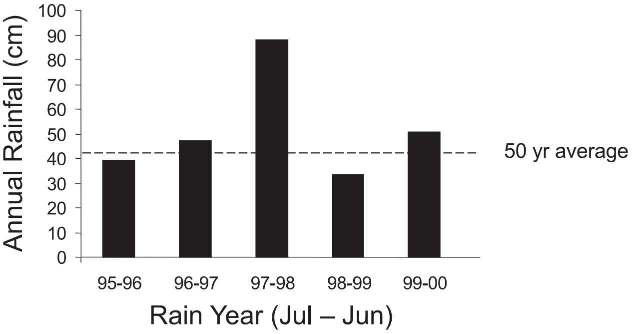

FIG. 3. Annual rainfall for years included in this study (1995–2000) at the Morro Bay Fire Station (35.386, −120.856), located approximately 3 km from the study sites. Dashed line indicates 50-year mean annual rainfall (42.1 cm). Rain years run from 1 July to 31 June.

The stand age was estimated to be 40 years in 1999, based on historical aerial photographs and ring counts of obligate-seeding shrubs present in the stand (Tyler and Odion 1996).

The second site was north of Hazard Canyon, also in Montaña de Oro State Park, relatively close (<400m) to site 1, but farther inland and upslope. This site was a mix of *Quercus agrifolia* Née and dense *A. morroensis*. The percent cover of *A. morroensis* ranged from 50–75% to 75–100% (Mullany 1990). This stand of Manzanita is intermediate in age between sites 1 and 3, and was ≥ 47 yrs old in 1999, also based on historical aerial photographs and stem ring counts.

The third site was the Elfin Forest Natural Area. This area was a mix of maritime chaparral (with *Ceanothus cuneatus* and *Adenostoma fasciculatum* Hook. & Arn.), coastal sage scrub (with *Ericameria ericoides*, *Salvia mellifera* Greene, and *Artemisia californica* Less.), and oaks (*Quercus agrifolia*). The percent cover of *Arctostaphylos morroensis* was low, ranging from <1% to 5–25%, with considerable open space (10–60% cover bare ground). The Manzanita stands at this site were older than 50 years in 1999, with no evidence of burning or clearing observed on available historical aerial photographs, starting in 1949. Some individual Manzanitas at this site appeared to be very old, as they were large and arborescent with canopy heights up to 7.5 m high and db of 1 m. Unlike in the other sites, here we found large dead *A. morroensis*, indicating that individuals in this stand might be approaching the age of natural shrub senescence. This stand is also relatively isolated, as it is separated from the other two sites by residential development (Fig. 2).

Self-pollination

To determine whether *A. morroensis* is capable of self-pollination, inflorescences were bagged to exclude all pollinators. Open flowers were removed from the inflorescence prior to bagging and closed buds were counted. Bags were left in place until all of the flowers within the bag had senesced. The stems were then examined for fruit.

In 1998 a total of 1243 flowers on 14 plants were bagged to exclude cross pollination. Inflorescences were covered beginning on March 3, 1998, until all of their flowers dropped their corolla. In 1999 flowers were selected at an earlier developmental stage to ensure that all of the bagged flowers did not receive pollen before being enclosed; a total of 226 flowers on 15 plants were bagged to exclude cross pollination. Inflorescences were covered beginning on February 24, 1999, until all of their flowers dropped their corolla.

Pollinators

Pollinators were observed during March–April 1998, and February–May 1999. Insect specimens were captured using nets and collected for identification. Counts of pollinators visiting plants were recorded for each site. In 1998, we conducted a total of 22 observation periods of at least 10 minutes per period over seven different days. In 1999, a total of 17 observation periods were conducted over six different days for a total of 890 minutes. Observations were made at multiple shrubs, selected haphazardly, across sites.

Flower and Fruit Production, and Fruit Set

To examine fruit set, plants were selected haphazardly within each site—six plants per site in 1998 and ten per site in 1999. Ten stems that were new in bud were selected and banded for identification on each plant. Stems were followed weekly to determine the cumulative number of buds and subsequent flowers produced by the stem from February through April. Fruits were counted on stems from March through the first week in June in 1998 and from March through September in 1999. The counts of flowers and fruit on the ten stems on each plant were used to determine a mean value for flower number and fruit number per stem for each plant. This mean value per plant was used for analysis (i.e., sample size per site was six in 1998 and ten in 1999). The ratio of fruit number to flower number was calculated to determine the average fruit set per plant. We used one-way analysis of variance (ANOVA) to detect statistically significant differences in flower production, fruit production and fruit set among study populations.

Estimate of Mature Fruit Reaching the Soil

The average number of fruits falling from a plant was estimated by placing trays under each of the six plants at each site. When possible (i.e., an individual plant's canopy was distinct from adjacent vegetation), four trays were placed under the outer canopy edge of each plant in each of the compass quadrants. In some cases, a plant was at the edge of a dense cluster of other Manzanitas, with overlapping canopies; here we were only able to place trays at one or two of the plant's clearly defined canopy edges. Trays were 25 cm by 25 cm. They were constructed of wood frames, wire screen bottoms, and hardware cloth tops that were slightly v-shaped; the top was contoured in this way so that fruits hitting the cage would roll toward the center and fall into the tray. Thus, once the fruit entered the tray rodents were excluded. Fruit falling into the trays was used to estimate the mean number of fruits that reached the ground per 0.625 m^2, under each study plant. Fruits in the trays were counted and emptied throughout the spring and summer until no fruit remained on the plant. The total number of trays placed in the field was 72 in1998, and 70 in 1999.

