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STATUS AND LIMITING FACTORS OF THREE RARE PLANT SPECIES IN THE COASTAL LOWLANDS AND MID-ELEVATION WOODLANDS OF HAWAI`I VOLCANOES NATIONAL PARK

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SUMMARY

Two endangered plant species (*Portulaca sclerocarpa*, `ihi mākole, and *Sesbania tomentosa*, `ōhai) and a species of concern (*Bobea timonioides*, `ahakea) native to the coastal lowlands and dry mid-elevation woodlands of Hawai`i Volcanoes National Park were studied for more than two years to determine their stand structure, short-term mortality rates, patterns of reproductive phenology, success of fruit production, seed germination rates in the greenhouse, presence of soil seed bank, and survival of both natural and planted seedlings. The role of rodents as fruit and seed predators was evaluated using exclosures and seed offerings in open and closed stations or cages. Rodents were excluded from randomly selected plants of *P. sclerocarpa* and from branches of *S. tomentosa*, and flower and fruit production were compared to that of adjacent unprotected plants. Tagged *S. tomentosa* fruit were also monitored monthly to detect rodent predation.

Natural populations of all three rare plant species showed declines over the period of monitoring. *Bobea timonioides* had the stand structure of a senescent population, and about a third of these long-lived trees have died since a previous survey 13 years ago. The size of monitored natural *P. sclerocarpa* plants decreased during the study, and mortality rate was 23% over two years. A comparison of current and long-term population data showed the same declining trend. Stand structure and mortality of natural *S. tomentosa* could not be determined at Kīpuka Nēnē, but half of monitored plants died over a year at coastal `Āpua Point. *Portulaca sclerocarpa* and *S. tomentosa* showed pronounced seasonal patterns in their reproductive phenology, and *B. timonioides* appeared to have a continuous pattern of flower and fruit production. Buds and flowers of *P. sclerocarpa* at its natural population peaked during spring and fall months, and fruit capsules were borne most of the year. At the upland *S. tomentosa* site, peak bud and flower production occurred in spring and summer, and greatest fruit abundance was in summer and winter months. The coastal site for this species showed greatest flowering in the fall and mature fruit were persistent year-long. Fruit set was high for *P. sclerocarpa*, very low for *S. tomentosa*, and undetermined for *B. timonioides*. Pollination was studied for only *S. tomentosa* at Kīpuka Nēnē, where six insect species were floral visitors, and native *Hylaeus*, or yellow-faced bees, and *Apis mellifera* honeybees were found to be transporting pollen of the rare plant.

Seed germination rates determined by greenhouse studies were moderately high for *B. timonioides* and *S. tomentosa* and low but variable for *P. sclerocarpa*. Field-sowed seeds of *B. timonioides* and *P. sclerocarpa* did not germinate, but up to 31% germination was observed for *S. tomentosa* seed-sowing trials. No difference in germination or seedling survival was observed for *S. tomentosa* in plots with and without grass. A small seed bank was detected for *S. tomentosa* during one season at both Kīpuka Nēnē and `Āpua Point. Mortality of planted seedlings or cuttings was high for all three rare species, but recent plantings of *P. sclerocarpa* seedlings showed a low mortality rate at one site. Natural seedlings were observed at two *P. sclerocarpa* planting sites, but all succumbed during dry periods. Rodents were found to be seed predators of both *P. sclerocarpa* and *S. tomentosa*, but had no detected impact on *B. timonioides*. A third of tagged seed pods of *S. tomentosa* displayed signs of rat predation, and another third disappeared.

The most important limiting factors identified for *P. sclerocarpa* were loss of seeds to rodent predation and low seedling recruitment. *Sesbania tomentosa* shared these two limiting

factors and also lost flowers to alien insect predation and displayed very low fruit set caused by either a lack of effective pollination or self-compatibility problems. Lack of natural seedling recruitment, perhaps caused by current harsh site conditions, appeared to be the most significant limiting factor for *B. timonioides*.

INTRODUCTION

Hawai`i Volcanoes National Park (HAVO), including the recently-acquired Kahuku Unit, stretches from the sea coast to the summit of Mauna Loa at 4,169 m elevation and protects the summit and much of the land area of Kīlauea Volcano. There are at least seven major ecological zones within the boundaries of HAVO (Stone and Pratt 1994), and the park supports a broad range of plant communities including wet, moist, and dry forests, shrublands, and grass communities in multiple elevation zones. HAVO contains more than 400 native vascular plant species, and rare plant species comprise about 15% of the recorded flora (Higashino *et al.* 1988, Benitez *et al.* 2008). Among the park's flora are 25 listed endangered and threatened plants, 5 candidates for endangered status, and 29 species of concern (U.S. Fish and Wildlife Service 2008, 2009). Every ecological zone of the park supports populations of rare native plant species. At least eight endangered plants, one threatened plant species, and another nine species of concern are currently found or formerly occurred in the coastal lowlands and mid-elevation woodlands below the Kīlauea summit.

The park lowlands and dry woodlands of Kīlauea were negatively impacted by feral ungulates in the past. Feral goats (*Capra hircus*) had been present in HAVO for more than 120 years when organized and effective feral goat removal from HAVO began in the 1970s (Baker and Reeser 1972). Despite the harvest of more than 70,000 animals by public hunters from 1920 to 1970, there remained at least 15,000 goats in HAVO (Katahira and Stone 1982). Much of the coastal lowlands and mid-elevation woodlands were considered major feral goat range, and the goat population in the area below Hilina Pali was estimated at 13,500 in 1970–71 (Baker and Reeser 1972). Removal of goats from the coastal lowlands led to an increase in native woody plants and alien perennial grasses (Mueller-Dombois and Spatz 1975). Feral pigs (*Sus scrofa scrofa*) remain in the woodlands and grasslands below a fence near Puhimau Crater that protects the Kīlauea summit area (Katahira *et al.* 1993), but pigs are thought to have low densities and less impact than goats in dry open woodlands and coastal vegetation, except where alien kiawe trees (*Prosopis pallida*) are present (Stone 1985). Wildfire is aggressively suppressed in the coastal lowlands and mid-elevation woodlands, as it is throughout HAVO (Tunison *et al.* 1994).

Nine non-rainforest areas of HAVO below the summit of Kīlauea are considered Special Ecological Areas (SEAs), the most intact natural areas of the park in which feral ungulates and highly invasive alien plant species are removed or reduced (Tunison and Stone 1992, Loh and Tunison 2009). Natural vegetation within the managed SEAs has responded positively, but most of the known endangered and rare plant populations have not increased in size or expanded their ranges despite decades of protection from feral animals and reduction of invasive alien plants. More than 80 of the park's rare and depleted plant species were recently targeted for augmentation or re-introduction in a stabilization project, which included many plants native to the coast and dry woodlands of the park (Belfield *et al.* in prep.). If the factors causing the rarity and low reproduction of these plant populations were better understood, the success of the park's stabilization program might be enhanced and additional tools might be developed to better manage the park's endangered species in their natural habitat. Determination of the causes of reproductive failure of both extant and restored rare species may allow managers to stabilize remaining rare plant populations and prevent further losses.

Within the special ecological areas of the coastal lowlands and mid-elevation woodlands, two endangered plant species (*Portulaca sclerocarpa* and *Sesbania tomentosa*) and a species of concern (*Bobea timonioides*) were selected for a limiting factors study. In addition to selected natural park populations of the three species, planting sites were also included in the study. *Bobea timonioides*, `ahakea, is currently considered a species of concern (U.S. Fish and Wildlife Service 2008) and has in the past been a candidate endangered species (U.S. Fish and Wildlife Service 1980). An endemic Hawaiian tree in the coffee family (Rubiaceae), *B. timonioides* is known from dry and mesic forests of Hawai`i, Maui, O`ahu and Kaua`i (Wagner *et al.* 1999, Lorence *et al.* 1995). In HAVO, *B. timonioides* is found in Nāulu Forest and an adjacent kīpuka, where less than 50 individuals were mapped in the 1990s (Abbott and Pratt 1996), and the species probably persists in remote rainforests of Kīlauea's East Rift (Pratt *et al.* 1999). A small to medium-sized tree, *B. timonioides* has shiny, opposite leaves with conspicuous, often reddish venation and small white flowers followed by purplish-black fleshy fruit 1 cm in diameter (Wagner *et al.* 1999). The bark of the tree is smooth and typically pale tan or almost white.

Portulaca sclerocarpa, `ihi mākole or po`e, is a perennial herbaceous plant in the purslane family (Portulacaceae) endemic to Hawai`i Island and an offshore islet of Lanā`i (Wagner *et al.* 1999), and it was recently reported from a site on Maui (American Technologies, Inc. 2004). The species was listed as endangered in 1994. On the island of Hawai`i, *P. sclerocarpa* is known from 11 populations, the largest of which is found within HAVO (U.S. Fish and Wildlife Service 1996). At HAVO, the species occurs naturally at Puhimau Geothermal Area and in the Ka`ū Desert near Keanakāko`i Crater, and plants formerly were found near the Ka`ū Desert/Mauna `Iki Trail and along the Hilina Pali Road near Kalanaokuaiki Pali. Plantings have been made at five areas in the park: near the Ka`ū Desert Trail, near the Hawaiian Volcano Observatory (HVO), on the Crater Rim Trail in Keanakāko`i SEA, at Kalanaokuaiki Pali, and at several other sites along the Hilina Pali Road (Belfield *et al.* in prep.). The plant is a small succulent with fleshy, pale green, linear leaves and flowers with white petals, bright red sepals, and many yellow stamens. The tiny round capsules are thick-walled and indehiscent (Wagner *et al.* 1999). Like other members of the genus *Portulaca*, *P. sclerocarpa* is self-fertilized before flowers open (Kim and Carr 1990).

Sesbania tomentosa, `ōhai, is a sprawling or occasionally upright shrub in the pea family (Fabaceae). Currently this endangered species is found on six of the main Hawaiian Islands, as well as in the Northwest Hawaiian Islands. On Hawai`i Island the main regions inhabited by the species are near South Point, or Ka Lae, and within HAVO; a few plants persist on the northwest coast of the island (U.S. Fish and Wildlife Service 1999). Within HAVO, *S. tomentosa* occurs at five general sites (or sub-populations): `Āpua Point, Kīpuka Nēnē to Hilina Pali, Kīpuka Pepeiau to Kukalau`ula, Kamo`oali`i, and Kū`ē`ē. A few plants are also found near the coast at Ka`aha, and a single planting from the 1970s (1-2 plants) persists near Lae`apuki. There is also a recent planting near the coast at Kahue (Belfield *et al.* in prep.). This fast-growing shrub has pinnately compound leaves and brilliant red to salmon-pink pea-shaped flowers; its fruits are narrow, indehiscent legumes to 23 cm long with constrictions between the seeds (Wagner *et al.* 1999). Previously recognized species and varieties (including a species with two named varieties within HAVO) (Char 1983) are not currently accepted and have been interpreted as morphological variation among relictual populations of a formerly widespread, polymorphic species (Wagner *et al*. 1999).

The objectives of this study were 1) determine population size and stand structure for *B. timonioides* and *P. sclerocarpa* and determine mortality and growth of selected branches or patches of *S. tomentosa*; 2) evaluate the success of planted populations of *P. sclerocarpa* and *S. tomentosa* and monitor plantings augmenting a natural population of *B. timonioides*; 3) measure flower and fruit production by monthly or bimonthly monitoring of phenology of three species; 4) investigate the cause of reproductive failure by following the fate of a sub-sample of flowers and fruit, identifying pollinators and soil seed banks for one species, and quantifying seed germination rates; 5) monitor natural seedling establishment; and 6) determine the role of rodents in seed or fruit predation for all three species.

METHODS

Description of the Study Areas

Nāulu Forest

Nāulu Forest, a kīpuka on Hōlei Pali in the southeastern section of HAVO, contains the largest known population of *Bobea timonioides* in the park (Abbott and Pratt 1996). This heavily-vegetated kīpuka is positioned between two stretches of the Chain of Craters Road at an elevation of 250–600 m (Fig. 1). Surrounded by lava flows from the 1970–1972 eruption of Mauna Ulu, the Nāulu Forest kīpuka substrates date from 500 to 750 years ago and include both \`a\`ā and pāhoehoe (Holcomb 1987). The climate of Nāulu Forest is warm and dry with summer droughts (Doty and Mueller-Dombois 1966). Mean annual rainfall in this area is 1,500–2,000 mm. At the nearby Kalapana station to the southeast, mean annual rainfall is 1,441 mm, and the driest months are June and July with less than 25% of the mean January rainfall (Giambelluca *et al*. 1986). Mean temperature in this region is 21–24°C (Hawaii Department of Land and Natural Resources 1970).

Vegetation within Nāulu is composed of a dry lowland forest of *Diospyros sandwicensis* (lama) and *Metrosideros polymorpha* (\`ōhi\`a lehua) with other native trees in the forest understory, and a stand of the Polynesian introduction *Aleurites moluccana* (kukui) is prominent on the eastern edge of the kīpuka. Several rare tree and shrub species persist in Nāulu Forest, and others have been lost in historical times (Abbott and Pratt 1996). Nāulu Forest is treated as a Special Ecological Area (SEA) (Tunison and Stone 1992), and alien plants such as *Lantana camara* (lantana), *Nephrolepis brownii* (*N. multiflora*; Asian swordfern), and grasses have been periodically controlled (R. Loh, pers. comm.). Feral goats were removed from this region in the 1970s (Baker and Reeser 1972). The forest has been used as a restoration site for several rare and endangered plant species (Belfield *et al*. in prep.).

Puhimau Geothermal Area

A geothermal area southwest of Puhimau Crater near the Chain of Craters Road at 1,200 m elevation (Fig. 2), Puhimau "Hotspot," was formed in 1937–1938 when magma intruded close to the surface and killed most of the original forest cover (Hazlett 1987). This site currently supports the largest population of *Portulaca sclerocarpa* known in the Hawaiian Islands (U.S.

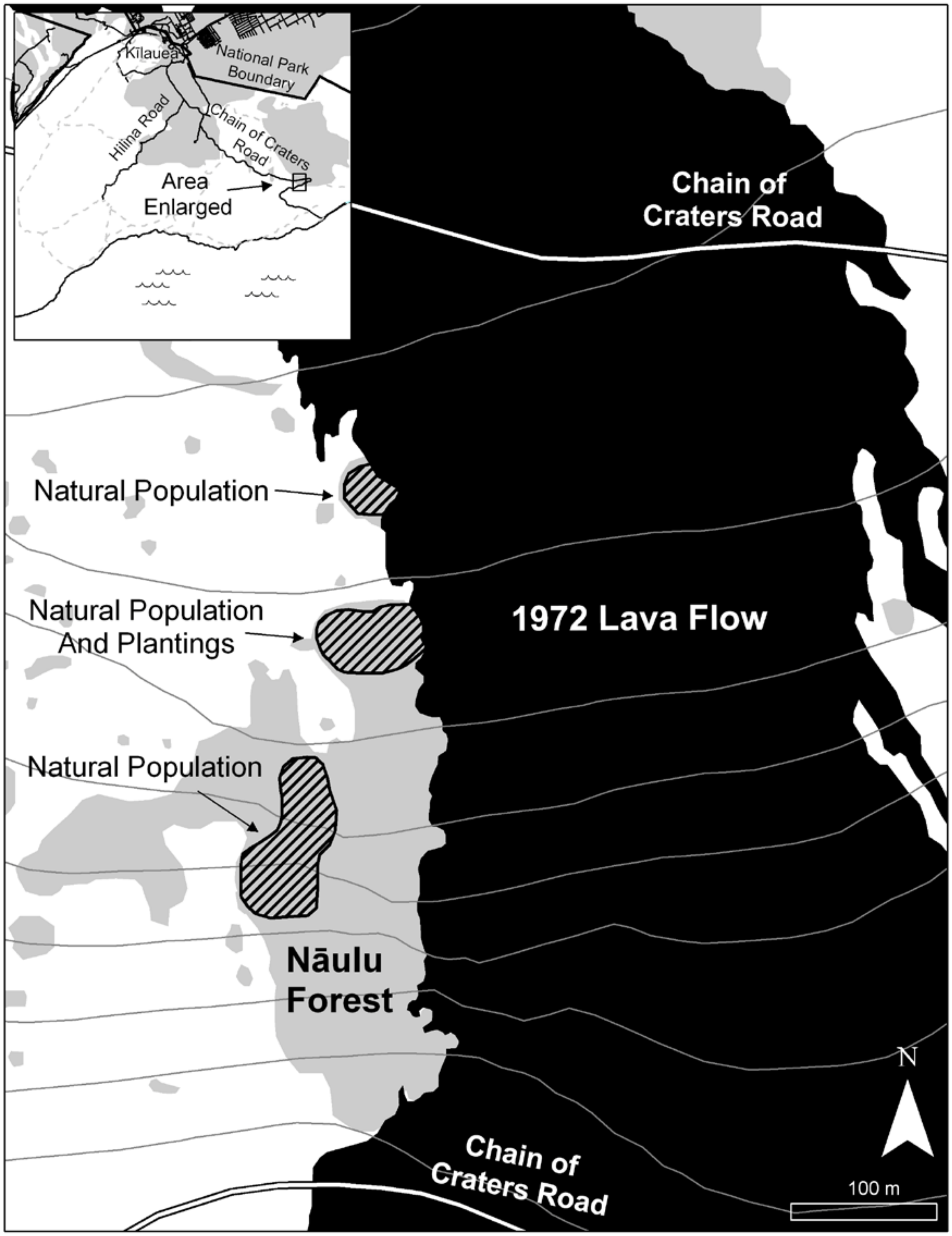

Figure 1. Location of the natural population and plantings of *Bobea timonioides* at Nāulu Forest, Hawai`i Volcanoes National Park.

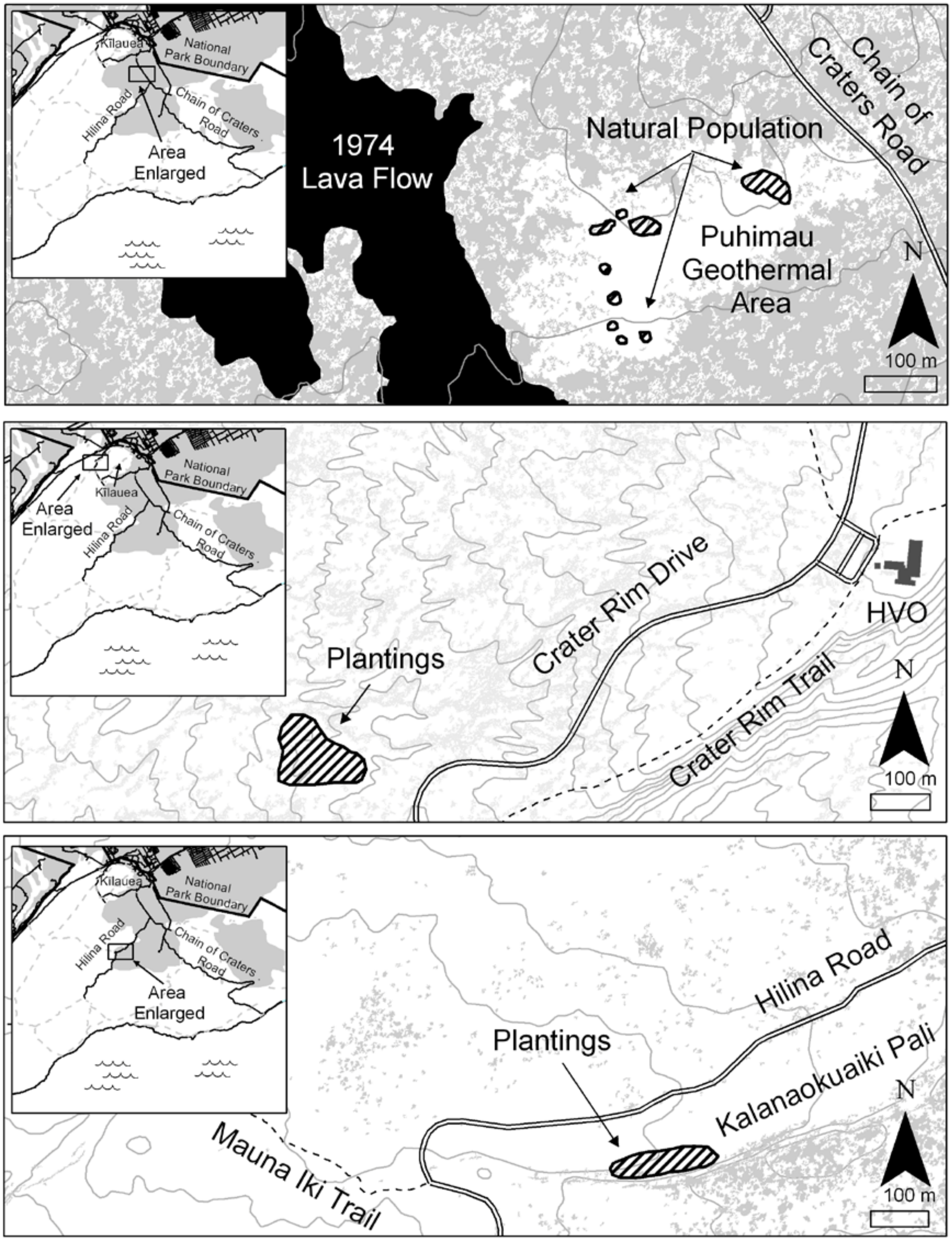

Figure 2. Location of the natural population of *Portulaca sclerocarpa* at Puhimau Geothermal Area and plantings near Hawaiian Volcano Observatory (HVO) and at Kalanaokuaiki Pali, Hawai`i Volcanoes National Park.

Fish and Wildlife Service 1996). Soils of the site are silt loam formed in ash and pumice (Sato *et al.* 1973), and ground temperatures may reach 48–89°C (Smith 1981). The underlying substrate is part of the Ko`oko`olau flows dated at 250–350 years ago (Holcomb 1987). The climate of the surrounding area is seasonal with a dry and warm period in the summer (Doty and Mueller-Dombois 1966). Rainfall averages 2,200 mm a year and the mean annual temperature is 16.3°C (Smith 1981).

Vegetation of the surrounding area is *Metrosideros polymorpha* woodland of medium stature with a ground cover of native shrubs and alien grasses (primarily *Andropogon virginicus*, broomsedge) that has been invaded by the fast-growing alien tree *Morella faya* (firetree or faya). The central zone of the geothermal area is sparsely vegetated with native lichens, mosses, sedges, and the indigenous shrub *Waltheria indica* (`uhaloa), as well as with alien ferns, sedges, *Portulaca pilosa* (purslane), and the grass *Andropogon virginicus* (Smith 1981). Peripheral areas of the hotspot have more grass and scattered stunted *Metrosideros* trees. Puhimau Geothermal Area is treated as a SEA (Tunison and Stone 1992) and is included within a feral pig management unit (Katahira *et al.* 1993).

Hawaiian Volcano Observatory Site

A planting of 500 *P. sclerocarpa* was made at a site southwest of the Hawaiian Volcano Observatory (HVO) in 2003 (Belfield *et al.* in prep.). This site is at 1,100 m elevation near the Crater Rim Road (Fig. 2) on consolidated ash over pāhoehoe from the Observatory flows 250–350 years old (Holcomb 1987). Annual rainfall in this area is approximately 1,500 mm (Giambelluca *et al.* 1986). Annual rainfall over the last seven years averaged 1,709 mm at the nearby HVO Uwēkuna weather station (HAVO Fire Cache, unpublished data). The climate of the site is seasonal with a dry period during summer months, and the mean annual temperature is 25°C (Doty and Mueller-Dombois 1966). Vegetation of the study site is *Metrosideros polymorpha* woodland with patchy low-stature trees, native shrubs, and alien grasses. Plantings of *P. sclerocarpa* were made on the edge of vegetation patches. The site is considered pig-free and is within a unit that receives alien plant control of the most invasive species, such as *Morella faya* (R. Loh, pers. comm.).

Kalanaokuaiki Pali and Hilina Road

Plantings of both *Portulaca sclerocarpa* and *Sesbania tomentosa* were made at the base of Kalanaokuaiki Pali (cliff) near Hilina Pali Road at 980 m elevation (Figs. 2 and 3); plantings were part of the current study and were also a component of a park rare plant stabilization project (Belfield *et al.* in prep.). Kalanaokuaiki is a section of the Koa`e Fault system (Hazlett 1987), and the substrates at the base of the cliff in this area are from the Kīpuka Nēnē flows that are approximately 1,100 years old (Holcomb 1987). Rainfall ranges from 1,000 to 1,500 mm per year in this region (Giambelluca *et al.* 1986), and the climate is seasonal with dry summers (Mueller-Dombois 1966). Vegetation is an open woodland of *Metrosideros polymorpha* with scattered native shrubs, such as *Leptecophylla tameiameiae* (pūkiawe), *Dodonaea viscosa* (`a`ali`i) and *Dubautia ciliolata* (kūpaoa). Alien grasses, particularly *Andropogon virginicus* and *Schizachyrium condensatum* (bush beardgrass) have sparse cover (Mueller-Dombois 1966). This site is within the Hilina SEA, where *Morella faya* is controlled, feral goats are absent, and feral pigs are present in low numbers (Tunison and Stone 1992).

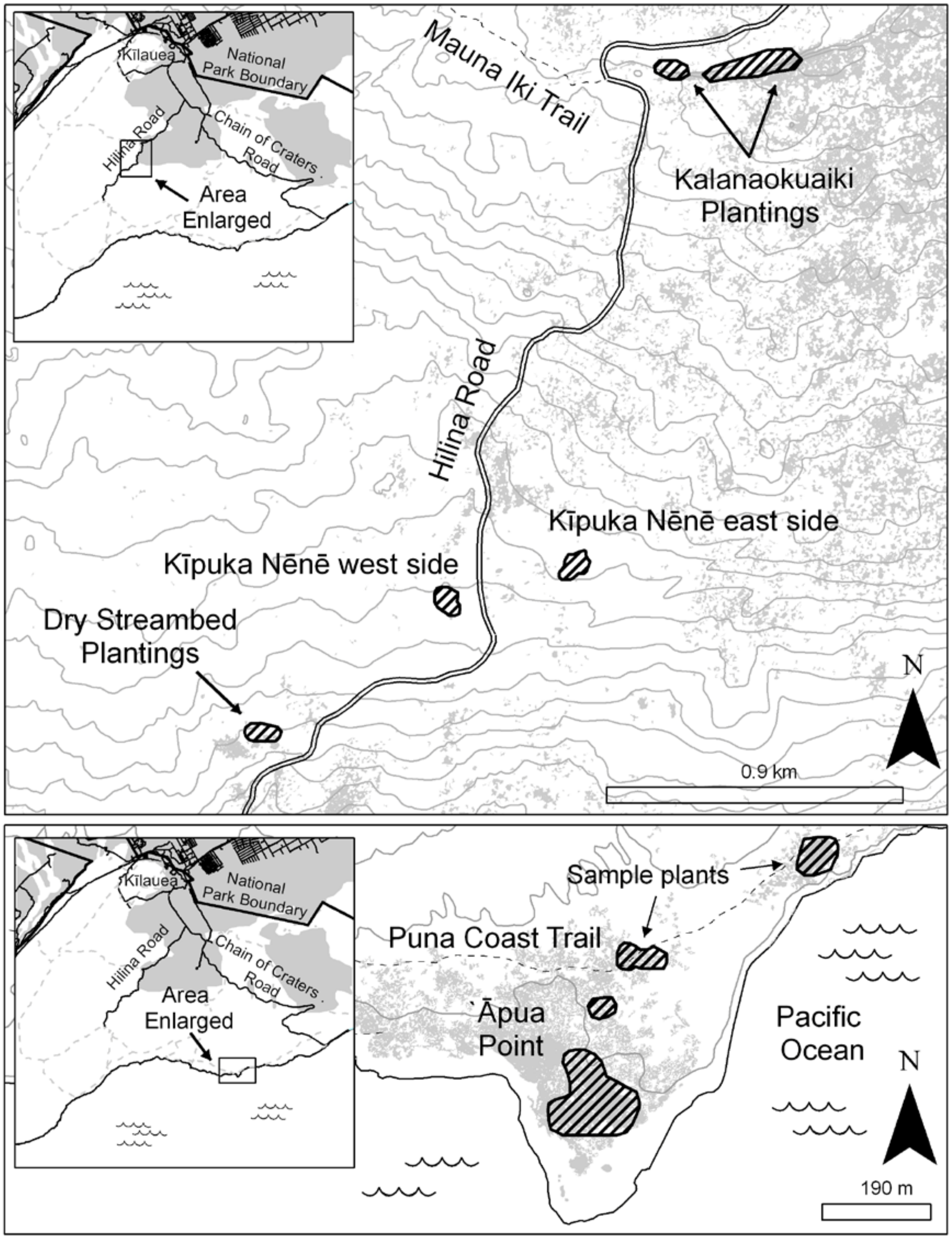

Figure 3. Location of natural populations of *Sesbania tomentosa* at Kīpuka Nēnē and `Āpua Point and plantings at Kalanaokuaiki Pali and a dry streambed near Hilina Road, Hawai`i Volcanoes National Park.

A second site on Hilina Road was also used for planting *S. tomentosa*. This site is on the edge of a dry streambed north of Hilina Road at 840 m elevation. The soil is ash over pāhoehoe lava from the Kālu`e flows, 500–750 years old (Holcomb 1987). The climate and vegetation are as described for the Kalanaokuaiki site.

