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STATUS AND LIMITING FACTORS OF TWO RARE PLANT SPECIES IN MONTANE DRY COMMUNITIES OF HAWAI`I VOLCANOES NATIONAL PARK

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ABSTRACT

Two rare plants native to montane dry forests and woodland communities of Hawai`i Volcanoes National Park (HAVO) were studied for more than two years to determine their stand structure, short-term mortality rates, patterns of reproductive phenology, success of fruit production, floral visitor composition, seed germination rates in the greenhouse, and survival of both natural and planted seedlings. *Phyllostegia stachyoides*, a shrubby Hawaiian mint (Lamiaceae) that is a species of concern, was studied within two small kīpuka at a natural population on the park's Mauna Loa Strip, and three plantings at sites along the Mauna Loa Road were also monitored. *Silene hawaiiensis*, a threatened shrub species in the pink family (Caryophyllaceae), was monitored at two natural populations, one on Mauna Loa at the Three Trees Kīpuka and the second on Kīlauea Crater Rim south of Halema`uma`u. *Silene hawaiiensis* plantings were also made inside and outside ungulate exclosures at the park's Kahuku Unit.

Phyllostegia stachyoides appeared to have a relatively stable natural population in HAVO with approximately 19% adult plant mortality over three years and recruitment of natural seedlings. Despite high mortality (~98%), some seedlings persisted for more than a year, and recruitment of new plants into the population exceeded the losses of adult plants. Flowering and fruiting phenology was annual and seasonal with peak appearance of buds and flowers in spring and greatest abundance of mature fruit in the summer and fall. Successful production of green fruit from buds and flowers was very high (45%), and green fruit transitioned to mature fruit at a rate of 17.8%. Five insect species were observed visiting flowers, and those with the greatest visitation rates were the alien hover fly *Allograpta obliqua* (Syrphidae) and the endemic yellow-faced bee *Hylaeus difficilis* (Colletidae). Both insect species were shown to be carrying pollen of *P. stachyoides*. Seed germination rates in the greenhouse were variable but ranged as high as 80.4%. Mortality of seedlings planted at three sites along the Mauna Loa Road was very high (~90%) within 2–3 years of planting. There was no significant difference in the mortality or growth of seedlings planted in areas with little grass compared to those in adjacent areas with high grass cover.

Silene hawaiiensis had a stable population structure at the Mauna Loa study area, but its population structure at the Kīlauea study site was flat to declining. Mortality of adult plants was low on Mauna Loa (6.5%), but was greater than 30% at the Kīlauea Crater Rim site. Among regularly monitored plants at the Kīlauea site, losses were observed in all size classes between 2006 and 2008. Natural seedling recruitment was observed in stand structure plots at both sites between 2006 and 2007, but numbers of seedlings were low and did not compensate for losses of adult plants. Reproductive phenology was annual with buds and flowers observed in summer and fall, and fruit formed in the fall and winter. The production of immature fruit capsules from buds and flowers was high (51.2%) and tagged immature fruit became mature fruit at a high rate of 66.7%. Floral visitation rates were very low in timed observations and only three insect species were identified visiting *S. hawaiiensis* flowers: native yellow-faced bees *Hylaeus difficilis* and *H. volcanicus*, and the alien hover fly *Allograpta exotica*. A seed dispersal experiment at the Kīlauea Crater Rim site demonstrated that wind dispersed seeds could travel at least 40 m from *S. hawaiiensis* plants with mature open capsules. Seed germination rates varied from 7.0 to 73.0% in greenhouse trials. Mortality of planted seedlings at Kahuku was not significantly greater outside ungulate exclosures than inside, but growth in height and production of reproductive structures was significantly greater in protected areas inside exclosures. In the current study, the seedling stage was the most vulnerable part of the life cycle for both *P.*

stachyoides and *S. hawaiiensis*, and low seedling recruitment appeared to be the most important limiting factor for these species.

INTRODUCTION

Hawai`i Volcanoes National Park (HAVO) has a flora of more than 1,000 species, with more than 400 native taxa (Higashino *et al.* 1988, Benitez *et al.* 2008). Among these park natives are 25 listed endangered species, 1 threatened species, 5 candidate threatened or endangered, and 28 species of concern (U.S. Fish and Wildlife Service 2009, Pratt *et al.* 2011). While most of the endangered and rare plants of HAVO inhabit rain forests or mesic forests, a few are restricted to dry montane habitats of the park. Two of these rare inhabitants of dry montane communities were selected for a limiting factors study, because they had accessible, previously documented populations of at least 50 to several thousand individuals growing within Special Ecological Areas (SEAs). The montane section of the Mauna Loa Strip that supports populations of both *Phyllostegia stachyoides* and *Silene hawaiiensis* is a unit of the Mauna Loa SEA; it is fenced to exclude feral ungulates and has few invasive alien plants (Tunison and Stone 1992). Feral pigs (*Sus scrofa*) and goats (*Capra hircus*) were removed from the Mauna Loa SEA in the 1980s (Katahira *et al.* 1993), and an incipient invasion of mouflon sheep (*Ovis gmelini* subsp. *musimon*) was repelled in the early 2000s (H. Hoshide, pers. comm.). The upper Ka`ū Desert near the Kīlauea Crater Rim south of Halema`uma`u Crater contains a second population of *Silene hawaiiensis* and is included within a buffer zone between other SEAs, where it is protected from feral ungulates by boundary and internal fences (Benitez *et al.* 2012).

Phyllostegia stachyoides, a *Stachys*-like Hawaiian mint with no common name (Family Lamiaceae), is endemic to the islands of Hawai`i, Maui, and Moloka`i, where it has been collected at elevations of 880–1,400 m (Wagner *et al.* 1999). On Hawai`i Island, the mint is known from North and South Kona districts but has also been collected at Kīpuka Puauulu, HAVO, in Ka`ū District (Bishop Museum *Herbarium Pacificum* n.d.). This early collection from Ka`ū was mistakenly reported from Hualālai by Sherff (1935). *Phyllostegia stachyoides* disappeared from Kīpuka Puauulu, probably before the creation of the national park in 1916. In 1987 and 1991, the mint was observed and collected during forest bird surveys on the western side of the Mauna Loa Strip near 1,830 m elevation, although specimens were originally misidentified as *P. racemosa* (Belfield and Pratt 2002). Plants could not be subsequently relocated at the forest bird survey site, but in 2004, *P. stachyoides* plants were found in five small kīpuka on the western side of the Mauna Loa Strip just east of the boundary with Kapāpala Ranch. Recently (in 2011), *P. stachyoides* was collected on Keauhou Ranch just east of HAVO (A. Christie, pers. comm.). Plantings of *P. stachyoides* have been made at four sites along the Mauna Loa Road in areas with vegetation similar to that of the natural populations (Belfield *et al.* 2011).

Phyllostegia stachyoides is currently considered a species of concern (U.S. Fish and Wildlife Service 2008), and the species was previously listed as of uncertain status without enough information to determine if it warranted endangered status (Fosberg and Herbst 1975). This mint is an erect low shrub with multiple stems, rough ovate leaves covered with stiff hairs, and complex multi-branched terminal inflorescences of small white tubular flowers. A detailed description of the flowers and inflorescences is found in Appendix I. Like other members of the genus, the mint has fleshy four-parted fruits, which are shiny black when mature with a single small seed in each section (Wagner *et al.* 1999).

Silene hawaiiensis or Hawaiian catchfly, a shrub in the Pink Family (Caryophyllaceae), is endemic to the island of Hawai`i, where it is restricted to dry areas on lava and ash substrates of Kīlauea, Mauna Loa, Hualālai, and Mauna Kea at elevations of 900–3,050 m (Wagner *et al.* 1999). In HAVO, *S. hawaiiensis* is known primarily from two populations: on prehistoric lava flows of the Mauna Loa Strip between 1,525 and 2,130 m elevation, occasionally at higher elevation; and on ash and cinder substrates of Kīlauea between the summit caldera at 1,240 m elevation and the lower reaches of the Ka`ū Desert near 900 m elevation. The dry habitats that support scattered individuals of this rare shrub typically have sparse vegetation. *Silene hawaiiensis* is listed as a threatened species and is thought to occur in at least 11 populations on Hawai`i Island with a total of more than 11,000 plants (U.S. Fish and Wildlife Service 1996). Although more than 5,000 plants have been counted within HAVO, the species is vulnerable to browsing damage and death caused by mouflon sheep (Belfield and Pratt 2002). The species was previously known as *S. struthioides* var. *gracilis* (Sherff 1946). In a study of Hawaiian *Silene* species, *S. hawaiiensis* was shown to differ genetically from *S. struthioides* (Westerbergh and Saura 1994), a related species from subalpine and alpine regions of Hawai`i and Maui (Wagner *et al.* 1999).

Silene hawaiiensis is a sprawling to upright shrub, sometimes >1 m tall, with linear, curved leaves covered in sticky hairs. The shrub has an enlarged, swollen taproot. Flowers are borne in inflorescences at the ends of branches, and individual flowers have five white petals with a tubular dull maroon base. A detailed description of the flowers is found in Appendix I. Fruits are dry urn-shaped capsules, straw-colored when mature, with many tiny seeds (Wagner *et al.* 1999).

The objectives of this study were to 1) determine population size, stand structure, growth, and mortality rates for two rare plant species of dry montane vegetation communities of the Mauna Loa Strip and Ka`ū Desert near Halema`uma`u Crater in HAVO and to evaluate the success of plantings of both species; 2) measure flower and fruit production through monthly or bimonthly monitoring of phenology; 3) identify potential pollinators and quantify floral visitation rates; 4) determine the success of seedling recruitment by quantifying seed germination rates and following natural seedling establishment; 5) evaluate the role of grasses in the survival of plantings of *Phyllostegia stachyoides*; and 6) compare mortality and growth of planted *Silene hawaiiensis* inside and outside ungulate exclosures.

METHODS

Study Area

Kīpuka of the Western Mauna Loa Strip

Five small kīpuka of the HAVO Mauna Loa Strip were found to contain individuals of *Phyllostegia stachyoides* in 2004 (Figure 1). These kīpuka were west of the edge of Kīpuka Mauna`iu and east of the boundary with Kapāpala Ranch and were surrounded by `a`ā lava. The uppermost kīpuka near 1,830 m elevation was the site of the original discovery of the species in HAVO in 1987 (Belfield and Pratt 2002). Because of logistical difficulties reaching plants on a monthly schedule, only two of the lower three kīpuka were monitored in the current study. The lowest kīpuka (designated kīpuka 4) was near the park boundary at 1,620 m elevation and the next highest kīpuka (kīpuka 5) was approximately 100 m northwest of kīpuka 4 at 1,630 m elevation; this small forest patch had only three *P. stachyoides* plants and was not regularly visited. The