Fruit and Seed Predation

We examined the effect of vertebrate predators on fruit survival and whether there are differences in the intensity of predation beneath versus away from the canopy/cover of the shrub. We used three treatments to determine the rate of fruit removal from trays in which known numbers of fruit were placed. These treatments were: 1) under the plant canopy and screened to prevent vertebrate predator access, 2) under the plant canopy and open to predators, and 3) away from the plant canopy (1–3 m from canopy edge) and open to predators. The first treatment served as a control to determine if fruits were either lost to a factor other than vertebrate predators, or if fruits were added to the trays via fruit drop from the shrub. The trays were rectangular 10 cm by 20 cm, and 3 cm high, made of a wood frame with a screen bottom; those that prevented predators (treatment 1) had hardware mesh tops. Ten mature fruits were placed in each tray; trays were placed in association with each of the six study plants at each of the three sites. The number of fruit and seeds remaining were counted at approximately weekly intervals for six weeks. In both years the experiment was initiated when natural fruit drop was first recorded: in 1998 on June 2nd, and in 1999 on April 14th.

RESULTS

Self-pollination

In 1998, the vast majority (99%) of bagged flowers did not set fruit; however, eight out of 1243 flowers did set fruit. We hypothesized that these eight flowers had already opened and been pollinated before being bagged. Thus, during the following year's study in 1999 flowers were selected at an earlier developmental stage to ensure that none of the bagged flowers received pollen before being enclosed. In 1999 no bagged flowers set fruit.

Pollinators

In both years the pollinators most often observed visiting *A. morroensis* flowers were yellow-faced bumblebees (*Bombus vosnesenskii*). In 1998, during 18 out of the 22 observation periods only bumblebees were observed. The other bees observed were the common anthoporid bee, *Anthophora urbana*, and halictid bees. Other pollinators that were observed visiting *A. morroensis* flowers at least once were a *Colletes* sp., a Syrphid fly, a Monarch butterfly (*Danus plexxipus*), and several bee flies (family Bombyliidae, *Bombylius* sp.).

The most striking observation in both years was the paucity of pollinators on *A. morroensis* blooms, even on warm, sunny days. During the observation periods, which ranged from 5 to 120 minutes, approximately half of the periods had no pollinator visits on *A. morroensis*, even when abundant blooms were present. For the remainder of the periods, the most frequent number of pollinator visits was 1 per observation, but there were a few observations when we recorded 3 to 4 pollinator visits to *A. morroensis*.

Flower and Fruit Production, and Fruit Set

In 1998 the mean number of flowers produced per stem per plant ranged from 80 to 135, and fruit production averaged between 8–12 fruits per stem (Table 1). There was wide variation within the sites and no statistically significant differences among the sites in either flower (ANOVA, P = 0.243, F = 1.556, df = 2,15) or fruit production (ANOVA, P = 0.516, F = 0.691, df = 2,15). Fruit set over all study populations was low, averaging 10.0% (Fig. 4). The Hazard Canyon site had less than half the fruit set of the Dune site, due to both higher flower production and lower fruit production at Hazard Canyon. However, this difference in fruit set was not statistically significant (ANOVA, P = 0.125, F = 2.398, df = 2,15).

In 1999 the mean number of flowers produced per stem per plant ranged from 52 to 66 (Table 1), roughly half that produced in the previous year. However, fruit production was only slightly below that in the previous year, and averaged between 5–10 fruits per stem (Table 1). We detected no statistically

TABLE 1. REPRODUCTIVE OUTPUT IN *A. MORROENSIS*: NUMBERS OF FLOWERS AND FRUITS PER STEM (I.E., PER INFLORESCENCE), AND FRUITS DROPPED PER 0.0625 M^2 AT EACH STUDY SITE. Data are means (plus one standard error). Also given are the numbers of shrubs (n) sampled per site, and the P-values resulting from one-way analysis of variance to detect differences among sites for a given parameter in each year.

Year	Site	# Flowers/stem (SE)	# Fruits/stem (SE)	# Fruits dropped per 1/16 m^2 (SE)
1998	Dune area	111.3 (31.0)	11.6 (3.4)	23.8 (6.7)
	Hazard Canyon	134.6 (21.1)	8.0 (2.0)	10.8 (2.4)
	Elfin Forest	79.6 (8.1)	8.8 (0.7)	16.5 (3.0)
	n per site =	6	6	24
	P =	0.243	0.516	0.128
1999	Dune area	65.7 (11.4)	9.3 (2.5)	9.9 (2.5)
	Hazard Canyon	51.8 (8.3)	10.4 (2.5)	15.3 (2.7)
	Elfin Forest	54.2 (9.4)	5.2 (1.2)	8.5 (3.0)
	n per site =	10	10	24
	P =	0.567	0.218	0.181

significant differences among the sites in either flower (ANOVA, P = 0.567, *F* = 0.580, df = 2,27) or fruit production (ANOVA, P = 0.218, *F* = 1.615, df = 2,27). Fruit set across all study populations averaged 18% (Fig. 4). Although the Hazard Canyon site had twice the fruit set of the Elfin Forest site, there was high variation within sites, and this difference was not statistically significant.

Interestingly, the patterns observed differed between the two years. At all sites, flower production was nearly twice as high in 1998—a year of twice average rainfall—as in the following year, when rainfall was below average. However, at two of the three sites, the Dune area and the Elfin Forest, fruit set was comparable within each site over the two years, despite the very different rainfall and flower production. At the third site, Hazard Canyon, fruit set varied greatly between the years and was almost five times higher in 1999 than in 1998.