Kīpuka Nēnē

Kīpuka Nēnē at 890 m elevation along the Hilina Road supports a natural population of *Sesbania tomentosa* (Fig. 3). Two sections of the population, east and west, are separated by approximately 400 m and the Hilina Road. The substrate here is ash over pāhoehoe from the Kīpuka Nēnē flows estimated as 1,100 years old (Holcomb 1987). The climate is as described for the nearby Kalanaokuaiki Pali site. Annual rainfall at Kīpuka Nēnē has averaged 1,598 mm over the last seven years (HAVO Fire Cache, unpublished data). Vegetation is an open woodland of *Metrosideros polymorpha* and *Sophora chrysophylla* with native shrubs and a relatively dense cover of alien grasses, particularly *Melinis minutiflora* (molasses grass), *Schizachyrium condensatum*, and *Andropogon virginicus*. The kīpuka has burned twice in the last 40 years (Hughes *et al*. 1991). *Morella faya* is controlled within the kīpuka, but feral pigs remain in the area, although attempts are made to reduce their numbers during the breeding season of the endangered nēnē (*Branta sandvicensis*; R. Loh, pers. comm.). The area near the road was used as a rare plant restoration site in the 1950s and 1960s (Morris, unpublished) and has recently been planted with native species utilized by nēnē.

`Āpua Point

The only coastal site investigated in this study was `Āpua Point, approximately 9 km west of the coastal portion of the Chain of Craters Road in the eastern section of HAVO (Fig. 3). `Apua Point supports a large natural population of *Sesbania tomentosa* that has been previously recognized as two species (Char 1983). The substrate of the point is patchy coral and lava sand (Mueller-Dombois 1966) over pāhoehoe of the Keauhou flows, dated at 350–500 years before present (Holcomb 1987). The climate of this coastal area is warm with summer droughts and a mean annual temperature of 23°C (Mueller-Dombois 1966). Rainfall records are poor at this remote coastal site, but mean annual rainfall here falls between 1,000 and 1,500 mm (Giambelluca *et al*. 1986). Annual rainfall at Pu`uloa in the coastal lowlands about 8 km to the east has averaged 1,452 over the last seven years (HAVO Fire Cache, unpublished data).

Vegetation at `Āpua Point is dominated by *Scaevola taccada* (naupaka kahakai) among which *Sesbania* shrubs are scattered. Native vines, particularly *Ipomoea pes-caprae* (pōhuehue) and *Vigna marina* (nanea), are common as are the native shrubs *Waltheria indica* (`uhaloa) and *Sida fallax* (`ilima). A number of alien shrubs and herbs are present with low cover (Smith 1980). Feral goats were removed from the coastal lowlands in the 1970s (Baker and Reeser 1972), and the area likely does not support feral pigs, as it is surrounded by vast fields of recent lava flows. `Āpua Point is managed as an SEA (Tunison and Stone 1992).

Sampling Methods

Size Class Structure, Growth, and Mortality

Natural populations – For *Bobea timonioides*, 24 of the 36 trees previously known from Nāulu Forest were relocated and their diameters at breast height (dbh) were measured in both

2006 and 2007. Those trees that had died since the previous survey were found either standing or on the ground. The natural population of *Portulaca sclerocarpa* at Puhimau was revisited and every live plant was given a numbered tag and measured in April 2006. Heights and plant width in two directions (north/south and east/west) were measured to the nearest cm. All plants were revisited and measured two years later to detect mortality in the entire population. A subset of *P. sclerocarpa* (64) that was randomly selected for phenology monitoring was re-measured monthly for 19 months in 2006 and 2007.

Two natural populations of *Sesbania tomentosa* were monitored, but we did not have previous data on the size of the populations, and individual plants could not always be distinguished. At `Āpua Point, 30 distinct patches of *S. tomentosa* (possibly individuals) were randomly selected, and the width of patch was measured in two directions (north/south and east/west). Measurements were used to estimate the area covered by the plant. Plants were visited bimonthly from April 2006 to May 2007 when final measurements were taken and mortality was evaluated.

Two groups of *S. tomentosa* at Kīpuka Nēnē were sampled. East of the road a systematic grid was established over the large spreading patch of *Sesbania*. Starting from a randomly selected point on the northern perimeter of the patch, lines were established in a north-south direction at ten-meter intervals. Sample branches were selected at five-meter intervals along each of five lines for a total of 50 branches. Branches were marked at the base with a metal tag and flag and lengths were measured at each monthly monitoring period. Branch mortality was evaluated after 14 months. During the first year of monitoring, branches that died were replaced by the nearest branch to the original selected point, so that an adequate sample was available for phenology and rodent predation studies. In May 2007, monitoring continued on 23 surviving branches until September 2009 when final measurements and mortality evaluation were made. Monitoring began for plants on the western side of the Hilina Road in May 2007 when 23 branches were randomly selected on the perimeter of the *Sesbania* patch at random points measured along a tape measure. Branches were tagged and measured for length at monthly intervals until September 2009 when final evaluation of branch mortality was made.

Plantings – At Nāulu Forest, 59 *Bobea timonioides* seedlings were randomly selected from a planting of 129 made in 2005 (Belfield *et al.* in prep.; Fig. 1). Each seedling was given a numbered tag and had height measured in December 2005, soon after planting. Seedlings were visited at intervals of six months until July 2007 when final measurements and mortality evaluations were made.

Three plantings of *Portulaca sclerocarpa* were monitored (Fig. 2). One planting of 500 was made by Thomas Belfield of HAVO Natural Resources Management Division in 2004 at a site near Hawaiian Volcano Observatory (HVO), and we marked 300 healthy plants to monitor in 2005. As with plants at the natural population, heights and plant width in two directions (north/south and east/west) were measured to the nearest cm. All 300 plants were revisited in 2007, re-measured, and evaluated for mortality. A subset of 67 randomly-selected plants monitored for phenology was visited and had height and width re-measured monthly for 18 months.

Two plantings were made at the base of Kalanaokuaiki Pali near Hilina Road. In July 2006, an equal number of *P. sclerocarpa* (25) was planted in both bare soil sites and adjacent areas covered with alien grass, primarily *Melinis minutiflora* and *Schizachyrium condensatum*. Plantings were made in groups of five with grass and no-grass groups separated by a distance of no more than three meters. Soil depths were taken at the time of planting, and only sites with soil at least 15 cm deep were used. A second planting was made in the same area in March 2008, which consisted of 30 seedlings and 30 cuttings rooted in the greenhouse. Groups of 10 plants made up of half seedlings and half cuttings were planted together in grass-free sites, and soil depths were measured at the time of planting. The 2006 and 2008 plantings were visited monthly for 24 and 18 months, respectively. At each visit, heights and width in two directions were measured, and dead plants were recorded. A final visit was made to the 2008 planting in April 2010 to determine mortality after two years.

Two plantings of *Sesbania tomentosa* were monitored; the first was at the base of Kalanaokuaiki Pali and the second was at a site along a dry streambed near Hilina Pali Road south of Kīpuka Nēnē (Fig. 3). Plantings were made in February 2006 with seedlings propagated from seeds collected at Kīpuka Nēnē (Belfield *et al.* in prep.). Individual plants were tagged with a unique number and were first measured a month after planting. Mortality was evaluated and heights were re-measured at 2–7 month intervals for two years; a final visit was made in September 2009, 3.5 years after planting.

Density, Cover, and Frequency of *Portulaca sclerocarpa* and Other Plants at Puhimau

Density of *P. sclerocarpa* was sampled in 10 by 10 m plots throughout the central zone of the Puhimau Geothermal Area. One hundred plots were randomly selected from a total of 347 plots sampled in 1993 (L. Pratt, unpublished data). Location of the randomly-selected plots was facilitated by permanent markers at 10 m intervals on the periphery of the geothermal area and along an east/west baseline in the central zone. All *P. sclerocarpa* plants were counted within each sampled plot. The mean number of *P. sclerocarpa* per plot and the number of plots supporting the rare plant were compared with numbers from the same plots sampled in 1993. The cover of alien grass in the 100 sampled plots in 2008 was estimated in categories of 0, <25%, 25–50%, and >50%.

The cover and frequency of all plants in both the central zone and the periphery of the geothermal area were sampled following the methods of Smith (1981). Three transects 50 m in length were established in the central zone by randomly selecting plots and using the northeastern corner of each selected plot as a starting point. The transect azimuth was randomly selected from a possible 360°, and any transects whose trajectories took them into the peripheral zone were rejected. Three transects 50 m in length were also selected in the peripheral zone by randomly selecting three points from among the permanent markers on the periphery of the central zone of the geothermal area. A random azimuth was selected for these transects in the same way as those of the central zone. Percentage cover of each plant species was measured along each transect using a point intercept frame with five points per meter (Mueller-Dombois and Ellenberg 1974). Plant frequency was determined by placing a pvc frame 1 m^2 in size at 2 m intervals along each transect and recording all the species that occurred within the plot frame. Vascular plants, mosses, and lichens were all sampled.

A reference collection of mosses and lichens at the HAVO Natural History Collection (Herbarium) was consulted to assist with plant identification. One moss identified by Smith 1981 as *Campylopus praemorsus* is now considered to be two species (*C. praemorsus* and *C. exasperatus*), so all mosses of the genus were combined for sampling in 2008. Waite (2007) found that *Dicranella integrifolia* was actually the most common moss at Puhimau Geothermal Area in 2004, and he noted that this moss was reported to be common in the area as early as 1933. This moss is very similar in appearance to *Campylopus exasperatus*, so it was combined with members of that genus during sampling in 2008. The plant frequency was calculated by dividing the number of plots in which the species occurred by the total number of plots in the three transects of each zone.

Reproductive Phenology

Natural populations – Reproductive phenology was monitored bimonthly on relocated *Bobea timonioides* trees at Nāulu Forest for 17 months in 2006 and 2007. The number of buds and flowers, green fruit, and mature black fruit were estimated on each tree in categories: 0, 1–10, 11–50, 51–100, and >100. Buds and flowers were similar in appearance and were not distinguished. Estimates were made using Leica (8 x 32) binoculars.

At the *P. sclerocarpa* population at Puhimau, 64 plants were randomly selected to monitor monthly. At each selected plant the total number of branches was counted and the numbers of branches bearing buds, flowers, or fruit were recorded for 19 months in 2006 and 2007.

At the \`Āpua Point population of *S. tomentosa*, the number of buds, flowers, immature green fruit, and mature fruit on 30 plants was estimated in categories (none, 1–5, 6–25, 26–50, and >50) at bimonthly monitoring periods for 14 months. For 10 months, the numbers of immature and mature fruits were counted (and tagged) on randomly selected branches at each plant. At Kīpuka Nēnē, the numbers of buds, flowers, immature fruit, and mature fruit were counted on each selected branch monthly. Large buds fully expanded but not yet open were counted as flowers. Fruit was considered mature if the pod was dry and brown or if it was green-, red-, or yellow-mottled and full size. At the Kīpuka Nēnē East site, phenology counts were made on 50 selected branches and replacements for 14 months. After May 2007, bud, flower, and fruit counts were made on 23 surviving branches in good condition at the eastern site and 23 newly-selected branches at the western patch of *Sesbania* (Kīpuka Nēnē West); monitoring continued for 2.5 years.

Insect predation of buds and flowers at Kīpuka Nēnē – For two years (2007–2009), predation by caterpillars of the alien bean butterfly (*Lampides boeticus*, Lycaenidae) was quantified monthly on *S. tomentosa* branches at Kīpuka Nēnē West by counting the number of buds and flowers with feeding damage, exit holes, or attached eggs.

Plantings – *Bobea timonioides* plantings remained small and did not produce flowers and fruits during the study. At the *P. sclerocarpa* planting at HVO 67 plants were randomly selected to monitor for phenology monthly for 18 months in 2006–2007. At each selected plant the total number of branches was counted and the numbers of branches bearing buds, flowers, or fruit were recorded. Monthly phenology of all plants in the 2006 and 2008 plantings at Kalanaokuaiki was monitored in the same way, for 24 and 18 months, respectively. The *S. tomentosa* plantings at Kalanaokuaiki and the dry streambed near Hilina Road were visited too infrequently for collection of phenology data, but some incidental information on flowering was collected.

Success of Fruit Production

The success of fruit production was not evaluated for *Bobea timonioides*, because trees were tall and buds and flowers were inaccessible for tagging. The successful transition of buds and flowers to fruit capsules was determined for *Portulaca sclerocarpa* by tagging branches of randomly selected phenology plants at Puhimau Geothermal Area when they bore buds and flowers. Branches were marked with a colored wire and were re-monitored monthly and examined for fruit. If fruit capsules were present on a branch which previously bore buds or flowers, this was counted as a successful transition. If no fruit appeared, fruit formation was considered unsuccessful. *Sesbania tomentosa* flowers and very young developing fruit were tagged with paper twist ties on randomly selected phenology branches at both east and west Kīpuka Nēnē sites. All flowers in good condition (not predated or dried out) on the selected branches were tagged and monitored monthly until they either formed a mature fruit or disappeared.

Pollination Studies

Floral visitor observations – Composition of the floral visitor community and the rates of visitation were quantified by observing insect activity at flowers of *Sesbania tomentosa*. A single inflorescence of 1–10 flowers was observed for 15-minute periods between 0900 and 1500 on dry days with sunny weather and light to moderate wind speeds. Observations were made on 25 August 2006, 5 September 2006, 13 September 2006, 15 September 2006, 28 November 2006, 29 November 2006, 7 December 2006, 8 December 2006, 1 June 2007, 21 September 2007, 25 September 2007, and 15 October 2007, totaling 46.8 hours of observation. Flowers were observed at a close range (one meter) through close-focusing 8.5 x 21 Pentax Papilio binoculars. For each floral visitor, the following data were recorded: identity of the visitor, whether or not it entered the floral chamber formed by the wing and keel petals, floral resource collected if any, and the duration of the visit. Prior to the study, a species-level reference collection of insect visitors was made to facilitate identifications during the timed observations.

Pollen transport – To examine the extent to which floral visitors were capable of transporting *S. tomentosa* pollen, insects observed foraging on flowers during June of 2007 were collected and examined for presence of pollen (Kearns and Inouye 1993). Insects were first collected with either a butterfly net or captured directly into a one-dram glass vial with a loosely closed top. The vial was then placed into a killing jar with a layer of plaster of Paris saturated with ethyl acetate. Once the insect was euthanized, it was washed by adding a 50:50 ethanol and water solution and shaken vigorously for two minutes (Krause and Wilson 1981). To ensure that most of the pollen was removed, the insect was withdrawn from the wash, allowed to dry, and then dabbed with a 1 mm^3 section of hardened glycerin gel (Beattie 1971) under a dissecting microscope. The small cube of gel was added to the insect wash and centrifuged for four minutes at 12,000 rpm. The supernatant was then decanted and the remaining pellet mounted and sealed on a slide with a droplet of 50:50 glycerin and Calberla's stain solution. A reference collection of pollen from plants on the study site was used to identify pollen washed from insects.

Pollen viability and stigma receptivity – A chemical test was used to determine the length of pollen viability after anther dehiscence. In June 2007, 71 mature buds were randomly assigned a floral age to be collected, and then enclosed in nylon bags with a fine mesh to be isolated from pollen-collecting floral visitors. Floral ages assessed were the day before anthesis or mature bud (n = 21), the day of anthesis or flower opening (n = 20), one day following anthesis (n = 16), and two days following anthesis (n = 14). The pollen was stained with a droplet of DAB (*Sigmafast*™ 3,3′-Diaminobenzidine), which tests for the presence of dehydrogenases in pollen as an indication of viability (Khatum and Flowers 1995). The droplet was allowed to dry and then a second application of the stain was applied. Once the second droplet dried, a droplet of glycerin and a cover slip were added to the pollen sample and sealed with nail polish. From a random field on the slide, 100 grains were counted and tallied as viable or nonviable. Viable pollen grains stain a dark brown while non-viable pollen remains colorless. As a control, a sample of pollen was killed with FAA (Formalin, acetic acid, and ethanol; 5:5:90, by volume) and then stained with a droplet of DAB to demonstrate the appearance of non-viable pollen to which viable pollen could be compared.

To determine the developmental stage at which *S. tomentosa* stigmas are most receptive, stigma receptivity was examined at various floral ages. In June 2007, 67 mature buds were emasculated and bagged in fine mesh nylon to avoid a false positive reaction due to presence of pollen on a stigma. Floral ages assessed were the day before anthesis or mature bud (n = 20), the day of anthesis (n = 18), one day following anthesis (n = 15), and two days following anthesis (n = 14). Stigma receptivity was identified with the same DAB chemical technique used to examine pollen viability. Receptive stigmas stain a dark brown while non-receptive stigmas remain colorless.

Pollen limitation experiment – Fruit set of *S. tomentosa* was compared between naturally-pollinated flowers and flowers artificially supplemented with pollen by hand, to determine whether female reproductive success was limited by insufficient deposition of pollen on stigmas (Kephart 2005, Dafni *et al.* 2005). From June to July of 2007, *S. tomentosa* flowers found east of Hilina Road were tagged as buds and randomly assigned to either control (no manipulation) or experimental (hand-pollinated) treatments. Upon anthesis, flowers in the experimental treatment were hand-pollinated with fresh pollen gathered from a mix of donor plants also located east of Hilina Road. Because the sprawling growth pattern of *S. tomentosa* made it difficult to differentiate between individual plants, an effort was made to pollinate flowers with pollen from flowers located at a distance greater than five meters from the recipient flower. Pollen was applied by gently rubbing recently dehisced anthers across the stigmatic surfaces of the recipient flower. In total, there were 102 control flowers and 99 flowers in the experimental treatment. Flowers were revisited after a month to determine the presence or absence of developing seed pods.

Rodent Exclusion Experiments

At the natural population of *P. sclerocarpa* at Puhimau Geothermal Area, 19 phenology plants were randomly selected to be protected from rodents by a small cage exclosure made of hardware cloth; hardware cloth has an opening in the wire squares of approximately 1.2 cm (½ inch). The size of the cage was 40 by 40 cm square with a height of 30 cm; this was adequate to accommodate even the largest *P. sclerocarpa* plant at the site. The exclosure had a hinged top so that it could be opened during monitoring; after monitoring the top was securely fastened with twist ties. The exclosure was secured tightly to the ground using landscape cloth pins. Exclosures were installed in October 2006 and were in place through October 2007. All branches bearing buds, flowers, or fruit capsules were counted monthly at each exclosure plant and an adjacent unprotected plant.

Exclosures were also constructed around 20 *S. tomentosa* branches at the Kīpuka Nēnē East. Branches were randomly selected from those 50 branches already established for phenology monitoring. Exclosures were cylindrical sleeves at least 1.2 m long made of hardware cloth closed off at the branch end by screening material sewed to the cylinder with a small hole for the stem to pass through. Within the exclosure sleeve, all buds, flowers, immature fruit, and mature fruit were counted at monthly intervals, as part of the overall phenology monitoring at the site. The numbers of reproductive structures inside the exclosure sleeves were compared with those on unprotected branches monitored monthly. Exclosures were installed in May 2006 and were in place for a year, when they had to be removed because of the growth of branches at the distal tip end.

Natural Seedlings

No natural seedlings were observed at the *Bobea timonioides* population at Nāulu Forest or at either the `Āpua Point or Kīpuka Nēnē populations of *Sesbania tomentosa*. Seedlings were, however, observed at both planted populations of *Portulaca sclerocarpa* at HVO and Kalanaokuaiki Pali. When seedlings were first seen at the HVO site, they were marked with small plastic-headed pins and recounted at monthly intervals. A plot 1 m by 1 m in size was marked around each of 10 plants that produced seedlings to facilitate searching for new seedlings. When seedlings appeared at the Kalanaokuaiki plantings, they were marked with a wooden toothpick and counted with reference to the tag number of the parent plant. Plot perimeters with flagging tape were established around those plants that produced large numbers of seedlings. All seedlings were counted monthly, new seedlings were marked with a toothpick, and seedlings that died were noted and had their toothpicks removed.

Seeds and Seed Germination

Field seed plots in and outside rodent exclosures – At the *Bobea timonioides* population in Nāulu Forest just down slope from several monitored trees, 10 small exclosures were placed in an area with soil under partial shade. Exclosures were boxes made of hardware cloth open on the end attached to the ground with stakes. Twenty fresh seeds were planted inside each exclosure in April 2007, and an equal number of seeds was planted in 10 adjacent open plots the same size as the exclosure (16 by 16 cm). Seed plots were examined for seedling recruitment bimonthly for 10 months.

Field seed plots with and without grass – At both the Kīpuka Nēnē East and West monitoring sites, a 50-m-long transect was placed along the perimeter of the *Sesbania tomentosa* patches. Five pairs of seed plots were selected at random points along each of these lines. Each plot was 1 by 1 m in size and was marked with flagsticks on the corners. One plot of each pair was established in an area with alien grass cover, and the adjacent plot had all alien grass pulled by hand. Predominant alien grasses were *Melinis minutiflora* and *Schizachyrium condensatum*. Soil depths were measured with a soil probe (>1 m long) at the time of plot establishment with 10 soil depth measurements per plot, and any randomly-selected plot with an average depth <15 cm was rejected.

In April 2007, each plot at the Kīpuka Nēnē East site had 51 seeds sowed in five rows. Seeds were a mixture of freshly collected seeds and seeds collected two to four months previously and stored in the refrigerator. Plots were monitored for seedlings monthly for 2.5 years. At the Kīpuka Nēnē West site plots were each sowed with 51 fresh seeds in February

2008. Plots were monitored monthly at this site for a year and eight months. All seedlings at both sites were counted, measured for height, and marked with numbered tags, and their death or disappearance was recorded monthly.

Seed plots for *S. tomentosa* could not be placed at `Āpua Point, because this remote site could not be visited monthly. Instead, coastal seed plots were placed at the end of the Chain of Craters Road near Hōlei Sea Arch. Three pairs of plots were selected in flat areas with soil cover between the road and the shoreline; a plot of each pair was covered with alien grass (primarily *Digitaria* sp., crabgrass) and the second was grass-free. Soil depths were measured with a soil probe at the time of planting (two measurements per plot); all plots had a minimum soil depth of 18 cm. Sixty-six seeds from the `Āpua Point plants were planted in each plot in April 2007; seeds were a mix of freshly collected seeds and those stored for 10 months in a refrigerator. Starting three weeks after planting, plots were monitored at two-week intervals for four months. All seedlings were counted and marked with a wooden toothpick. Seedling heights and disappearance were recorded at each monitoring interval.

Field seed plots in moss and soil – At the natural *P. sclerocarpa* population at Puhimau we established pairs of seed plots 20 by 40 cm in size at each of 10 randomly-selected monitored plants. One plot of each pair was set up in bare soil adjacent to a *P. sclerocarpa* plant, and the second was placed in a nearby area covered by native moss (*Campylopus* spp.). Seed plots were not placed on obvious trails to steam vents. Plot corners were marked with tacks and the sides were delineated with white thread. In October 2006, 200 fresh seeds were sowed in each plot, and plots were examined monthly for two years to detect the appearance of seedlings.

Seed and fruit predation by rodents – At the natural *Bobea timonioides* population at Nāulu Forest, offerings of 20 fresh cleaned seeds were made in each of three open rat bait stations (Protecta brand) and in three adjacent bait stations with the opening sealed off with screen. Pairs of stations were placed beneath randomly selected *B. timonioides* trees. Offerings were made in March 2007, and seeds were counted and examined for rodent chewing at two-month intervals for six months.

At both the natural Puhimau population and the planting site near HVO, offerings of *Portulaca sclerocarpa* capsules (with seeds intact) were made inside and outside rodent-proof small exclosures made of hardware cloth affixed securely to the ground. At Puhimau these were the same exclosures that protected randomly selected *P. sclerocarpa* plants for a year. At HVO, small boxes 16 x 30 cm in size made of hardware cloth were used to protect the offerings of fruit from rodents. Twenty seed capsules were offered in plastic trays inside and outside the rodent-proof cages, and the offerings were monitored monthly for three months to record disappearance and rodent chewing.

Sesbania tomentosa seeds were offered as intact seed pods at the Kīpuka Nēnē East site. Sites selected for the seed pod offering were randomly selected points along a north/south transect on the western perimeter of the patch of monitored plants. In October 2006 an intact mature legume 20 cm in length was offered in each of three rodent-proof hardware cloth cages and in three adjacent open trays tacked to the ground; the full-size legumes were mottled green with red or yellow blotches. A second offering was made in December 2006 using two to three mature seed pods in each of five cages and adjacent open sites. Four pair of cages and controls had two large (20 cm) legumes offered, and the fifth pair each had three small (ca. 10 cm long) seed pods offered. The October and December offerings of fruit were examined for rodent predation after 1–1.5 months.

At Kīpuka Nēnē West, samples of green developing fruit were tagged with numbered flags and examined monthly for rodent predation or disappearance. These green fruit were not typically on randomly-selected monitored branches, but were scattered throughout the *S. tomentosa* population. Tagging started in March 2007 and continued until September 2009. When pods matured, dried, and turned brown they were left on branches for a minimum of three months before they were collected for seed germination projects.

Soil seed bank – The soil seed bank of *Bobea timonioides* was not sampled, because it was impossible to collect soil cores beneath monitored trees in the rocky `a`ā substrate of the study site. The *Portulaca sclerocarpa* seed bank was not sampled because the tiny seeds of this species could not be consistently sifted out of soil samples. *Sesbania tomentosa* soil seed banks were sampled at both `Āpua Point and Kīpuka Nēnē by collecting soil cores taken from beneath the canopy of randomly selected plants and sifting the air-dried soil through a soil sieve with 2 mm apertures (smaller than the target seed). All seeds, whole or partial, were collected from sieved soil and rocks, counted, and examined for rodent damage. Whole seeds were planted in pots with a medium of mixed cinder, perlite, and potting soil. The soil coring device was a bulb planter 10 cm long and 6 cm wide (at the base).

The `Āpua Point plants were sampled in both March and May 2007 with five cores collected at each of five randomly selected plants. If the substrate did not have soil as deep as the coring device beneath a plant, that plant was rejected and the next randomly selected plant was chosen. Kīpuka Nēnē plants were sampled in October 2006 at the eastern site and in December 2007 at both the eastern and western sites; sampling was carried out beneath randomly selected branches used for phenology monitoring. In October 2006 10 branches were sampled, and in December 2007, five branches were sampled; each branch had five soil cores taken from beneath the foliage of *S. tomentosa*.

Seed germination in the greenhouse – Seeds of *Bobea timonioides*, *Portulaca sclerocarpa*, and *Sesbania tomentosa* were collected from multiple plants at several seasons throughout the study. Germination trials used fresh seeds when possible, but for some trials seeds were stored in a refrigerator for up to six months until an adequate sample could be collected for a germination trial. No special treatment was given to seeds before sowing, except in the last two trials with *S. tomentosa* when seeds were soaked in warm water before planting. Seeds were planted in replicated pots or flats filled with a potting medium of equal parts vermiculite, perlite, and cinder. Because of the small size of *P. sclerocarpa* seeds, pots in those trials had a top layer of fine sifted cinder above the standard potting medium. Germination trials were carried out in the HAVO Natural Resources Management greenhouse, which is located north of Kīlauea Iki Crater at 1,180 m elevation. Flats and pots were misted with water three times a day. The time of first germination was noted for each pot or flat, and counts of seedlings were made weekly. Trials were terminated when seedlings ceased to appear or after seven to eight months with no germination.

Three germination trials were carried out with *B. timonioides* seeds; each trial used 50 to 57 cleaned, air-dried seeds per flat with three replicate flats. The first trial was sown in April 2007 using two-month-old seeds; the second was sown in July 2007 with seeds five months old; and the third was planted in February 2008 using seeds six months old. Trials were monitored for four to six months.

Portulaca sclerocarpa had four germination trials each with three to five replicated pots. Four trials used 100 seeds in each pot, and one used 50 per replicate. Seed capsules were collected from both the natural and planted populations and were stored for a month. Seeds were removed from the dry capsules and counted into vials before sowing. Trials were sowed in November 2005, May 2006, June 2007, and January 2009. Trials were monitored for seven to eight months.

Four germination trials were carried out with *S. tomentosa* seeds. Two trials used 50 seeds per flat with five replicates in each trial. Two trials used 23 or 40 seeds in each of three replicate flats. Seeds were removed from the dry seed pods (legumes) and air-dried. All seeds were planted a few days after being collected, except those of the second trial, which were stored in a refrigerator for five months before sowing, and those of the fourth trial, which were a mix of fresh seeds and seeds stored for two months. In the latter two trials, seeds were soaked in warm water for six hours before sowing. Seeds in the trials were sowed in July 2006, October 2006, February 2009, and June 2009. The first two trials were terminated 15 to 20 months after planting, and the latter two trials were monitored for three to four months before termination.

Seed viability test – To complement germination trials and estimate seed viability, a tetrazolium test was used on ungerminated seeds of *P. sclerocarpa* (20). Seeds of *S. tomentosa* and *B. timonioides* were not tested with this method, which results in destruction of the seed sample, because at the time of the study park managers were collecting seeds of these species to propagate for restoration projects. Seeds of *P. sclerocarpa* were prepared by opening the seed coat and bisecting the endosperm and embryo with a razor blade. The internal parts of the healthy seeds were not removed from the bisected halves of the seed coat before treatment. Prior to opening, the seeds were first imbibed in tap water for 24 hours. Each seed was individually treated with a 0.1% solution of 2,3,5-triphenyl tetrazolium chloride in a buffer of 66 mM KH_2PO_4 and 33 mM Na_2HPO_4 (pH ~7.0). Solution was added to completely cover both halves of the bisected seed. Hydrogen ions released as products of respiration in a healthy embryo reduce tetrazolium chloride to form formazan, which appears red and stains healthy tissues (Cottrell 1947, Baskin and Baskin 1998).