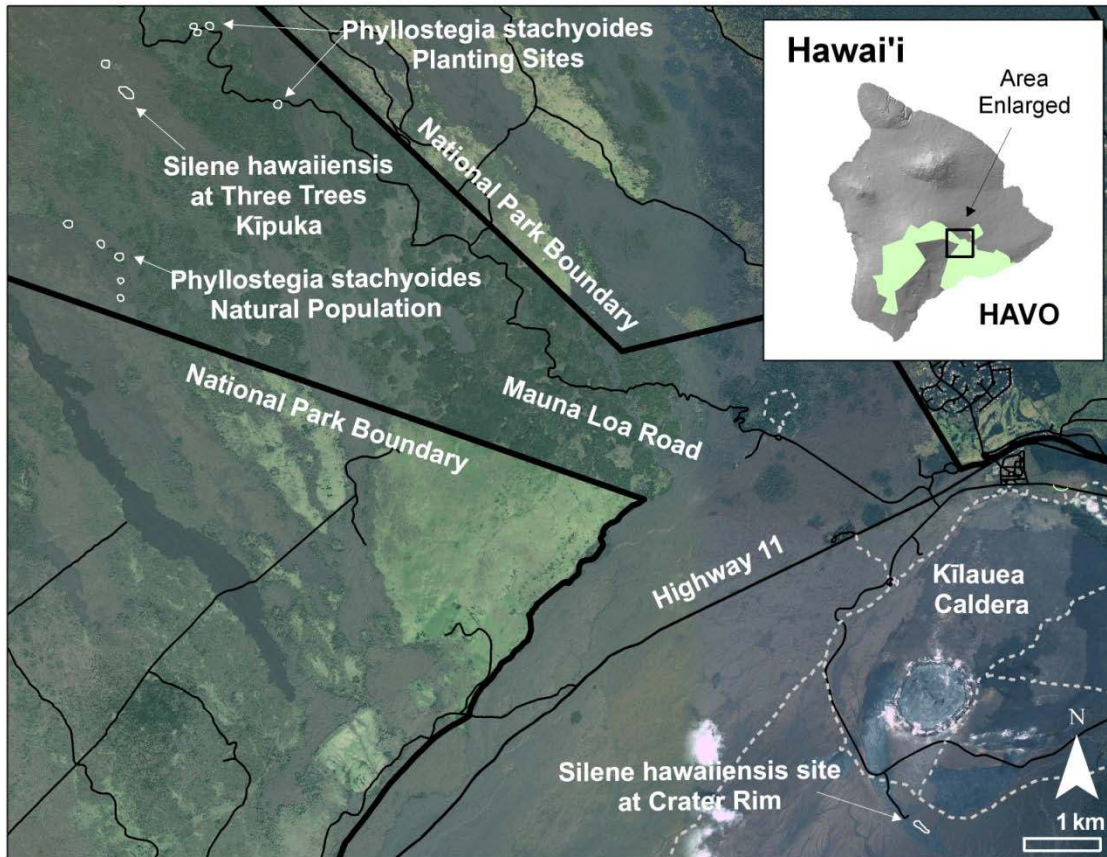


Figure 1. Location of the natural populations and planting sites of *Phyllostegia stachyoides* and two natural populations of *Silene hawaiiensis* at Hawai`i Volcanoes National Park (HAVO).

third kīpuka studied (kīpuka 3) was 700 m northwest of kīpuka 4 at 1,630 m elevation. Vegetation of the small kīpuka studied was open *Acacia koa* (koa) and *Sophora chrysophylla* (māmane) with an understory of *Dodonaea viscosa* (‘a‘ali‘i) trees and scattered tall individuals of *Myoporum sandwicense* (naio), *Myrsine lessertiana* (kōlea lau nui), and *Santalum paniculatum* (‘iliahi or sandalwood). Ground cover of the kīpuka forests was a mix of native grasses (*Panicum tenuifolium*, *Deschampsia nubigena*), alien grasses (*Ehrharta stipoides* or meadow ricegrass), native sedges (*Carex wahuensis*), and alien shrubs. The alien shrubs *Physalis peruviana* (poha) and *Bidens pilosa* (beggar’s tick) were prominent in the understory of kīpuka 4.

The lava substrates of the small forested kīpuka that supported *Phyllostegia stachyoides* were relatively old, dated in the range of 1,500 to 3,000 or 4,000 years bp (before present; Lockwood *et al.* 1988, Trusdell *et al.* 2005). Soils of the kīpuka were shallow, discontinuous ash soils. Lava surrounding the small kīpuka were ‘a‘ā flows of the early historic and late prehistoric period (100–750 years old). This area of Mauna Loa has a summer-dry climate with an annual mean temperature of approximately 14°C (Doty and Mueller-Dombois 1966). Mean annual rainfall is in the 1,000–1,500 mm range (Giambelluca *et al.* 1986).

The entire Mauna Loa Strip (below 3,000 m elevation) is managed as a SEA and is fenced against feral animals (Tunison and Stone 1992). Previously, this section of the park was used to graze domestic cattle (*Bos taurus*), but they were removed in 1948 (Apple 1954). Feral pigs and goats were removed from the SEA in the 1980s (Katahira *et al.* 1993), and mouflon sheep are not currently resident within the fenced portions of the Mauna Loa Strip. The SEA is, for the most part, free of highly invasive alien plants (Tunison and Stone 1992); *Verbascum thapsus* (common mullein) is perhaps the most serious threat to the dry montane and subalpine communities of the SEA (Loh *et al.* 2000).

Planting Sites on Mauna Loa Road

Four sites accessible along the Mauna Loa Road were selected for plantings of *Phyllostegia stachyoides* (Belfield *et al.* 2011). The first site (site 1) was just south of the road at 1,845 m elevation, and sites 2 and 3 were across the road at the same elevation (Figure 1). The fourth site selected for planting was south of the Mauna Loa Road at 1,720 m elevation upslope from the road crossing of a lobe of the Ke`āmoku Lava Flow. Vegetation at all four planting sites was closed *Acacia koa* forest with a dense understory of *Dodonaea viscosa* trees and scattered *Sophora chrysophylla*. Ground cover was relatively sparse and composed of the same mixed native and alien grasses and native sedges found at the natural population. At the fourth site, plantings were split between a shady area beneath koa trees with little ground cover other than leaf litter and an adjacent, more open stand of koa with a denser cover of mixed grasses. Substrates of all four planting sites were old weathered lava flows dated in the range of 1,500 to 3,000 or 4,000 years bp (Lockwood *et al.* 1988, Trusdell *et al.* 2005) with shallow, discontinuous ash soils undesignated by a soil series name (Sato *et al.* 1973). The summer-dry climate and mean rainfall were the same as that of the natural populations of *P. stachyoides* to the west.

Three Trees Kīpuka on Mauna Loa

A natural population of *Silene hawaiiensis* was sampled at two sites near 1,890 m elevation on the Mauna Loa Strip within a sparsely vegetated kīpuka of old pāhoehoe lava surrounded by more recent `a`ā flows; the kīpuka is locally known as the Three Trees Kīpuka because of the presence of three large *Metrosideros polymorpha* trees along a partially collapsed lava tube (Figures 1 and 2). The two sites that supported *S. hawaiiensis* were the area adjacent to the large lava tube (Three Trees Kīpuka proper) and a similar area along a lava flow channel, approximately 300 m south and downslope of the lava tube; the lower site was fenced about 10 years ago against mouflon sheep with strands of razor wire. Vegetation of the Three Trees Kīpuka was very scattered *Metrosideros polymorpha* trees and native shrubs, such as *Leptecophylla tameiameia* (pūkiawe), *Vaccinium reticulatum* (`ōhelo), *Dubautia ciliolata* (kūpaoa), and *Coprosma ernodeoides* (kūkae nēnē). Mixed native and alien grasses, a few alien forbs, and native ferns composed the very sparse ground cover of the sites. Lava substrates of the Three Trees Kīpuka are in the age range of 750–1,500 years bp (Lockwood *et al.* 1988, Trusdell *et al.* 2005), with the pāhoehoe of the kīpuka appearing to be older than the surrounding `a`ā flows. No soil development was noted within the kīpuka or downslope flow channel. Climate and rainfall of the Three Trees Kīpuka were the same as for the previously described sites that supported *P. stachyoides*.

Ka`ū Desert and Crater Rim South of Halema`uma`u

A second natural population of *Silene hawaiiensis* was sampled in the upper Ka`ū Desert near the summit of Kīlauea Volcano at a site on the caldera rim south of Halema`uma`u (Figures 1 and 2). The site chosen for intensive monitoring was an area approximately 100 x 200 m in size

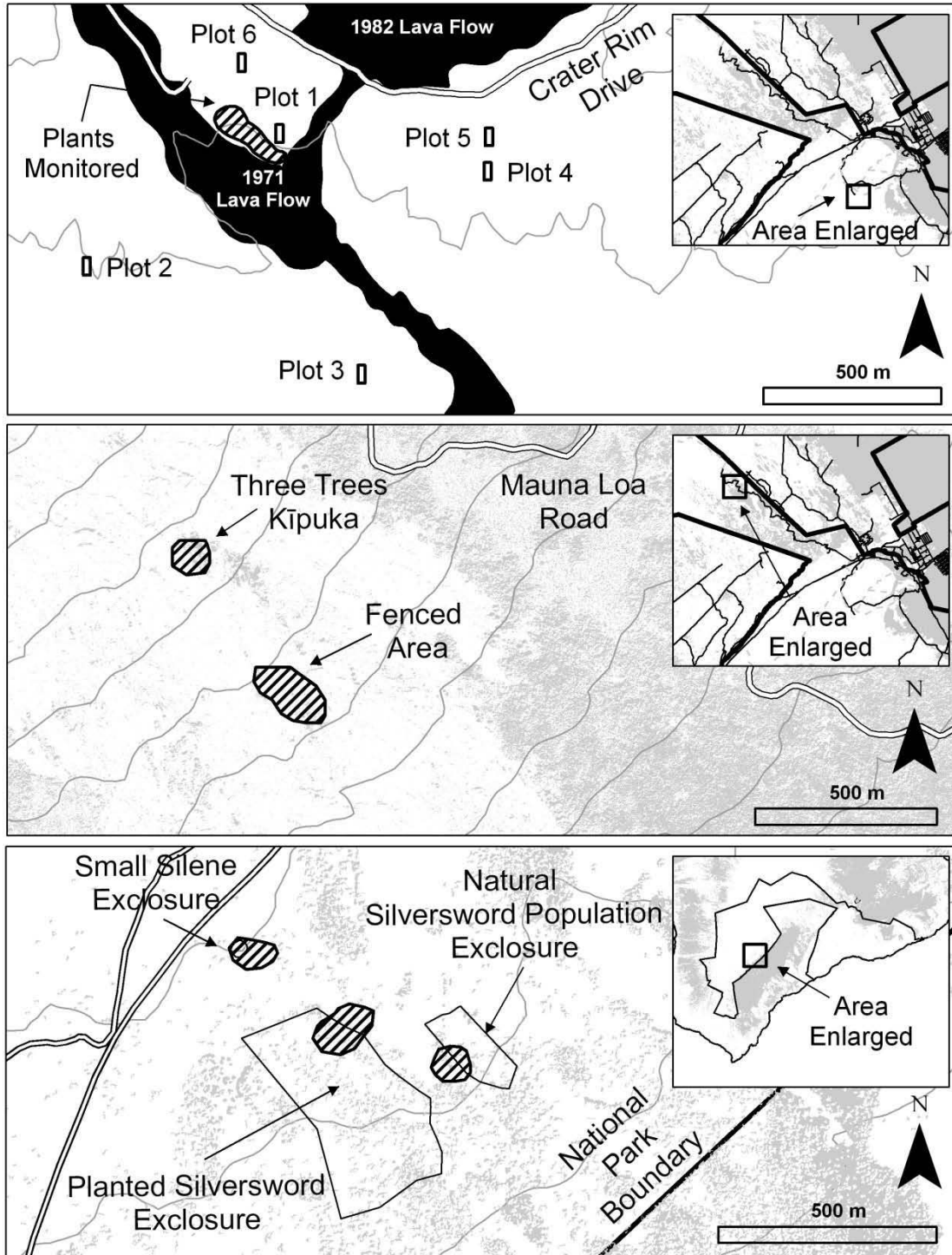


Figure 2. Study sites at two natural populations (top and middle) of *Silene hawaiiensis* in HAVO and planting sites (bottom) near silversword exclosures at Kahuku Unit.

adjacent to the 1971 lava flow; this site was previously known to have a dense population of *S. hawaiiensis* (L. Pratt, pers. obs.). A larger area of 1 x 2 km was circumscribed, centered on the

intensive monitoring area; in this section of the Ka`ū Desert, six points were randomly selected for establishing *S. hawaiiensis* stand structure plots. The vegetation of the Ka`ū Desert and Crater Rim study site was very sparse, scattered native shrubs and ferns with almost no grasses. Predominant shrubs were *Vaccinium reticulatum*, *Leptecophylla tameiameiae*, *Dubautia ciliolata*, *Coprosma ernodeoides*, and *S. hawaiiensis*. The endemic fern *Sadleria cyatheoides* (‘ama`ū) was frequently encountered along the edges of eroded gullies at the site.