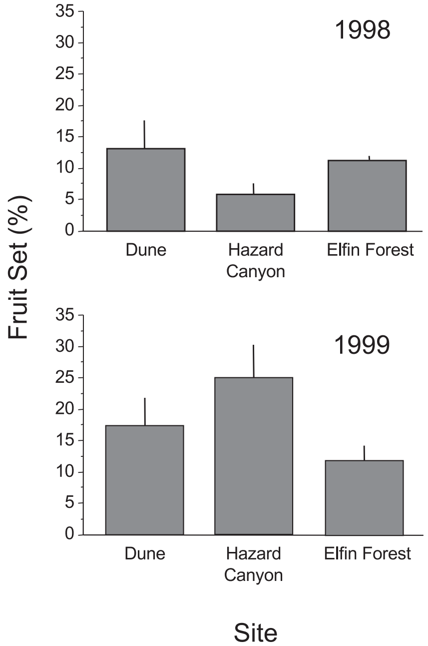

FIG. 4. Differences in fruit set (% of flowers that produced fruit) among study populations in 1998 and 1999. Data are means (+ 1 s.e.) of 6 plants per site in 1998, and 10 plants per site in 1999.

Estimate of Mature Fruit Reaching the Soil

In 1998 fruit drop began in early June, and the majority of fruits fell from the plants during June and early July. Of the total 1223 fruits collected at all sites (through September 1998), 93% were collected by mid-July. Combining all sites, shrubs dropped an average of 17 fruits per tray (area = 0.0625 m^2), or 272 per m^2. There was no significant difference among sites in the number of fruits reaching the ground (P = 0.128, *F* = 2.115, df = 2,69) (Table 1).

In 1999 though fruit drop began in mid-April, the majority of fruits fell from the plants between August and early October—much later than in the previous year. Of the total 808 fruits collected at all sites (through October 1999), only 46% were collected by mid-August. Combining all sites, shrubs dropped an average of 12 fruits per tray (area = 0.0625 m^2), or 185 per m^2. There was no significant difference in the number of fruits reaching the ground among sites (P = 0.181, *F* = 1.750, df = 2,69). The site with the greatest number of fruits produced per stem also had the highest number of fruits dropped—the Hazard Canyon site. However, in the previous year this site had the lowest number of fruits produced and dropped. At the other two sites, Dune and Elfin Forest, fruit drop was correlated with flower production: in 1998 when the number of flowers per stem was twice as high compared to 1999, fruit drop was also roughly twice as high.

Fruit and Seed Predation

In both years predators removed a significant number of fruits and relatively quickly—from 60–70% within a month and a half. In 1998 combining all sites, after 46 days there was an average of 4 fruits

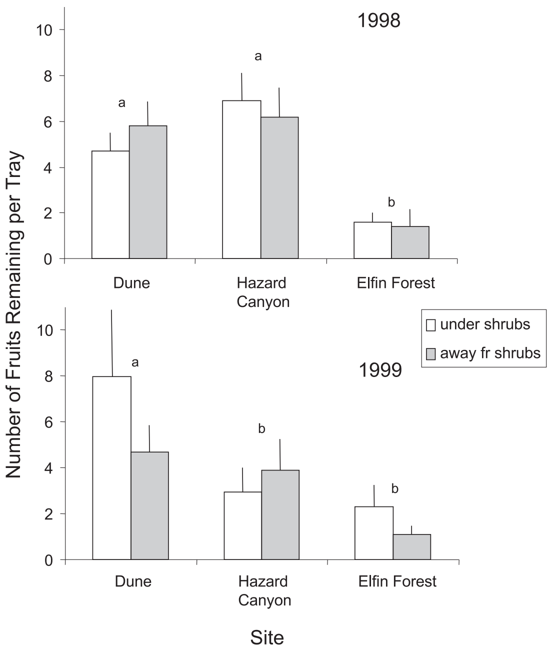

FIG. 5. Loss of fruit due to predation. Shown are numbers of fruit remaining (out of 10) in open trays at 3 sites, under shrub canopy and 1–3m away from shrubs. Data are means (+ 1 s.e.) on sampling dates when approximately half of the fruits had been removed overall in that year: 1998, 46 days after study initiation; 1999, 26 days after study initiation. Different letters above bars indicate a significant difference between sites in that year.

remaining per tray in both open treatments (i.e., predators present) compared to 11 fruits in the controls (ANOVA, $P < 0.001$, $F = 40.591$, df = 2,87; posthoc Scheffe test indicate that both open treatments were significantly lower than the control, but not different from each other). Similarly, in 1999 with all sites combined there was an average of 3 fruits remaining per tray in both open treatments compared to 10 fruits in the screened controls (ANOVA, $P < 0.001$; posthoc Scheffe test indicate that both open treatments were significantly lower than the control, but not different from each other); however, in 1999 this removal of a similar number of fruits occurred much sooner than in the previous year—after only 26 days.

To determine whether seed predation varied among sites and location (i.e., under canopy vs. away from canopy) we conducted two-way analyses of variance (Fig 5). We found no "location" effect in either year, i.e., there was no significant difference in loss of fruit in trays that were underneath versus away from plant canopies for all sites (2-way ANOVA, location: $P > 0.500$ in both years). However, in both years, predation rate varied among sites (Fig. 5). In 1998 the number of fruit lost to predation was significantly higher at the Elfin Forest site (mean predation rate = 85%) than at the other two sites (2-way ANOVA, site: $P < 0.001$). There was no significant difference between the Hazard Canyon and Dune sites (mean predation rates = 35% and 48%, respectively). In 1999, the number of fruit lost to predation was significantly higher at the Elfin Forest and Hazard Canyon sites (mean predation rates = 83% and 66%, respectively) than at the Dune site (mean predation rate = 37%). There was no significant difference between the Elfin Forest and Hazard Canyon sites. We found no location by site interaction in either year indicating that patterns of seed predation in relation to shrub cover did not differ significantly among all sites (2-way ANOVA, location by site interaction: 1998, $P = 0.632$; 1999, $P = 0.179$). Overall, the site with the highest fruit predation rates was the Elfin Forest—the eldest stand with the largest *A. morroensis* individuals.