Results of the tetrazolium test were recorded 24 hours after treatment. Each seed was individually inspected for staining using a dissecting microscope. Viability was assessed by assigning each seed to a category representing the level of embryo staining (negative = no staining, weakly positive = embryo with barely detectable pink color, positive = embryo clearly pink, strongly positive = embryo with dark reddish staining).

Data Analysis

The majority of analyses were performed using two methods. For data recorded as categories, including phenology observations of structures that were too numerous to count efficiently or accurately (e.g., buds) and dichotomous variables such as survival, comparisons were made using chi-square tests of independence in contingency tables. For data that incorporated continuous variables, such as counts from phenology observations, growth, diameter, number of leaves, number of germinants, and frequency of events such as rat or insect predation, means were compared using two-sample t-tests assuming unequal variance. The t-tests were run using the Analysis ToolPak in Excel (Microsoft 2003). In comparing the mean density of *P. sclerocarpa* plants in plots surveyed in 1993 and again in 2008, a Wilcoxon signed-rank test was used because the mean densities did not meet parametric assumptions due to the large number of plots without any *P. sclerocarpa* plants. Likewise, a Mann-Whitney U test was used to compare the mean decrease in *P. sclerocarpa* density between plots with high grass cover and those with low grass cover. With all statistical tests, a probability level of 0.05 or lower was considered significant.

The mean proportion of *Portulaca sclerocarpa* branches with fruit and the mean number of buds, flowers, and fruit on *Sesbania tomentosa* branches were compared between rodent-excluded and control plants using repeated measures analysis of variance (ANOVAR). This was run with SAS® 9.1 using the MIXED procedure (SAS Institute, Cary, NC). Repeated measures analysis was used to improve model accuracy by fitting a variance-covariance structure. The analysis was run with four different variance-covariance structures (Autoregressive 1; AR1), Compound Symmetry (CS), Toeplitz (TOEP), and Unstructured (UN), and then compared using AICc values. The results of those comparisons indicated that for both the *P. sclerocarpa* data and all three *S. tomentosa* data sets UN was the best fit variance-covariance structure. Denominator degrees of freedom were adjusted using the Kenward-Roger adjustment statement. The *S. tomentosa* data contained a large number of zeros associated with periods where some plants were not producing, so count data was ln (count+1) transformed in order to meet the parametric assumptions of the ANOVAR and to stabilize the error variance. Multiple comparisons were made using Tukey's adjustment to control experiment-wise Type I error rate.

Mean visitation rates for each floral visitor species in the pollination study were calculated as the total number of flowers visited per total number of flowers observed per 15-minute observation period and then converted to the number of visits per flower per hour. The mean visitation rate was based on the average across all observation periods. Mean visit duration was calculated as the total time spent visiting a flower and averaged across individual visits independent of observation period. In the insect transport study, the Wilcoxon rank-sum test was used to compare the mean number of *S. tomentosa* pollen grains removed from washed insects. The results of the average pollen viability among floral ages were compared with ANOVA. All statistical tests in the pollination studies were performed using SPSS 10.0 statistical package (SPSS Inc., Chicago, IL).

RESULTS

Bobea timonioides, **`Ahakea**

Size Class Structure, Growth, and Mortality

In 2006, 24 of 36 *Bobea timonioides* trees previously mapped in Nāulu Forest (Abbott and Pratt 1996) were relocated (Fig. 1); 16 were found alive and 8 were dead. The mortality rate of relocated trees was 33.3% over 13 years. The diameter class distribution of trees in 2006–2007 was similar to that displayed in 1993 (although the number of trees was different in the two time periods; Fig. 4). No trees with diameters less than 10 cm were seen in either monitoring period, and most trees were mature trees with diameters 20–40 cm.

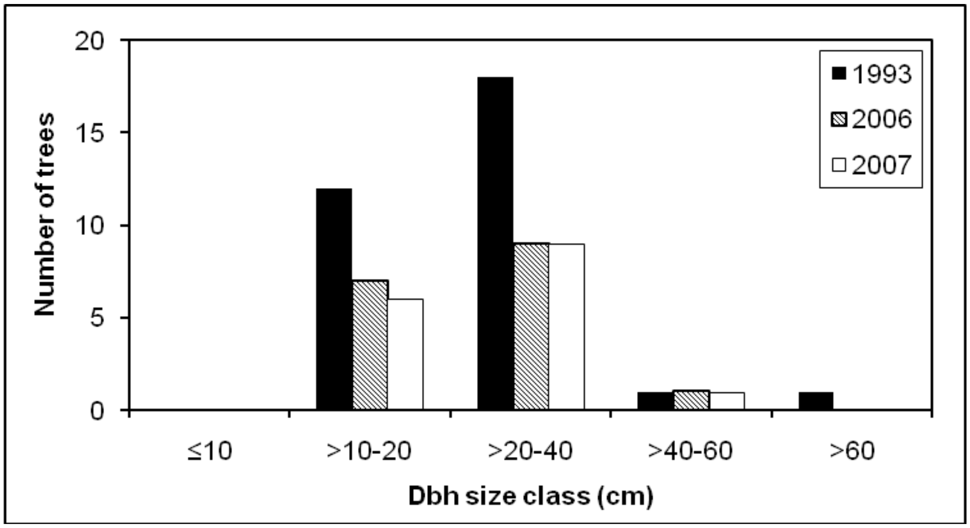

Figure 4. Size class distribution of *Bobea timonioides* at Nāulu Forest in 1993 (36 trees) and 2006–2007 (16 trees).

Very little growth in diameter was observed between 1993 and 2006–2007. The mean diameter of the 16 trees surviving in 2007 was 25.9 cm (± 11.9 SD), and this was a very slight increase over the mean diameter of 25.5 cm (±11.2 SD) measured for the same trees in 1993. Only seven trees exhibited growth during the 13-year period; the others remained the same diameter or showed a decrease.

Reproductive Phenology 2006–2007

During the 17 months of monitoring from June 2006 until October 2007, a high percentage of trees (ca 80%) bore buds and/or flowers at every monitoring period except summer (June and August) 2007, when less than 20% of trees were observed with buds (Fig. 5). Summer is typically a dry season based on long-term HAVO weather records collected at nearby Pu`uloa, which showed June through August as the driest months of the year. In May 2007, rainfall was only 33 mm at Pu`uloa (HAVO Fire Cache, unpublished data), and a rain gauge at Nāulu collected only 35 mm in the two months prior to June (T. Belfield, pers. comm.). Based on estimated abundance of buds and flowers, there were repeated peaks of bud production in fall, winter, and spring. Green fruit were observed on more than 60% of monitored trees in every bimonthly interval except August 2007, when no fruit were seen on *Bobea* trees (Fig. 6). There was no clear pattern of seasonal abundance of immature fruit, as peaks of production were noted in summer and fall 2006 and in winter 2007.

Fewer trees were observed bearing mature black fruit than were seen with green fruit; the proportion of trees with mature fruit exceeded 50% only in August 2006 and February–April 2007 (Fig. 7). Typically most trees bore <50 mature fruit even during months when most trees had fruit. The pattern of peak production of mature fruit was not consistent between the years 2006 and 2007, because August 2006 showed a peak in mature fruit, but in August of the following year only half as many trees bore ripe fruit and estimated abundance was low.

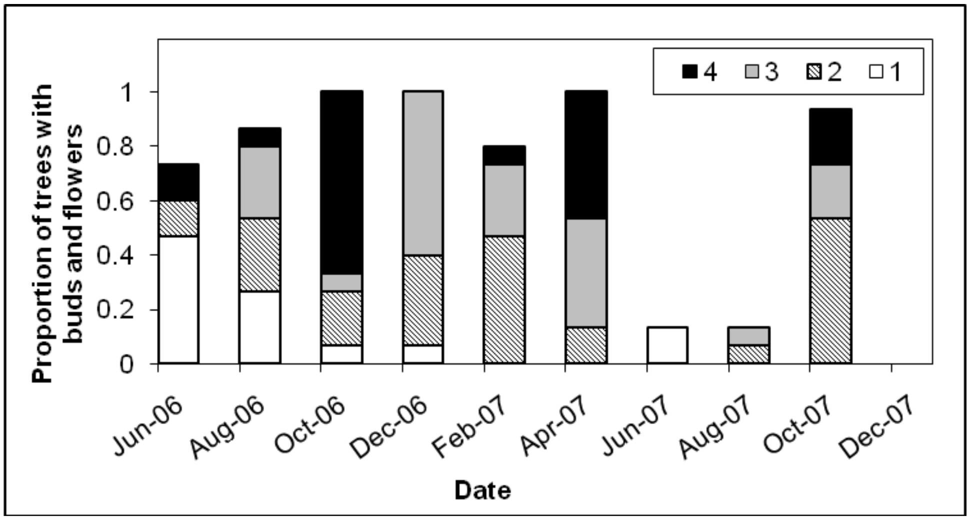

Figure 5. Estimated abundance of buds and flowers in four categories for *Bobea timonioides* trees at Nāulu Forest, 2006–2007 (categories: 1 = 1–10, 2 = 11–50, 3 = 51–100, 4 = >100).

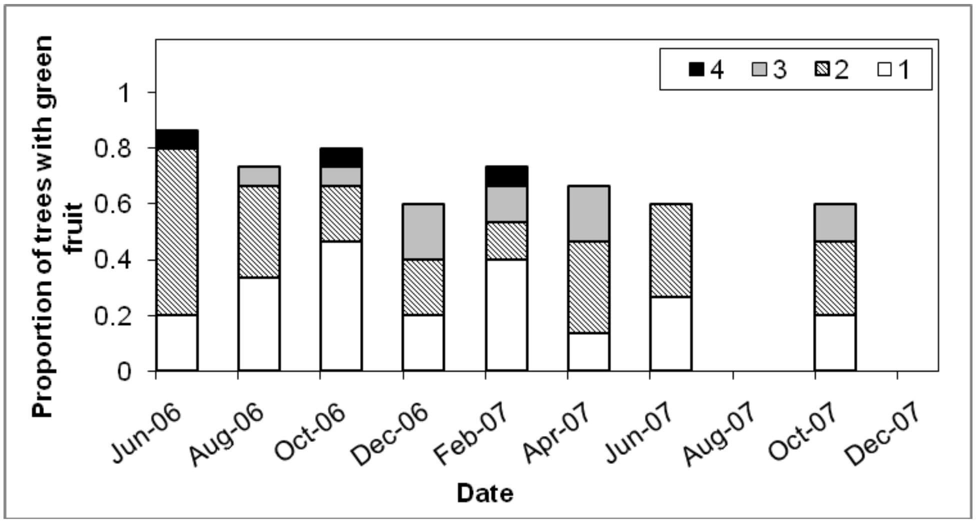

Figure 6. Estimated abundance of green fruit in four categories for *Bobea timonioides* trees at Nāulu Forest, 2006–2007 (categories: 1 = 1–10, 2 = 11–50, 3 = 51–100, 4 = >100).

Planted Seedlings

The mortality rate of a sample of 59 *B. timonioides* seedlings planted within the tree's natural habitat at Nāulu Forest in 2005 was low (6.8%) after the first six months, but mortality increased to 79.7% a year post-planting (Fig. 8). By June 2007, almost all seedlings had died (93.2%). When the site was revisited in March 2010 by NPS botanists, there were no live *B. timonioides* plantings (T. Tunison, pers. comm.). Relatively little growth in height was observed over 1.5 years. The mean height of seedlings was 35.7 cm (±11.1 SD) after planting, and by June 2007 the surviving seedlings had achieved a mean height of 46.8 cm (± 6.7 SD).

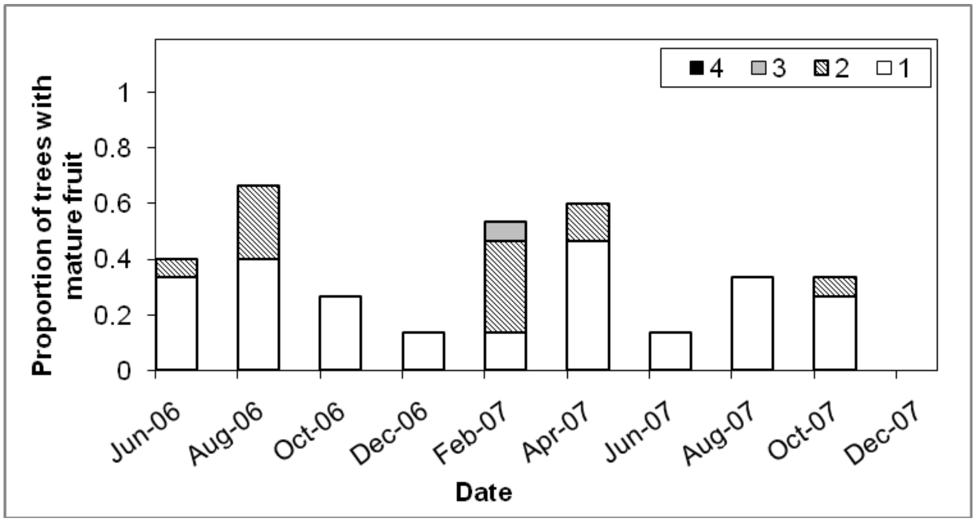

Figure 7. Estimated abundance of mature fruit in four categories for *Bobea timonioides* trees at Nāulu Forest, 2006–2007 (categories: 1 = 1–10, 2 = 11–50, 3 = 51–100, 4 = >100).

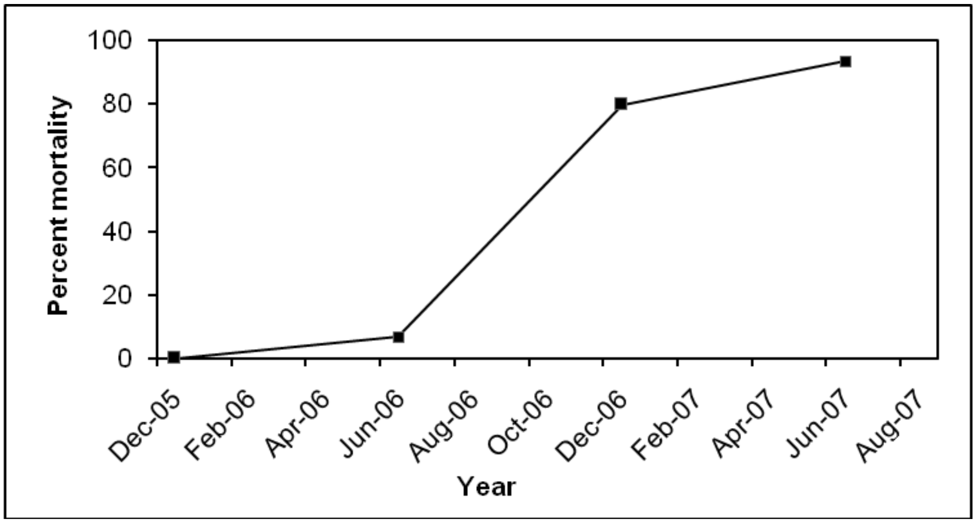

Figure 8. Mortality (%) of *Bobea timonioides* seedlings planted in 2005 at Nāulu Forest, HAVO.

Seeds and Seed Germination

Field seed plots in and outside rodent exclosures – After six months of monitoring, no germination was observed in either caged or open seed plots sown in April 2007 near adult *B. timonioides* trees at Nāulu Forest.

Seed predation by rodents – Of 20 fresh seeds offered in each of three open bait stations in March 2007, only two seeds were missing from a single station after three months (3% of the total offering). No disturbance was noted in control bait stations closed to rodents. The small difference in seed disturbance between the treatments was not significant ($\chi^2 = 2.0$, df = 1, p = 0.15).

Seed germination in the greenhouse – The overall germination rate of three trials with *B. timonioides* seeds in the HAVO greenhouse was 39%. The first trial using seeds collected during the previous two months and planted in April 2007 had the highest mean germination rate (59%) of all trials (Appendix I, Table 1). The second trial in July 2007 used five-month-old seeds and had a mean germination rate of 39%. In the third trial, seeds were six months old and were sown in February 2008; the mean germination rate was 21%. The proportion of seeds germinating in each of the first two trials was significantly higher than that seen in the third trial ($\chi^2 = 12.5$, df = 1, $p < 0.001$ and $X^2 = 5.4$, df = 1, $p = 0.02$). Seedlings were first observed four to six weeks after sowing.

Portulaca sclerocarpa, **`Ihi mākole**

Growth and Mortality at the Natural Puhimau Population

In 2006, 300 *P. sclerocarpa* plants were found and tagged at Puhimau Geothermal Area (Fig. 2). The total Puhimau population consisted mostly of small plants ≤100 cm^2 in area at both the initial measurement and the final visit two years later (Fig. 9). Plants in larger size classes were much less abundant, and few plants were found in the >300 cm^2 size class. After two years there were 229 survivors, and the mortality rate over the monitoring period was 23%. Losses were noted in all size classes between 2006 and 2008, but were most pronounced in the two smallest groups of plants. In a t-test comparing the mean size of 229 surviving plants in 2008 (111.2 cm^2, ± 123.5 SD) with that of the same plants in 2006 (123.0 cm^2, ± 111.5 SD), there was a significant decrease in plant size over the two-year period (t = 2.0, df = 228, p = 0.045).

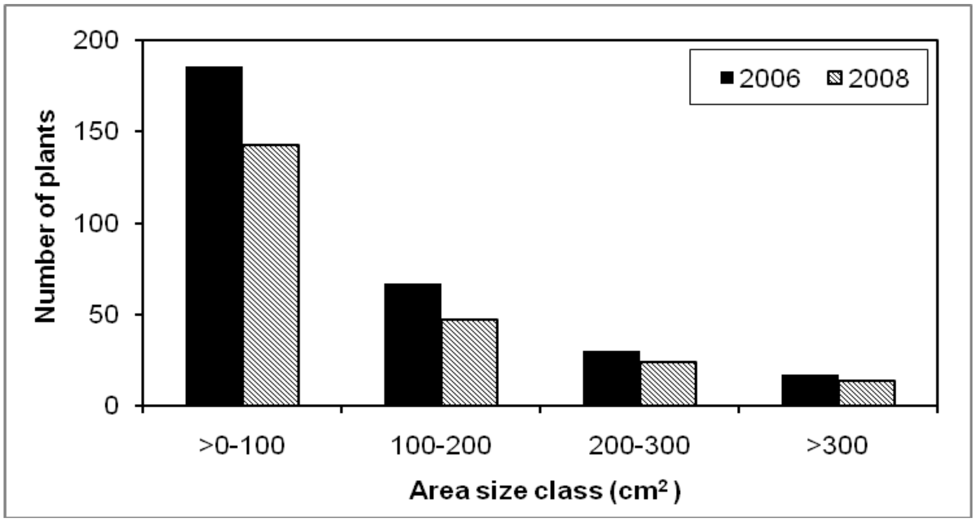

Figure 9. Size class distribution of all *Portulaca sclerocarpa* plants in a natural population at Puhimau Geothermal Area, 2006–2008.

A higher mortality rate was displayed by the subset of plants randomly selected for phenology monitoring; 31% of these were lost between 2006 and 2008. Mortality was relatively low in 2006, but steadily increased in 2007 (Fig. 10). Care was taken to avoid damage to plants during regular visits, but this higher mortality rate for frequently monitored plants indicates that the species may be sensitive to disturbance. As was seen in the total population, size decreased in the monitored subset of plants over a two-year period. The mean size of 47 surviving plants in 2008 (103.9 cm^2, ± 125.8 SD) was significantly smaller (t = 2.1, df = 46, p = 0.04) than that of the same plants in 2006 (130.2 cm^2, ± 108.1 SD).

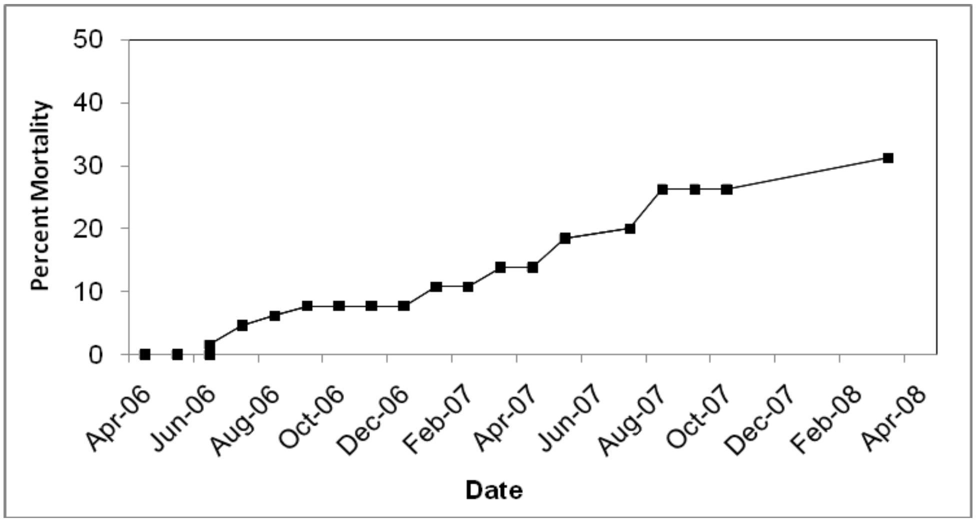

Figure 10. Mortality (%) of a subset of 64 *Portulaca sclerocarpa* plants in a natural population at Puhimau Geothermal Area, 2006–2008.

<u>Growth and Mortality at Plantings</u>

Cuttings at Hawaiian Volcano Observatory (HVO) – Mortality was very high in rooted cuttings planted in June 2004 at the HVO site. Between December 2005 and May 2007, 84% of the total monitored planting of 300 died. When last visited, 71% of 49 surviving plants displayed poor vigor with few leaves and many dead branches. Mortality was lower in a subset of plants randomly selected for phenology observations. In this group 49% of plants died by May 2007, and there was a steady decline in the number of live plants over the monitoring period of 18 months (Fig. 11). We were unable to revisit the site in 2008 because a summit eruption caused access restrictions in the area. When we visited the site in April 2010 to remove tags and markers, only a single *P. sclerocarpa* plant remained alive at HVO.

Individuals in the monitored planting of 300 decreased steadily in size over 18 months (Fig. 12). The mean size (area) of surviving plants in 2007 (29.8 cm^2, ± 37.78 SD, n = 49) was significantly smaller (t = 11.6, df = 48, p < 0.0001) than the mean size of the same plants in December 2005 (245.6 cm^2, ± 143.2 SD, n = 49).

Seedlings at Kalanaokuaiki Pali with and without grass – Mortality of 50 seedlings planted at Kalanaokuaiki in July 2006 was 20% overall after more than two years in the ground. Mortality among 25 seedlings in plots without grass was 24%, higher than the 16% observed for 25 plants in plots with grass cover (Fig. 13). The difference in mortality in grass and grass-free treatments was not statistically significant (X^2 = 0.5, df = 1, p = 0.480). Losses were observed during the first 6 months of monitoring, after which all plants survived.

Size of seedlings in both treatments increased in the first six months after planting, and then remained the same for more than 10 months (Fig. 14). By January 2008, plants in the

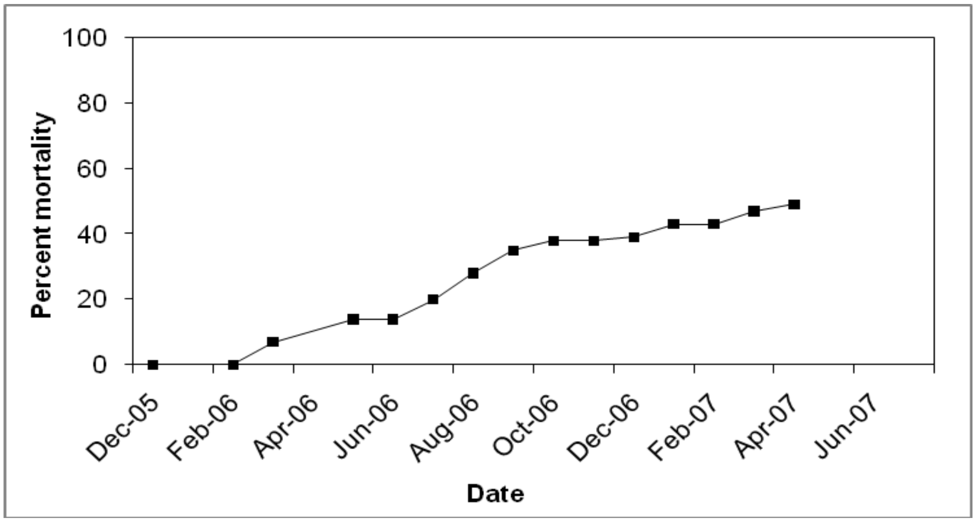

Figure 11. Mortality (%) of a subset of 67 *Portulaca sclerocarpa* in a planting at Hawaiian Volcano Observatory, 2005–2007.

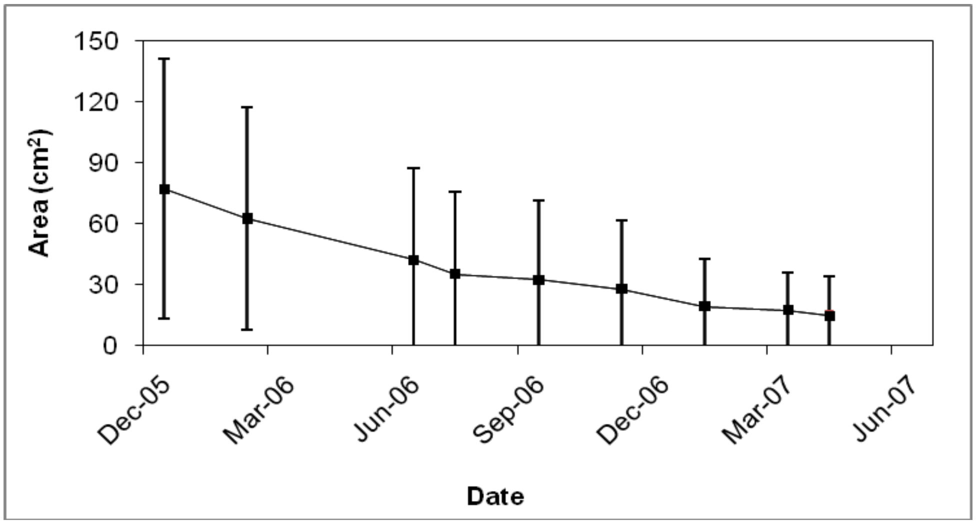

Figure 12. Mean (±SD) areal size (cm^2) of 49 survivors of 300 *Portulaca sclerocarpa* planted at Hawaiian Volcano Observatory, 2005–2007.

grass treatment began to increase in size, while those planted without grass decreased. During the observation period, the mean maximum size of plants in the grass treatment was 476.2 cm^2 (± 191.4 SD, n = 25), significantly larger (t = 2.1, df = 48, p = 0.04) than the mean maximum of 347.2 cm^2 (± 232.7 SD, n = 25) in the no-grass treatment. The maximum height of seedlings in the grass treatment was 11.4 cm (± 4.0 SD) compared with 6.1 cm (± 2.0 SD) in the no-grass treatment. There was no difference in the mean maximum number of branches in plants of the two treatments (t = 0.2, df = 48, p = 0.84).

Seedlings and cuttings at Kalanaokuaiki Pali – The overall mortality of the seedlings and cuttings combined was 10% when measured 17 months after planting in March 2008. Mortality of 30 cuttings (17%) was more than five times greater than that of 30 seedlings (3%), although

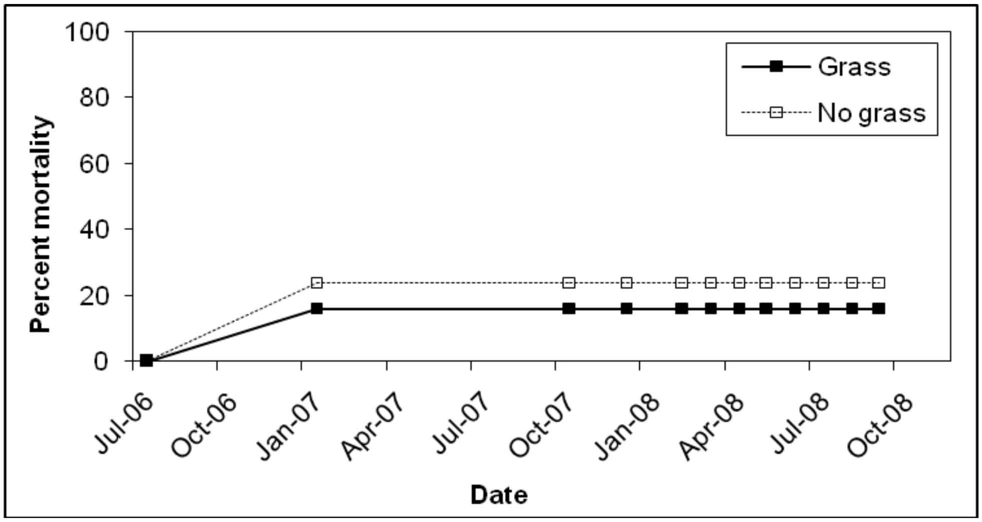

Figure 13. Mortality (%) of *Portulaca sclerocarpa* seedlings planted in treatments with and without alien grass at Kalanaokuaiki Pali, 2006–2008 (25 seedlings in each treatment).