The young substrates of the crater rim/Ka`ū Desert study area comprises ash, pumice, and blocks of lava dating from the explosive Kīlauea eruption of 1790 (Holcomb 1987, Trusdell *et al.* 2005). Although the Ka`ū Desert is one of four rainfall minima on Hawai`i Island, the study area south of Halema`uma`u Crater receives 1,296 mm mean annual rainfall with winter months much wetter than summer months (Giambelluca *et al.* 1986). The area typically experiences drought between June and September (Doty and Mueller-Dombois 1966). The study area of the upper Ka`ū Desert and Crater Rim is within a buffer zone between Ke`āmoku and Keanakāko`i SEAs and receives the same level of management as the SEAs. Although not specifically fenced, the area is protected by boundary and internal wing fences and is considered to have a very low level of feral ungulates (H. Hoshide, pers. comm.).

Kahuku Unit Planting Sites

Plantings of *Silene hawaiiensis* were made inside and outside two existing exclosures that HAVO staff built to protect a natural population and plantings of *Argyroxiphium kauense* (Ka`ū or Mauna Loa silversword) at the Kahuku Unit of HAVO; a third small temporary exclosure composed of a circle of fencing material was placed just northwest of the existing exclosures (Figure 2). *Silene hawaiiensis* occurs naturally very rarely at Kahuku (Benitez *et al.* 2008); plantings of seedlings from germination trials in the current study allowed us to evaluate the impact of mouflon sheep on young *S. hawaiiensis*, while potentially boosting the numbers of the rare shrub at Kahuku. The silversword exclosures were on the eastern side of Kahuku near 1,850 m elevation between a jeep road and the boundary of the park with the Ka`ū Forest Reserve. Vegetation of this area was an open woodland of low-stature *Metrosideros polymorpha* trees with an understory of native shrubs, particularly *Leptecophylla tameiameiae*, *Vaccinium reticulatum*, and *Coprosma ernodeoides*. Native sedges and ferns and mixed native and alien pasture grasses made up the sparse ground cover. Substrates of this area of Kahuku were very old weathered lava and have been dated at >4,000 years bp (Lockwood *et al.* 1988) and alternatively at 1,000–3,000 years bp (Trusdell *et al.* 2005). The lava substrates were covered by shallow soils derived from ash and weathering (Sato *et al.* 1973). Climate of the eastern slope of Kahuku is strongly influenced by the northeast tradewinds, and the area has dry summers (Benitez *et al.* 2008). The mean annual rainfall falls between 1,000 and 1,500 mm (Giambelluca *et al.* 1986). While domestic cattle have been removed from Kahuku Unit, a former cattle ranch, the planting sites are in an area that continues to support populations of mouflon sheep (Hess *et al.* 2006) as well as feral pigs.

Sampling Methods

Plant Growth and Mortality at Natural Populations

In May 2005, *Phyllostegia stachyoides* plants were counted and marked with a unique number within four of five kīpuka known to support the species in HAVO (Figure 1). Plants selected for intensive monitoring were those in the lowermost kīpuka 3 and 4 (kīpuka 5 had only three plants and was not regularly monitored). All plants in kīpuka 3 (12) and 17 of the 29 plants in kīpuka 4 (randomly selected) were visited at six-month intervals in 2006 and at one-to-two-

month intervals from February 2007 to July 2008. Heights of the tallest stem were measured (to the nearest cm) and plant condition was evaluated at each monitoring period. Final mortality was evaluated for all plants at both kīpuka 3 and 4 in July 2008.

Two natural populations of *Silene hawaiiensis* were monitored; one on Mauna Loa and one on Kīlauea. All plants in a previously known group at the Three Trees Kīpuka on Mauna Loa (Belfield and Pratt 2002) were monitored, as were a randomly selected group of plants in the flow channel approximately 300 m downslope of the kīpuka. The lower plants had been protected from periodic ingress of mouflon sheep in 1997–2000 by a circle of temporary fencing installed by the HAVO Natural Resources Management Division. A total of 200 *S. hawaiiensis* were tagged with unique numbers, measured for height, and evaluated for condition in March 2006 and were re-monitored at bimonthly intervals until February 2008. In 2008, we included in the final monitoring an additional 50 tagged plants at the flow channel site and compared the size and mortality of all 250 plants with data from the same plants collected in a previous monitoring project in 2000.

A second natural population of *S. hawaiiensis* was monitored in the cinder fields of Kīlauea Crater Rim south of Halema`uma`u, an area previously known to support a dense population of the threatened plant. All plants (200) were located within a randomly chosen large plot (50 x 250 m) directly adjacent to the 1971 lava flow with the long side of the plot at 120° azimuth magnetic. Plants were marked with numbered tags. A randomly selected subset of 50 plants was revisited at monthly or bimonthly intervals from May 2006 through February 2008 (no data were collected in July and September 2007). At each monitoring interval the height or length (of tallest or longest stem) was measured and plant condition evaluated; growth and mortality were summarized at the end of the study.

Stand Structure of Silene hawaiiensis

In order to evaluate the stand structure of a larger portion of the natural population of *Silene hawaiiensis* beyond the subset of plants selected for regular monitoring, we established stand structure plots 20 x 50 m in size at both the Mauna Loa and Kīlauea Crater Rim populations. At the Mauna Loa Three Trees Kīpuka and nearby flow channel site, three plots were placed at randomly selected points in the confined area of the kīpuka and flow channel that supported *Silene* plants. Plots were oriented with the long (50 m) side at 310–130° magnetic azimuth, which was the direction in which the topography sloped naturally. In 2006, all plants within the plots were marked with a numbered metal tag, measured for height, and evaluated for vigor (good, fair, poor) based on the plant's color, leaf cover, and number of dead branches. Plots were revisited a year later in 2007, and all plants were relocated and re-measured. Tagged dead plants were recorded, and small plants without tags were counted as seedling recruitment.

At the Kīlauea Crater Rim site south of Halema`uma`u, an area 1 km (north-south) by 2 km (east-west) centered on the monitored *S. hawaiiensis* population was delineated on a map. Random points were selected within the 1 x 2 km area, and we navigated to six of these points using a global positioning system (GPS) device. Plots 20 x 50 m in size were established at the random points, with the point representing the center of the short (20 m) line of the plot on the north side. Each plot was oriented at 335–155° azimuth magnetic. Plots were established whether or not *S. hawaiiensis* was present. All *S. hawaiiensis* plants within each plot were marked with a metal tag, measured for height or length (for decumbent [reclining with an ascending tip] plants), and evaluated for vigor. A year later in 2007, all six plots were revisited,

and plants were recounted and re-measured. Dead plants were recorded, and young untagged plants were considered to be new seedlings recruited.

Growth and Mortality of Plantings

Plantings of *Phyllostegia stachyoides* were made at four sites along the Mauna Loa Road at elevations similar to those of the natural populations to the west. Site 1 was planted with a mix of seedlings and cuttings in 2005 and 2006 (25 total) by Natural Resources Management Division personnel prior to the beginning of the current study (Belfield *et al.* 2011). We observed this planting starting in 2007 and report only mortality rates. As part of the current rare plant limiting factors study, sites 2 and 3 were each planted with 25 seedlings in January 2007. The lower site 4 was planted with 83 seedlings in May 2007; 43 were in a nearly grass-free area beneath *Acacia koa* (koa) trees, and 40 were in an adjacent sunny area with grasses in an open koa grove. All seedlings were watered once after planting. Heights of seedlings were measured (to the nearest cm) at planting and at monthly or bimonthly intervals for 14–17 months. At each monitoring, the condition of seedlings was noted. Plantings were revisited 1 and 1.5 years after monthly monitoring ceased to evaluate mortality.

Plantings of *Silene hawaiiensis* were made inside and outside three ungulate exclosures at the HAVO Kahuku Unit, in a region where the species had been previously observed (Figure 2). Two of the exclosures were existing protected areas in which silverswords, *Argyroxiphium kauense*, had been planted. The third exclosure was a small ring of tall (1.8 m or 6 ft) fencing material staked to the ground. Exclosures protected the plants inside from browsing by mouflon sheep and other feral ungulates. An equal number of *S. hawaiiensis* seedlings (8) were planted both inside and immediately outside of all three exclosures in November 2006, and a second planting of three seedlings was made at each of the same sites in May 2007. Heights were measured at planting and at 3–6 month intervals for 1.5 years (1 year for the second planting). Plants were revisited May 2009 to determine final mortality. At each monitoring period plant condition and browse damage were noted.

Ground Cover at the Population and Planting Sites of Phyllostegia stachyoides

Ground cover at the natural population of *P. stachyoides* at kīpuka 4 was sampled with five point-intercept transects each 10-m long and centered on a randomly selected *P. stachyoides* plant. The point-intercept frame was 1-m wide and tall and had five points per meter (Mueller-Dombois and Ellenberg 1974). The number of points hit was recorded for each plant species, as well as for bare soil, rock, and litter (dead and detached leaves and woody debris). The points struck for each species were divided by the total points to determine percentage cover. The results from all five transects were pooled for the kīpuka. At planting sites 2 and 3 on the Mauna Loa Road, a baseline was established in a north-south direction in the center of the planting and three point-intercept transects were placed at randomly selected points on the baseline. Each transect was 10-m long and ran perpendicular to the baseline. At planting site 4, a north-south baseline was established through the center of the grass-free and adjacent grassy planting sites. At each treatment, three point-intercept transects, each 20-m long, were placed perpendicular to the baseline at randomly selected points. Cover data were collected with the point-intercept frame in the same manner as was done at the kīpuka 4 natural population.

Reproductive Phenology

Reproductive phenology of *Phyllostegia stachyoides* was monitored at two kīpuka supporting natural populations, as well as at planting sites 2, 3, and 4 along the Mauna Loa Road.

Monitoring was monthly during the spring and summer months and bimonthly at the end of the fruiting season in the fall through the winter. At the natural population, data were collected between March 2006 and July 2008, while at the planting sites phenology monitoring was limited to the period between May 2007 and July 2008, with a final visit in June 2009. Sampled plants were all plants (13) at the natural population in kīpuka 3, a randomly selected subset of 17 plants at kīpuka 4, and all plants at the three monitored planting sites on Mauna Loa Road. At each monitoring interval, the number of inflorescences on each sampled plant bearing buds, flowers, immature green fruit, or mature fruit were counted and the total number of inflorescences per plant were also counted.

Reproductive phenology of *Silene hawaiiensis* was monitored at both natural populations studied. At the Three Trees Kīpuka on Mauna Loa, data were collected monthly from July through September 2006, after which monitoring was bimonthly until February 2008 with a gap of no data for September 2007. A random subset of 53 plants was selected from the total monitored population of 250. At each monitoring interval on each sampled plant, the number of buds, flowers, immature green fruit, mature fruit, and old dry capsules was estimated in 4 categories: 1–10, 11–50, 51–100, and >100 structures. At the Kīlauea site, on the crater rim south of Halema`u`ma`u, phenology monitoring was monthly from May 2006 through February 2008 with a gap in data collection in July and September 2007. Phenology data were collected on 50 plants randomly selected from the population of 200 within the designated study area, 250-m long by 50-m wide. For each sampled plant, the number of buds, flowers, immature fruit, mature fruit, and old dry capsules was estimated in the same categories used at the Mauna Loa population. At the planting sites inside and outside ungulate exclosures at Kahuku, systematic phenology monitoring was not done, but the presence of any reproductive structures (buds, flowers, fruit) was noted at each of the six-month monitoring intervals.