Although we did not trap or use similar methods to identify or quantify the abundance of small mammal species in these sites, we made several observations that indicate the presence of woodrats (*Neotoma fuscipes*) and brush rabbits (*Sylvilagus bachmani*). Rat feces were deposited in several trays, and large wood rat nests were nearby, notably in the Elfin Forest. We also found scat of brush rabbits in some trays at the Elfin Forest site only.

Seed Input

We used our data on fruit drop, fruit predation, and previous data on numbers of seeds per fruit (Tyler and Odion 1996) to estimate the annual contributions to the soil seed bank under shrub canopies (Table 2). The addition of seeds to the soil seed bank ranged considerably over the two years from 248 to 1608 seeds/m^2, but the relative addition of seeds was similar within sites across both years. The estimated number of seeds added to the Dune site was highest,

TABLE 2. ESTIMATES OF NUMBERS OF SEEDS ADDED TO THE SEED BANK IN 1998 AND 1999 AT THREE STUDY SITES. This estimate was derived with the following formula: (number of fruits dropped per m^2 – number of fruits lost due to predation) × (number of seeds per fruit). Average number of seeds per fruit is eight (Tyler and Odion 1996).

	1998			1999		
Site	# Fruits per m^2	% Loss due to predation	# Seeds added per m^2	# Fruits per m^2	% Loss due to predation	# Seeds added per m^2
Dune	379	47	1608	158	20	1008
Hazard Cyn	173	34	912	245	68	624
Elfin Forest	263	85	316	136	77	248

moderate at the Hazard Canyon site, and lowest at the Elfin Forest.

DISCUSSION

We found that maximum fruit set in *Arctostaphylos morroensis* required pollinators; in fact, when they were excluded before any inflorescences had opened (in year 2), no fruit set occurred. Though in our first year, a few of the bagged flowers (0.6%) did set fruit, we suspect that these had already been pollinated by insects prior to bagging. Based on our results, we cannot rule out the possibility that these few flowers self-pollinated, but even if they did, and if indeed *A. morroensis* is self-compatible, the rates of fruit set would be exceptionally low in the absence of pollinators. The dependence of *A. morroensis* on pollinators for successful reproduction is consistent with previous studies that demonstrated self-incompatibilty in *A. pringlei* var. *drupacea* (Parry) P.V. Wells and *A. glauca* Lindl. (Brum 1975) and in *A. pungens* Kunth (Richardson and Bronstein 2012).

We found that the most frequent pollinators were bees, particularly bumblebees. Bees have been shown to be important pollinators in other Ericaceae (Cane et al. 1985; Kasagi and Kudo 2003) including *Arctostaphylos* congeners (Gankin and Major 1964; Brum 1975; Fulton and Carpenter 1979). Recent observations (January 2023) of pollinators visiting *A. morroensis* flowers at the Elfin Forest and Hazard Canyon sites included Anna's hummingbirds, *Calypte anna*, and numerous European honeybees, *Apis mellifera* (Fig. 1) (Tyler unpublished data). Since the latter were never recorded in the pollinator studies conducted in 1998 and 1999, they may represent naturalized honeybee colonies. Given that European honeybees compete with native bees (Goulson 2003) this development could have implications for native bee communities in the area as well as the plant species dependent on them, and warrants further investigation.

As might be expected given its need to attract insect pollinators and to accumulate sufficient seed bank stores, *A. morroensis* produced abundant flowers—from 50–135 per stem. Other obligate seeders have been shown to allocate significant resources to flowering and to attracting pollinators, especially compared to congeners that resprout (Carpenter and Recher 1979; Fulton and Carpenter 1979). For example, *Arctostaphylos pringlei* Parry, an obligate-seeder, produces significantly more flowers per unit plant size and attracts close to two times the number of pollinator visits compared to the resprouting *A. glandulosa* Eastw. (Fulton and Carpenter 1979).

For *A. morroensis* flower production was especially high in a wet year—nearly twice as many flowers were produced per stem in 1998, an El Niño year with rainfall two times the average, compared to the following year when rainfall was below average. Similarly, the subsequent number of fruits produced were also higher in 1998. The relationship between rainfall and fruit or flower production in *Arctostaphylos* appears to be complex and to vary among species based on previous studies. Keeley (1977) found that rainfall in the previous winter-spring was positively correlated with numbers of fruits produced in both *A. glauca* and *A. glandulosa*, and conjectured that resources in the previous year determined numbers of buds produced, which then determined the extent of the following season's floral display. Flowering in *A. viscida* also appears to be strongly influenced by water availability in the year of bud development (i.e., the year before flowering) (Baker et al. 1982). However, Mahall et al. (2010) suggested that flower production in *A. glauca* is influenced by rainfall in two periods—the previous year, in which buds (nascent inflorescences) are formed, as well as the present year in which flower and fruit development occur. In this way if many flower buds develop in wet/favorable years, but the following year is dry/unfavorable, they may fail to develop or be aborted (Mahall et al. 2010). Richardson and Bronstein (2012), who also examined Manzanita flowering in the same years as our study (1998 and 1999), found a similar pattern in *A. pungens* to ours: many flowers and subsequent fruits in the wet year (1998) and no strong "population-level bloom" nor fruit production in the following, dry year (1999). In the present study we found that in *A. morroensis* the final development and display of flowers was primarily affected by rainfall amount in the present season, suggesting that, for this species, present environmental resources were most important in determining the realized floral output. In addition, it is possible that abundant flower and fruit production in 1998, depleted stored resources of the individual shrubs, negatively impacting floral bud production for the following year, contributing to lower flower and fruit numbers in 1999.