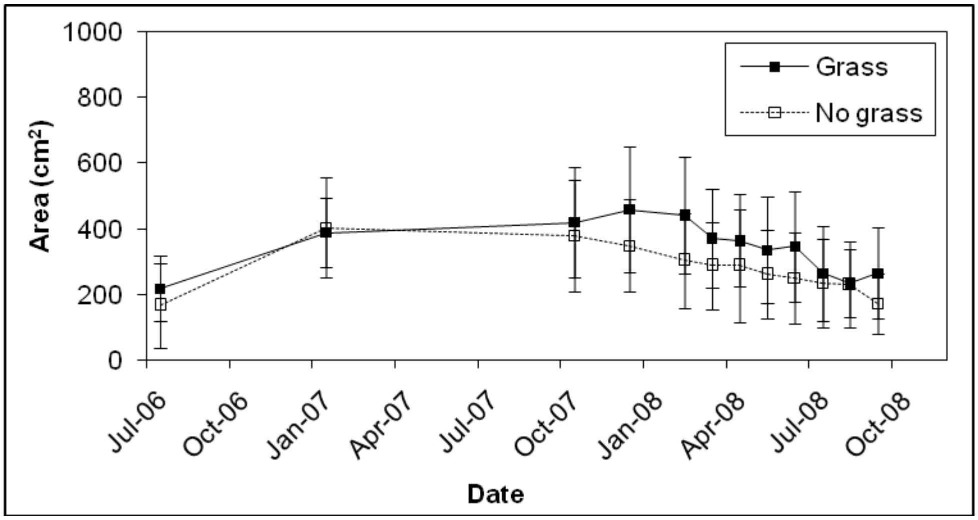

Figure 14. Mean (±SD) areal size (cm^2) of seedlings planted in treatments with and without alien grass at Kalanaokuaiki Pali, 2006–2008.

the difference was not highly significant (χ^2 = 3.0, df = 1, p = 0.09). First losses were observed nine months after planting, and cuttings continued to accrue losses until the end of monthly monitoring in August 2009.

When re-visited in April 2010, eight months after the final monthly monitoring, mortality of cuttings was 40%, while that of seedlings had not increased (3%). The mortality of cuttings was significantly greater than that of seedlings at this re-visit more than two years after planting (X^2 = 9.0, df = 1, p = 0.003). The size of seedlings was also much larger than that of cuttings. The differences were noticeable at planting in March, and while seedlings steadily increased in size for nine months, cuttings gained very little in area at the beginning of the study period. Both seedlings and cuttings were smaller on average in August 2009 than when they were planted (Fig. 15).

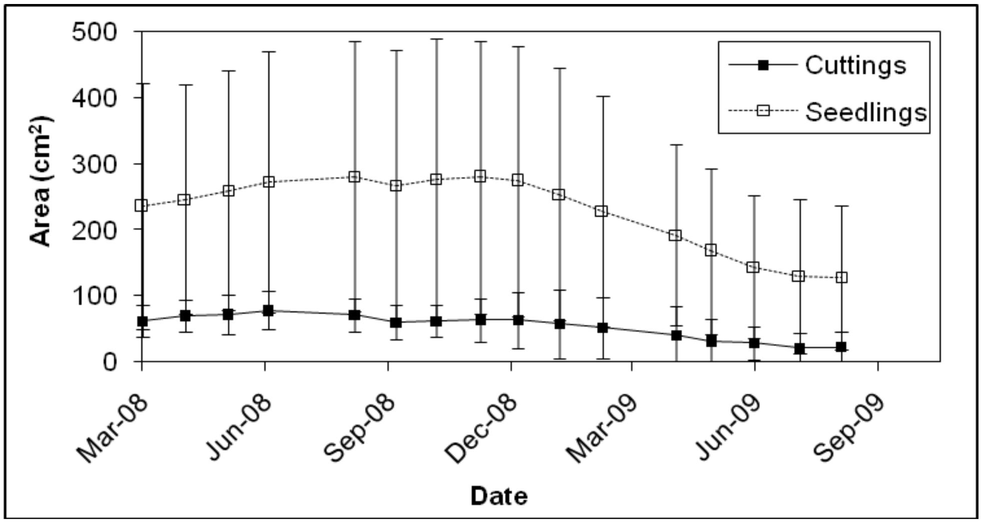

Figure 15. Mean (±SD) areal size (cm^2) of seedlings and cuttings planted at the same time at Kalanaokuaiki Pali, 2008–2009.

Density, Cover, and Frequency of Plants at the Puhimau Population

Portulaca sclerocarpa density 1993–2008 – When the natural population of *P. sclerocarpa* was surveyed throughout the Puhimau Geothermal Area in 1993, 970 plants were found at the site (L. Pratt, unpublished data). In 2008, 100 of 347 potential plots 10 x 10 m in size covering the entire geothermal area were randomly selected to recount and compare with the density observed in the last survey 15 years before. In 1993, 301 *P. sclerocarpa* plants were observed in the 100 plots combined for a calculated density of 0.03/m^2. Forty of the 100 sampled plots contained at least one *P. sclerocarpa* plant.

By 2008, only 38 *P. sclerocarpa* plants were counted in the same 100 sampled plots for a density of 0.004/m^2. In this recount, only 10 of the 100 plots supported *P. sclerocarpa* plants, revealing a loss of plants from 30 plots that supported *P. sclerocarpa* in 1993. Nine additional plots had decreased numbers of *P. sclerocarpa* between 1993 and 2008, while new plants were found in only a single plot in 2008. A comparison of the mean number of plants in the paired plots with a Wilcoxon signed-rank test indicated a significantly lower number of plants in 2008 compared with 1993 ($S = 418$, $p < 0.0001$). There was no significant difference in the decrease of *P. sclerocarpa* in plots with high alien grass cover (>25%) compared with those that had little grass cover (<25%) in 2008 (Mann-Whitney $U = 883.5$, $n_1 = 82$, $n_2 = 18$, $p = 0.80$).

Cover and frequency of all plants 1981–2008 – The species encountered on three transects in the central zone of the geothermal area were similar in 2008, compared with those listed 27 years prior (Smith 1981; Table 1). The cover of the most common alien grass, *Andropogon virginicus* appeared to decrease slightly in the central zone, despite a large increase in the frequency of the grass. The native mosses *Campylopus* spp. and *Dicranella integrifolia* combined showed a dramatic downward trend in cover in 2008, although their frequency was similar in 1981 and 2008. The lichens *Cladonia* (*Cladina*) *skottsbergii* and

Table 1. The percent frequency and percent cover of species in the central zone of the Puhimau Geothermal Area in 1981 [1] and 2008.

Species	% Frequency 1981	% Frequency 2008	% Cover 1981	% Cover 2008
Andropogon virginicus	30	61	6.5	4.0
Bulbostylis capillaris	1	44	0	2.7
Campylopus spp./*Dicranella integrifolia*	94	93	11.5	2.8
Carex wahuensis	29	-	0	-
Chamaesyce hirta	4	7	0	0
Cladonia fimbriata	11	27	0	0.1
Cladonia oceanica	93	85	4.0	1.3
Cladonia (*Cladina*) *skottsbergii*	18	16	1.0	0.1
Cyperus polystachyos	-	4	-	0
Digitaria violascens	-	9	-	0.1
Diploschistes sp.	11	28	0.5	0.4
Fimbristylis dichotoma	-	56	-	1.2
Lindsaea ensifolia	-	1	-	0.0
Nephrolepis brownii or *N. exaltata*	1	1	0	0
Portulaca pilosa	-	39	-	2.0
Portulaca sclerocarpa	2	0	0	0
Stereocaulon spp.	36	37	0.5	1.3
Waltheria indica	6	8	1.0	0.4
Litter	100	100	19.0	1.5
Bare ground	100	100	56.0	81.9

[1] Smith, C. W. 1981. Bryophytes and lichens of the Puhimau Geothermal Area, Hawaii Volcanoes National Park. The Bryologist 84:457–466.
- Not seen in frequency plots or cover transects that year.

Cladonia spp. also declined in cover between the two surveys. No *P. sclerocarpa* was encountered in either the frequency plots or the cover transects in 2008, which was a decrease from the 2% frequency observed in 1981. By contrast, the alien *P. pilosa* (`ihi) had high frequency and 2% ground cover in 2008 but was not observed at the geothermal area in 1981.

In the peripheral zone of the geothermal area, the alien grasses *A. virginicus* and *Schizachyrium condensatum* and the alien sedge *Bulbostylis capillaris* showed large increases in cover between 1981 and 2008 (Table 2). The native mosses *Campylopus* spp. and *D. integrifolia* had similar cover in both surveys, as did the terrestrial lichen *Cladonia oceanica*. The alien fern *Nephrolepis brownii* (formerly *N. multiflora*) appeared in the peripheral zone between 1981 and 2008, and it had high ground cover in the recent survey. Other alien plants observed in 2008 but not in 1981 were *Paspalum conjugatum* (Hilo grass), *Emilia javanica* (Flora's paintbrush), *Hypochoeris radicata* (gosmore), and *Portulaca pilosa*. *Portulaca pilosa* had low frequency and no measurable cover along the peripheral transects in 2008. No plants of the rare *P. sclerocarpa* were seen in plots or along cover transects of the peripheral zone in either year. Two native sedges (*Fimbristylis dichotoma* and *Cyperus polystachyos*) and the fern

Table 2. The percent frequency and percent cover of species in the peripheral zone of the Puhimau Geothermal Area in 1981 [1] and 2008.

Species	% Frequency 1981	% Frequency 2008	% Cover 1981	% Cover 2008
Andropogon virginicus	97	96	27.6	49.7
Arundina graminifolia	13	21	0	2.7
Bulbostylis capillaris	2	17	0	0.7
Campylopus spp./*Dicranella integrifolia*	68	77	6.4	7.5
Carex wahuensis	19	-	0	-
Cladonia fimbriata	35	1	0	0
Cladonia oceanica	45	100	2.4	2.7
Cladonia (*Cladina*) *skottsbergii*	42	31	0	0
Ctenidium decurrens	12	0	0	0
Cyperus polystachyos	-	24	-	0.7
Digitaria setigera	2	0	1.6	0
Diploschistes sp.	0	25	0	0.1
Dodonaea viscosa	1	20	0	2.9
Emilia javanica	-	15	-	0
Fimbristylis dichotoma	-	19	-	0.5
Hypochoeris radicata	-	3	-	0
Isopterygium spp.	-	31	-	0.1
Lepraria sp.	1	0	0	0
Leucobryum gracile	5	1	0	0
Lindsaea ensifolia	-	3	-	0
Lycopodiella cernua	-	13	-	0.1
Melinis repens	2	1	0	0.1
Metrosideros polymorpha	5	7	0	0
Nephrolepis brownii	-	71	-	7.2
Nephrolepis exaltata	19	0	2.4	0
Paspalum conjugatum	-	4	-	0
Portulaca pilosa	-	4	-	0
Portulaca sclerocarpa	0	0	0	0
Psilotum nudum	20	11	0	0.1
Pyrrhobryum spiniforme	3	0	0	0
Racomitrium lanuginosum	5	0	0	0
Schizachyrium condensatum	12	48	0	6.8
Stereocaulon spp.	34	15	0	0.1
Vaccinium reticulatum	-	7	-	0
Waltheria indica	23	15	3.6	1.1
Litter	100	93	52.0	9.5
Bare ground	32	41	3.6	7.3

[1] Smith 1981.

- Not seen in frequency plots or cover transects that year.

ally *Lycopodiella cernua* (wawae`iole) were first observed in 2008, suggesting some recovery of native plants in the peripheral zone during the last several decades.

Reproductive Phenology

Natural population at Puhimau 2006–2007 – Buds were borne by most (40–60%) of the natural plants at Puhimau during the monitoring period, except for a single month in summer in each of the monitored years (Fig. 16). Flowers were produced by a similar proportion of plants as bore buds, and the summer decline in plants bearing flowers mirrored the decline in plants with buds. Fruit capsules were found on more than 60% of plants except in summer 2006.

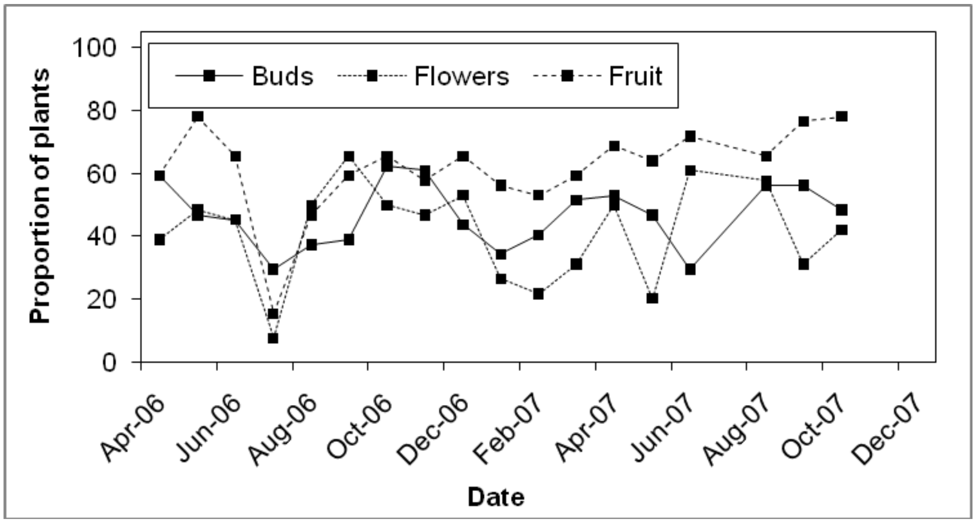

Figure 16. Proportion (%) of *Portulaca sclerocarpa* plants producing buds, flowers, and fruit at Puhimau, 2006–2007.

The mean proportion of branches bearing buds, flowers, and fruit showed a similar pattern to the population phenology. The proportion of branches with buds and flowers was almost always lower than the proportion bearing fruit capsules (Fig. 17). Seasonal declines in bud and flower production were noted during summer months, and peak flowering was in September 2006 and June the next year. Fruit capsules were typically seen on 10–20% of branches throughout the year except in July 2006, which had no fruit present, and September 2007, which showed a peak fruit production on approximately 30% of branches of monitored plants. At the nearby park headquarters, May through August had low mean monthly rainfall totals (<150 mm/month) during the years 2003–2009 (Appendix II, Fig. 1; HAVO Fire Cache, unpublished data).

Planting at Hawaiian Volcano Observatory 2006–2007 – Plants of *P. sclerocarpa* were fertile within two years of planting. Bud production appeared to be seasonal (Fig. 18) with declines in the number of plants bearing buds noted in July 2006 and April 2007. The peak in number of plants with buds was noted in the fall, October 2006. This was also the peak time for plants to bear flowers; throughout the study fewer plants were observed with flowers than were seen bearing buds. Fruit capsules were seen on most (40–80%) planted individuals at HVO throughout the 18-month monitoring period. A peak in fruit production was noted in December of both 2005 and 2006, and June 2006 was the time with fewest plants bearing fruit.

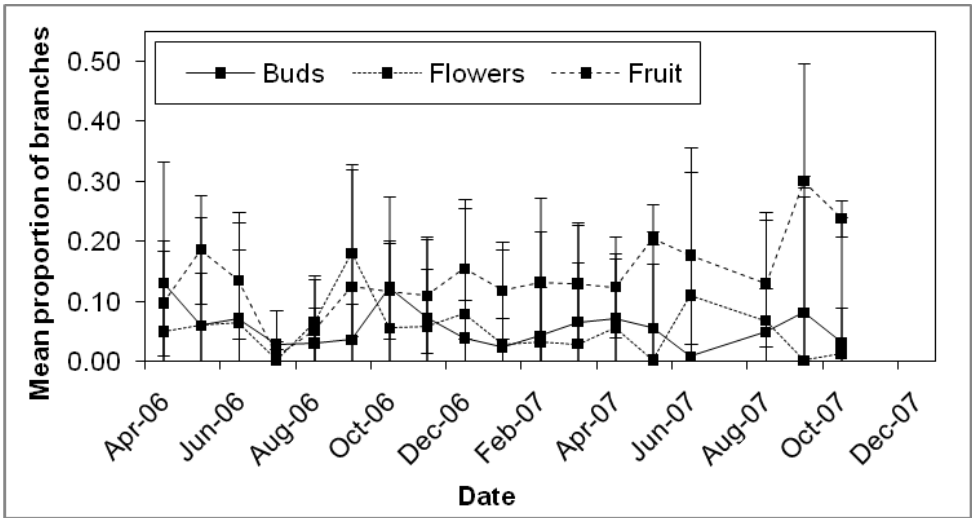

Figure 17. Mean proportion (±SD) of *Portulaca sclerocarpa* branches bearing buds, flowers, and fruit at Puhimau, 2006–2007.

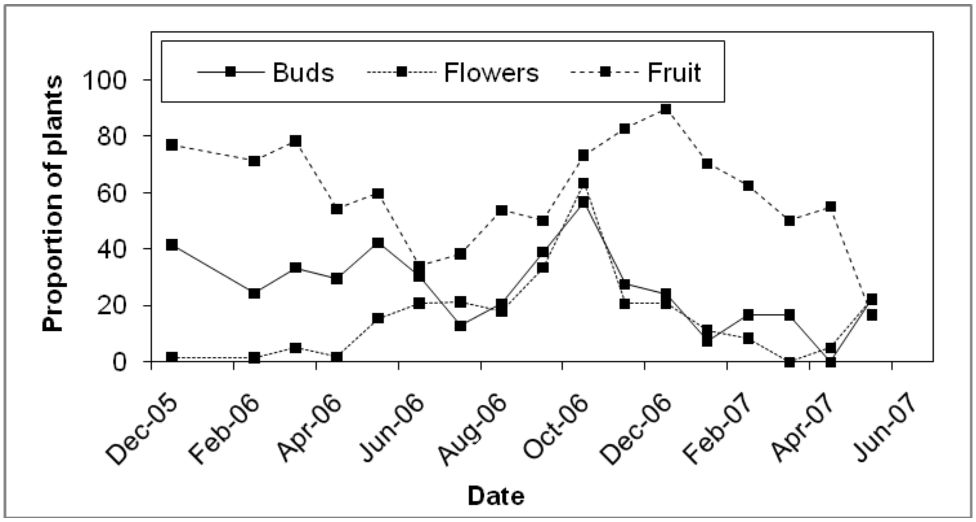

Figure 18. Proportion (%) of *Portulaca sclerocarpa* plants producing buds, flowers, and fruit at the Hawaiian Volcano Observatory site, 2005–2007.

Rainfall data from nearby HVO Uwēkahuna showed that the months from May through September were dry and most rain fell from October to April (Appendix II, Fig. 2).

Among the plants sampled for phenology at HVO, the mean proportion of branches of bearing buds and flowers was consistently low with only a moderate peak in buds in May and a slightly larger peak in October (Fig. 19). Both May and October 2006 had rainfall totals >250 mm at HVO, while summer months of June through August each had rainfall <50 mm (HAVO Fire Cache, unpublished data). The proportion of branches bearing fruit was consistently higher than that of buds and flowers. A low point in fruit production was observed in summer 2006 and was followed by the beginning of a decrease in late spring 2007. Peaks in fruit production were not pronounced, but plants had the greatest proportion of branches with fruit (60%) in winter 2006 (Fig. 19).

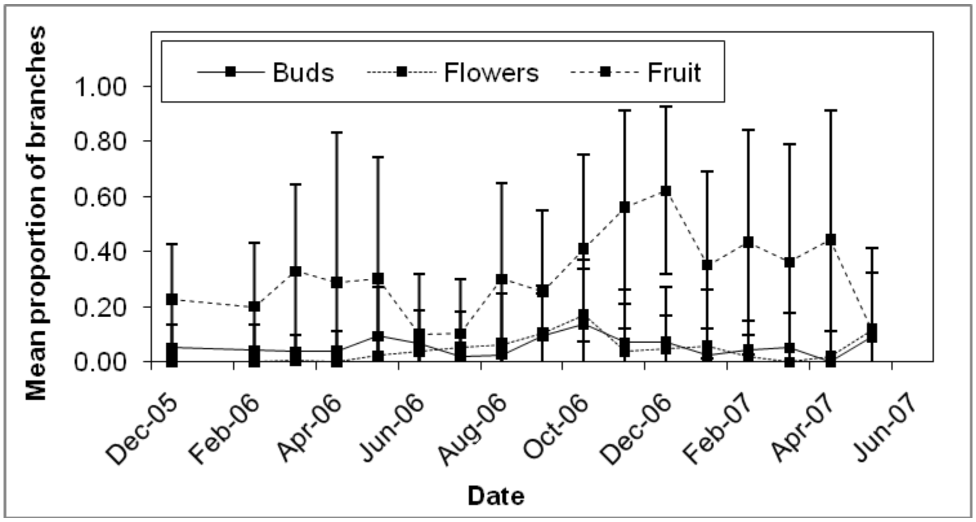

Figure 19. Mean proportion (±SD) of *Portulaca sclerocarpa* branches bearing buds, flowers, and fruit at the Hawaiian Volcano Observatory site, 2005–2007.

Planted seedlings at Kalanaokuaiki Pali with and without grass 2006–2008 – Fifty seedlings were planted at the Kalanaokuaiki Pali site in July 2006, but their phenology was not followed for their first six months in the ground. When first monitored in January 2007, there was no difference in the proportion of branches bearing buds in the grass and no-grass treatments; each treatment had on average 20% of branches with buds. Throughout the study period, fewer than 25% of branches bore buds or flowers in either treatment. Fruits were borne on more than 20% of branches in both treatments in January 2007, and this increased to more than 60% of branches in October (Fig. 20). At this peak in fruit production, the mean proportion of branches with fruit in the grass treatment (0.76, ± 0.15 SD, n = 19) was significantly higher than in the no-grass treatment (0.67, ± 0.10 SD, n = 21; t = -2.15, df = 38, p = 0.038). Peak fruit production was not related to high rainfall, as the month of October 2007 had only 11.4 mm total precipitation at nearby Kīpuka Nēnē, and preceding summer months had also been dry (HAVO Fire Cache, unpublished data).

Planted seedlings and cuttings at Kalanaokuaiki Pali 2008–2009 – A second planting of *P. sclerocarpa* was accomplished at the Kalanaokuaiki Pali site in March 2008; this consisted of 30 rooted cuttings and 30 seedlings planted together in grass-free sites. Both cuttings and seedlings bore buds and flowers when they were planted, but seedlings consistently had a greater proportion of branches bearing buds and flowers than did cuttings (Fig. 21 and Fig. 22). Both cuttings and seedlings demonstrated moderate seasonality in bud and flower production with low points in the summer and fall of their first year. Summer and early fall were months with low rainfall totals at the nearby weather station at Kīpuka Nēnē (Appendix II, Fig. 3).

Fruit capsules were not seen until two months post-planting, after which fruit were present on 20–80% of seedling branches and a lesser percentage of those of cuttings (Fig. 23). There was no obvious annual seasonality to fruiting in this planting, but peak fruit production occurred in June 2008 when cuttings had a mean proportion of 0.63 branches with fruit (± 0. 23 SD, n = 30) and the proportion of seedling branches with fruit was 0.80 (± 0.21 SD, n =

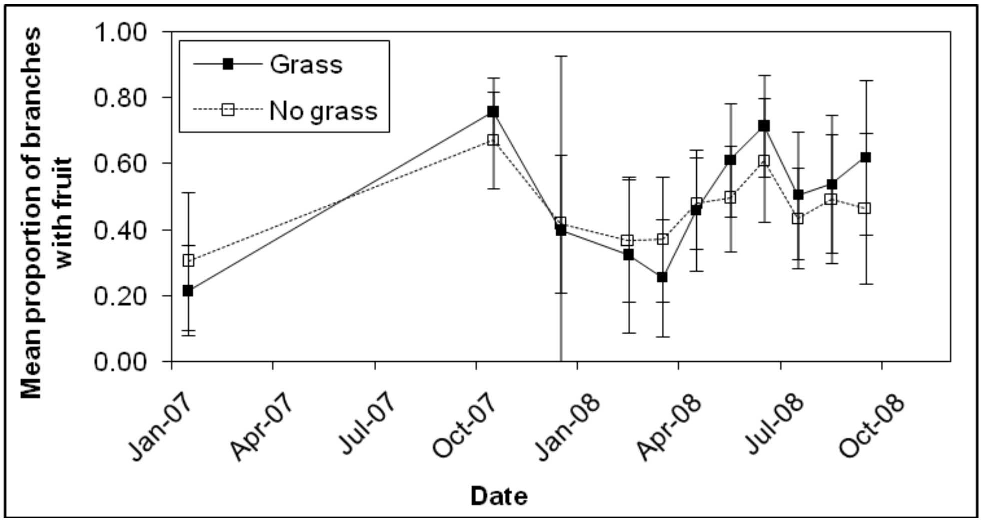

Figure 20. Mean proportion (±SD) of *Portulaca sclerocarpa* branches bearing fruit in grass and no-grass treatments at Kalanaokuaiki Pali, 2007–2008.

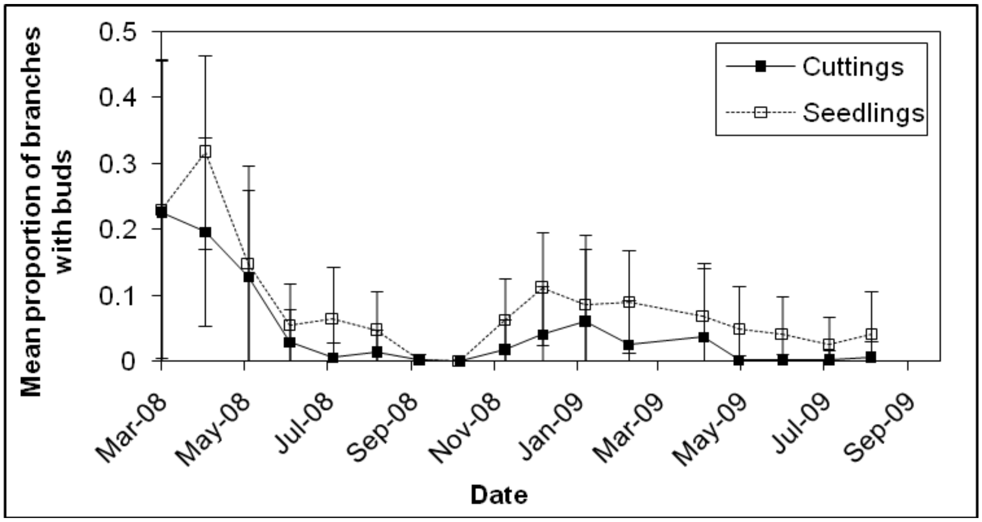

Figure 21. Mean proportion (±SD) of *Portulaca sclerocarpa* branches bearing buds in seedling and cutting plantings at Kalanaokuaiki Pali, 2008–2009.

30). This difference in fruit production was statistically significant (t = -3.2, df = 58, p = 0.002).

Success of Fruit Production

Based on 1136 tagged reproductive structures in 64 sampled plants at the natural Puhimau population, 47% of buds and flowers successfully formed fruit capsules. More than 90% of transitions to fruit took place within a month (Fig. 24). Fruit remained on plants for 1.7 months on average (± 1.2 SD, n = 883) before dispersing.

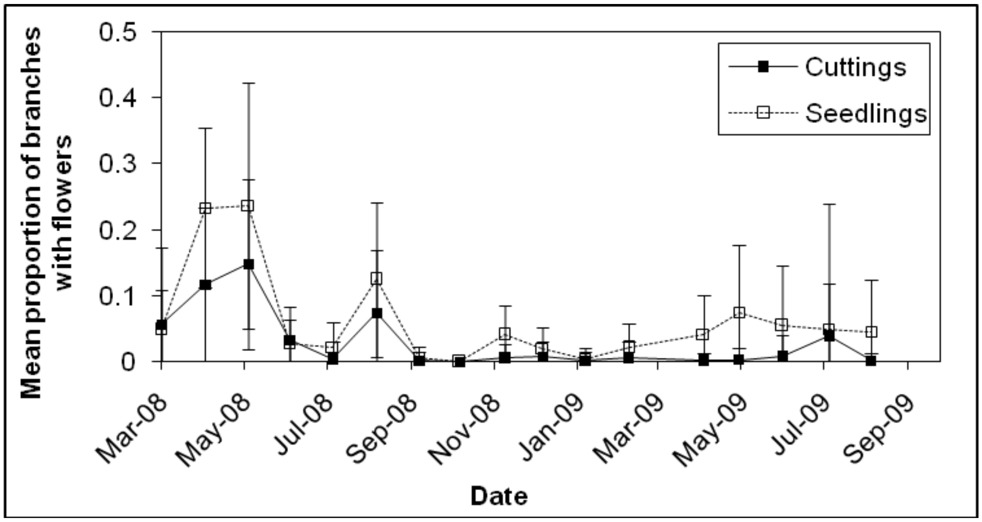

Figure 22. Mean proportion (±SD) of *Portulaca sclerocarpa* branches bearing flowers in seedling and cutting plantings at Kalanaokuaiki Pali, 2008–2009.