Success of Fruit Production

To determine the rate of successful transition of *Phyllostegia stachyoides* buds and flowers to fruit, a sample of inflorescences was randomly selected on 15–20 plants in each of the months between March and May 2008. An additional five plants were sampled at the end of the flowering season in June. Plants sampled were a mix of natural plants at the kīpuka 4 site and planted individuals at planting sites 2 and 3. Each plant had a single inflorescence sampled (for a total of 55 throughout the study). On each sampled inflorescence, the lowermost whorl with buds and developing flowers was selected and marked with a numbered paper twist tie. The number of buds and flowers was counted on the whorl at the first visit, and the same whorl was monitored at monthly intervals for three to five months. The transition from bud and flower to immature green fruit was recorded first, and monitoring continued until mature fruits formed, dispersal occurred, or the structures aborted or otherwise disappeared. Dispersed fruits leaving behind empty, reflexed calyx lobes were considered successful transitions to mature fruit.

For *Silene hawaiiensis*, success of fruit production was studied only at the Kīlauea Crater Rim population south of Halema`u`ma`u. In July 2007, 30 buds and 30 flowers were tagged on 22 randomly selected plants. Tags were numbered paper twist ties light enough to mark the bud or flower on the inflorescence without damaging it. Buds and flowers were revisited three times at two- to three-day intervals, and a final monitoring visit was made a month after tagging. At each monitoring visit, the state of development of each tagged structure was recorded (flower, green fruit, mature fruit, dry capsule). Successful transitions of buds to flower and flower to green fruit were summarized in July, and the successful transition of green fruit to either mature fruit or dry capsules was detected in the final visit in August. Data on flower and fruit

production were presented as the proportion of the total number of tagged buds that produced flowers, the percentage of the total number of buds and flowers together that produced green fruit, and the percentage of green fruit that continued to develop and formed mature or dry capsules. The number of seeds within each of 22 randomly selected, dry, unopened capsules was counted and the mean number of seeds/capsule was calculated.

Pollination

Floral visitor observations. Composition of the floral visitor community and the rates of visitation were quantified by observing insect activity at flowers of *Phyllostegia stachyoides* at both the natural population and at three of the planting sites. Flowers were observed for 10-minute periods between 0900 and 1500 on dry days with sunny weather and light to moderate wind speeds. Observations were made in 2008 on 12 March, 14 March, 31 March, 2 April, 7 April, and 9 May, totaling 9.7 hours of observation. Flowers were observed at a close range (one meter) through close-focusing 8.5 x 21 Pentax Papilio binoculars.

Composition of the floral visitor community and the rates of visitation at the *Silene hawaiiensis* population of the Kilauea Crater Rim were quantified by monitoring insect activity at adjacent flowers using digital video cameras (Super Circuits PC219ZWPH) mounted on tripods. The video was recorded onto a digital video recorder (Lorex DXR4280UQA) at a rate of two frames per second to conserve memory space on the hard drive of the recorder. The entire unit was powered by 12-volt deep cycle marine batteries. Recordings were conducted on 2–12 *S. hawaiiensis* flowers continuously throughout the day and into the night over five days (9–13 July 2007), totaling 70.15 hours of observation. Observations were made on dry days with moderate wind speeds.

For each floral visitor to both species, the following data were recorded: identity of the visitor to the lowest possible taxonomic level allowed by the observation or video recording; 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 at the study sites to facilitate identifications during the timed observations. For both plant species, mean visitation rate for each visitor species was calculated as the total number of flowers visited per total number of flowers observed per hour. Mean visit duration was calculated as the total time spent visiting a flower and averaged across individual visits.

Pollen transport. To examine the extent to which floral visitors of *P. stachyoides* were capable of transporting pollen, insects observed foraging on flowers at the natural population during June 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 mm³ 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.

Natural Seedlings

Natural seedlings of *Phyllostegia stachyoides* were observed at monitored plants in kīpuka 4. When they appeared, seedlings had their height measured and they were marked with a numbered plastic pot marker. At each subsequent monitoring period, seedlings were relocated to determine mortality, and the heights of living seedlings were measured. At a few plants, seedlings were too numerous to mark with tags, and the area supporting seedlings was delineated with flagging tape and all seedlings were counted and measured. For *Silene hawaiiensis*, the presence of natural seedlings was detected during the one-year remonitoring of stand structure plots at both Mauna Loa and Kīlauea Crater Rim, Halema`uma`u, sites.

Seeds and Seed Germination

Field seeding in grass and no-grass plots: Field seeding was only carried out for *Phyllostegia stachyoides*. In September 2007, three pairs of plots were established at randomly-selected monitored plants in kīpuka 4. Grass was manually removed from an area 1 m² and the plot was marked with flagsticks at each corner. An adjacent area of the same size was not manipulated and was used as a control. A total of 50 fresh, cleaned seeds was planted in each grass-removal and non-manipulated grassy plot. Plots were visited at monthly or bimonthly intervals, and any seedlings that appeared were marked with a plastic pot tag and measured for height. Field seedling plots were monitored until July 2008 (10 months).

Seed germination in the greenhouse: Seeds of *Phyllostegia stachyoides* and *Silene hawaiiensis* were collected from multiple plants during several summer fruiting seasons throughout the study. Seeds were cleaned of fleshy pulp or removed from the capsules and air dried. Germination trials of *P. stachyoides* generally used fresh seeds, although for two trials seeds were stored in a refrigerator for one to two months until an adequate sample could be collected. Seeds used in *S. hawaiiensis* trials varied from fresh to 10 months old; when not used immediately, air-dried seeds were stored in a refrigerator. No special treatment was given to seeds before sowing. Equal numbers of seeds were planted in three to six replicated pots or flats filled with a potting medium of equal parts vermiculite, perlite, and cinder. The pots sowed with *S. hawaiiensis* were topped with fine sifted cinder to prevent downward movement of the tiny seeds. Germination was carried out in the HAVO Natural Resources Management greenhouse, 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, and counts of seedlings were made weekly. Trials of *P. stachyoides* germination were terminated after 10 to 12 months, and those of *S. hawaiiensis* were finished after 3 to 8 months when germination ceased.

Seed dispersal experiment for Silene hawaiiensis: At the monitored *S. hawaiiensis* population south of Halema`uma`u, a baseline was established along the edge of the 1971 lava flow adjacent to a relatively dense concentration of the plants (Figure 2). Because the prevailing winds are from the northeast, the seed dispersal experiment was set up southwest of the *S. hawaiiensis* population. Five parallel transects were placed on the lava flow at 20-m intervals along the baseline and perpendicular to the edge of the *S. hawaiiensis* population. Transects ran at 220° azimuth (magnetic). In August 2006, during a peak time of mature seed capsule production, blue sticky cards were placed along the transects on the lava at intervals of 1, 5, 10, 20, 30, and 40 m from the edge of the *S. hawaiiensis* population. The corners of the sticky cards were staked to the ground and weighted down with small rocks to prevent their blowing away in the wind. Cards were left in place for one month, after which they were retrieved and brought into the lab for seed counting. All seeds of *S. hawaiiensis* stuck to the cards were

counted, and the mean number of seeds on the five replicates at each of the six distance intervals was determined.

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, and number of germinants, means were compared using two-sample t-tests assuming unequal variance. The chi-square and t-tests were run using the Analysis ToolPak in Excel (Microsoft 2003). With all statistical tests, a probability level of 0.05 or lower was considered significant.

The mean number of *Phyllostegia stachyoides* inflorescences with buds, flowers, or fruit at site 4 on the Mauna Loa Road were compared between plantings in a grassy area and adjacent plantings in an area with low grass cover (called no-grass) using repeated measures analysis of variance (ANOVAR). This was run with SAS® 9.1 using the MIXED procedure (SAS Institute 2002–2003). 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 corrected Akaike information criterion (AICc) values. The results of those comparisons indicated that TOEP was the best fit variance-covariance structure for the data sets. Denominator degrees of freedom were adjusted using the Kenward-Roger adjustment statement.

RESULTS

***Phyllostegia stachyoides*, *Stachys*-like Hawaiian Mint**

Plant Growth and Mortality at Natural Populations

When first found in 2004, individual plants were not counted. When the four lower kīpuka were revisited prior to the beginning of the current project in 2005, there were 29 plants in kīpuka 2, 13 in kīpuka 3, 29 in kīpuka 4, and only 3 in kīpuka 5 (Figure 1). Only plants in kīpuka 3 and the lowermost kīpuka 4 were monitored in 2006–2008. Between February 2006 and July 2008, 8 of the 42 total monitored plants in the two kīpuka died (19.1%). The mortality rate in kīpuka 3 was 15.4% (n = 13) and that of kīpuka 4 was 20.7% (n = 29).

Plants were first measured in May 2005, when the mean height of *P. stachyoides* plants in the two kīpuka was 1.0 m. Growth over 40 months averaged 47.1 cm (\pm 60.2 SD) in kīpuka 3 and 29.1 cm (\pm 34.2 SD) in kīpuka 4. Heights of *P. stachyoides* fluctuated over the monitoring period, with no obvious pattern to declines and increases. The greatest mean heights were observed in winter or spring of the three monitoring years (Figure 3).

Growth and Mortality at Planting Sites

Overall mortality at all four *P. stachyoides* planting sites along the Mauna Loa Road was 89.9% (n = 158). The first planting of 25 mixed seedlings and cuttings was made by T. R. Belfield in June, July, and October 2005 and January 2006 (Belfield *et al.* 2011); only one seedling remained after more than four years, amounting to a mortality rate of 96.0%. Plantings at sites

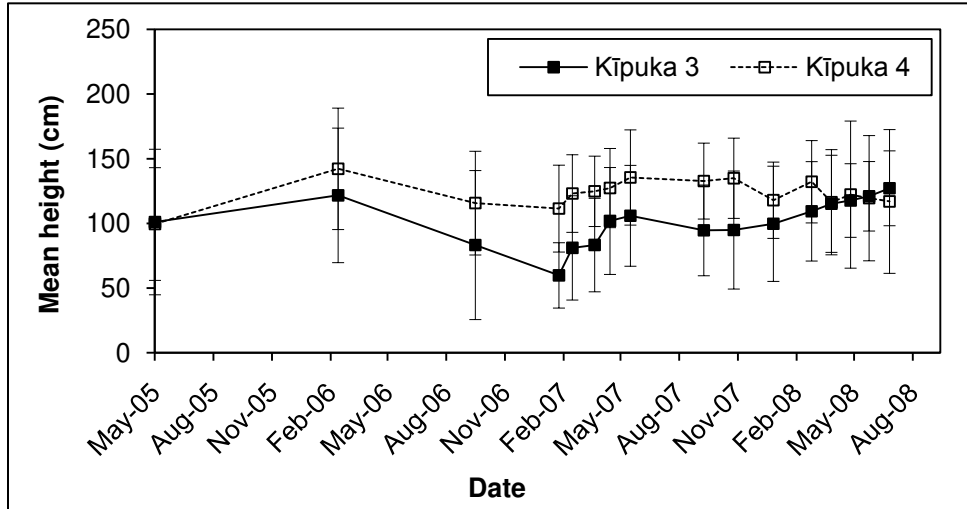


Figure 3. Mean height in cm (\pm SD) of *Phyllostegia stachyoides* in natural populations of two kīpuka in the western Mauna Loa Strip, 2005–2008.

2 and 3 in January 2007, across the road from site 1, were seedlings placed in adjacent areas with heavy grass cover (site 2) and light grass cover (site 3). Mortality of 25 seedlings at site 2 was 84%, and that of 25 plants at site 3 was 92.0% after 38 months (Figure 4). Overall mortality of 83 seedlings planted in May 2007 at site 4 was 89.2% after 34 months (Figure 4); site 4 was at a slightly lower elevation (1,710 m) than the other planting sites (1,830 m). At all planting sites, initial losses occurred in the first six to eight months after planting, after which the plants were relatively stable with little mortality for almost a year. After July 2008, we ceased monthly visits and do not know the specific months when mortality began to increase. However, increased mortality was noted in both June 2009 and March 2010, the final visit.