Many obligate seeding species have high fruit set (i.e., fruit: flower ratios) or seed set (i.e., viable seed: ovule ratios), especially relative to species capable of resprouting after fire (Carpenter and Recher 1979; Kelly and Parker 1990; Lamont and Weins 2003). For *A. morroensis*, we found that fruit set (% of flowers producing a fruit) varied among sites and years, ranging from an annual average across sites of 10–18%. There is little information published on fruit set in Manzanitas to help put these numbers in context. Vasek and Clovis (1976) report findings for fruit set in the obligate-seeder *A. glauca* as ranging from 7–49%, and the obligate-seeder *A. pungens* has been found to have a fruit set of 30% (Rafferty et al. 2016), 36% (Richardson and Bronstein 2012), and 40–73% (Eliyahu et al. 2015). More broadly, within the family Ericaceae, fruit set has been found to range from 20–72% in the genus *Vaccinium* (Jacquemart 1997), from 41–71% in *Rhododendron aureum* (Kudo 1993) and 65% in *Kalmia latifolia* (Rathcke 2003). Thus, although data on other congeners are lacking in order for this to be confirmed, given the ranges of published fruit set in related species, we suspect fruit set is comparatively low in *A. morroensis*.

We did not conduct the appropriate experiments to determine pollen limitation (i.e., comparison of fruit or seed set in hand-pollinated flowers to that in naturally-pollinated flowers), but if our conjecture is correct that fruit set is relatively poor in in *A. morroensis,* there are several observations that suggest pollinator limitation was a likely cause. First, resources do not appear to limit fruit set. In spite of the large variation in rainfall in the two years of this study, fruit set was relatively constant at two out of the three sites. In the site that did vary between the two years, it was in the year of highest resource (water) availability that fruit set was lowest. Second, insect pollinators, though found to be necessary for fruit set, were relatively rare in both years, even in 1998 when flowers were abundant. Lacking information on why pollinators were uncommon in these stands, we do not know if the reduced and fragmented nature of populations of *A. morronesis* contribute to the low numbers of bees and other insect pollinators present in both years. It is possible that insect activity was low in 1998 because that winter and spring, though wet, was also frequently stormy and windy—common conditions that characterize an El Niño. Whether environmental conditions limited insect movement or insect reproduction or development, it is clear that successful fruit set was relatively low even when soil moisture and flower abundance was high, suggesting pollinator limitation.

Previous studies in small populations (Agren 1996) and in fragmented or isolated stands (Steffan-Dewenter and Tscharntke 1999; Cunningham 2000) have demonstrated that pollinator limitation can be responsible for low seed set. If in fact small population size, fragmentation, or isolation are impacting pollination rates in *A. morroensis*, we should expect to see lowest fruit set in the most isolated stand, the Elfin Forest, which also has relatively few individuals. It was indeed in this site that fruit set was consistently low both years, though at one site (Hazard Canyon) fruit set was lower in 1998. Unfortunately, the likelihood is that existing stands of *A. morroensis* will become smaller and more isolated, rather than expanding, given the surrounding residential development. If so, pollinator limitation may pose a threat to adequate fruit and seed production. Such a threat would be greatly exacerbated if the decline in bumblebee and other bee populations reported in the Midwest and Eastern United States (Kearns et al. 1998; Colla and Packer 2008; Grixti et al. 2009) extends to the west coast. An additional and related concern, given dependence on pollinators, is the potential for phenological mismatches resulting from climate change (Renner and Zohner 2018; Visser and Gienapp 2019). Parker (2021) reported that flowering time in *Arctostaphylos* appears to have remained unchanged in the past century in spite of warming trends. If, for example, insects foraging behaviors were to shift to an earlier or later seasonal period, while *A. morroensis* flowering phenology remains constant, such a trophic asynchrony could result in even lower pollination rates.

Post-dispersal fruit predation was intense at all sites, particularly at the Elfin Forest, limiting input to the soil seed bank. We believe that the dominant fruit/seed predators were woodrats (*Neotoma fuscipes*), based on observations of rat feces, and on the proximity of large wood rat nests, especially in the Elfin Forest. Brush rabbit scat was present but only observed at the Elfin Forest site. Rodents are known to be attracted to fruit and/or seeds of *Arctostaphylos* (Horton and Wright 1944; Keeley and Hays 1976). Similarly high intensities of seed predation have been reported for other species of *Arctostaphylos* (Keeley 1977; Kelly and Parker 1990) and other obligate seeding species (Auld and Denham 2001; O'Neil and Parker 2005). We also found fruit predation rates to be higher (i.e., most fruit removed after 26 days vs. 46 days) in 1999 when there were fewer fruits produced, perhaps as expected since resources/fruits were more scarce. This combination of factors—low fruit production and high fruit predation—resulted in especially low seed input in that year.