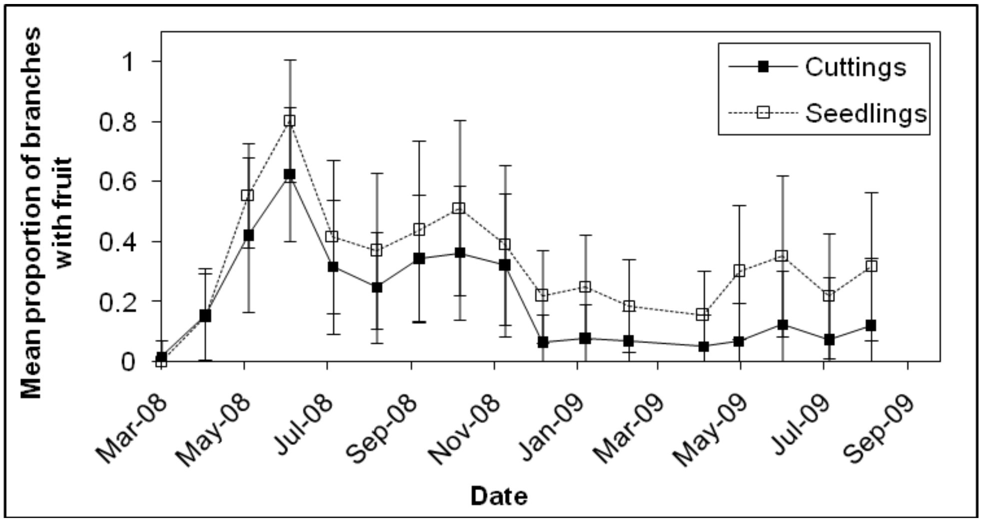

Figure 23. Mean proportion (±SD) of *Portulaca sclerocarpa* branches bearing fruit in seedling and cutting plantings at Kalanaokuaiki Pali, 2008–2009.

Fruit Production in and Outside Rodent Exclosures

Rodent-proof cages were installed around a sample of 19 plants at Puhimau in October 2006. Within two months of cage installation, caged plants had more branches with fruit than did control plants outside cages, and this difference continued throughout the study period (Fig. 25). Overall, caged plants had a higher mean proportion of branches bearing fruit (0.24 ± 0.40 SD, n = 332) than did unprotected plants (0.11 ± 0.21 SD, n = 329), but the difference was not significant using a repeated measures Analysis of Variance ($F_{1,35.8}$ = 2.0, p = 0.169). However, when fruit production was compared between caged and control plants at the peak month of fruiting (September 2007), there was a significant difference in the mean proportion

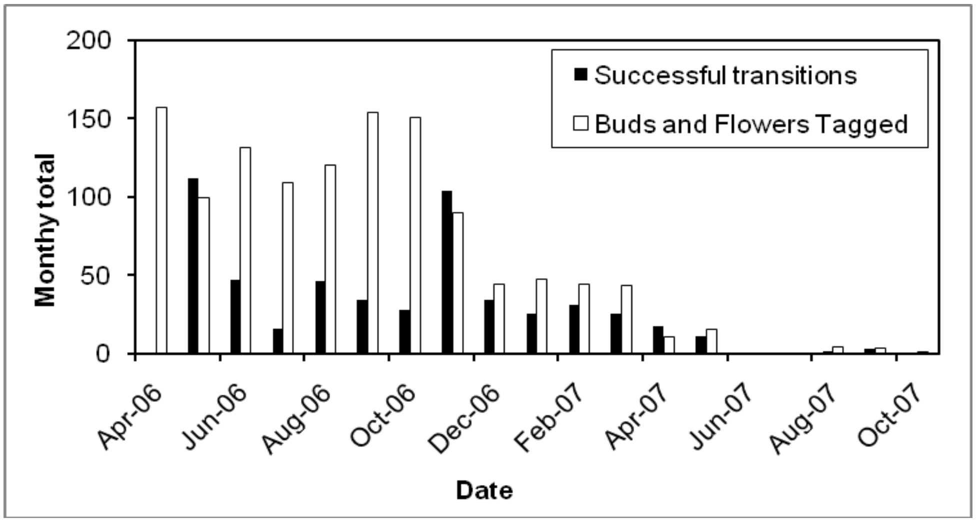

Figure 24. Monthly totals of successful fruit set from tagged buds and flowers at the natural population of *Portulaca sclerocarpa* at Puhimau.

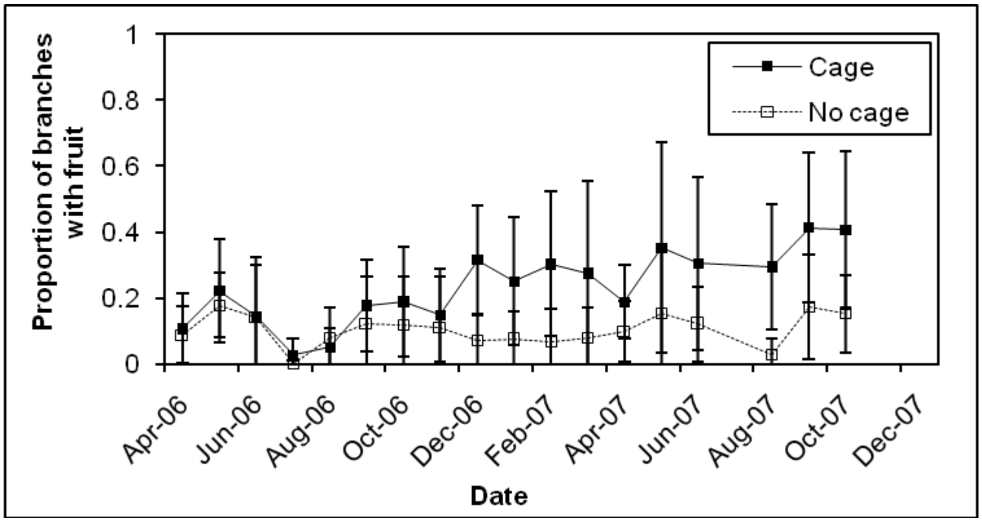

Figure 25. Mean proportion (±SD) of *Portulaca sclerocarpa* branches bearing fruit in cage and no cage treatments at Puhimau, 2006–2007. (Rodent-proof cages were installed in October 2006.)

of branches with fruit in caged plants (0.41 ± 0.23 SD, n = 18) and unprotected controls (0.17 ± 0.16 SD, n = 14; t = 3.4, df = 30, p = 0.002). (Several caged plants and controls died between October 2006 and the end of the study.)

Natural Seedlings

Natural seedlings were observed repeatedly throughout the study at planting sites near Hawaiian Volcano Observatory (HVO) and Kalanaokuaiki Pali. At HVO, seedlings were first noted around planted *P. sclerocarpa* in November 2005, when 257 tiny germinants were counted at sites surrounding 10 planted individuals. All these seedlings died or disappeared within seven months. A few seedlings (3) were noted in May 2006, but died within a month of first sighting. The last observation at the HVO planting site was in November 2006, when 41 seedlings appeared but were not followed.

At the Kalanaokuaiki Pali planting site seedlings were first sighted in December 2007 around plants placed in grass-free areas as seedlings in 2006. A total of 56 seedlings was counted and marked with pins, but all had disappeared after three months. Seedlings appeared again in December 2008 at both the 2006 planting and at the seedling/cutting planting installed in March 2008. A total of 422 seedlings was observed over an eight-month period; 97% of tiny seedlings appeared between December 2008 and February 2009 (Fig. 26). All seedlings disappeared by July 2009.

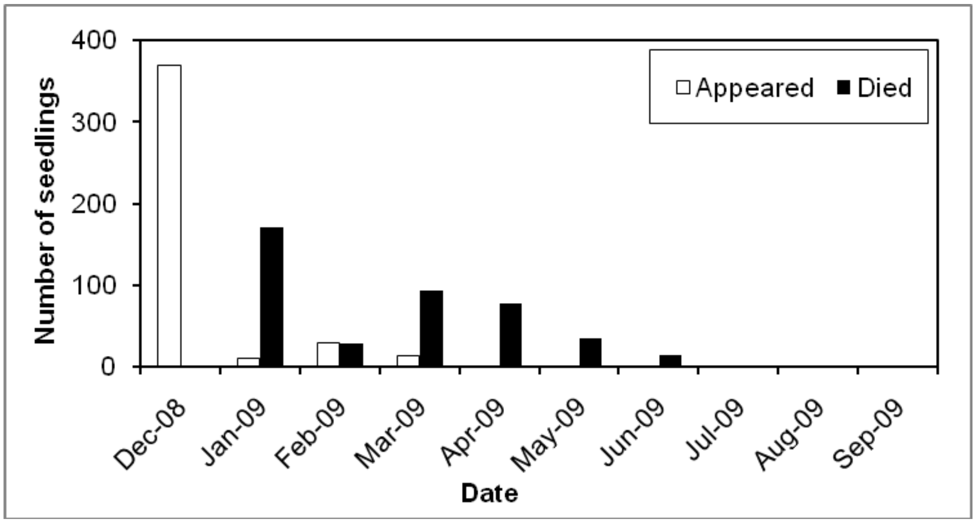

Figure 26. Appearance and death of natural seedlings near planted *P. sclerocarpa* at Kalanaokuaiki Pali, December 2008–September 2009.

Seeds and Seed Germination

Field seed plots in moss and soil – During a year of monitoring 10 paired plots at Puhimau Geothermal Area sown with fresh *P. sclerocarpa* seeds in October 2006, there was no germination or seedling establishment observed in either bare soil plots or adjacent plots with moss cover. Other species, such as the sedges *Bulbostylis capillaris* and *Cyperus polystachyos* appeared and established in two plots of each of the treatments (bare soil and moss) during the monitoring period.

Seed capsule predation by rodents – In an offering of 20 capsules (with intact seeds) in each of three pairs of rodent-proof cages and adjacent unprotected controls at the HVO site, a larger number of capsules disappeared or were predated in the open offerings than in the cages. The difference in the number of missing and predated capsules in the two treatments was highly significant ($X^2 = 39.2$, df = 1, $p < 0.0001$). The mean number of fruit still present after three months was 17.0 (± 1.0 SD) in the cages and 5.7 (SD = 6.4) in the unprotected offerings. On average 3.0 (± 1.0 SD) capsules (15%) were missing in the rodent-proof cages, and 14.3 (± 6.4 SD) fruit (72%) were either missing or predated in the unprotected controls. The loss of offered capsules inside cages was probably due to the action of wind, which may have blown some light capsules out of the seed tray and away from the cage.

Similarly at Puhimau, a significantly larger number of capsules disappeared in unprotected controls than in offerings protected from rodents by small cages ($\chi^2 = 67.0$, df = 1, $p < 0.0001$). In three pairs of offerings of 20 capsules each inside and outside rodent exclosures monitored for six weeks (October to December 2006), the mean number of undisturbed capsules was 14.7 (± 8.4 SD) inside the cages and 0.3 (± 0.6 SD) outside in the control offerings. The mean number of missing and predated capsules was 5.3 (± 8.4 SD) inside the cages. All 20 (100%) capsules eventually disappeared from all unprotected adjacent offerings, and two of the three open trays contained obviously predated capsules. Predated capsules were noted in a single caged offering, where a small gap had developed on the hinged top of the cage. This compromised exclosure contributed to the loss of 28% of the offerings inside the cages. If data from the cage with the temporary gap are excluded, only 2.5% of capsules within the caged offerings disappeared.

Seed germination in the greenhouse – Seed germination rates were variable in greenhouse trials (Appendix I, Table 2). The mean germination of four replicate pots sown in November 2005 was 23.8%. The second trial sown in May 2006 achieved an average germination rate of only 2.4%. The third germination trial sown in June 2007 had a mean germination of 19.7%, although one of the three replicate pots showed no sign of seedlings. The final trial sown in January 2009 had a very low mean germination rate of 0.4%. Time from sowing to first germination was also highly variable, ranging from 12 days in the summer to 96 days in the winter sowing. Seeds used were typically one month old and were collected from the natural population at Puhimau, as well as from the plantings at HVO and Kalanaokuaiki Pali. The average number of seeds per capsule was 229.6 (± 75.4 SD, n = 25) for fruit collected at the natural population at Puhimau and 106.0 (± 57.7 SD, n = 9) for those from the planted individuals at the HVO study site.

Seed viability test – Two viability trials each using 20 seeds from multiple capsules were carried out in October 2009. Only mature black seeds were used, and all seeds appeared healthy when bisected. All 20 fresh seeds tested positive for viability with 13 (65%) showing a strongly positive or positive reaction and 7 (35%) with a weakly positive result. Of 20 seeds stored for five weeks, 4 (20%) were strongly positive or positive, 13 (65%) were weakly positive, and 3 (15%) were negative and apparently non-viable.

***Sesbania tomentosa*, `Ōhai**

Growth and Mortality at Natural Populations

*`Āpua Point plants* – During 14 months of monitoring the natural *S. tomentosa* population at coastal `Āpua Point, 43.3% of the randomly selected plants died. Most of the mortality occurred after January 2007. The size of live plants decreased between July 2006 and May 2007 from 3 m^2 to an estimated mean area of 2 m^2.

Kīpuka Nēnē branches – At Kīpuka Nēnē East, we sampled randomly-selected branches of *S. tomentosa* rather than whole plants, because it was impossible to discern individuals in the large patch of plants we studied. Over 3.5 years of monitoring, mortality was nearly 100% in both the original randomly selected branches and those chosen to replace them (Fig. 27). Growth of original branches was steady over the course of several years, and the mean length of branches increased from <100 cm to >400 cm by the end of the study (Fig. 28). At the Kīpuka Nēnē West site, *S. tomentosa* branches grew steadily over 2.5 years from an original mean length of 123.7 cm (± 50.5 SD) to a final length of 196.1 cm (± 98.7 SD). Mortality of selected branches at the western site was 30% after 2.5 years of measurement.

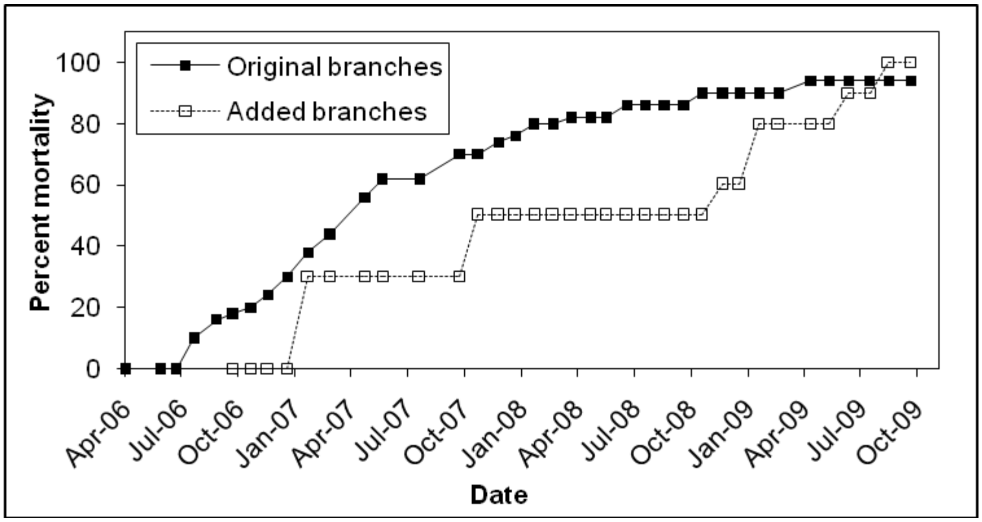

Figure 27. Mortality (%) of original and additional randomly selected branches of *Sesbania tomentosa* at Kīpuka Nēnē East, April 2006–September 2009.

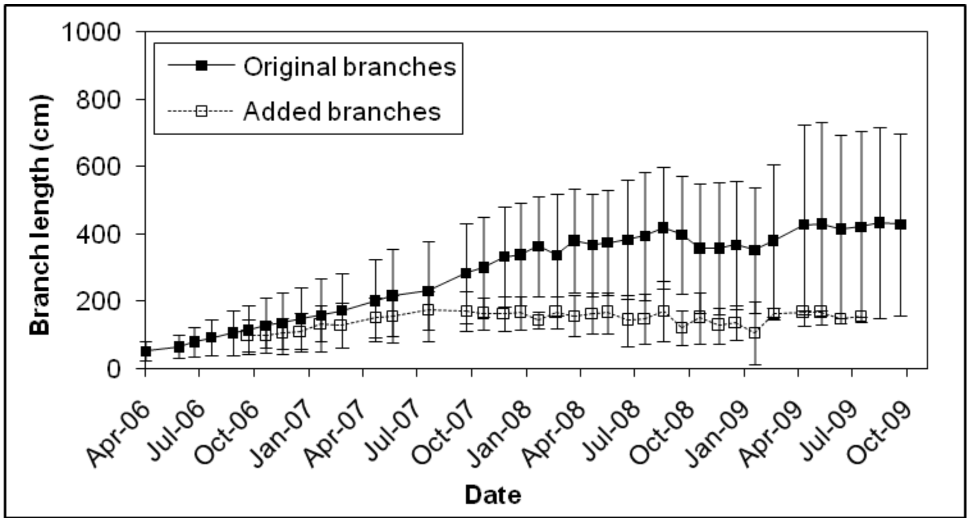

Figure 28. Mean branch length (±SD) in cm of randomly selected branches of *Sesbania tomentosa* at Kīpuka Nēnē East, April 2006–September 2009.

Growth and Mortality of Plantings

Mortality of seedlings planted at two sites along Hilina Road in 2006 was very high over 3.5 years of monitoring (Fig. 29). Initially, mortality was greater among seedlings at the dry stream bed site than at Kalanaokuaiki Pali, but by the end of the study mortality rates were almost the same (96.7%, n = 30 at the dry stream bed and 96.9%, n = 32 at Kalanaokuaiki); one vigorous plant remained at each of the two sites. Soil depths were similar at the planting sites; mean soil depth was 31.6 cm (± 18.1 SD, n = 96) at Kalanaokuaiki and 30.3 cm (± 15.6 SD, n = 90) at the dry stream bed near Hilina Road.

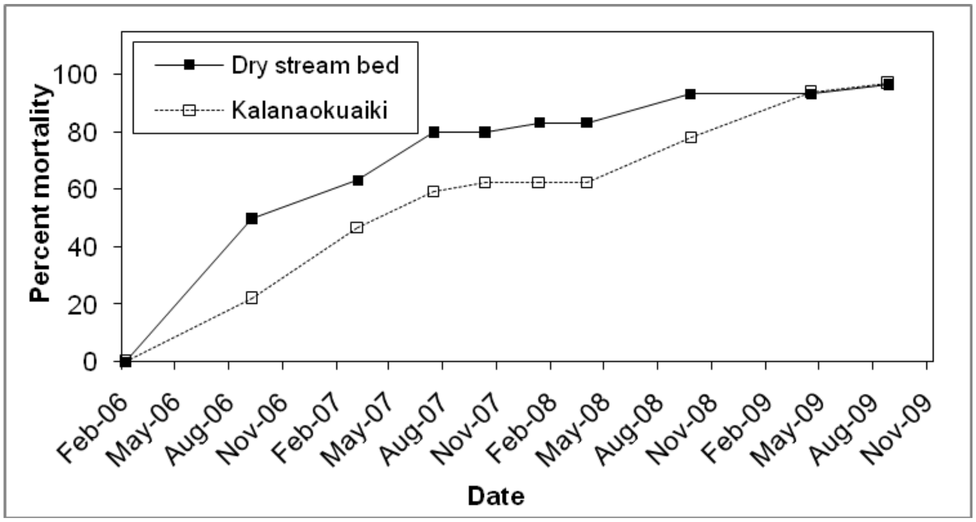

Figure 29. Mortality (%) of *Sesbania tomentosa* seedlings planted at two sites along Hilina Road in 2006.

At planting, the mean height of Kalanaokuaiki seedlings was 25.4 cm (± 14.7 SD), and that of seedlings at the dry stream bed was 30.4 cm (± 18.6 SD); heights of plants at both sites increased steadily for a year and nine months before any decline was noted. The greatest mean height achieved at Kalanaokuaiki was 144.0 cm (± 89.1 SD, n= 2) in May 2009, and the surviving plant was 310 cm tall when revisited in April 2010. The remaining plant at the dry stream bed site was 350 cm tall when last visited in October 2009.

Reproductive Phenology

*`Āpua Point 2006–2007* – Phenology was monitored at `Āpua Point *S. tomentosa* plants for less than a year. During this period a peak in buds was observed during the fall (Fig. 30), and peaks in flower abundance were noted in both summer and fall, when more than half of plants bore flowers and higher abundance categories were recorded (Fig. 31). Immature fruit pods were also most abundant in the summer, although a smaller peak was also seen in winter (January) (Fig. 32). Mature fruit pods were persistent and were observed in every monitoring interval; typically more than 40% of plants bore 1–5 pods each (Fig. 33). Summer months were dry at the nearby Pu`uloa weather station; monthly totals for June through September were about 20–50% the rainfall of other months (HAVO Fire Cache, unpublished data).

Kīpuka Nēnē East 2006–2009 – Bud production at Kīpuka Nēnē East was highly seasonal with peaks in mean number of buds per branch observed in the spring or summer of four years. Peak months for buds were June, May, or March in 2006–2008 and an extended period from April to August in 2009. The mean number of flowers per branch was less than that of buds, typically 15–25% of the bud means, but a similar seasonal pattern of peaks was recorded in spring and summer months (Fig. 34). Bud and flower production was highest during months of low rainfall as measured at the HAVO Kīpuka Nēnē weather station (Appendix II, Fig. 3 and Fig. 4).

The mean number of immature green fruit on branches was far less than was counted for either flowers or buds, and seasonal peaks in immature fruit followed peaks for flowers by

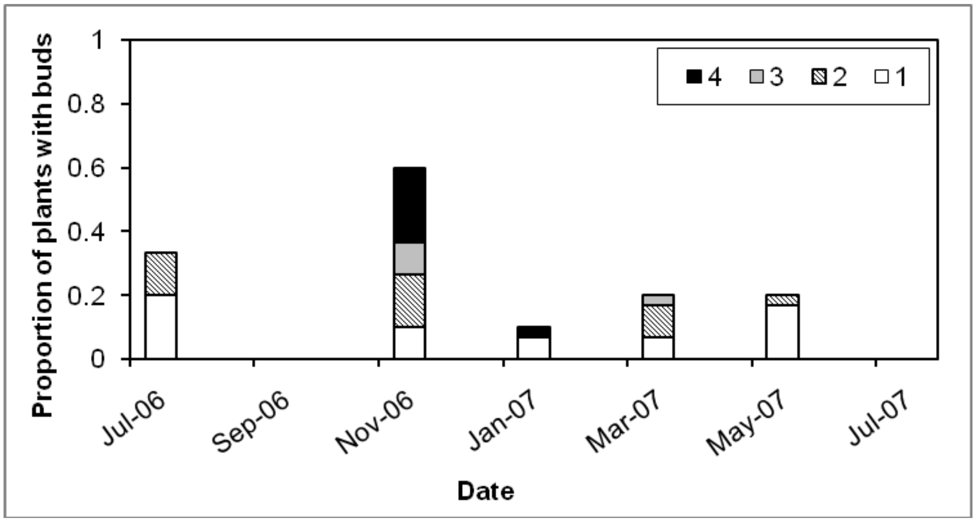

Figure 30. Estimated abundance of buds in four categories for *Sesbania tomentosa* plants at `Āpua Point (categories: 1 = 1–5, 2 = 6–25, 3 = 26–50, 4 = >50).

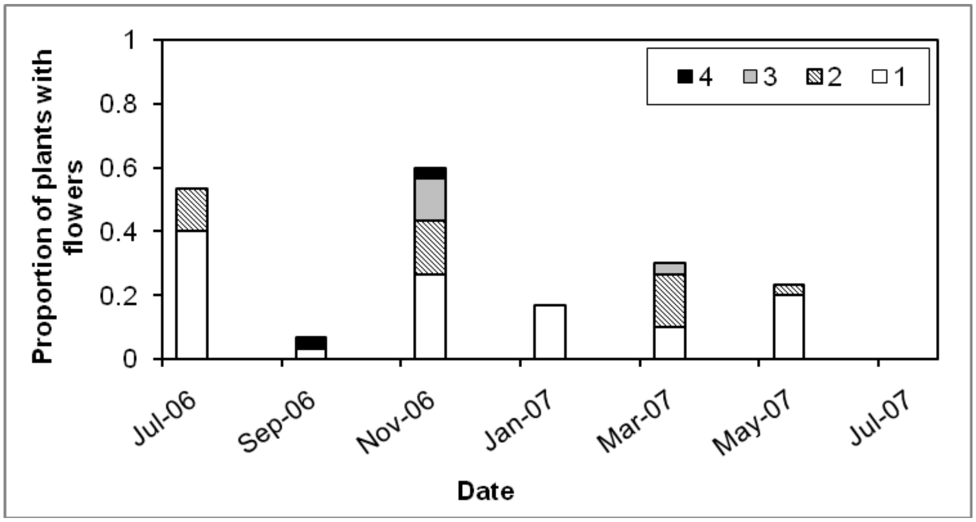

Figure 31. Estimated abundance of flowers in four categories for *Sesbania tomentosa* plants at `Āpua Point (categories: 1 = 1–5, 2 = 6–25, 3 = 26–50, 4 = >50).

about a month (Fig. 35). On average <1 immature fruit was noted at monthly monitoring intervals (0.02 ± 0.14 SD to 0.91 ± 2.11 SD), except in summer 2009 when a mean of 4.8 (± 5.7 SD) green fruit was recorded in July. The pattern for mature fruit at Kīpuka Nēnē East was less pronounced than those for immature fruit or flowers (Fig. 35). Small peaks in mature fruit with means < 0.14 fruit per branch (± 0.47 SD) were seen during the summer and fall months of two years (June to November 2006 and July to October 2007), but no mature fruits at all were observed in the following two years (November 2007 to September 2009).

Kīpuka Nēnē West 2007–2009 – Bud production was also seasonal at the *S. tomentosa* plants monitored at Kīpuka Nēnē West, but the peaks were less pronounced than those at the eastern site. High bud numbers were observed during summer months of three years, but at

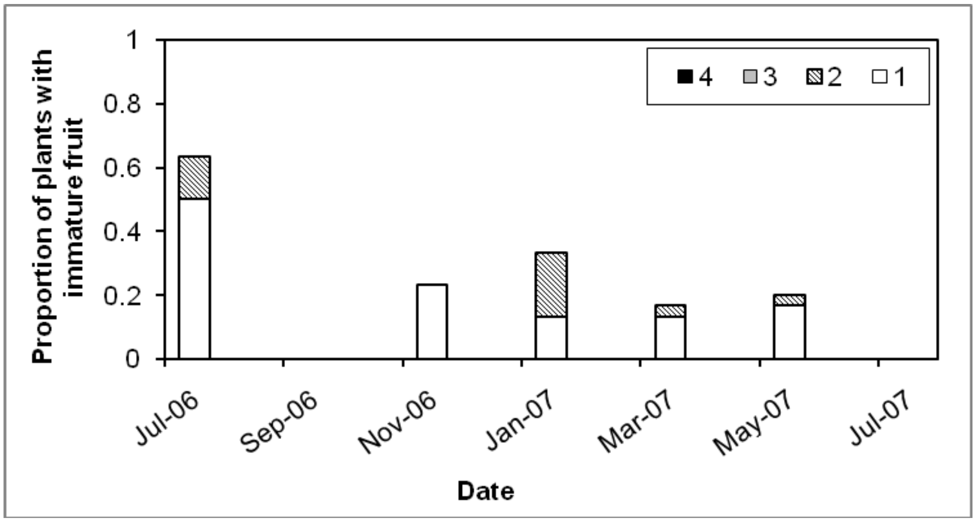

Figure 32. Estimated abundance of immature fruit in four categories for *Sesbania tomentosa* plants at `Āpua Point (categories: 1 = 1–5, 2 = 6–25, 3 = 26–50, 4 = >50).

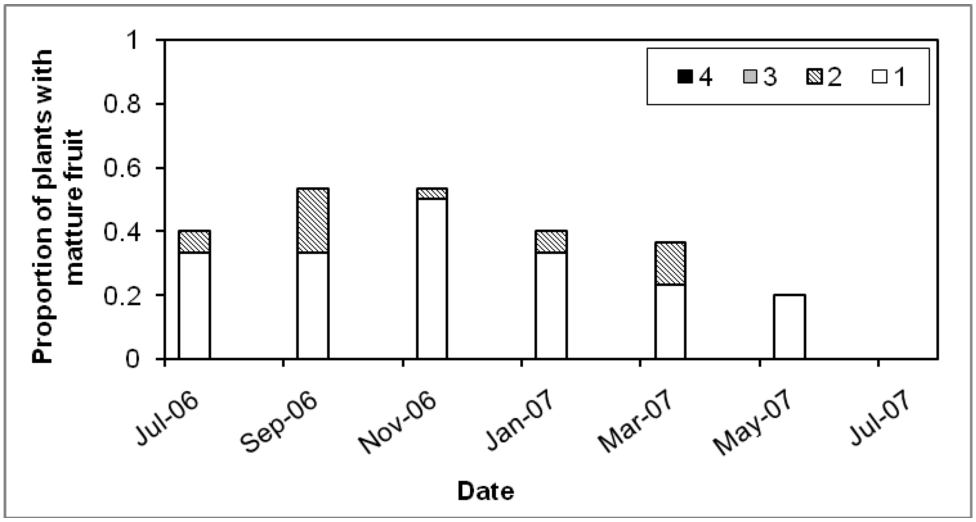

Figure 33. Estimated abundance of mature fruit in four categories for *Sesbania tomentosa* plants at `Āpua Point (categories: 1 = 1–5, 2 = 6–25, 3 = 26–50, 4 = >50).

least in 2008, buds seemed to be present for a prolonged period throughout the year (Fig. 36). Low points in bud production appeared to be December and January. Flowers peaked during fall months in 2007 and 2008, but there was a prolonged period of flowering throughout the summers in both 2008 and 2009 (Fig. 36). The mean number of flowers per branch was typically 10–20% the mean number of buds counted, except during peak flowering in summer 2009. As was seen at the eastern monitoring site, bud and flower numbers were greatest during the driest months at Kīpuka Nēnē (Appendix II, Fig. 3 and Fig. 4).