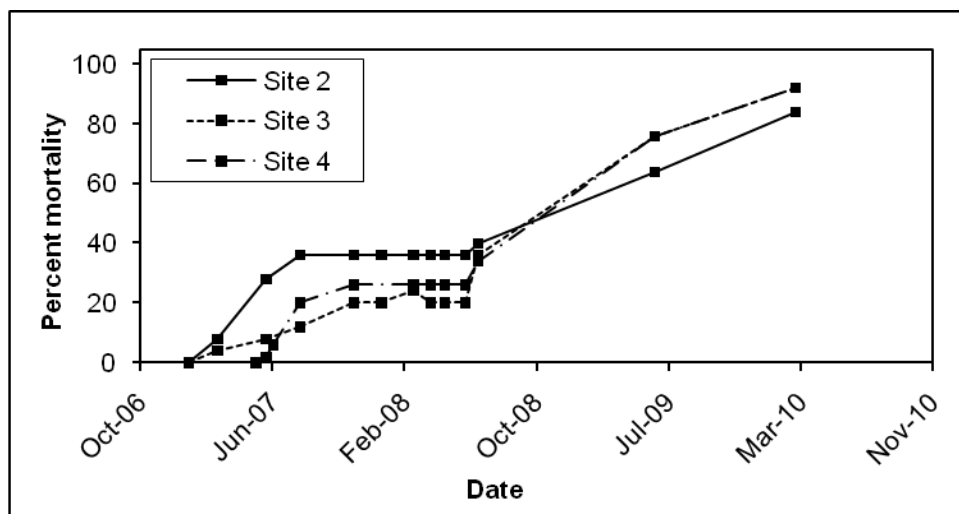


Figure 4. Mortality (%) of *Phyllostegia stachyoides* seedlings planted at three sites on the Mauna Loa Road, 2007–2010.

At site 4, plantings were split between a shady area beneath koa trees with little grass and an adjacent grassy area with fewer trees. After 34 months, seedlings in the no-grass area had a mortality of 86.1% (n = 43), and those in the grassy area had a mortality rate of 92.5% (n = 40). There was no statistical significance to the difference in the number of plants that died in the 2 areas ($\chi^2 = 0.89$, df = 1, p = 0.345). As was seen at the other planting sites, losses occurred in the first few months after planting, after which the plantings were stable for about a year (Figure 5). Mortality of seedlings began to increase in July 2008, and the mortality rate doubled between summer 2008 and summer 2009 in both grass and no-grass areas.

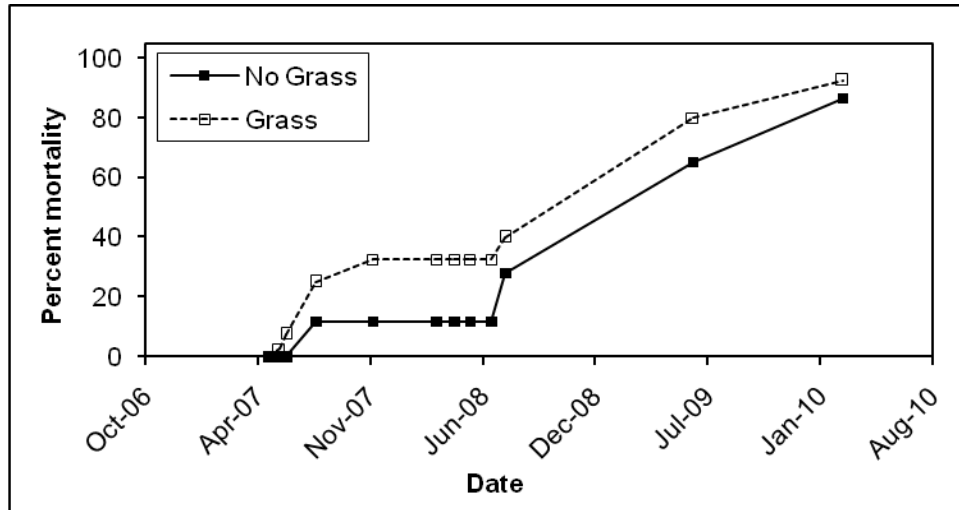


Figure 5. Mortality (%) of *Phyllostegia stachyoides* seedlings planted in adjacent grass and no-grass areas at site 4 on the Mauna Loa Road, 2007–2010.

At planting, seedlings at site 2 averaged 11.7 cm in height (± 4.5 SD), and those at the adjacent site 3 were 14.5 cm tall (± 3.0 SD). The greatest mean height achieved at site 2 was 83.6 cm (± 29.1 SD) in May 2008 and that at site 3 was 66.3 cm (± 29.1 SD) in April 2008, almost 1.5 years after planting (Figure 6). Heights of plantings declined to less than half their maxima, and in March 2010 the mean height of survivors was 37 cm (± 20.5 SD) at site 2 and 30 cm (± 4.2 SD) at site 3. Seedlings at site 4 in the no-grass area were on average 23.0 cm (± 5.5 SD) at planting in May 2007 and achieved a mean height of 71.8 cm (± 23.4 SD) a year later (Figure 7). The seedlings in the grassy area at this site averaged 29.1 cm (± 9.6 SD) at planting and reached a mean maximum of 76.8 cm (± 26.1 SD) in May 2008. After a year in the ground, the height of seedlings in both areas declined. At the end of monitoring in March 2010 survivors in the no-grass area had a mean height of 59.3 cm (± 23.5 SD, n = 6), and those in the grassy area averaged only 32.4 cm (± 18.9 SD, n = 3). The growth of seedlings in the grass and no-grass areas at site 4 was not significantly different (t = 1.43, df = 7, p = 0.171).

Ground Cover at the Natural Population and Planting Sites

The ground cover composition of the habitat of the natural population of *Phyllostegia stachyoides* at kīpuka 4 was dominated by grasses, with non-native grasses having more cover (36.4%) than native species (22.0%; Table 1). The most abundant alien grass was *Ehrharta stipoides* (meadow ricegrass) with 30% cover, and the most common native grass was *Panicum*

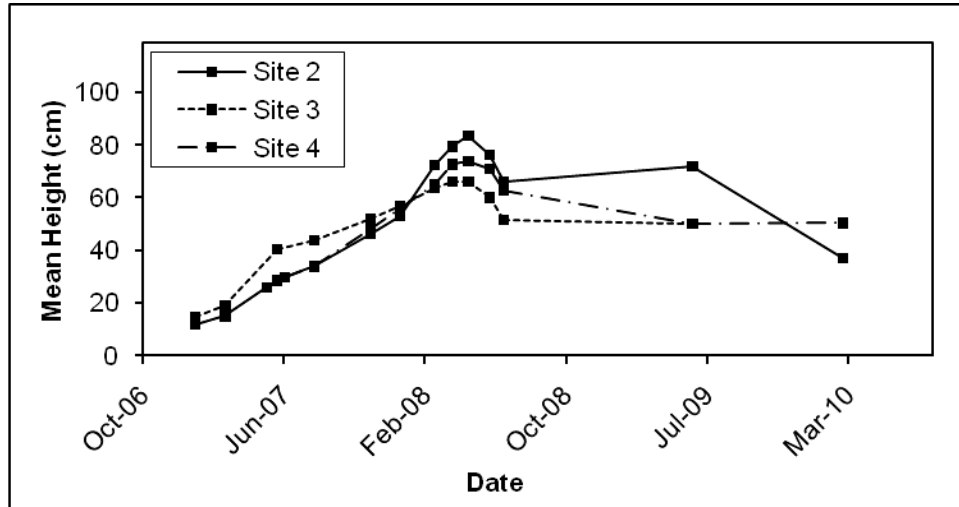


Figure 6. Mean heights (cm) of *Phyllostegia stachyoides* seedlings planted at three sites on the Mauna Loa Road, 2007–2010.

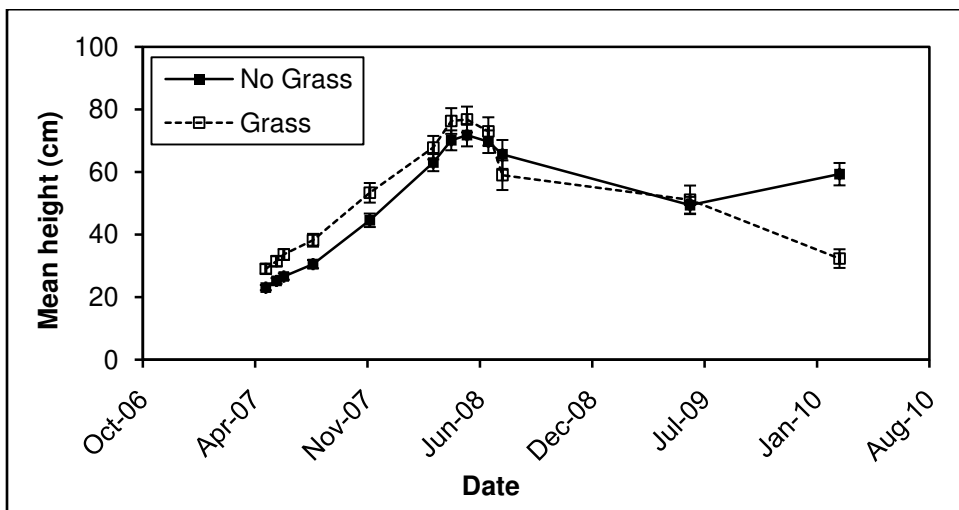


Figure 7. Mean heights in cm (\pm SD) of *Phyllostegia stachyoides* seedlings planted in grass and no-grass areas at site 4 on the Mauna Loa Road, 2007–2010.

tenuifolium (mountain pili) with 21.2% cover. Other native species with appreciable cover in the kīpuka were the native sedge *Carex wahuensis* and the native shrubs *Dodonaea viscosa* and *Leptocophylla tameiameia*. The alien shrub with the most cover was *Bidens pilosa* (6.4%). Litter (fallen leaves and woody debris) made up 14.4% of ground cover, and there was very little exposed soil or rock (1.6%).

The three planting sites along the Mauna Loa Road to the east of the natural population had species compositions similar to that of the habitat of *P. stachyoides* at kīpuka 4. The most notable differences in composition were the absence of the alien shrubs *Bidens pilosa*, *Physalis peruviana* (poha), and *Solanum pseudocapsium* (Jerusalem cherry) and lack of the alien forbs

Table 1. Percentage cover (%) of plant species in the ground layer at a natural population of *Phyllostegia stachyoides* (kīpuka 4) and at three planting sites on the Mauna Loa Road, HAVO.

Species	Kīpuka 4	Site 2	Site 3	Site 4 less grass	Site 4 grass
<i>Acacia koa</i>		0.0	0.7	0.0	0.0
<i>Acacia koa</i> root		0.7	1.3	1.0	0.0
<i>Anthoxanthum odoratum</i>	4.0		0.0	0.0	1.0
<i>Asplenium trichomanes</i>	0.4				
<i>Bidens pilosa</i>	6.4				
<i>Carex wahuensis</i>	8.4	11.3	8.7	3.7	4.3
<i>Cirsium vulgare</i>	0.8				
<i>Daucus pusillus</i>	0.4				
<i>Deschampsia nubigena</i>	0.8	30.7	16.0	10.0	23.0
<i>Dodonaea viscosa</i>	5.2	0.0	2.0	4.7	1.0
<i>Ehrharta stipoides</i>	30.0	0.0	0.0	6.0	32.0
<i>Holcus lanatus</i>	2.4	0.7	0.7	0.7	0.0
<i>Leptecophylla tameiameiae</i>	2.0	10.0	4.0	4.7	5.3
<i>Panicum tenuifolium</i>	21.2	21.3	5.3	1.7	21.0
<i>Phyllostegia stachyoides</i>	0.8	1.3	0.1	1.0	0.7
<i>Physalis peruviana</i>	1.2				
<i>Solanum pseudocapsicum</i>	0.1				
<i>Sophora chrysophylla</i>	0.1	0.7			0.1
<i>Stenogyne rugosa</i>	0.1				
Litter	14.4	20.0	59.3	32.3	27.7
Log		3.3	0.7	1.0	3.0
Moss				0.7	
Soil/rock	1.6	0.0	1.3	0.3	0.0

Daucus pusillus (wild carrot) and *Cirsium vulgare* (bull thistle) at the planting sites. Site 2 had a similar amount of grass cover as did the kīpuka 4 natural population with almost the same percentage cover of the native grass *Panicum tenuifolium*. However, the grass with the most cover at planting site 2 was the endemic *Deschampsia nubigena* (30%) rather than the alien *Ehrharta stipoides*. Litter cover and cover of the native sedge *Carex wahuensis* was also similar at site 2 and kīpuka 4, although both were slightly higher at the planting site. Planting site 3 had a total grass cover of 22%, made up mostly of the native *D. nubigena*. No *E. stipoides* was present at this planting site. Other species with appreciable cover included the native sedge *C. wahuensis* and the native shrubs *Leptecophylla tameiameiae* and *Dodonaea viscosa*. The most

prominent feature of the ground cover at site 3 was the very high amount of litter (59.3%) comprising mostly fallen *Acacia koa* leaves.