We do not know if fruit predation is unusually high in the remaining stands of *A. morroensis*. It is possible that rodents and brush rabbits are concentrated in these islands of shrub vegetation, especially since both types of animals tend to be strongly associated with bushes (Vestal 1938; Connell 1954). Alternatively, seed predators may be less abundant than in the past as a result of the reduction in their habitat and available shrub cover (e.g., Soule et al. 1992). In any case, it is clear that currently predators remove the majority of fruits dropped in a matter of weeks, regardless of production in a given year. It is possible that removal of fruits was not strictly predation, in that animals that take the fruit may scatter-hoard and thus bury some of them (Crowe and Parker 2023). However, previous studies on *A. morroensis* reveal that density of viable seed in the soil seedbank can be very low, so removal of a large fraction of fruits, even if some are buried and forgotten by animal foragers, may have a net negative effect.

For obligate seeding species in fire prone habitats input to the soil seed bank is essential to its long-term persistence. In *A. morroensis* seed input appears to be strongly limited by low fruit set and high seed predation. Our calculations of annual seed input (Table 2) are surely overestimates since our rates of seed/fruit predation are based on removal of fruits within a relatively short time period—only 26 to 46 days—and additional seed predation and mortality will undoubtedly occur before the seeds are incorporated in the soil seed bank. In other species of *Arctostaphylos*, Keeley (1977, 1987) documented that fruit/seed production of *A. glauca* and *A. glandulosa* fluctuated orders of magnitude among years, but more seeds were produced within some years than were found in the soil seed bank, suggesting that accumulation of seed in the soil seed bank over time is slow. In addition, over a ten-year period, Keeley (1987) found that despite the huge input of seed, estimated to be over 22 × 10^6 seeds per ha for the obligate-seeder *A. glauca*, no significant change in seed density was detected in the soil seedbank. Both Keeley (1977) and Keeley (1987) suggest that seed predation by small mammals were a likely cause of seed loss and lack of accumulation in the seed bank.

A critical question is what proportion of seeds in the soil seed bank is viable. Though we lack information on the viability of fresh *A. morroensis* seed, viability of seeds in the litter is very low—approximately 3–4% of intact seeds (Tyler and Odion 2020). Even if viability of fresh seed is significantly higher than viability of litter-stored seed, we suspect that the number of viable seed added to the seedbank is much lower than estimated in Table 2. Projected annual seed input is especially low in the oldest and most isolated stand (Elfin Forest), suggesting that this portion of the population may be most vulnerable to local extinction, unless the existing soil seed bank contains enough viable seed to ensure re-establishment after fire. This points to the other key information required to assess the status of this and similarly rare obligate seeders. In addition to reproductive output, density of viable seed in the seed bank and expected germination rates after fire will allow for more accurate predictions about the future of such species and the need for active management in their conservation.

ACKNOWLEDGMENTS

Co-authors Daniel Meade and Dennis Odion passed away before this manuscript was submitted for publication—Dan in November 2022, and Dennis in February 2020. They both contributed substantially to this work, in particular Dan's many hours of field observations and data collection, and Dennis' role in project conception, planning and literature review. They both made substantive comments on an earlier draft of this manuscript. This research would not have been conducted without them. Our work was funded in part by the California Department of Fish and Game (now California Department of Fish and Wildlife). Thanks to Diana Hickson for long-term support of our research, Sarah Cusser, Katja Seltmann, and Charlie Thrift for bee identification, and Peter Slaughter for photographs and additional assistance. Jon Keeley and two anonymous reviewers made comments and suggestions that greatly improved the manuscript.

LITERATURE CITED

AGREN, J. 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. Ecology 77:1779–1790.

AGUILAR, R., L. ASHWORTH, L. GALETTO, AND M. A. AIZEN. 2006. Plant reproduction susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecology Letters 9:968–980.

AIZEN, M. A. AND P. FEINSINGER. 2003. Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation. Pp. 111–129 *in* G. A. Bradshaw and P. A. Marquet, (eds.) How landscapes change. Springer-Verlag Berlin Heidelberg, New York.

AULD, T. D. AND A. J. DENHAM. 2001. The impact of seed predation by mammals on post-fire seed accumulation in the endangered shrub *Grevillea caleyi* (Proteaceae). Biological Conservation 97:377–385.

BAEZA, M. J., M. DE LUIS, J. RAVENTOS, AND A. ESCARRE. 2002. Factors influencing fire behaviour in shrublands of different stand ages and the implications for using prescribed burning to reduce wildfire risk. Journal of Environmental Management 65:199–208.

BAKER, G. A., P. W. RUNDEL, AND D. J. PARSONS. 1982. Comparative phenology and growth in three chaparral shrubs. Botanical Gazette 143:94–100.

BOND, W. J. AND B. W. VAN WILGEN. 1996. Fire and plants. Population and Community Biology Series, 14. Chapman and Hall, New York, NY.

BRUM, G. D. 1975. Floral biology and pollination strategies of *Arctostaphylos glauca* and *A. pringlei* var. *drupacea* (Ericaceae). Ph.D. dissertation. University of California, Riverside, CA.

CANE, J. H., G. C. EICKWORT, F. R. WESLEY, AND J. SPIELHOLZ. 1985. Pollination ecology of *Vaccinium stamineum* (Ericaceae: Vaccinioideae). American Journal of Botany 72:135–142.

CARPENTER, F. L. AND H. F. RECHER. 1979. Pollination, reproduction, and fire. The American Naturalist 113:871–879.

COLLA, S. R., AND L. PACKER. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. Biodiversity and Conservation 17:1379–1391.

CONNELL, J. H. 1954. Home range and mobility of brush rabbits in California chaparral. Journal of Mammalogy 35:392–405.

CROWE, R. AND V. PARKER. 2023. The morphological and ecological variation of *Arctostaphylos* (Ericaceae) fruit: a link between plant ecology and animal foraging behavior. Ecology and Evolution 13:e9801.