The mean number of immature fruit observed on branches at Kīpuka Nēnē West was noticeably higher than the mean recorded at Kīpuka Nēnē East (Fig. 37). During peak periods

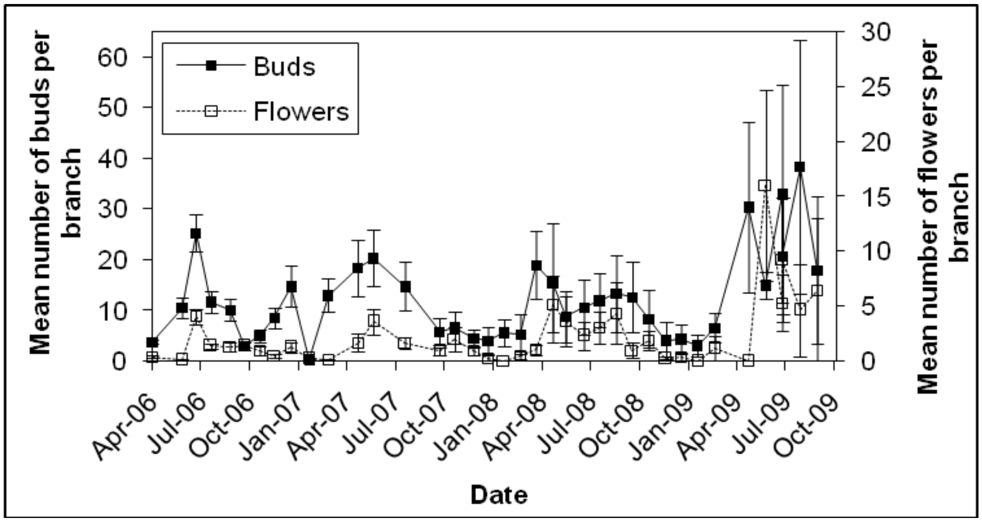

Figure 34. Mean number (±SD) of buds and flowers on branches of *Sesbania tomentosa* at Kīpuka Nēnē East, 2006–2009.

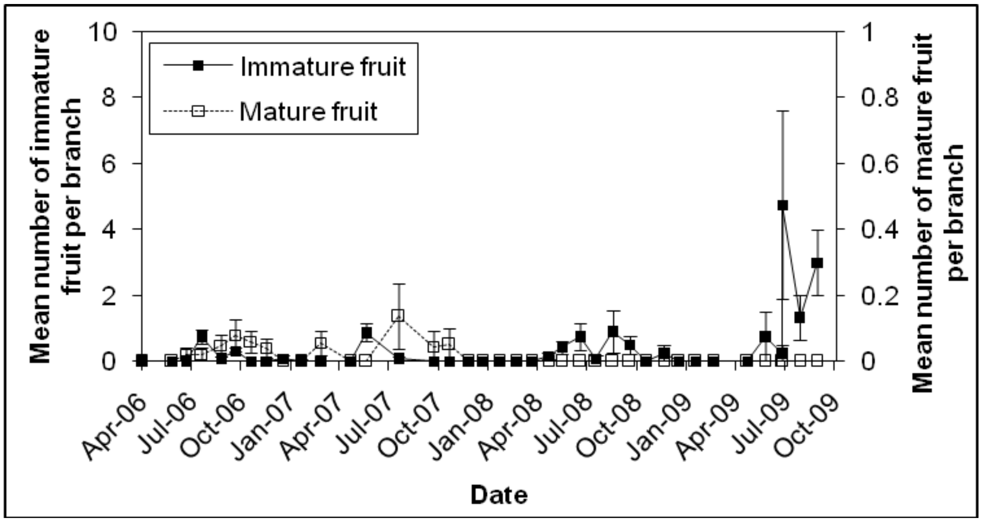

Figure 35. Mean number (±SD) of immature and mature fruit on branches of *Sesbania tomentosa* at Kīpuka Nēnē East, 2006–2009.

of immature fruit production, such as October 2007, September 2008, and November 2008, the mean number of fruit per branch ranged from 1.4 (± 2.9 SD) to 1.7 (± 3.2 SD). These means were almost double those observed in comparable time periods at Kīpuka Nēnē East. The highest peak in immature fruit at the western site was seen in September 2009, when a mean of 4.6 (± 5.9 SD) green fruit per branch was recorded. Mature fruit numbers were considerably lower than those counted for immature fruit at Kīpuka Nēnē West (Fig. 37), and the mean number per branch never exceeded 0.19 (± 0.4 SD). Peaks in mature fruit occurred somewhat erratically in the summer (July and August), fall (November), and winter months (January), but the highest mature fruit means seen were only 4–14% those recorded for immature fruit.

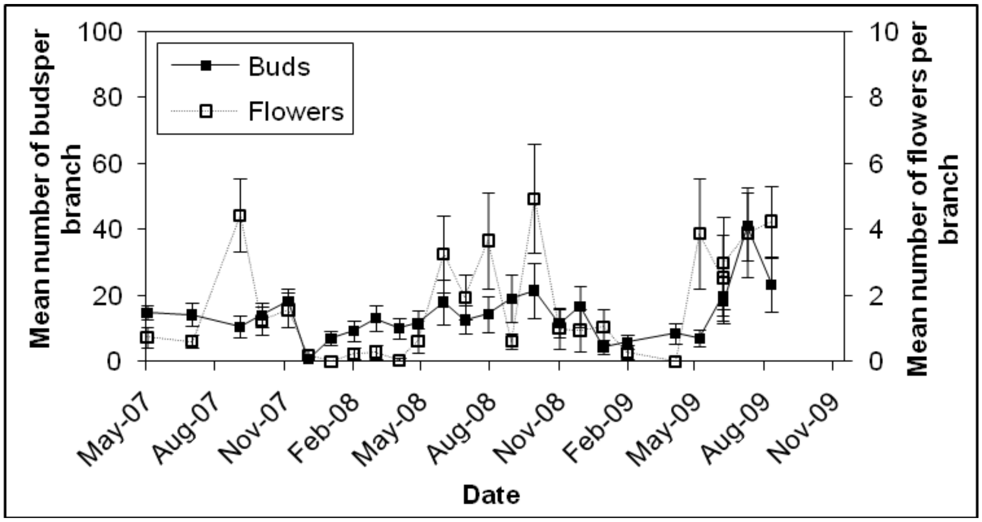

Figure 36. Mean number (±SD) of buds and flowers on branches of *Sesbania tomentosa* at Kīpuka Nēnē West, 2007–2009.

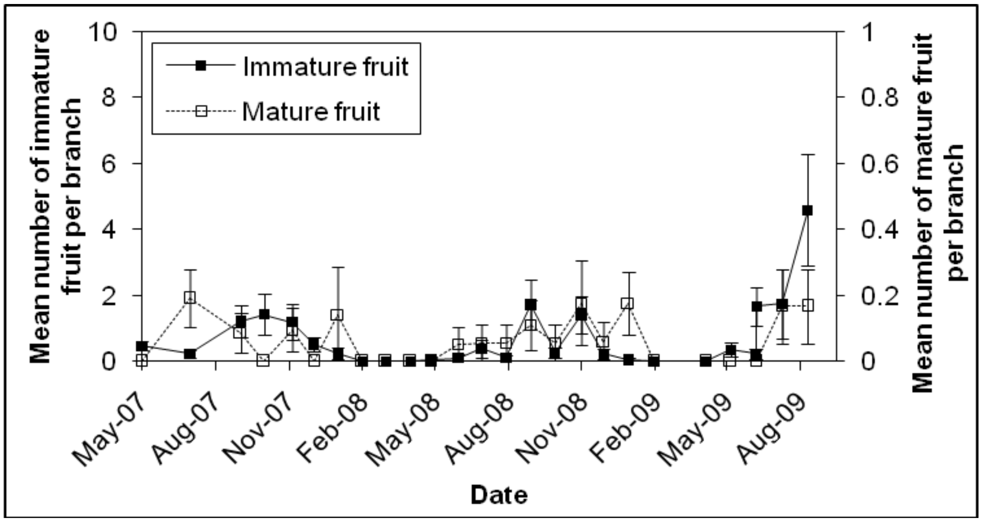

Figure 37. Mean number (±SD) of immature and mature fruit on branches of *Sesbania tomentosa* at Kīpuka Nēnē West, 2007–2009.

Insect predation of buds and flowers at Kīpuka Nēnē – When insect predation was noted on buds and flowers during phenology monitoring in fall 2007, we began to record how many buds and flowers exhibited insect damage, entry holes, or attached eggs. Adult bean butterflies (*Lampides boeticus*) were observed fluttering around *Sesbania tomentosa* flowers, and caterpillars of this species were found within large buds and flowers. Later the small, sparkling white eggs of the species (Harding 1971) were identified attached to the exterior of *Sesbania* buds. During two years of monitoring, bean butterfly damage was concentrated in May through November 2008 and July to September 2009 (Fig. 38). These periods roughly matched the times of greatest bud and flower production for those two years. The proportion of buds with damage by bean butterfly caterpillars was 10–20% from May to December 2008 and was even larger in July 2009, when > 40% of buds were affected. Prior to May 2008 and between December 2008 and July 2009, almost no predation was observed on buds of *S. tomentosa*.

Peaks in flower predation by the caterpillar were found in November 2008, July 2009, and September 2009, when approximately 50% of flowers were damaged.

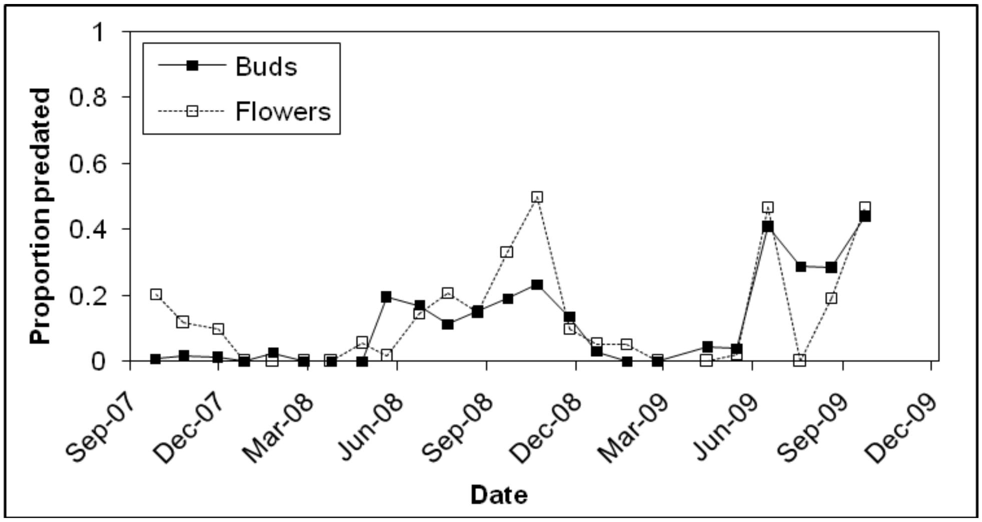

Figure 38. Predation of *Sesbania tomentosa* buds and flowers by caterpillars of the bean butterfly (*Lampides boeticus*) at Kīpuka Nēnē, 2007–2009.

Success of Fruit Production

The successful production of immature fruit by buds and flowers combined was very low overall at Kīpuka Nēnē. Only 0.7% of tagged buds and flowers produced immature fruit, and the percentage that formed mature fruit (0.6%) was even lower (n = 703). When immature fruit were tagged, the percentage that successfully became mature fruit was 4.9% (n = 185). When the data for Kīpuka Nēnē East and West were evaluated separately, some differences were apparent in fruit production at the two sites. Tagged buds and flowers at Kīpuka Nēnē East never successfully produced either immature or mature fruit (n = 380). However, immature fruit were seen (that had not been previously tagged as a flower), and those tagged as immature green fruit successfully became mature fruit at a rate of 5.8% (n = 185).

At Kīpuka Nēnē West, 1.6% of tagged buds and flowers successfully transitioned to immature fruit, and 1.2% became mature fruit (n = 323). The rate of successful formation of mature fruit from those tagged as immature fruit was 4.9% (n = 52). On average, buds or flowers became immature fruit in less than one month. The transition to mature fruit from bud or flower required 3.7 months on average (± 0.6 SD, n = 4). Immature fruit matured within 1.9 months (± 0.4 SD, n = 9).

Buds and flowers were not tagged at `Āpua Point, because this study site could not be visited at a monthly interval. However, a small sample of immature fruit was tagged on branches monitored for bimonthly phenology. This tagging resulted in detection of relatively high rates of successful maturation of fruit from immature green legumes. Between November 2006 and January 2007, 70% of 10 tagged immature fruit formed mature fruit. Lower success rates were observed later in the winter and spring. Between January and March 2007, 43% of tagged immature fruit became mature fruit (n = 91); from March to May 2007 the successful transition from immature to mature fruit was 30% (n = 15).

Pollination

Floral visitor observations – During 46.8 hours of observation, 425 floral visits to *S. tomentosa* were made by three orders of insects (Table 3). Hymenoptera were the most common visitors represented by at least two species of bees and two species of ants. Additional species of both Lepidoptera and Orthoptera were also observed.

Endemic *Hylaeus*, yellow-faced bees, were the most abundant visitors, with a total of 266 visits (60.2% of total visits) and a mean visitation rate of 0.55 visits/flower/hr (± 0.22 SD, n = 187). *Hylaeus* could not be identified to species level during the observations, but collections of visitors at flowers indicate that two species were present, *H. flavipes* and *H. laetus*. *Hylaeus* collected mainly pollen (67 total visits) rather than nectar (16 total visits) (Table 4). Since anthers of *S. tomentosa* begin to dehisce prior to anthesis of the mature bud, pollen collection by *Hylaeus* was initiated in flowers at the late stage of bud development. Like many other legume species of the Papilionoideae or pea subfamily, the anthers of *S. tomentosa* are concealed in a chamber formed by the wing and keel petals. *Hylaeus* bees were observed crawling into the distal end of the chamber to access the anthers during pollen collection.

The second most abundant visitor, the non-native honey bee (*Apis mellifera*), made 109 (24.7% of total visits) visits with a mean visitation rate of 0.30 visits/flower/hr (± 0.22 SD, n = 187; Table 3). Nectar collection was the predominant activity during floral visits by honey bees (69 total visits), while pollen foraging was rare (three total visits; Table 4). To feed on nectar, honey bees extended their tongues between the wing petals into the nectary at the proximal end of the floral chamber.

The remaining four species participated in less than 10.0% of all floral visits. The non-native Argentine ant (*Linepithema humile*) and little yellow ant (*Plagiolepis alluaudi*) represented 8.8% and 0.5% of visits, respectively. Frequency of visitation was higher for Argentine ants (0.10 visits/flower/hour, ± 0.09 SD, n = 39) than for little yellow ants (0.01 visits/flower/hour, ± 0.02 SD, n = 2). Both species were observed to crawl into the floral chamber to forage on nectar only.

The non-native longhorned grasshopper (*Conocephalus saltator*) and bean butterfly (*Lampides boeticus*) were also observed visiting flowers. The longhorned grasshopper fed mostly on pollen (77.1% of visits) by chewing on the anther, and had a visitation rate of 0.09 visits/flower/hour (± 0.12 SD, n = 7). The bean butterfly accounted for 0.7% of visits with a mean visitation rate of 0.01 visits/flower/hour (± 0.03 SD, n = 3) and fed only on nectar (66.7% of visits) by inserting its proboscis between the wing petals.

Pollen transport – Insects collected for pollen identification consisted of 9 *Hylaeus spp.*, 11 honey bees, and 3 bean butterflies. The mean number of *S. tomentosa* pollen grains removed from washed insects did not differ significantly between honey bees (158.4 pollen grains, SE = 158.4) and *Hylaeus* spp. (21.0 pollen grains, SE = 5.5; Wilcoxon rank-sum, z = 112.0, n_1 = 11, n_2 = 9, p = 0.42; Fig. 39 and Fig. 40). However, the sample size of insects was very low, and the differences in pollen on the insect species were relatively large. The comparison of pollen numbers between honey bees and native bees may be considered inconclusive. Low numbers of pollen grains from other species in the plant community were also removed from collected insects. Pollen of *S. tomentosa* made up 17.8% of the average

Table 3. Visitation rates and duration of visits of insects on *S. tomentosa* flowers during timed observation intervals at Kīpuka Nēnē, August 2006 to October 2007.

Floral Visitors	Status*	Total number of visits [1] (%)	Mean visitation rate [2] (SD) (n = 187)	Mean visit duration in sec [3] (SD) (n = # of visits)
HYMENOPTERA				
Colletidae				
Hylaeus spp. (*H. flavipes* & *H. laetus*)	end	266 (60.2)	0.55 (0.22)	29.8 (80.5)
Apidae				
Apis mellifera	pur	109 (24.7)	0.30 (0.22)	15.7 (19.7)
Formicidae				
Linepithema humile	adv	39 (8.8)	0.10 (0.09)	39.1 (59.0)
Plagiolepis alluaudi	adv	2 (0.5)	0.01 (0.02)	222.5 (38.9)
LEPIDOPTERA				
Lycaenidae				
Lampides boeticus	adv	3 (0.7)	0.01 (0.03)	29.5 (34.6)
ORTHOPTERA				
Tettigoniidae				
Conocephalus saltator	adv	7 (1.6)	0.09 (0.12)	230.1 (341.9)

* Status: adv = adventive or accidentally introduced; pur = purposely introduced; end = endemic to Hawaiian Islands (Nishida 2002)

[1] Total number of visits to an individual flower by each observed insect species

[2] Rates represent the total number of flowers visited per total number of open flowers observed per hour for each observation period. Mean visitation rate is based on the average across all observation periods.

[3] Mean duration of a visit to a flower based on individual visits independent of observation period

pollen load for honey bees and 15.7% of that on *Hylaeus* spp. The bean butterfly washes resulted in no pollen.

Pollen viability and stigma receptivity – Average pollen viability was 85.4% (± 9.2% SD, n = 21) for mature buds, 85.3% (± 10.9% SD, n = 20) at the day of anthesis (when flowers were fully open), 87.6% (± 10.0% SD, n = 16) at one day following anthesis, and 87.5% (± 8.2% SD, n = 14) at two days following anthesis. There was no significant difference in average pollen viability among floral ages (ANOVA, F (3, 63) = 0.35, p = 0.79). Stigmas were 100% receptive at each stage of flower development tested.

Table 4. Total number of pollen and nectar collection visits by floral visitors to *S. tomentosa* during timed observation intervals at Kīpuka Nēnē, August 2006 to October 2007.

Floral Visitors	**Status***	**Total # of visits pollen collected (%)**	**Total # of visits nectar collected (%)**	**Total # of visits no floral resource collected (%)**
HYMENOPTERA				
Colletidae				
Hylaeus spp. (*H. flavipes* & *H. laetus*)	end	67 (25.2)	16 (6.0)	183 (68.8)
Apidae				
Apis mellifera	pur	3 (2.8)	69 (63.3)	37 (33.9)
Formicidae				
Linepethima humile	adv	0 (0)	3 (7.7)	36 (92.3)
Plagiolepis alluaudi	adv	0 (0)	2 (100.0)	0 (0)
LEPIDOPTERA				
Lycaenidae				
Lampides boeticus	adv	0 (0)	2 (66.7)	1 (33.3)
ORTHOPTERA				
Tettigoniidae				
Conocephalus saltator	adv	4 (57.1)	1 (14.3)	2 (28.6)

* Status: adv = adventive or accidentally introduced; pur = purposely introduced; end = endemic to Hawaiian Islands (Nishida 2002)

Pollen limitation – Only two seed pods total were produced in the control treatment (no manipulation; n = 102). Four seed pods were produced in the experimental treatment (hand-pollinated; n = 99).

Rodent Exclosures on Branches at Kīpuka Nēnē

In 2006, rodent-proof exclosure sleeves were placed over randomly-selected branches of *S. tomentosa* at Kīpuka Nēnē East. In more than a year of monitoring there was no significant difference in the number of buds between protected branches and unprotected control branches, based on a repeated measures analysis of variance ($F_{1,53.1}$ = 2.09, p = 0.160). The mean number of buds per branch was 6.7 (± 10.7 SD, n = 223) on branches protected by rodent-proof sleeves, and the mean number of buds on unprotected branches was 13.6 (± 22.0 SD, n = 333). There were also slightly more flowers on average on unprotected branches (1.4 ± 3.0 SD, n = 331) than were counted on branches protected by exclosures (1.1 ± 2.7 SD, n = 222). This small difference in flowers was not significant ($F_{1,60.1}$ = 0.86, p = 0.37).

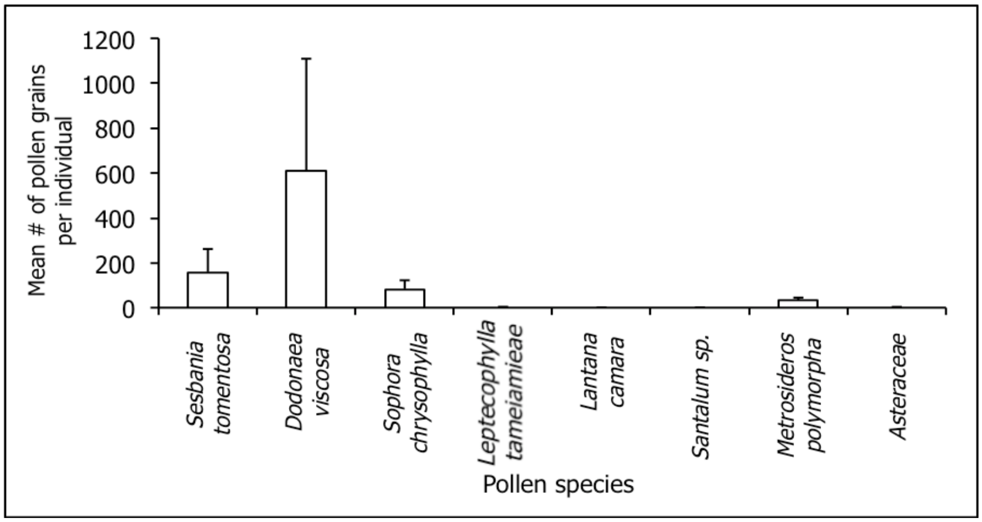

Figure 39. Pollen load composition of honey bees (*Apis mellifera*) collected on flowers of *Sesbania tomentosa* in Kīpuka Nēnē.

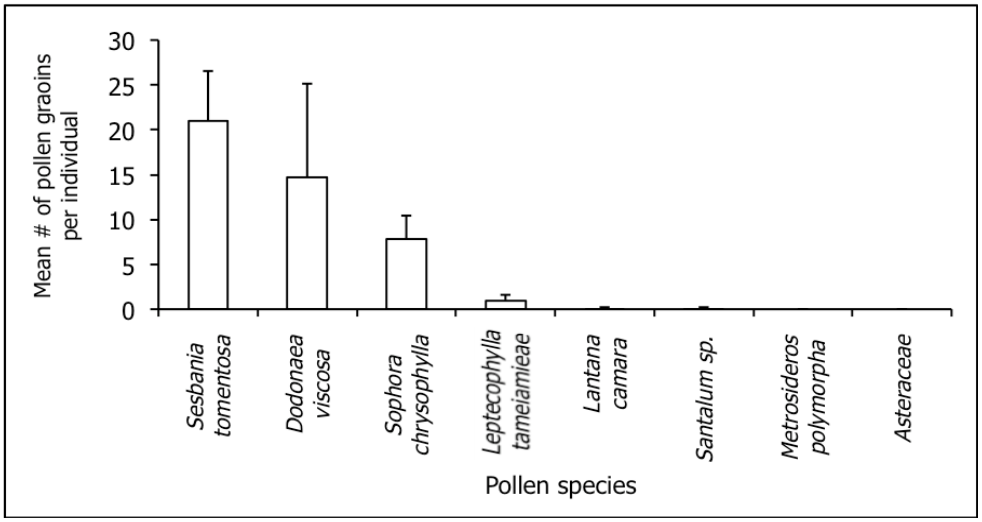

Figure 40. Pollen load composition of yellow-faced bees (*Hylaeus* spp.) collected on flowers of *Sesbania tomentosa* in Kīpuka Nēnē.

Most importantly for the reproduction of the plant, there was no significant difference in the number of fruit per branch between branches in exclosure sleeves and those unprotected ($F_{1,64.6}$ = 2.69, p = 0.11). No fruit pods were seen in more than a year of monitoring inside exclosures (n = 220), and unprotected branches had a mean of 0.05 fruit per branch (± 0.23 SD, n = 321).

Seeds and Seed Germination

Field seed plots with and without grass at Kīpuka Nēnē – Seedlings first appeared at Kīpuka Nēnē East in September 2007, almost five months after sowing. Seedlings continued to appear in both grass-covered and grass-free plots until the following summer, with a larger number of seedlings seen where grass had been removed (Fig. 41). After a hiatus in germination during the dry summer months (Appendix II, Fig. 4), low numbers of seedlings began to appear in November 2008 through May 2009, at least in the grass-covered plots. Individual seedlings continued to appear occasionally in grass plots until the end of the study in September 2009, more than two years after sowing. Overall in the seed plots sowed in spring 2007, a total of 9% of seeds germinated in the grass-covered plots, and 7% germinated in the no-grass plots. There was no significant difference in the number of seedlings germinated per plot between the grass and grass-free treatments (t = 0.45, df = 7, p = 0.445).

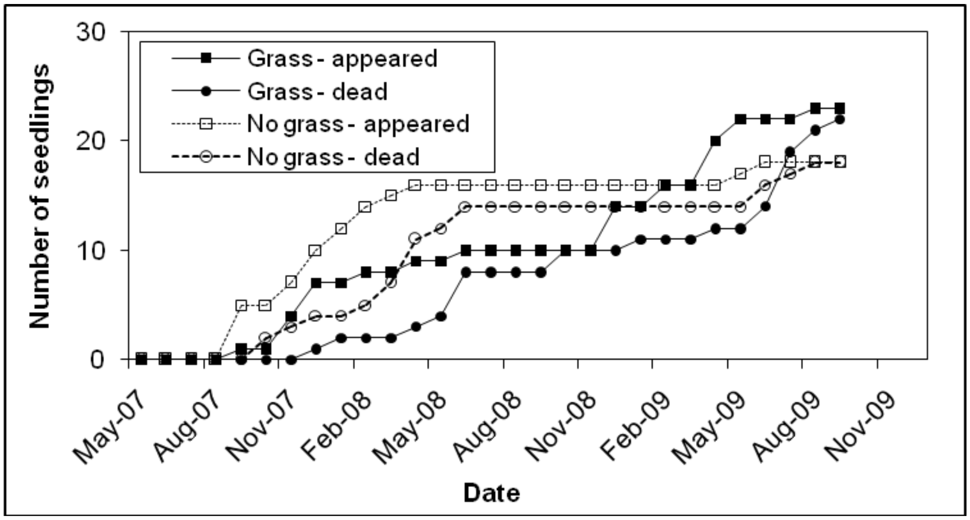

Figure 41. Cumulative appearance and death of *Sesbania tomentosa* seedlings in seed plots with and without alien grass cover at Kīpuka Nēnē East. Seeds were sowed in April 2007 with 51 seeds in each of 10 plots.

Seedlings in the no-grass treatment began to die in October after the spring 2007 sowing, and losses continued until almost all seedlings had disappeared by July 2008 (Fig. 41). Seedlings in the grass-covered plots started dying in December 2007 and losses were seen throughout the following two years. A second cycle of loss of newly-appeared seedlings began within the grass plots in October 2008 and peaked in September 2009.

By the end of the study, all except two seedlings (that germinated in 2009 in one grass plot) had been lost from the Kīpuka Nēnē East plots. There was no statistical difference between the number of seedlings that survived in the grass and no-grass treatments (t = 1.00, df = 4, p = 0.374). Mean soil depths were similar in the grass plots (26.9 cm ± 9.3 SD, n = 50) and the no-grass plots (23.7 cm ± 7.9 SD, n = 50).

In the seed plots established at Kīpuka Nēnē West in January 2008, most of the seedlings that germinated did so immediately within a month of planting (Fig. 42); Kīpuka Nēnē received an exceptionally high rainfall of 537 mm in February 2008 (HAVO Fire Cache, unpublished data; Appendix II, Fig. 4). No new seedlings appeared after June 2008 until April 2009, following high rainfall in March totaling >300 mm. A total of 30% of seeds germinated and recruited seedlings in the grass cover treatment, and a similar percentage (31%) germinated in the grass-free plots. There was no significant difference in the number of seedlings that appeared in the two treatments (t = 0.09, df = 7, p = 0.931). The mean soil depth was almost the same in plots of both treatments; grass-free plots had a mean depth of

19.6 cm (± 4.8 SD, n = 50), and the mean depth of grass plots was 19.5 cm (± 6.9 SD, n = 50).