At site 4 near the Ke`āmoku Lava Flow, plantings were made in either an open *A. koa* grove with high grass cover or an adjacent shady area with dense leaf litter and less grass. The grassy area had 77% cover of mixed grasses, made up of 44% native grass and 33% alien grass (mostly *E. stipoides*). The grassy planting site was similar in grass composition and cover to that of the natural population at kīpuka 4, except the cover of the native bunchgrass *D. nubigena* was higher. Two native shrubs (*D. viscosa* and *L. tameiaemeiae*) and a sedge (*Carex wahuensis*) each had <5% cover at both grass and less-grass planting areas. Both areas had high litter cover (27.7–32.3%), more than double the litter value at the natural population.

Reproductive Phenology 2006–2008

Natural population: At the natural populations of *P. stachyoides* in kīpuka 3 and 4, most plants (>80%) produced both buds and flowers in each of three years of monitoring (2006–2008). The peak in buds was observed in spring all three years: May in 2006, May–June in 2007, and March–April in 2008 (Figure 8). Flower peaks followed those of buds about two to three months later. Immature fruits were also produced by most (>80%) plants in all three monitoring years, but mature fruits were observed on a lower proportion of monitored plants in 2007 and 2008 (Figure 9). Immature fruits were present on a high percentage of plants in spring and summer into the fall; peaks were observed from March through August in 2006 and from June to November in 2007. Mature fruiting peaks were of shorter duration and were observed in August through October and September through November.

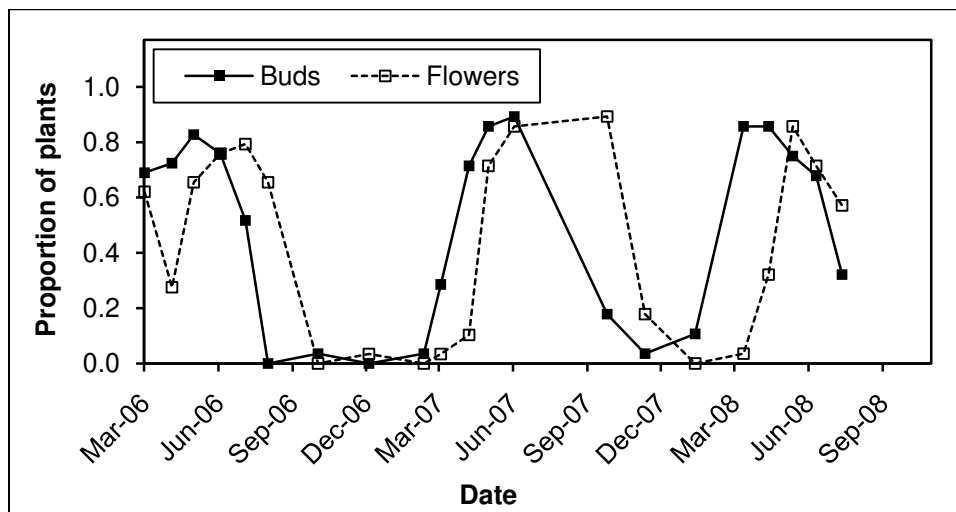


Figure 8. Proportion (%) of *Phyllostegia stachyoides* plants producing buds and flowers at natural populations in kīpuka 3 and 4 (combined).

The abundance of buds and flowers on plants at kīpuka 3 and 4 was greatest during the spring of both 2007 and 2008 (Figure 10). Peaks in the mean number of inflorescences with buds were in April or May, and numbers began to decline in June of both years. The number of inflorescences bearing flowers was lower than that observed for those bearing buds, but

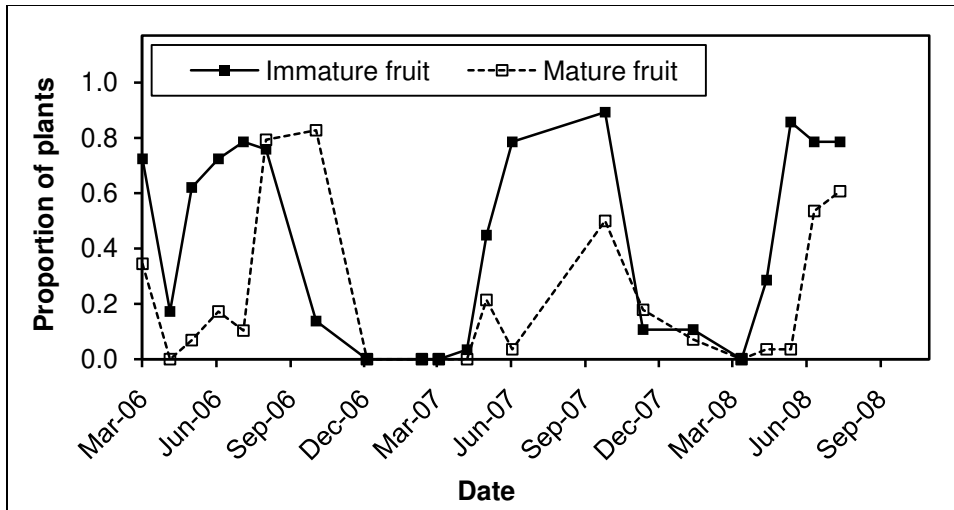


Figure 9. Proportion (%) of *Phyllostegia stachyoides* plants producing immature and mature fruit at natural populations in kīpuka 3 and 4 (combined).

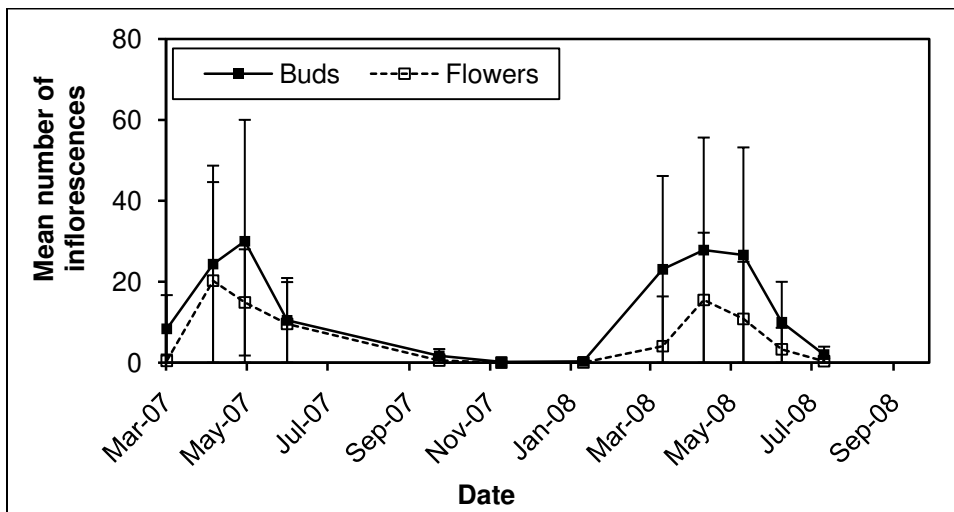


Figure 10. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing buds and flowers at natural populations in kīpuka 3 and 4 (combined).

followed the same pattern. The peak month for flower numbers was April in both years. Flowers began to appear in March and had all disappeared by the summer (around July). No buds or flowers were observed on plants between September and January.

Immature fruits were most abundant on the *P. stachyoides* plants of kīpuka 3 and 4 in May and June of both years (2007–2008; Figure 11). Immature fruit began to appear in March and April. Few immature fruits were seen between September and March. Inflorescences with mature fruits were far less abundant than were those bearing immature, green fruits; very small peaks in abundance were observed in the period between May and July in both years.

At the nearby Ke`āmoku weather station at 1,680 m elevation on the Mauna Loa Road, rainfall occurred primarily during winter and spring months (Appendix III, Table 1). There was a lag of

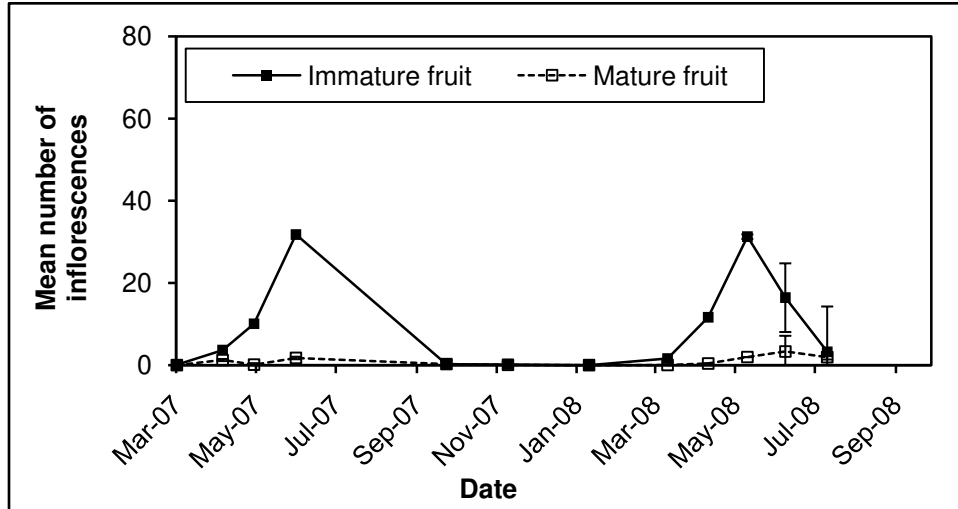


Figure 11. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing immature and mature fruit at natural populations in kīpuka 3 and 4 (combined).

one to two months between the peak in mean monthly rainfall in March and the peak production of buds of *P. stachyoides*. During the peak time for mature fruit in summer months, mean monthly rainfall was low; the driest month at this station was June.

Throughout multiple years of monitoring in both kīpuka, the average total number of inflorescences per plant with either buds or flowers was 139.7 (\pm 110.7 SD). The mean number of buds or flowers per inflorescence was 58.4 (\pm 15.71 SD, $n = 27$). If every bud and flower produced fruit with four seeds, the estimated mean number of seeds per plant produced during the monitoring period (17 months) was 32,623.5 (\pm 25,852.5 SD). Adjusting for the success rate of 45% of buds/flowers to immature fruits and 17.5% success rate of immature to mature fruits, there were potentially 2,569 seeds produced per plant during the monitoring period, or 1,285 estimated seeds per plant per year.

Plantings. Plantings of *P. stachyoides* seedlings were made at sites 2 ($n = 25$) and 3 ($n = 25$) in January 2007 and at site 4 ($n = 83$) in May 2007. Few plants produced buds during the first year, but bud production began in January 2008 of the second year and peaked in April at all three sites (Figure 12). Flower production followed the same pattern at the sites. Immature fruit was not detected the year of planting, but approximately 40% of plants at site 3 produced mature fruit in summer (July) of the planting year (2007; Figure 13.). Almost all plants (>80%) at all three sites bore both immature and mature fruit during 2008. The peak month for immature fruit was May, and the peak production of mature fruit was June at all sites. Phenology monitoring ceased after summer 2008, but in a revisit to the sites in June 2009, mature fruits were seen on more than half of plants at site 2 and on a few plants at site 4 (Figure 13).