CUNNINGHAM, S. A. 2000. Effects of habitat fragmentation on the reproductive ecology of four plant species in Mallee woodland. Conservation Biology 14:758–768.

DUNN, A. T. 1989. The effects of prescribed burning on fire hazard in the chaparral: toward a new conceptual synthesis. Presented at the Symposium on Fire and Watershed Management, October 26–28,1988, Sacramento, California. USDA Forest Service Gen. Tech. Rep. PSW-109:23–29.

ELIYAHU, D., A. C. MCCALL, M. LAUCK AND A. TRAKHTENBROT. 2015. Florivory and nectar-robbing perforations in flowers of pointleaf manzanita *Arctostaphylos pungens* (Ericaceae) and their effects on plant reproductive success. Arthropod-plant Interactions 9:613–622.

FRANKLIN, J., A. D. SYPHARD, H. S. HE, AND D. J. MLADENOFF. 2005. Altered fire regimes affect landscape patterns of plant succession in the foothills and mountains of Southern California. Ecosystems 8:885–898.

FULTON, R. E. AND F. L. CARPENTER. 1979. Pollination, reproduction, and fire in *Arctostaphylos*. Oecologia 38:147–157.

GANKIN, R. AND J. MAJOR. 1964. *Arctostaphylos myrtifolia*, its biology and relationship to the problem of endemism. Ecology 45:792–808.

GLEMIN, S., T. BATAILLON, J. RONFORT, A. MIGNOT, AND I. OLIVIERI. 2001. Inbreeding depression in small populations of self-incompatible plants. Genetics 159: 1217–1229.

GOULSON, D., 2003. Effects of introduced bees on native ecosystems. Annual Review of Ecology, Evolution, and Systematics 34:1–26.

GRIXTI J. C., L. T. WONG, S. A. CAMERON, AND C. FAVRET. 2009. Decline of bumble bees (*Bombus*) in the

North American Midwest. Biological Conservation 142:75–84.

Horton, J. S. and J. T. Wright. 1944. The wood rat as an ecological factor in southern California watersheds. Ecology 25:341–351.

Jacquemart, A. L. 1997. Pollen limitation in three sympatric species of *Vaccinium* (Ericaceae) in the Upper Ardennes, Belgium. Plant Systematics and Evolution 207:159–172.

Jepson, W. L. 1916. Regeneration in manzanita. Madroño 1:3–12.

Jules, E. S. 1998. Habitat fragmentation and demographic change for a common plant: Trillium in old-growth forest. Ecology 79:1645–1656.

Kasagi, T. and G. Kudo. 2003. Variations in bumble bee preference and pollen limitation among neighboring populations: comparisons between *Phyllodoce caerulea* and *Phyllodoce aleutica* (Ericaceae) along snowmelt gradients. American Journal of Botany 90:1321–1327.

Kauffmann, M., V. T. Parker, and M. Vasey. 2021. Field guide to manzanitas: California, North America, and Mexico. Backcountry Press, Kneeland, CA.

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics 29:83–112.

Keeley, J. E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecology 58:820–829.

Keeley, J. E. 1987. Ten years of change in seed banks of the chaparral shrubs, *Arctostaphylos glauca* and *A. glandulosa*. The American Midland Naturalist 117:446–448.

Keeley, J. E. 1991. Seed germination and life history syndromes in the California chaparral. The Botanical Review 57:81–116.

Keeley, J. E. 1992. Demographic structure of California chaparral in the long-term absence of fire. Journal of Vegetation Science 3:79–90.

Keeley, J. E. and C. J. Fotheringham. 2003. Impact of past, present, and future fire regimes on North American mediterranean shrublands. Pp. 218–262 *in*: T. T. Veblen, W. L. Baker, G. Montenegro and T. W. Swetnam (eds.), Fire and climate change in temperate ecosystems of the western Americas. Springer, New York, NY.

Keeley, J. E. and R. L. Hays. 1976. Differential seed predation on two species of *Arctostaphylos* (Ericaceae). Oecologia 24:71–81.

Keeley, J. E. and S. C. Keeley. 1977 Energy allocation patterns of a sprouting and a nonsprouting species of *Arctostaphylos* in the California chaparral. American Midland Naturalist 98:1–10.

Keeley, J. E. and S. C. Keeley. 1988. Temporal and spatial variation in fruit production by chaparral shrubs. Pp. 457–463 *in* F. Di Castri, C. Floret, S. Rambal, J. Roy (eds.), Time scales and water stress, Proceedings of the 5th International Conference on Mediterranean Ecosystems, IUBS, Paris, France.

Keeley, J. E. and P. H. Zedler. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. American Midland Naturalist 99:142–161.

Keeley, J. E., C. J. Fotheringham, and G. Ne'eman. 1999. Immaturity risk in a fire dependent pine. Journal of Mediterranean Ecology 1:41–48.

Kelly, V. R. and V. T. Parker. 1990. Seed bank survival and dynamics in sprouting and nonsprouting *Arctostaphylos* species. American Midland Naturalist 124:114–123.

Klinger, R. and M. Rejmanek. 2009. The numerical and functional responses of granivorous rodent and the fate of Neotropical tree seeds. Ecology 90:1549–1563.

Kudo, G. 1993. Relationship between flowering time and fruit set of the entomophilous alpine shrub, *Rhododendron aureum* (Ericaceae), inhabiting snow patches. American Journal of Botany 80:1300–1304.

Lamont, B. B. and D. Wiens. 2003. Are seed set and speciation rates always low among species that resprout after fire, and why? Evolutionary Ecology 17:277–292.

Mack, M. C. and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution 13:195–198.