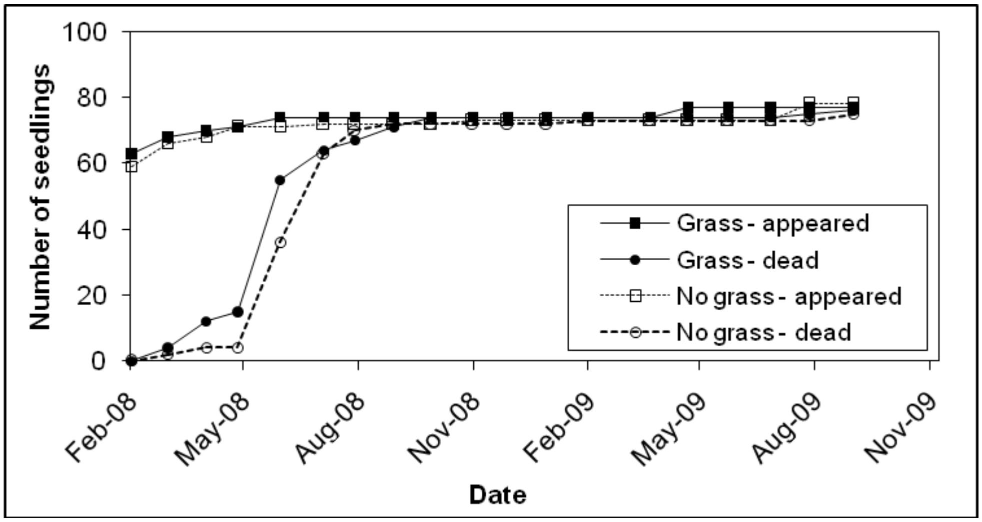

Figure 42. Cumulative appearance and death of *Sesbania tomentosa* seedlings in seed plots with and without alien grass cover at Kīpuka Nēnē West. Seeds were sowed in January 2008 with 51 seeds in each of 10 plots.

A few seedlings were lost within the first three months after germination, but most disappeared in June and July 2008 (Fig. 42); June 2008 was very dry at Kīpuka Nēnē, with only 8 mm total rainfall (HAVO Fire Cache, unpublished data). By the end of the study in September 2009, there were 4 seedlings remaining, one in each of four plots at Kīpuka Nēnē West (three no-grass and one grass plot). There was no difference in survival of seedlings in the grass and no-grass treatment plots (t = 1.27, df = 8, p = 0.242).

Field seed plots with and without grass at coastal Hōlei – Seed plots were sowed at the coastal site near Hōlei Sea Arch on April 5, 2007, following three months with >100–240 mm rainfall each at the nearby Pu`uloa weather station (HAVO Fire Cache, unpublished data). Germination was observed within 20 days (Fig. 43). Over almost four months of monitoring a total of 6 seedlings (3.0%) appeared in grass plots, and 7 seedlings (3.5%) were counted in plots without grass. There was no significant difference between the number of seedlings recruited in the grass and no-grass treatments (t = 1.1, df = 4, p = 0.17). The mean soil depth within grass plots was 20.3 cm (± 1.9 SD, n = 6), and that of no-grass plots was 23.0 cm (± 4.0 SD, n = 6).

Seedlings began to die within two weeks of their first appearance, and most seedlings were lost during the months of May and June, which were dry months (33–55 mm monthly rainfall) at Pu`uloa weather station (HAVO Fire Cache, unpublished data). The greatest height attained by seedlings was 2 cm. Two seedlings persisted throughout July (Fig. 43) but succumbed before mid-August. We stopped monitoring plants after August, but when plots were revisited in January 2008, there was 1 live seedling present in a plot. The final seedling likely germinated in December or January, at least nine months after sowing; its fate is unknown.

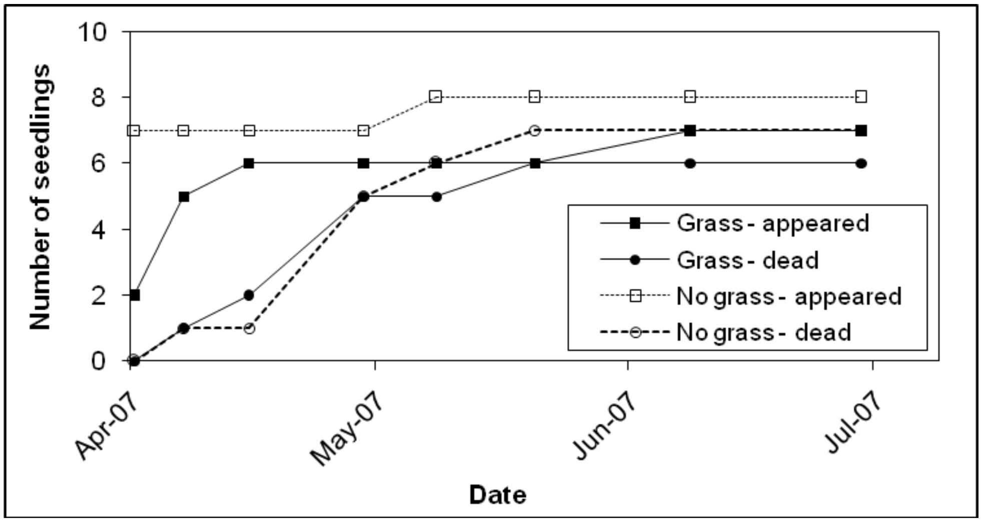

Figure 43. Cumulative appearance and death of *Sesbania tomentosa* seedlings in seed plots with and without alien grass cover at coastal Hōlei. Seeds were sowed in April 2007 with 66 seeds in each of six plots.

Soil seed bank – The soil seed bank was investigated in two seasons at the `Āpua Point *S. tomentosa* population. An equal number of soil cores (5) collected from each of five plants in March 2007 resulted in no *S. tomentosa* seeds, although many seeds of the common naupaka kahakai (*Scaevola taccada*) were recovered. The soil sampling was repeated in May 2007 at five different randomly-selected plants, when 7 whole *S. tomentosa* seeds were found in the pooled samples. Recovered seeds were planted in the HAVO greenhouse, but no germination was observed.

The soil seed bank at Kīpuka Nēnē East was also sampled during two seasons. Five cores were collected from beneath each of 10 randomly selected branches in October 2006, but no seeds of *S. tomentosa* were recovered. When sampling was repeated in December 2007 at five randomly selected branches, 3 seeds were found in the pooled samples. As with the seeds from `Āpua, no seedlings resulted from the recovered seeds after planting in the HAVO greenhouse.

Seed and fruit predation by rodents – Seed pod offerings inside and outside rodent-proof cages were made only at Kīpuka Nēnē East; the `Āpua Point site was too windy and remote for this experiment. When one mature fruit was offered in each of three cages and adjacent open trays in October 2006, only one seed pod was missing from an open tray after 28 days. Fruit offerings were repeated in December 2006, this time with two large or three small pods in each of five cages and adjacent unprotected trays. After 46 days, 2 pods total, one from each of two control trays, were missing; no pods showed any sign of rodent feeding. Pooling the data from the two offerings, there was no significant difference in fruit disappearance between the caged and unprotected fruit (X^2 = 3.36, df = 1, p = 0.07).

In a second attempt to detect rodent predation we monitored mature-size seed pods still attached to the *S. tomentosa* plants at Kīpuka Nēnē West from March 2007 to October 2009 and examined them monthly for rodent chewing or predation; we revisited tagged fruit a final time in January 2010. Variable numbers of legumes were tagged each month when pods were available. The number of predated pods observed was typically 25–41% of the total available during the peak months of pod production from October to April (Fig. 44). Overall, during this period of almost three years, 33.2% of tagged pods showed obvious signs of rat predation. Rat-predated fruit were typically cut on an angle at the base, and examination of the angled cut showed striations or tooth marks. An additional 33.6% of tagged fruit were missing in the monthly pod monitoring. Adding the missing fruit to the group of predated fruit, potentially 66.8% of all tagged seed pods may have been lost to rodents (n = 202).

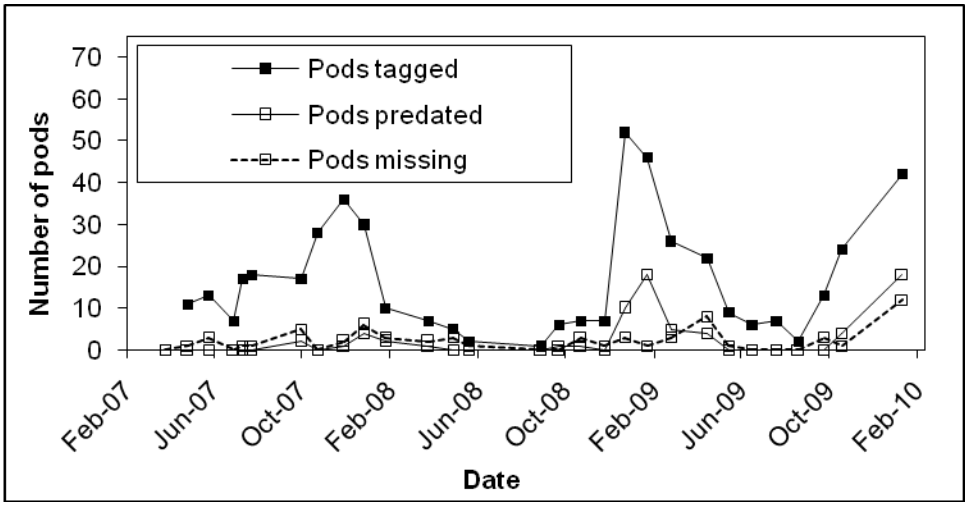

Figure 44. Number of tagged *Sesbania tomentosa* fruit pods predated by rodents or missing at the Kīpuka Nēnē West site, March 2007–January 2010.

Seed germination in the greenhouse – Seed germination rates were variable in four greenhouse trials (Appendix I, Table 3). The trial sown in July 2006 achieved an average germination rate of only 14.0%. The mean germination of five replicate flats sown in October 2006 was 24.8%. The third germination trial sown in February 2009 had a mean germination of 62.3%; this was the highest rate achieved by any of the four trials. The final trial sown in June 2009 had the second highest mean germination rate observed, 36.7%. Seeds used in the first two trials were not treated before sowing, while those of the last two trials were soaked in warm water for six hours before sowing. The medium was the same for all trials. Seeds tested in trials 2, 3, and 4 were collected from the Kīpuka Nēnē site, and those in germination trial 1 came from `Āpua Point. Time from sowing to first germination was variable, ranging from 17 days in June to 49 days in the October sowing with unsoaked seeds. Seeds used were typically less than one month old, but seeds in the second trial were stored for five months before sowing, and seeds used in trial 4 were a mixture of freshly collected and two-month-old seeds.

Potential Limiting Factors of Three Rare Plant Species in this Study

For two of the three species in this study, a comparison of the stand structure at the end of the monitoring period with that of an earlier period revealed declining populations; this conclusion was supported by the high adult mortality rates observed for all three studied species (Table 5). Fruit production was high for *B. timonioides* and *P. sclerocarpa*, but was very

Table 5. Potential limiting factors of three rare plant species investigated in this study.

Factor	*Bobea timonioides*	*Portulaca sclerocarpa*	*Sesbania tomentosa*
Stand structure	Declining	Declining	Unknown
Adult mortality	33%[1]	23%[2]	43%[2]
Flower/fruit phenology	Continuous	Annual	Annual
Fruit production	High	High	Low
% Bud/flower to green fruit	n/a	47%	1.6%[3]
% Green fruit to mature	n/a	n/a	4.9%[3]
# Potential insect pollinators observed [4]	n/a	n/a	4
Seed germination (greenhouse)	21–59%	<1–24%	14–62%
Seed viability test positive & strong	n/a	65%	n/a
Soil seed bank	n/a	n/a	Yes
Rodent predation of fresh seeds/fruit	3%	72–100%	33%[5]
Natural seedlings observed	No	Yes	No
Natural seedling mortality	n/a	100%	n/a
Planted seedling mortality	93%	20–84%[6]	97%

n/a Not tested or not observed

[1] Mortality of trees between 1993 and 2006 (13 years)

[2] During study period. Apparently separate *S. tomentosa* plants at `Āpua Point

[3] % from *S. tomentosa* at Kīpuka Nēnē West

[4] Insects observed collecting pollen, including two species of *Hylaeus*

[5] % of tagged fruit attached to plants predated by rodents at Kīpuka Nēnē West

[6] % mortality at 2006 planting at Kalanaokuaiki Pali and % mortality at HVO

low for *S. tomentosa*. Seed germination was relatively low for *P. sclerocarpa* but was high, at least in some trials, in the other two species. Seed viability was examined only for *P. sclerocarpa* and was found to be high. The soil seed bank was investigated only for *S. tomentosa*, which was found to have a small seed bank, at least in a single season. Rodents were implicated as seed and fruit predators of *P. sclerocarpa* and *S. tomentosa*, but they had no detected impact on *B. timonioides*. Natural seedlings were observed only at planted populations of *P. sclerocarpa*, but all were lost within a year of appearance. Mortality of planted seedlings was high for all three species.

DISCUSSION

Population Structure, Growth, and Mortality

All species followed in this study had declining populations when compared with either previous studies or the data from the first year of the current study; the size and structure of the population could not be determined for the Kīpuka Nēnē *Sesbania tomentosa* plants. *Bobea timonioides* had a diameter-class distribution indicating a senescent population composed of old trees with no young trees to replace them (Barbour *et al*. 1980). The number of trees of this species growing in the upper part of Nāulu Forest in 2006–2007 had decreased by a third since the last rare plant survey of the area (Abbott and Pratt 1996). The lack of growth in diameter of surviving trees between 1995 and 2007 is another indication of the old age of the trees and the senescent nature of the remaining population. The park population of *B. timonioides* has apparently declined since 1973, when Warshauer and Jacobi (unpublished) reported 65 trees along Hōlei Pali. Many of the trees observed in the 1970s were growing on an `a`ā flow north of Kamoamoa, an area that was covered by lava from Pu`u `Ō`ō in the last two decades.

The natural population of *Portulaca sclerocarpa* at Puhimau Geothermal Area also showed a pronounced mortality rate between the beginning of the current study, when 300 plants were present, and a previous survey of plants in 1994 (L. Pratt, unpublished data), when more than 900 plants were counted at the site. During the two years of monitoring for this study >23% of plants in the total population were lost from the site, and an even greater percentage of plants monitored for phenology disappeared, indicating that conditions causing loss of plants were continuing. Further evidence for decline of *P. sclerocarpa* at Puhimau was the decrease in frequency of the plants along transects between 1981 (Smith 1981) and 2008. While it is difficult to assess the current size class structure of this small herbaceous plant, a decrease in the size of live plants was observed between 2006 and 2008, indicating a loss of vigor of individual plants as well as a decline in the total population size. Losses were experienced in every size class of the population between 2006 and 2008. The study years 2006–2008 were not particularly dry as measured at the park headquarters weather station; the annual rainfall for both 2006 and 2007 exceeded the seven-year average by >500 mm (HAVO Fire Cache, unpublished data).

The reverse J-shape of the Puhimau *P. sclerocarpa* population measured in the current study was deceptive. Typically, such a population distribution curve would indicate a growing population (Barbour *et al.* 1980). The individuals of this herbaceous population are mostly small, but this does not necessarily indicate the youth of the plants. In this perennial species, a small-sized plant may be many years old, and the trend toward a decrease in size noted in our study may indicate senescence of the natural population. The longevity of *P. sclerocarpa* plants is not known (U.S. Fish and Wildlife Service 1996).

The *S. tomentosa* population at `Āpua Point showed a dramatic decline during more than a year of monitoring. The loss of almost half of the monitored plants and the decrease in areal size of survivors were evidence that this population of the rare plant is declining at the coastal site. The decline we detected in 2006–2007 at `Āpua did not seem to be related to low rainfall, as the years of the study had greater than average rainfall at the nearby lowland weather station at Pu`uloa (HAVO Fire Cache, unpublished data). Our study was not long enough to determine the actual age of plants that were lost. Hopper (2002) reported longevity of 3–10 years for *S. tomentosa* at a coastal site on O`ahu. By contrast, the Kīpuka Nēnē population did not appear to be decreasing in area, but we were unable to recognize individual plants here because of the sprawling growth form of the species. Our monitoring indicated that individual branches of *S. tomentosa* were not long-lived; few branches lived more than two years.

The growth of individual branches was pronounced at Kīpuka Nēnē, where the typical surviving branch increased from 1 to 4 m in length during the study period. Because of this capacity for rapid growth, stands of *S. tomentosa* may change dramatically in shape and size over short periods. This rapid growth rate and the tendency of the species to sprawl near the ground and root from branch nodes contribute to the dynamic nature of stands of *S. tomentosa*. Groups of plants that appear as distinct individuals may be a single tangled mass the next year. Conversely, a large single plant may break up into distinct patches that resemble multiple individuals. Char (1983) reported that lower branches of *Sesbania* near Kīpuka Nēnē (recognized in her work as *S. kauensis* var*. intermedia*) reached a length of 14 m, so an individual plant could likely be twice this size. An ongoing study examining the genetics of park plants may provide information on how many individual plants actually occur at several HAVO sites supporting *S. tomentosa*. Preliminary results indicate that the sampled branches at Kīpuka Nēnē East may all be part of a single enormous plant, while several individual plants appear to be present at Kīpuka Nēnē West (D. Cole, pers. comm.).

Patterns of Reproductive Phenology

Two of the species studied showed pronounced seasonal patterns in their reproductive phenology, and the third appeared to have a continuous pattern of flower and fruit production. *Bobea timonioides* was only visited for about a year, but during this time buds and flowers were continuously present on most of the trees, except during the months of June through August. These three months are typically dry in this area of HAVO, and each have <46 mm mean monthly rainfall at Pu`uloa, approximately 2 km from Nāulu. The study years 2006 and 2007 did not have atypical rainfall patterns (HAVO Fire Cache, unpublished data). Even during the summer months of low bud and flower production, these structures were present on >20% of the trees. Fruit production was continuous throughout the monitored period in 2006 and 2007, except for August 2007 when only mature fruit persisted on trees. Warshauer (unpublished) also reported the presence of fruit on *B. timonioides* trees of Kealakomo in winter, spring, and fall.

Portulaca sclerocarpa was highly seasonal in bud and flower production at least at the natural Puhimau population. Bud and flower production fluctuated throughout the year but dropped to zero in at least one month, either May, June, or July depending on the year. Peaks in bud production were bimodal and were observed in both April and September to October. Flower peaks typically trailed bud peaks by one to two months. Long-term rainfall patterns at the HAVO Headquarters weather station, approximately 4 km from Puhimau, show that the months from October through April each averaged >197 mm total rainfall from 2003 to 2009 (HAVO Fire Cache, unpublished data). Fruit capsule production was continuous at Puhimau, except for the month of July in 2006. In a study of uniform culture of Hawaiian *Portulaca*, the fruit capsules of *P. sclerocarpa* matured within 28 days of formation (Kim and Carr 1990).

The annual pattern of spring and fall production of *P. sclerocarpa* buds and flowers and continuous fruit production was also observed at the planting site near Hawaiian Volcano Observatory. Seedlings planted at Kalanaokuaiki Pali showed a less distinct seasonal pattern of reproduction, but as with the natural population, low points in bud and flower production were noted during the summer months of June or July. These months have the lowest mean rainfall at the nearby Kīpuka Nēnē weather station (HAVO Fire Cache, unpublished data). Few buds or flowers were seen on Kalanaokuaiki seedlings between July and October in 2008, although the summer pattern was less pronounced in 2009. As was seen at Puhimau, fruit capsules were present most of the year; fruiting began soon after the young seedlings and rooted cuttings were planted. In previous greenhouse studies with propagated Hawaiian *Portulaca*, cuttings were capable of flowering within a few weeks, and seedlings flowered 6–8 weeks after germination (Kim and Carr 1990).

Sesbania tomentosa showed an annual pattern of bud and flowers with peak seasons for buds and flowers in the spring and summer (between April and October) and greatest production of both green and mature fruit in summer (July to September). At Kīpuka Nēnē East most buds and flowers appeared between March and either June or August, and fruit had peak production between June and August during several years. Similarly at Kīpuka Nēnē West, most buds and flowers were produced seasonally in the spring and summer from May to at least August. Fruit production at this western site also followed an annual seasonal pattern, and peaks were observed for mature fruit in July, August, or September, as well as January. Unlike the pattern observed for *P. sclerocarpa*, peak bud and flower production in *S. tomentosa* occurred at Kīpuka Nēnē during dry months rather than those with high rainfall (HAVO Fire Cache, unpublished data). Flowering peaks at Kīpuka Nēnē were longer and started later than those observed for *S. tomentosa* at Ka`ena Point, O`ahu, where most flowering occurred between February and May (Hopper 2002).

The annual cycle of *S. tomentosa* bud and flower production at the coastal site of `Āpua Point had different seasonal peaks from those at the upland site of Kīpuka Nēnē. Here buds and flowers peaked in November and immature fruit were observed in greatest abundance in July and January. Mature fruit were persistent throughout the year on *S. tomentosa* plants at `Āpua. The retention of mature fruit on `Āpua *Sesbania* plants for extended periods is more like the pattern observed for *Portulaca sclerocarpa*; it is unclear why mature *S. tomentosa* fruit were persistent at `Āpua Point but not at Kīpuka Nēnē. We have no evidence of rat predation on fruit at `Āpua and no data on rodent populations there. The level of rat predation of *Sesbania* fruit may have been greater at the upland site of Kīpuka Nēnē than at the coastal site.

The annual pattern of reproduction has been reported in most native Hawaiian plant species for which phenology has been studied. Annual patterns of flowering and fruiting were observed for nine tree and shrub species in rain forest on Maui (Berlin *et al.* 2000). *Metrosideros polymorpha*, the dominant tree species of most Hawaiian forests, has also been shown to have a strongly seasonal annual pattern of flowering (Carpenter and MacMillen 1973, Porter 1973). *Acacia koa* (koa) the dominant tree of many dry and mesic forests, as well as a co-dominant of diverse wet forests, has a strongly seasonal annual pattern for flowering and fruiting (Lanner 1965), as does *Sophora chrysophylla* (māmane) the primary tree of subalpine forests in Hawai`i (van Riper 1980, Pratt *et al.* 1997, Banko *et al.* 2002). In a study carried out within HAVO, the flowering phenology of 12 tree species distributed from the coastal lowlands to the upper Mauna Loa Strip was found to be strongly seasonal and annual, although the season of greatest flowering varied among the species studied (Lamoureux *et al.* 1981). A recent study of rare plant species in HAVO found continuous patterns of flowering and fruiting in three species of mesic forest (Pratt *et al.* 2010) and annual reproductive phenology for two shrub species of the `Ōla`a wet forest (VanDeMark *et al.* 2010).

Pollination

Sesbania tomentosa flowers require specialized handling by pollinators to effect pollination because the stamens and pistil are enclosed in a chamber formed by the wing and keel petals. In order to transfer pollen onto the stigma, a visitor must part the tip of the petals at the distal end of the chamber to expose the stigma and adjacent anthers. Only visitors collecting pollen demonstrated this specialized behavior. Visitors accessing nectar inserted their mouthparts between the wing petals at the proximal portion into the nectary. Since the nectary is well separated from the reproductive organs, nectar-collecting visitors failed to inadvertently contact the stigma and therefore did not provide a pollination service.

Hylaeus, native yellow-faced bees, were the dominant foragers of pollen, and thus appeared to be the most important visitors to *S. tomentosa*. Even though honey bees on average carried a greater number of *S. tomentosa* pollen grains than did *Hylaeus*, most visits by honey bees were for nectar removal. Only on rare occasions did honey bees and the longhorned grasshopper collect pollen. A previous study by Hopper (2002) found that *Hylaeus* were the only foragers of pollen at coastal populations of *S. tomentosa* at Ka`ena Point, O`ahu. In addition, since self-pollination (autogamy) was rare (0.8%) in this plant species (Hopper 2002), *Hylaeus* bees appeared to be providing critical pollination services for *S. tomentosa*.

Pollen load analyses of insects collected near *S. tomentosa* indicated that two species of *Hylaeus* and honey bees were all carriers of pollen of this species. Honey bees typically focus their foraging activities on a single flowering plant species (Grant 1950), but pollen from other plant species found in the pollen loads of both the honey bees and *Hylaeus* suggested that neither insect taxon restricted their visits to the flowers of *S. tomentosa*. The small number of pollen types observed in the pollen loads of *Hylaeus* supports the description of *Hylaeus* as oligolectic insects that collect pollen primarily from a single species or genus of plants (Scott 1996, Hopper 2002, Daly and Magnacca 2003).

An important threat to *Hylaeus* bees is ants. Significantly fewer *Hylaeus* nests were found in habitats infested by Argentine ant (*Linepithema humile*) than in non-invaded areas at Haleakalā National Park (Cole *et. al.* 1992), severely impacting *Hylaeus* populations. At Ka`ena Point, the presence of little black ants (*Ochetellus glaber*) discouraged nectar feeding of *S. tomentosa* flowers by *Hylaeus*, significantly reducing their visit duration (Hopper 2002). Therefore the presence of two aggressive ant species, Argentine ants and long-legged ants (*Anoplolepis gracilipes*), at Kīpuka Nēnē is concerning. With the dependence of *S. tomentosa* on *Hylaeus*, any decline in these pollinators from predation may result in a loss of seed set, less vigorous offspring, and ultimately local extinction.

Despite the presence of *Hylaeus* and other pollinators at this population of *S. tomentosa* there was extremely low seed pod production. In flowering plants, low reproductive output can be attributed to various factors. Seed production may be limited by the quantity of pollen received because of insufficient pollinator visits (Ashman *et al.* 2004, Knight *et al.* 2005). However, manual supplemental hand pollination in this study failed to increase fecundity. A second factor limiting seed production may be a lack of female (Nayyar *et al.* 2005) and male fertility (Dafni and Firmage 2000, Huang *et al.* 2004, Gross and Caddy 2006), but our tests of pollen viability and stigma receptivity confirmed both male and female vigor.

To identify why there is such low seed set in the population, examination of pollen tube growth following hand pollination is necessary. Angiosperms frequently have self-incompatibility mechanisms encoded into their genotypes whereby stigmas of flowers are more likely to reject their own or closely related pollen to avoid inbreeding by stunting pollen tube growth before it reaches the ovaries (Newbigin *et al.* 1993). Since the population of *S. tomentosa* at Kīpuka Nēnē may be composed of only a few individuals, seed set may be limited by lack of potential mates due to restrictions in the breeding system.

Success of Fruit Production

The monitoring of tagged buds and flowers at two of the study sites indicated a high rate of successful fruit production at the natural population of *P. sclerocarpa* and a very low level of pod formation at the Kīpuka Nēnē population of *S. tomentosa*. Flowers were not tagged at the *B. timonioides* population of Nāulu because they were borne on tall trees out of reach from the ground. Almost half (47%) of *P. sclerocarpa* branches tagged with either buds or flowers produced fruit capsules, usually within a month. This high rate of fruit production is similar to the 55% fruit set reported for red-flowered *Metrosideros polymorpha* (\`ōhi\`a lehua) (Carpenter 1976), the most common tree in Hawai\`i forests. Like all other members of the *Portulaca* family, the rare *P. sclerocarpa* is self-pollinating (Geesink 1969), and wind is typically the agent when cross-pollination occurs. Under cultivation, the capsules of *P. sclerocarpa* require 28 days to mature, the longest maturation time observed for Hawaiian *Portulaca* species (Kim and Carr 1990).

The overall success of fruit production by *S. tomentosa* flowers at Kīpuka Nēnē was only 0.7% (0.6% for mature fruit). This level of fruit set is less than Hopper (2002) observed on bagged and self-pollinated *S. tomentosa* flowers in his study at coastal Ka\`ena Point, O\`ahu. Hopper reported fruit set of open-pollinated *S. tomentosa* flowers as 10 to 32% in the two years of his study. Fruit set lower than 1% is generally considered to be a very low level of productivity and is often interpreted as a lack of effective pollination (Armstrong and Irvine 1989, Zimmerman and Aide 1989, Anderson and Hill 2002). Because of the structure of *Sesbania* flowers, self-pollination is unlikely within an individual flower, and typically an insect agent of a particular size is required to move pollen from an anther onto the exserted stigma of the flower. Two species of native *Hylaeus* (yellow-faced) bees were observed visiting *S. tomentosa* flowers at Kīpuka Nēnē during this study (see previous section), and *Hylaeus flavipes* has been previously collected from *Sesbania* flowers at the site (Daly and Magnacca 2003). Hopper (2002) identified *Hylaeus* bees as the most effective pollinator of *S. tomentosa* among the bees and wasps he observed visiting his study plants at Ka\`ena Point. However, isolated plants at Ka\`ena were visited by bees at a much lower rate and had much lower fruit set than did plants in the main dune population.

The higher fruit set in the *S. tomentosa* plants at Kīpuka Nēnē West as compared to those across the Hilina Road at Kīpuka Nēnē East is difficult to explain. It is unlikely that the suite of pollinators is significantly different at two sites in the same vegetation type separated by less than 500 m. Magnacca (2007) considered *Hylaeus flavipes* to be abundant at Kīpuka Nēnē, and this species and/or *H. laetus* were observed as pollinators of *S. tomentosa* in our study. There is some evidence from a recent study at Kīpuka Nēnē that *S. tomentosa* at the eastern site is actually a single plant, while the western patch is composed of several individuals (D. Cole, pers. comm.). This lack of fruit set in the eastern site may be evidence for self-incompatibility in *S. tomentosa*, although Hopper (2002) reported that the species was selfcompatible and capable of self-fertilization with assistance of insect agents. Char (1983) reported low fruit set at plants she studied at Kīpuka Nēnē more than 30 years ago, which she considered a distinct variety (*S. kauensis* var. *intermedia*). Based on her specimen collection information, the plants Char studied were on the former trail to Halapē south of our study site at Kīpuka Nēnē East and may have been individuals isolated from the groups of plants we studied.