The abundance of buds and flowers was monitored from planting until July 2008. Buds began to appear at plantings before March and peaked in April at all three sites. The mean number of inflorescences with buds was greater at site 2 than at the other planting sites (Figure 14).

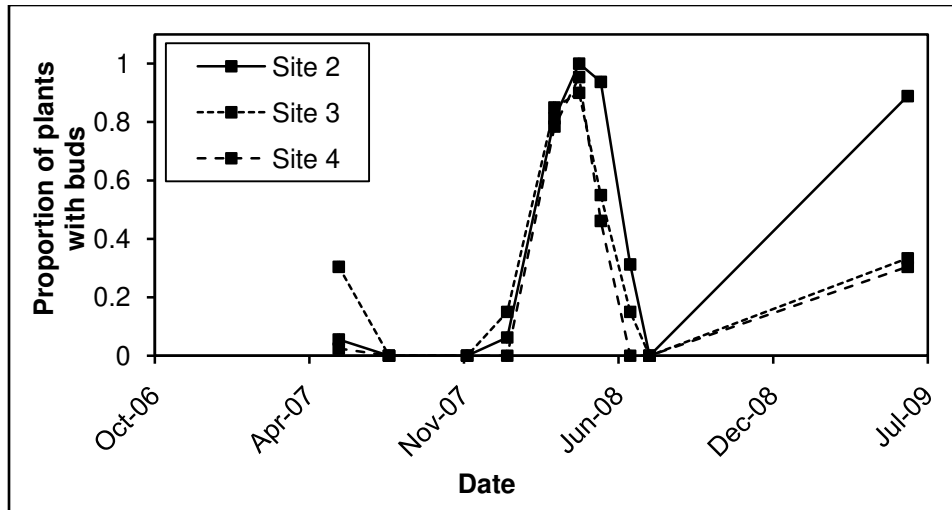


Figure 12. Proportion (%) of *Phyllostegia stachyoides* plants producing buds at three planting sites on the Mauna Loa Road.

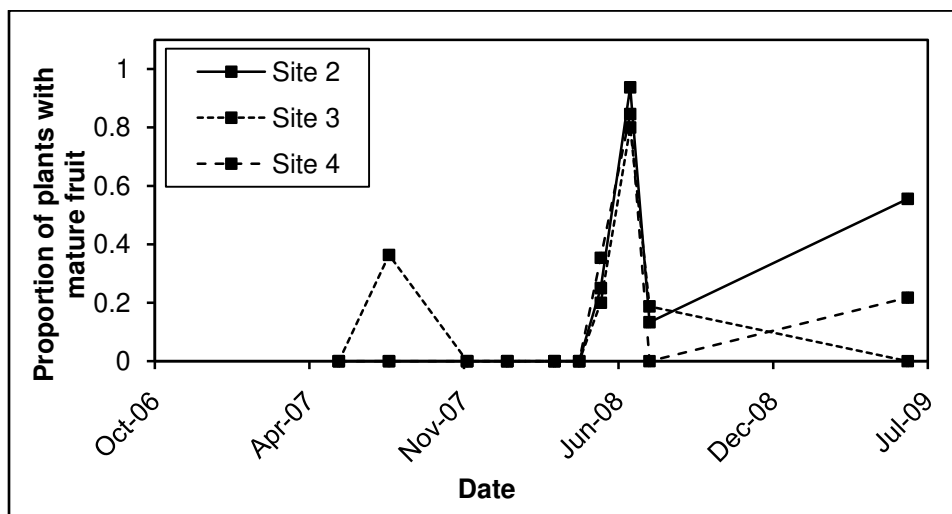


Figure 13. Proportion (%) of *Phyllostegia stachyoides* plants producing mature fruit at three planting sites on the Mauna Loa Road.

Flower abundance followed the same pattern as that of buds, except the peak in flower abundance was May at site 2 and April at sites 3 and 4 (Figure 15). Immature fruits were restricted to spring months with a peak in abundance in May at all sites (Figure 16). Mature fruits were less abundant than immature fruit and were observed primarily in June (Figure 17). As was true for buds and flowers, inflorescences with mature fruit were most abundant at site 2. Few mature fruits were seen in any month other than June, and they had disappeared from all planting sites by July.

At site 4, plantings were split between a grassy area and an adjacent area with dense leaf litter and no grass. The pattern of bud production and the mean number of inflorescences with buds was almost the same in the grass and no-grass areas (Figure 18). The abundance of flowers was also similar for plants in the two areas, although slightly more inflorescences with flowers

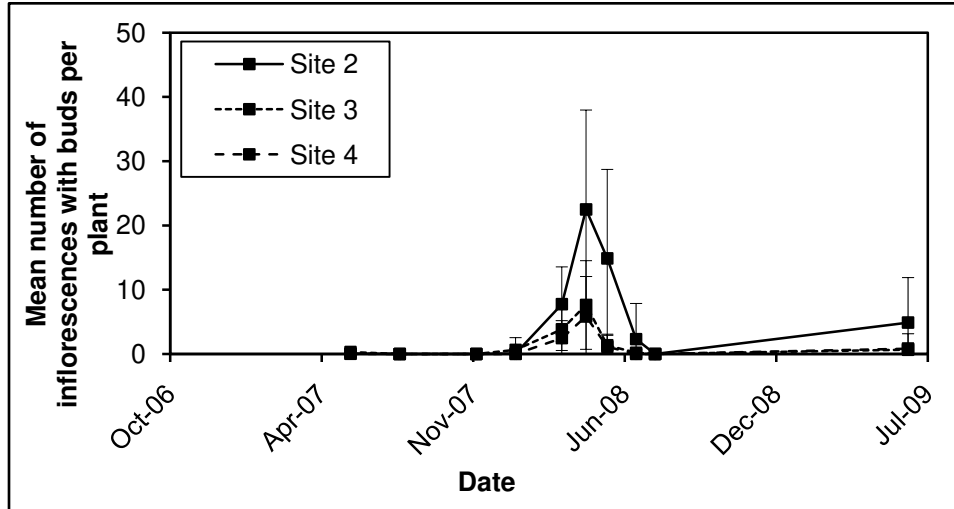


Figure 14. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing buds at three planting sites on the Mauna Loa Road.

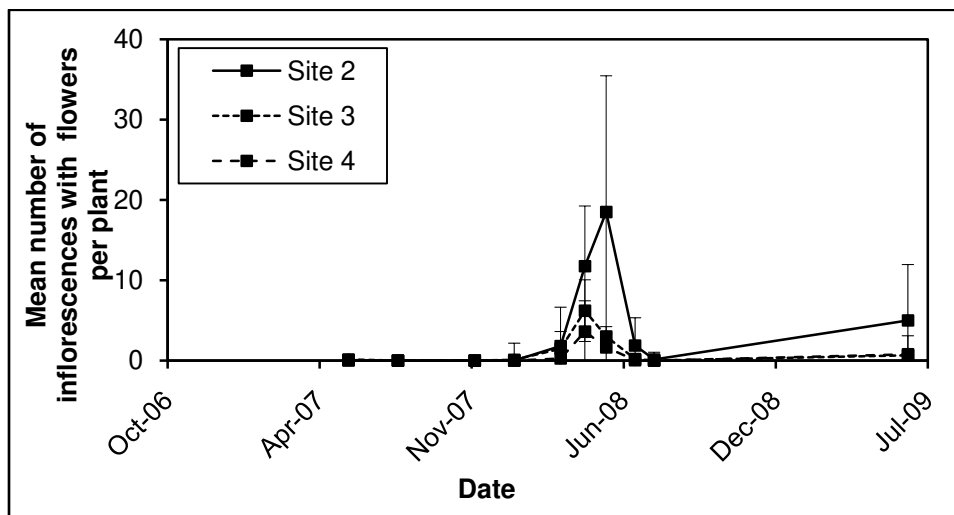


Figure 15. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing flowers at three planting sites on the Mauna Loa Road.

were seen in the no-grass area under dense koa (Figure 19). The only difference seen in immature fruit inflorescences at the two areas was a staggered peak in abundance with plants in the grassy area producing most of their immature fruit in May, a month earlier than plants in the no-grass area (Figure 20). The mean number of inflorescences bearing mature fruit was almost identical in the two adjacent areas (Figure 21). In a repeated measures analysis of variance of plants at the two areas (grass and no-grass), there was no significant difference in the mean number of inflorescences bearing buds ($F_{1,70.9} = 0$, $p = 0.935$), flowers ($F_{1,71.3} = 0.2$, $p = 0.678$), immature fruits ($F_{1,69.1} = 0$, $p = 0.968$), or mature fruits ($F_{1,68.3} = 1.5$, $p = 0.219$).

Success of Fruit Production

At the natural population of *P. stachyoides* in kīpuka 4, 45.0% of tagged buds and flowers

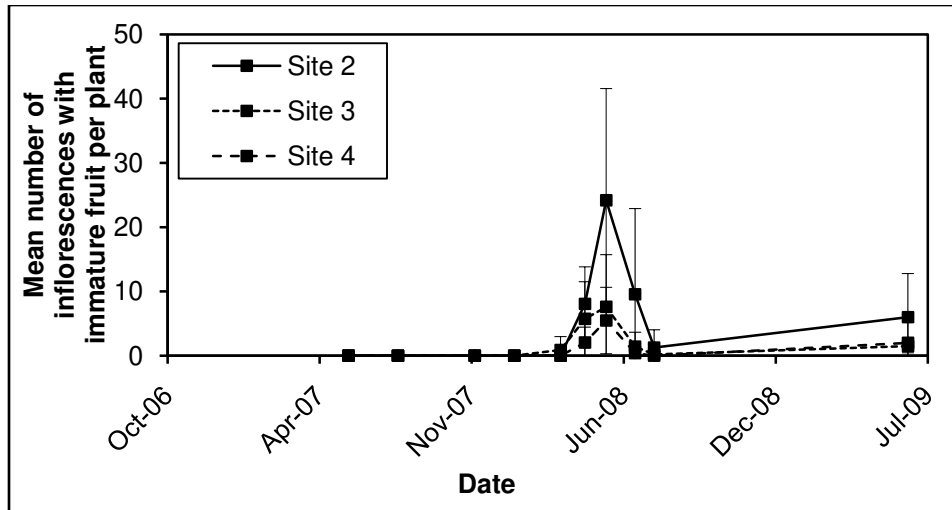


Figure 16. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing immature fruit at three planting sites on the Mauna Loa Road.

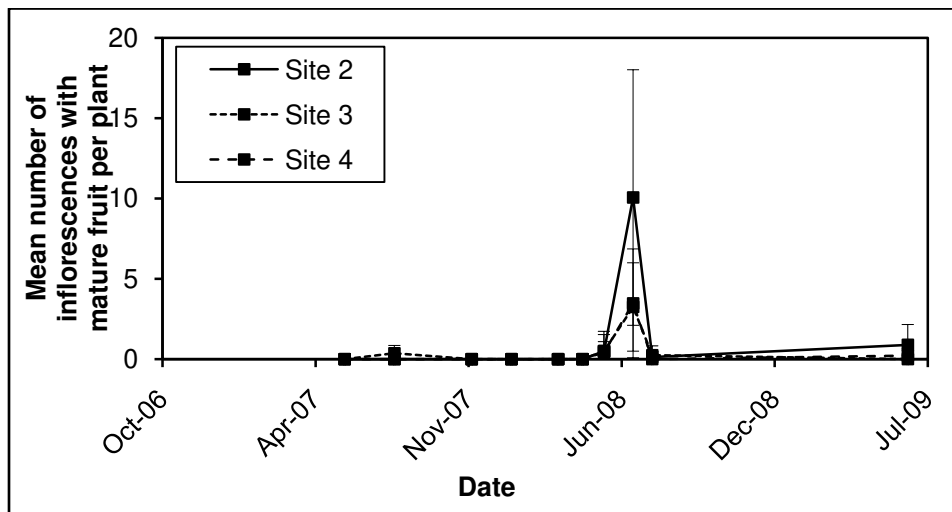


Figure 17. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing mature fruit at three planting sites on the Mauna Loa Road.

successfully transitioned to immature fruits ($n = 232$). The percentage of tagged immature fruits that matured, including expanded but empty calyces, was 17.8% ($n = 101$), less than half that of flower transitions. Tagged inflorescences at the planting sites on Mauna Loa Road showed a similar success rate for buds and flowers transitioning to immature fruits (46.0%; $n = 391$). The successful production of mature fruits from tagged immature fruits was also relatively high at the plantings, at 36.7% ($n = 215$). The number of tagged immature fruits successfully forming mature fruits was significantly higher at the plantings than at the natural population of *P. stachyoides* at kīpuka 4 ($\chi^2 = 11.57$, $df = 1$, $p = 0.0007$).