Mahall, B. E., L. K. Thwing, and C. M. Tyler. 2010. A quantitative comparison of two extremes in chaparral shrub phenology. Flora-Morphology, Distribution, Functional Ecology of Plants 205:513–526.

Meyer, S. E. 2008. *Arctostaphylos* Adans.: manzanita. Pp. 266–270 *in* F. T. Bonner and R. P. Karrfalt (eds.), The Woody Plant Seed Manual. Agric. Handbook No. 727. Washington, DC. U.S. Department of Agriculture, Forest Service.

Mullany, M. 1990. The distribution and variation of *Arctostaphylos morroensis* (Ericaceae). M.S. thesis. California State Polytechnic University, San Luis Obispo, CA.

Odion, D. C. and C. M. Tyler. 2002. Are long fire-free periods needed to maintain the rare, fire recruiting shrub *Arctostaphylos morroensis* (Ericaceae)? Conservation Ecology 6:4.

O'Neil, S. E. and V. T. Parker. 2005. Factors contributing to the soil seed bank size of two obligate seeding *Ceanothus* species in Northern California. Madroño 52:182–190.

Parker, V. T. 2007. Diversity and evolution of *Arctostaphylos* and *Ceanothus*. Fremontia 35:8–11.

Parker, V. T. 2021. Absence of flowering shifts in *Arctostaphylos* and *Ceanothus* over the past century of climate warming. Madroño, 68:461–472.

Parker, V. T., M. C. Vasey, and J. E. Keeley. 2012. *Arctostaphylos*. Pp. 686–702 *in* The Jepson manual: vascular plants of California, 2nd edition. University of California Press, Berkeley, CA.

Rafferty, N. E., C. D. Bertelsen, and J. L. Bronstein. 2016. Later flowering is associated with a compressed flowering season and reduced reproductive output in an early season floral resource. Oikos 125:821–828.

Rathcke, B. J. 2003. Floral longevity and reproductive assurance: seasonal patterns and an experimental test with *Kalmia latifolia* (Ericaceae). American Journal of Botany 90:1328–1332.

Rathcke, B. J. and E. S. Jules. 1993. Habitat fragmentation and plant-pollinator interactions. Current Science 65:273–277.

Regan, H. M., J. B. Crookston, R. Swab, J. Franklin, and D. M. Lawson. 2010. Habitat fragmentation and altered fire regime create trade-offs for an obligate seeding shrub. Ecology 91:1114–1123.

Renner, S. S. and C. M. Zohner. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annual Review of Ecology, Evolution, and Systematics 49:165–182.

Richardson, L. and J. L. Bronstein. 2012. Reproductive biology of pointleaf manzanita (*Arctostaphylos pungens*) and the pollinator-nectar robber spectrum. Journal of Pollination Ecology 9:115–123.

SCOBIE, A. R. AND C. C. WILCOCK. 2009. Limited mate availability decreases reproductive success of fragmented populations of *Linnea borealis*, a rare, clonal self-incompatible plant. Annals of Botany 103:835–846.

SOULE, M. E., A. C. ALBERTS, AND D. T. BOLGER. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63:39–47.

STEBBINS, G. L. AND J. MAJOR. 1965. Endemism and speciation in the California flora. Ecological Monographs 35:2–35.

STEFFAN-DEWENTER, I. AND T. TSCHARNTKE. 1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia 121:432–440.

SYPHARD, A. D., V. C. RADELOFF, J. E. KEELEY, T. J. HAWBAKER, M. K. CLAYTON, S. I. STEWART, AND R. B. HAMMER. 2007. Human influence on California fire regimes. Ecological Applications 17:1388–1402.

THOMSON, J. D. AND B. A. THOMSON. 1989. Dispersal of *Erythronium grandiflorum* pollen by bumblebees: implications for gene flow and reproductive success. Evolution 43:657–662.

TYLER, C. M. AND D. C. ODION. 1996. Ecological studies of Morro manzanita (*Arctostaphylos morroensis*). Technical report, California Department of Fish and Game, Endangered Plant Program, Sacramento, CA.

TYLER, C. M. AND D. C. ODION. 2020. Seed banks, seed germination, and implications for conservation of the endangered, fire-dependent shrub, *Arctostaphylos morroensis*. Natural Areas Journal 40:155–167.

VASEK, F. C. AND J. F. CLOVIS. 1976. Growth forms in *Arctostaphylos glauca*. American Journal of Botany 63:189–195.

VESTAL, E. H. 1938. Biotic relations of the wood rat (*Neotoma fuscipes*) in the Berkeley Hills. Journal of Mammalogy 19:1–36.

VISSER, M. E. AND P. GIENAPP. 2019. Evolutionary and demographic consequences of phenological mismatches. Nature Ecology & Evolution 3:879–885.

WEISLANDER, A. E. AND B. O. SCHREIBER. 1939. Notes on the genus *Arctostaphylos*. Madroño 5:38–47.

WELLS, P. V. 1969 The relation between mode of reproduction and extent of speciation in the woody genera of the California chaparral. Evolution 23:264–267.

WELLS, P. V. 1999. Nascent inflorescences in *Arctostaphylos pringlei*: response to Keeley. Madroño 46:49–50.

WHELAN, R. J. 1995. The ecology of fire. Cambridge University Press, Cambridge, Great Britain.

WILLI, Y., J. VAN BUSKIRK, AND M. FISCHER. 2005. Threefold genetic alle effect. Genetics 169:2255–2265.

ZEDLER, P. H., C. R. GAUTIER, AND G. S. MCMASTER. 1983. Vegetation changes in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64:809–818.