Impacts of Rodents and Alien Insects

Rodent seed or fruit predation was identified on two of the three species of this study. Predation of the small capsules of *P. sclerocarpa* was noted during monthly phenology monitoring, and all capsules offered outside exclosures at the natural population were either taken or gnawed open irregularly with the tiny seeds consumed. Sample plants protected within rodent-proof cages or exclosures exhibited a greater proportion of branches bearing fruit than did adjacent unprotected plants in every month for a year. Predation by rodents was not expected for this species because of the small size of both the seeds and the dry capsules. Rodents were not listed as reasons for decline in the recovery plan for the species (U.S. Fish and Wildlife Service 1996) or in a compilation of information on rare plants of Pōhakuloa Training Area, which supports a population of the species (Shaw 1997). Recent studies of the vulnerability of Hawaiian plants to black rats (*Rattus rattus*) indicated moderate vulnerability for seeds of *P. sclerocarpa* (A. Shiels, pers. comm.)

Typical rat depredation involves fleshy fruit with relatively large seeds (Clark 1982, Meyer and Butaud 2009). Seeds <5 mm long are thought to be less vulnerable to predation by the Polynesian rat (*Rattus exulans*; Campbell and Atkinson 2002). The tiny seeds of *P. sclerocarpa* are less than 0.5 mm in diameter and the capsule is only 4–4.5 mm long (Wagner *et al*. 1999). The identity of the depredating rodent is uncertain; the size of the wire mesh in exclosures was small enough to exclude both rats (*Rattus* spp.) and mice (*Mus musculus*). While black rats (*Rattus rattus*) are the dominant rodent in wet montane forests of Hawai`i (Stone 1985, Tomich 1986), mice are widespread in the Hawaiian Islands and are often abundant in grasslands (Lindsey *et al*. 2009) such as the woodland habitat surrounding the periphery of the natural *P. sclerocarpa* population at Puhimau with its dense ground cover of alien grasses (Smith 1981).

In a study of the food habits of rats and mice in high-elevation shrubland on Maui, monocot and dicot seeds together made up almost half the diet of mice, while rats were more likely to consume fleshy fruit (Cole *et al*. 2000). In studies of the diets of rats in Hawaiian rain forests, black rats ate more fleshy fruits than did Polynesian rats, but they also consumed the seeds of large dry capsular fruit, such as *Pittosporum* sp. (hō`awa; Sugihara 1997). On islands in the Southern Ocean that lack rats, house mice are seed predators of many grasses and sedges and have reduced populations of some species native to the islands (Angel *et al*. 2009).

Predation of *S. tomentosa* seeds and pods by rodents has been previously noted on O`ahu (Hopper 2002), and seed predation by rats and mice is listed as a reason for decline of the species in its recovery plan (U.S. Fish and Wildlife Service 1999). The results of the offering of seed pods inside and outside exclosures at Kīpuka Nēnē were not definitive, and the loss of some of the pods in the unprotected trays could have been due to feral pigs or even wind. The exclusion of rats from sample branches at Kīpuka Nēnē East did not result in increases in fruit production because no flowers borne by protected branches set fruit. However, in samples of pods marked and revisited for almost three years at Kīpuka Nēnē West, more than 33% of pods were obviously predated by rats, which left tooth marks on an angled cut at the base of the legume. The size of the tooth marks indicated predation by rats rather than mice (Wilmshurst and Higham 2004). Because many of the sampled pods were missing and likely taken by rats, the actual predation rate for pods at Kīpuka Nēnē West may have been higher than 60% of the monitored pods. Such a high level of fruit and seed predation, coupled with the very low fruit set observed at the site, indicated that few seeds were available for either immediate germination or seasonal replenishment of the soil seed bank.

The bean butterfly (*Lampides boeticus*), an alien blue or hairstreak butterfly (Lycaenidae) from Africa, Europe, and Asia, has been present in Hawai`i since 1882 and is known to attack the flowers of both introduced and native species of legumes (Fabaceae), including both *S. tomentosa* and *Sophora chrysophylla* (Zimmerman 1958). The butterfly has been reported from all the main Hawaiian Islands except Kaho`olawe (Nishida 2002). Flowers predated by the bean butterfly caterpillar at Kīpuka Nēnē were hollowed out by the insect's feeding; this resulted in the destruction of the ovary and stamens and the loss of ability to set fruit. We did not observe bean butterfly caterpillar damage to the fruit or seeds of *S. tomentosa*, as reported by Zimmerman (1958). We did not sample insect damage to flowers at `Āpua Point, although we noted the presence of adult butterflies at the site. High levels of damage to buds and flowers were seasonal at Kīpuka Nēnē, but in some months in the summer and fall almost half of the flowers and a quarter of the buds were attacked by this insect species. Buds that matured to flowers in the winter and early spring months may have been able to avoid attack by the bean butterfly, but these months were times of low bud production and few flowers were typically present. Predation of flowers by the alien bean butterfly likely contributed to the low fruit set observed at Kīpuka Nēnē and may have reduced the attractiveness of plants to pollinators, since predated flowers lacked pollen or nectar.

Seed Germination and Soil Seed Banks

Seed germination rates were variable for all three species studied, but high germination was achieved in some of the trials for both *B. timonioides* and *S. tomentosa*. Rates varying between 22 and 53% indicated that seed viability and germinability were not problems for the tree *B. timonioides*. Apparently *Bobea* seeds do not store well (Lilleeng-Rosenburger 2005), which may explain why germination trials using five-month-old seeds showed lower rates than did those with fresh seeds. Baskin *et al*. (2004) reported physiological dormancy in the related *B. elatior*, but the relatively rapid germination of *B. timonioides*, starting within a month in our study, suggested that seed dormancy was not a factor in this species.

Germination trials for *S. tomentosa* (14 to 62%) demonstrated high rates of seed germination under certain conditions. The low average was obtained using seeds from `Āpua Point. Seeds collected at this coastal site showed a greater degree of insect infestation than did those collected at Kīpuka Nēnē. While an attempt was made to collect only unaffected seeds, some may have been damaged by seed weevils, which are known to impact seed germination (Staples and Herbst 2005). *Sesbania tomentosa* seeds reportedly display physical dormancy (Baskin *et al*. 2004), which apparently was broken in latter trials by soaking seeds in hot water. The trials using soaked seeds showed much higher rates of germination than did those with untreated seeds. Even higher rates might be achieved by scarifying seeds, as suggested by Lilleeng-Rosenberger (2005). Char (1983) achieved 100% germination following scarification of small samples of *S. tomentosa* seeds from near Kīpuka Nēnē. Our direct seeding plots at

Kīpuka Nēnē showed that seeds could remain viable in the soil for up to three years and produce seedlings. Lilleeng-Rosenberger (2005) reported that the seeds of *S. tomentosa* could be stored up to 10 years and still germinate. Other species of *Sesbania* are also known to remain viable for more than 10 years (Char 1983).

Sesbania tomentosa appeared to have a small soil seed bank at both the `Āpua Point and Kīpuka Nēnē populations. Because our sampling was only carried out during two seasons at each site, it is unclear whether the soil seed bank for this species is transient or persistent. Most seed bank studies carried out within forests of HAVO found no soil seed bank or only transient banks for native woody species (Drake 1998, Loh and Daehler 2008). However, the hard seed coat and longevity of *S. tomentosa* seeds (Lilleeng-Rosenberger 2005), the reported short life span of plants (Hopper 2002), and the persistence of the species in alien-dominated vegetation at sites both in HAVO and elsewhere on the island (U.S. Fish and Wildlife Service 1999) are evidence that the species is capable of forming persistent seed banks at some sites.

Seed germination rates were relatively low for the small-seeded *P. sclerocarpa*. Previous propagation of this species at HAVO was carried out using rooted cuttings (Belfield *et al*. in prep; N. Zimmer, unpublished data), so there are no comparisons with previous germination trials in the park. Results from the tetrazolium test indicated a loss of viability in *P. sclerocarpa* seeds in just five weeks. However, there was no obvious pattern of lower germination rates with stored seeds; the trial with the lowest percentage germination used seeds collected the previous day, and a trial with high average germination rates used seeds stored for nine months. Lilleeng-Rosenberger (2005) reported that Hawaiian *Portulaca* seeds stored well. The variable germination rates observed in our trials may relate more to the time of year they were sown; the trials with the lowest germination were sowed in January and May, while the more successful trials were sown in summer (June) and fall (November), when ambient temperatures are typically higher than those of winter and spring. While we did not examine the soil seed bank for *P. sclerocarpa*, species with small smooth seeds often form persistent seed banks, and persistent seed banks have been reported for several species in the family Portulacaceae (Baskin and Baskin 1998).

Planting Survival and Potential Restoration Strategies

All three of the species in the current study have been recently propagated and planted within HAVO (Belfield *et al*. in prep.). The decline in the natural populations of *B. timonioides*, *P. sclerocarpa,* and *S. tomentosa* and the lack of natural seedling recruitment and establishment indicate that these species may eventually be lost from the park without continued active management. Because the habitat of *B. timonioides* has been greatly altered and the rare trees persist only in small kīpuka subject to sulfur dioxide fumes and drying winds, alternative planting sites have been selected in more continuous forest to the north of Nāulu (Loh, unpublished). Alternatively, the natural habitat of *Diospyros sandwicensis* (lama) forest might be made more hospitable for rare tree regeneration by repeated removal of alien ground cover species and continued restoration of native understory trees and shrubs to restore more shady conditions and block the prevailing winds (T. Tunison, pers. comm.). In recent native plant stabilization projects, at least two common tree and shrub species (*Myoporum sandwicense*, naio, and *Nototrichium sandwicensis*, kului) and the endangered *Pleomele hawaiiensis* (hala pepe) had relatively good survival at Nāulu Forest (Belfield *et al*. in prep.), indicating that these and other untested appropriate native species could be used effectively to improve the understory and potentially enhance survival and regeneration of *B. timonioides* and several other rare tree species that have been planted.

Portulaca sclerocarpa has received management attention for the last 10 years, and more than 2,000 individuals have been planted in HAVO, grouped at five general sites (Belfield *et al.* in prep.). Mortality has been extremely high at planting sites and four of the five sites have no persistent plants. The results of the current study indicate that seedlings are longer-lived than cuttings, and produce larger plants with higher levels of fruit production, although a longer period of monitoring would be desirable to confirm this trend. It is unknown whether larger cuttings with more developed root systems would have greater success than the cuttings we planted. There is some evidence from Kalanaokuaiki that adult plants do not suffer from proximity to alien grass; mortality of planted seedlings was not higher in grass-covered areas, while growth and fruit production were actually greater in plantings with alien grass cover. The sample size of 25 in each treatment was moderately large, although it would be desirable to repeat the planting with a larger sample size before accepting these results and altering management actions. The finding of no or positive impact of alien grasses on a native plant is consistent with the results from grass removal experiments previously carried out in dry woodlands near Kīpuka Nēnē (D'Antonio *et al.* 1998), where grass removal plots had lower moisture than those covered with alien grass and at least one native shrub species lost biomass in grass-free plots.

In the current study, spontaneous *P. sclerocarpa* seedlings were never observed at grassy plantings, so recruitment may be impaired by the presence of alien grass. Alien grasses are generally considered to compete for resources with native plants, and their fibrous root systems may reduce water near the surface and impact seedlings (D'Antonio and Vitousek 1992). D'Antonio *et al.* (1998) found increases in seedling recruitment and growth of some native woody plants after removal of alien grasses in woodlands near Kīpuka Nēnē, but seedling increases were attributed to increased light and temperature rather than increased availability of water.

Since control of all alien grass is not feasible on a large scale in HAVO, continued selection of planting sites with low grass cover is likely warranted. Because the natural seedlings seemed to be vulnerable to loss during the summer, selection of sites with greater overall rainfall, particularly during the summer months, might allow for greater longevity and potential recruitment of seedlings at plantings. Sites at the same elevation as Kalanaokuaiki to the east in Kīpuka Kahali`i have little grass cover and greater annual rainfall, exceeding 2,000 mm annually with >100 mm in each month between June and September (Giambelluca *et al.* 1986). Other non-forested sites below 1,200 elevation in the Kīlauea summit region that have annual precipitation greater than 2,000 mm may also provide planting sites for *P. sclerocarpa* that are slightly wetter than those previously planted. The species is also known from higher elevations elsewhere on the island (Shaw 1997), but except for areas in the Kahuku Addition, upland woodlands in HAVO typically have dry summer months (Doty and Mueller-Dombois 1966, Giambelluca *et al.* 1986).

Sesbania tomentosa has been particularly difficult to establish at new coastal sites within HAVO in the past; park managers planted approximately 750 individuals at eight general sites in the 1970s and only one to two plants persist from this effort (N. Zimmer, unpublished data). More recent coastal plantings also had high mortality, but a few plants have persisted for more than 10 years at coastal sites east of `Āpua Point (Belfield *et al.* in prep.). In the current study, survival of planted seedlings was very poor at two upland sites only 1–2 km away from the natural population at Kīpuka Nēnē; these sites also had poor survival of other dry forest and woodland species (Belfield *et al.* in prep.). Only *Myrsine lanaiensis* (kōlea) and *Bidens hawaiensis* (ko`oko`olau) appeared to have survival rates >10% at these sites. The low success of plantings near Kīpuka Nēnē did not seem to be related to lack of rainfall, as the weather station there had above-average annual totals for the years 2006 and 2007, and the year 2008 had annual rainfall only slightly lower than the seven-year mean (HAVO Fire Cache, unpublished data).

Seeding experiments demonstrated that untreated *S. tomentosa* seeds were capable of germinating at the Kīpuka Nēnē natural population at micro-sites with and without alien grass. Seeds could persist for almost three years in the soil and germinate under favorable rainfall conditions. Presence of grass did not reduce seed germination or result in greater loss of germinated seedlings. However, in both 2007 and 2008 seed sowing trials, most seedlings were lost during the summer months in both grass and no-grass plots. Loh *et al.* (2009) found low germination of seeds of *S. tomentosa* at both burned and unburned sites of the HAVO coastal lowlands, but seedlings did not persist more than 3–5 years. *Sesbania* plants in the small plots we monitored did not show increased growth without grasses as was observed for saplings of common shrubs in a previous study of grass removal at Kīpuka Nēnē (D'Antonio *et al.* 1998), and seedlings were not more numerous or longer-lived in grass-free plots. D'Antonio *et al.* detected lower soil moisture where grasses were removed. Future restoration sites for seedling planting or seed broadcast might be sought in areas to the east with higher levels of summer precipitation to achieve better survival results from those at Kīpuka Nēnē and the nearby Kalanaokuaiki and dry stream bed sites. The long-term prospects of seedling recruitment at natural populations and establishment of new populations of *S. tomentosa* from plantings would likely be increased if effective rat control reduced the percentage of seeds and pods predated and allowed for development of a larger seed bank at natural or restoration sites.

CONCLUSIONS

Summary of Important Limiting Factors of Three Rare Species in this Study

Bobea timonioides – The natural population of this rare tree at Nāulu Forest had declined in size since it was surveyed in 1993, and a third of the re-located trees had died. No natural seedlings were observed, and almost all planted seedlings died within 18 months. Most trees monitored for a year bore buds, flowers, and fruit. Seed germination rates in the greenhouse were moderately high, although germination was lower with stored seeds. No seeds sowed at Nāulu germinated. No obvious seed predation by rodents was detected in seed offerings, and no damage to fruit was noted on trees. Harsh site conditions, resulting from forest fragmentation by lava flows from the 1969–1972 Mauna Ulu eruption, appear to be inhibiting natural seedling recruitment.

Portulaca sclerocarpa – The natural population of this herbaceous plant at Puhimau declined, and surviving plants decreased in size over two years. Most plants at both natural and planted populations bore flowers and fruits, and percentage fruit set was high. Rodents were implicated as fruit/seed predators, based on an exclosure experiment and fruit offerings. Planted seedlings had lower mortality than cuttings at one site, and the mortality of a planting of cuttings was very high at another site. The presence of grass did not increase mortality or decrease fruit production of planted seedlings. Natural seedlings appeared at both monitored planting sites but did not survive more than a few months. Greenhouse germination rates were variable, with the best germination observed at summer and fall trials. Loss of seeds to rodent predation and low seedling recruitment were the most serious limiting factors for this species.

Sesbania tomentosa – The monitored population of this sprawling shrub declined at `Āpua Point, but individuals could not be discerned at Kīpuka Nēnē. Individual branches were fast-growing but short-lived. Bud and flower production was high, but fruit set was very low at Kīpuka Nēnē. Caterpillars of an alien butterfly destroyed a high percentage of flowers, and rats predated at least a third of monitored pods. Planted seedlings at two sites along Hilina Road had very high mortality, as did seedlings that germinated at seed plots at Kīpuka Nēnē. A small soil seed bank was detected at both natural populations. Greenhouse seed germination was variable, but was greatest in trials with soaked seeds sowed in the summer. Multiple limiting factors were identified for *S. tomentosa*, including low fruit set caused by lack of effective pollination or self-compatibility problems, loss of flowers to alien insects, predation of seeds by rats, and low seedling recruitment.

Suggestions for Future Work

Bobea timonioides – Further experimental plantings of this species following control of alien ground cover and increase in native understory species at Nāulu would help determine the feasibility of maintaining a population of the species within its natural habitat.

Portulaca sclerocarpa – Identification of the rodent species responsible for seed predation in this species would allow for development of specific strategies to reduce the populations of the predating animal. Determination of the role of grasses in reducing recruitment of seedlings would help managers select appropriate sites for planting this species.

Sesbania tomentosa – Additional research to identify individual plants, establish the genetic diversity of isolated groups of plants, and define the significance of morphological differences in upland and coastal populations would help managers develop genetic management strategies for park plants. Further research on pollination and identification of effective pollinators is warranted at different populations or subpopulations in the park. Research on the impacts of alien ants on native *Hylaeus* bees might lead to management strategies that favor pollinators of *S. tomentosa*. Determination of the causes of low fruit set is critical to the long-term survival of the Kīpuka Nēnē population.

Management Recommendations

- Effective control of rodents during periods of peak fruit production and through the winter period of likely seed germination would likely benefit both *P. sclerocarpa* and *S. tomentosa*.

- Continued propagation and planting in suitable sites may improve chances of long-term survival of all three species in HAVO. Alternative planting sites less exposed to sulfur dioxide fumes and drying winds could be sought for *B. timonioides*.

- For *P. sclerocarpa*, seedlings appear to be more vigorous and produce more fruit than do cuttings. Although cuttings are easier to propagate, use of cuttings seems less likely to result in establishment of new populations. Alternatively, cuttings could be retained in the greenhouse longer and planted after achieving a larger size and greater vigor.

- To enhance seedling survival and recruitment, additional sites for planting *P. sclerocarpa* and *S. tomentosa* could be sought east of current planting sites where annual rainfall is greater.
- Manipulation of the remaining habitat of *B. timonioides* at Nāulu by removal of alien ground cover and continued establishment of native understory species might alter conditions enough to allow for germination and survival of seedlings of this species.

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APPENDIX I

Data from Greenhouse Germination Trials

Table 1. Germination of *Bobea timonioides* seeds in the greenhouse.

Trial/Rep #	# Seeds	Date Sown	Date 1st Germination	# Seeds Germinated	% Seeds Germinated	Date Terminated
1/1	50	4/5/2007	5/21/2007	22	44%	8/7/2007
1/2	50	4/5/2007	5/21/2007	30	60%	8/7/2007
1/3	50	4/5/2007	5/21/2007	27	54%	8/7/2007
2/1	50	7/3/2007	8/6/2007	17	34%	1/8/2008
2/2	50	7/3/2007	8/6/2007	20	40%	1/8/2008
2/3	50	7/3/2007	8/6/2007	22	44%	1/8/2008
3/1	57	2/21/2008	3/25/2008	14	25%	8/6/2008
3/2	57	2/21/2008	3/25/2008	10	18%	8/6/2008
3/3	57	2/21/2008	3/25/2008	13	23%	8/6/2008

Table 2. Germination of *Portulaca sclerocarpa* seeds in the greenhouse.

Trial/Rep #	# Seeds	Date Sown	Date 1st Germination	# Seeds Germinated	% Seeds Germinated	Date Terminated
1/1	100	11/3/2005	11/30/2005	23	23%	5/2/2006
1/2	100	11/3/2005	11/30/2005	16	16%	5/2/2006
1/3	100	11/3/2005	11/30/2005	36	36%	5/2/2006
1/4	100	11/3/2005	11/30/2005	20	20%	5/2/2006
2/1	50	5/2/2006	8/1/2006	2	4%	1/25/2007
2/2	50	5/2/2006	8/1/2006	2	4%	1/25/2007
2/3	50	5/2/2006	8/1/2006	1	2%	1/25/2007
2/4	50	5/2/2006	8/1/2006	1	2%	1/25/2007
2/5	50	5/2/2006	n/a [1]	0	0%	1/25/2007
3/1	100	6/27/2007	n/a [1]	0	0%	1/8/2008
3/2	100	6/27/2007	7/9/2007	19	19%	1/8/2008
3/3	100	6/27/2007	7/16/2007	40	40%	1/8/2008
4/1	100	1/23/2009	4/29/2009	1	1%	9/28/2009
4/2	100	1/23/2009	2/6/2009	1	1%	9/28/2009
4/3	100	1/23/2009	n/a [1]	0	0%	9/28/2009
4/4	100	1/23/2009	n/a [1]	0	0%	9/28/2009
4/5	100	1/23/2009	n/a [1]	0	0%	9/28/2009

[1] Not applicable, no germination observed.

Table 3. Germination of *Sesbania tomentosa* seeds in the greenhouse.

Trial/Rep. #	# Seeds	Date Sown	Date 1st Germination	# Seeds Germinated	% Seeds Germinated	Date Terminated
1/1	50	7/30/2006	no data [2]	9	18%	2/11/2008
1/2	50	7/30/2006	no data [2]	9	18%	2/11/2008
1/3	50	7/30/2006	no data [2]	5	10%	2/11/2008
1/4	50	7/30/2006	no data [2]	5	10%	2/11/2008
1/5	50	7/30/2006	no data [2]	7	14%	2/11/2008
2/1	50	10/19/2006	12/7/2006	10	20%	1/8/2008
2/2	50	10/19/2006	12/7/2006	10	20%	1/8/2008
2/3	50	10/19/2006	12/7/2006	15	30%	1/8/2008
2/4	50	10/19/2006	12/7/2006	10	20%	1/8/2008
2/5	50	10/19/2006	12/7/2006	17	34%	1/8/2008
3/1 [1]	23	2/9/2009	2/27/2009	17	74%	5/15/2009
3/2 [1]	23	2/9/2009	2/27/2009	17	74%	5/15/2009
3/3 [1]	23	2/9/2009	2/27/2009	9	39%	5/15/2009
4/1 [1]	40	6/19/2009	7/6/2009	18	45%	10/24/2009
4/2 [1]	40	6/19/2009	7/13/2009	13	33%	10/24/2009
4/3 [1]	40	6/19/2009	7/6/2009	13	33%	10/24/2009

[1] Seeds soaked in warm water for six hours.

[2] No data, date of first germination not recorded.

APPENDIX II

Rainfall Data at Selected Stations in HAVO from 2003 to 2009 (HAVO Fire Cache, unpublished data)

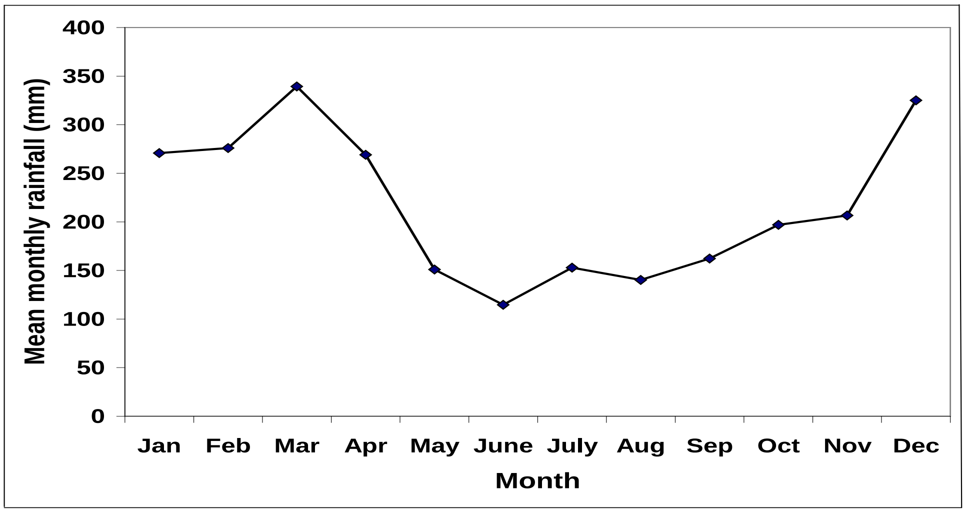

Figure 1. Mean monthly rainfall at Hawai`i Volcanoes National Park Headquarters, 2003–2009.

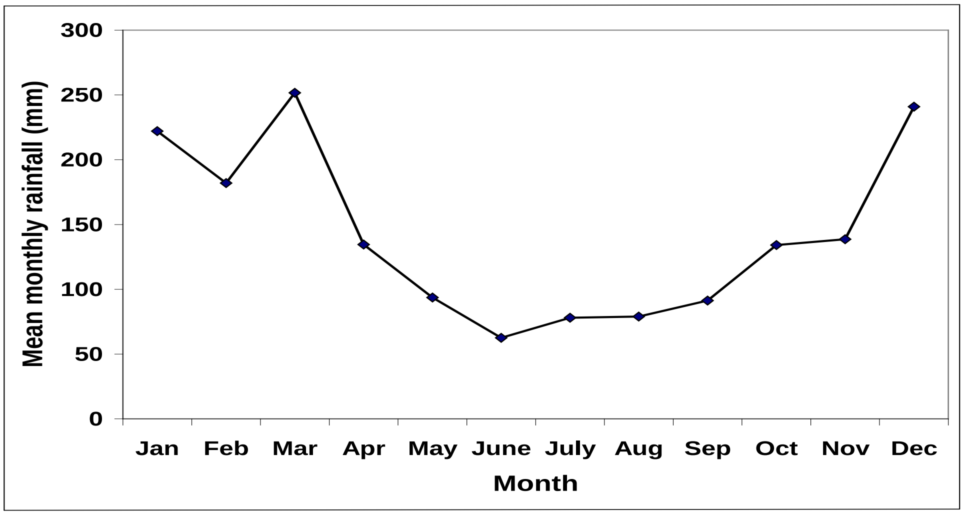

Figure 2. Mean monthly rainfall at Hawaiian Volcano Observatory - Uwēkahuna, 2003–2009.

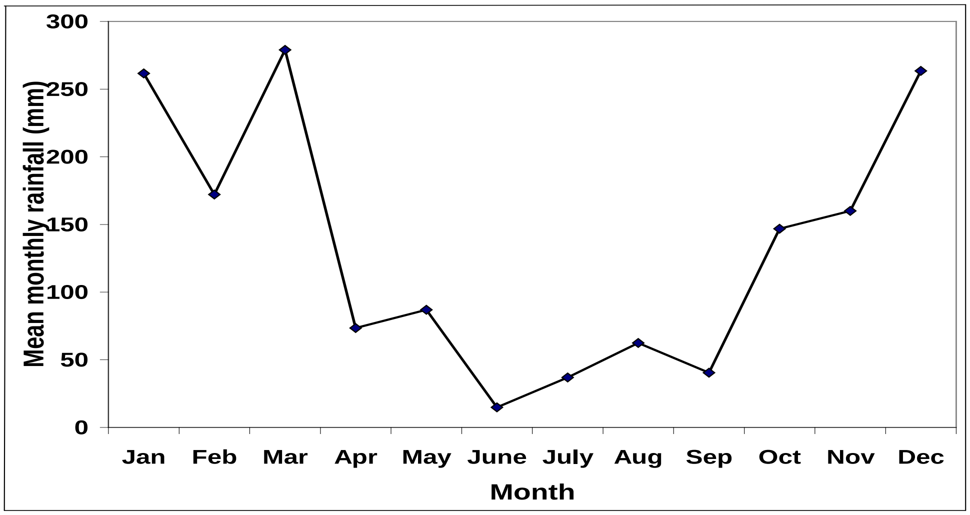

Figure 3. Mean monthly rainfall at Kīpuka Nēnē, 2003–2009.

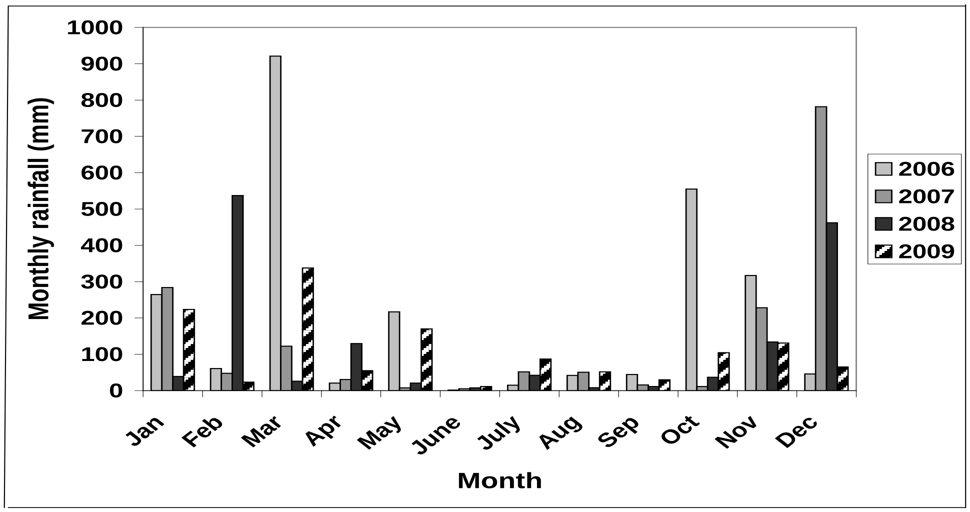

Figure 4. Monthly rainfall totals at Kīpuka Nēnē, 2006–2009.