Fruit development was rapid in monitored *P. stachyoides*. Very few tagged immature fruits remained in that state for a month; only 8.4% of immature fruits were still green after a month

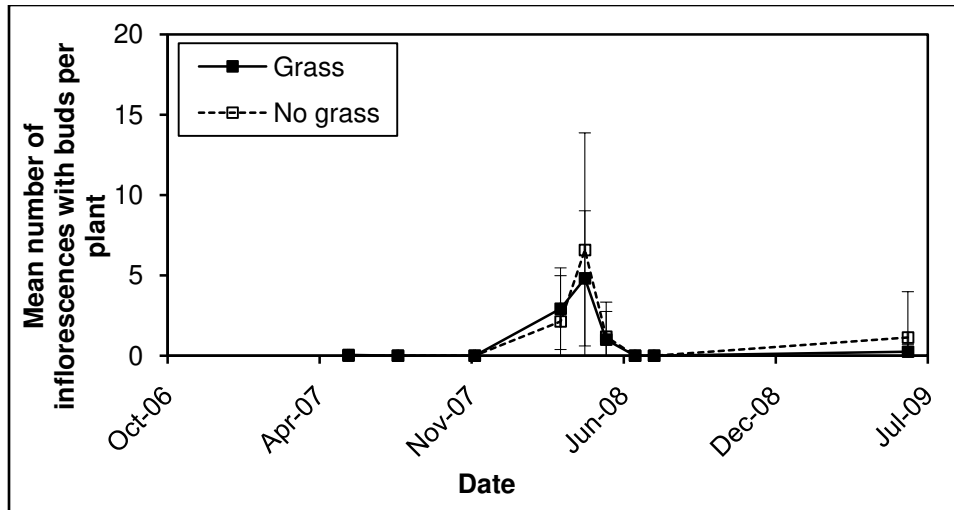


Figure 18. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing buds in adjacent grass and no-grass areas at site 4 on the Mauna Loa Road.

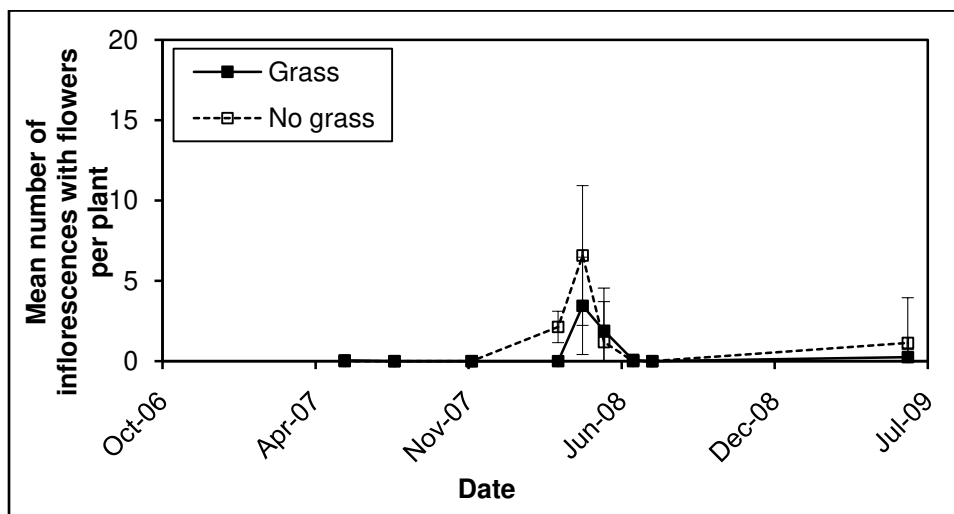


Figure 19. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing flowers in adjacent grass and no-grass areas at site 4 on the Mauna Loa Road.

at the plantings, and 6.9% of immature fruits were retained at the natural population. Mature fruits were never observed remaining on the plant for a month at the natural population, but 6.3% of mature fruits were retained for a month at the plantings. Two months after tagging, only empty calyces of dispersed fruits or dried, aborted fruits were observed at any of the monitored sites.

Pollination-Floral Visitor Observations and Pollen Transport

A total of 9.7 hours of observation of potential pollinators was obtained, during which native yellow-faced bees (*Hylaeus difficilis*), endemic koa butterfly (*Udara blackburni*), non-native honey bees (*Apis mellifera*), and alien hover flies (*Allograpta obliqua* and *Toxomerus marginatus*) visited flowers of *P. stachyoides*, resulting in 319 total floral visits (Table 2). The hover fly *A. obliqua* was the most abundant visitor with a total of 278 visits (87.1% of total

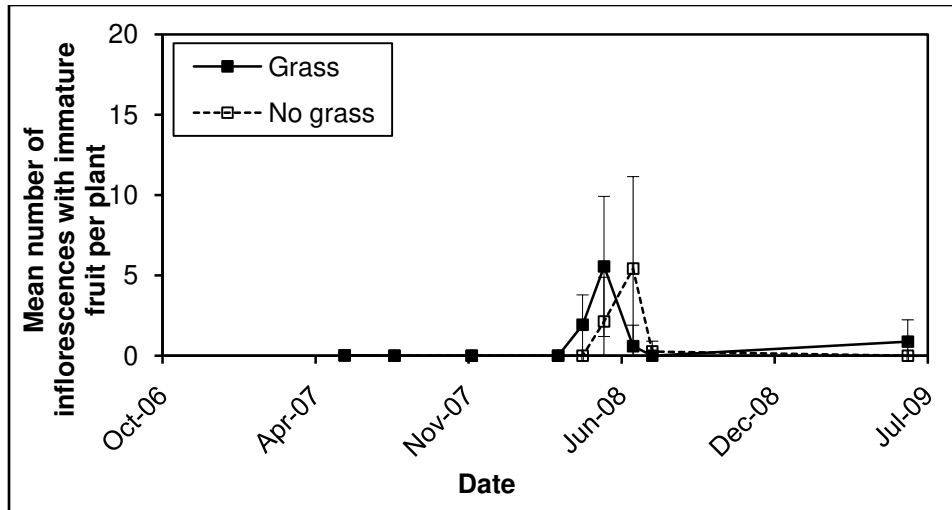


Figure 20. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing immature fruit in adjacent grass and no-grass areas at site 4 on the Mauna Loa Road.

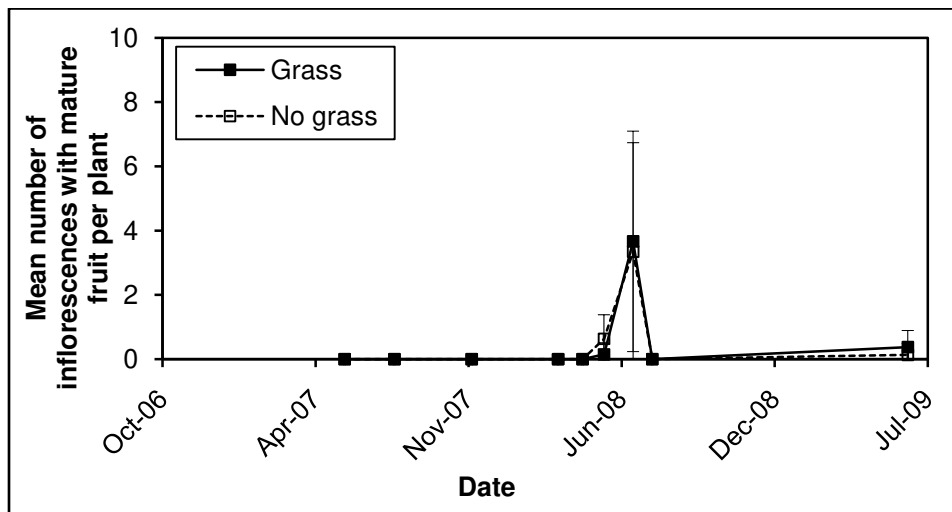


Figure 21. Mean number of inflorescences (\pm SD) on *Phyllostegia stachyoides* plants bearing mature fruit in adjacent grass and no-grass areas at site 4 on the Mauna Loa Road.

visits) and a mean visitation rate of 1.5 visits/flower/hr (SD = 3.1, n = 58). The second most abundant visitor, *H. difficilis*, made 27 visits (8.5% of total) with a mean visitation rate of 0.08 visits/flower/hr (SD = 0.3, n = 58). The remaining three species participated in less than 5% of all floral visits. The native yellow-faced bees and the single Blackburn's butterfly were observed only at the natural *P. stachyoides* population, while the alien flies and honey bees visited flowers at both the natural population and planting sites. All floral visitors exclusively foraged for pollen, except for honey bees, which collected nectar only.

Insects collected for pollen identification at the natural population of *P. stachyoides* consisted of 15 *H. difficilis* and 1 *A. obliqua*. Insect washing identified 7 *H. difficilis* and the single *A. obliqua* carrying *P. stachyoides* pollen. The average number of *P. stachyoides* pollen washed from *H.*

Table 2. Visitation rates and duration of visits of insects on *Phyllostegia stachyoides* flowers during timed observation intervals in kīpuka of the western Mauna Loa Strip and planting sites on the Mauna Loa Road, March to May 2008.

Floral Visitors	Status*	Total number of visits ¹ (%)	Mean visitation rate ² (SD; n = 58)	Mean visit duration in sec ³ (SD; n = # of visits)
DIPTERA				
Syrphidae				
<i>Allograpta obliqua</i>	adv	278 (87.1)	1.51 (3.14)	15.9 (31.8)
<i>Toxomerus marginatus</i>	adv	3 (0.9)	0.01 (0.07)	12.0 (17.3)
HYMENOPTERA				
Colletidae				
<i>Hylaeus difficilis</i>	end	27 (8.5)	0.08 (0.27)	4.5 (3.2)
Apidae				
<i>Apis mellifera</i>	pur	10 (3.1)	0.03 (1.13)	7.9 (9.0)
LEPIDOPTERA				
Lycaenidae				
<i>Udara blackburni</i>	end	1 (0.3)	0.01 (0.04)	33.0 (0.0)

* 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 flower 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

difficilis was 0.7 grains (SD = 1.1) while *A. obliqua* carried a single grain. Pollen grains from other species in the plant community were also removed (Figure 22). *P. stachyoides* pollen made up 6.6% of the average pollen load for *H. difficilis* and 33.3% of pollen on *A. obliqua*.

Natural Seedlings

Natural seedlings were observed during phenology monitoring at 16 *P. stachyoides* plants in kīpuka 4 (55.2% of all plants). In total, 608 seedlings were observed between November 2006 and July 2009. At the final monitoring in July 2009, there were 26 seedlings remaining, but 12 of these were new and only 14 were survivors from the previous year (2.3%). Mortality overall throughout the monitoring period was 97.7% (Figure 23). All of the surviving seedlings had persisted for more than 10 months. Most seedlings appeared during the months of December and January. The mean height of seedlings when first seen was 3.5 cm (\pm 4.7 SD) and the mean final height of seedlings was 6.9 cm (\pm 14.8 SD). The maximum height attained by any seedling was 190 cm. The average life span of seedlings was 4.4 months (\pm 4.0 SD). Losses of seedlings were pronounced from April through July 2008.

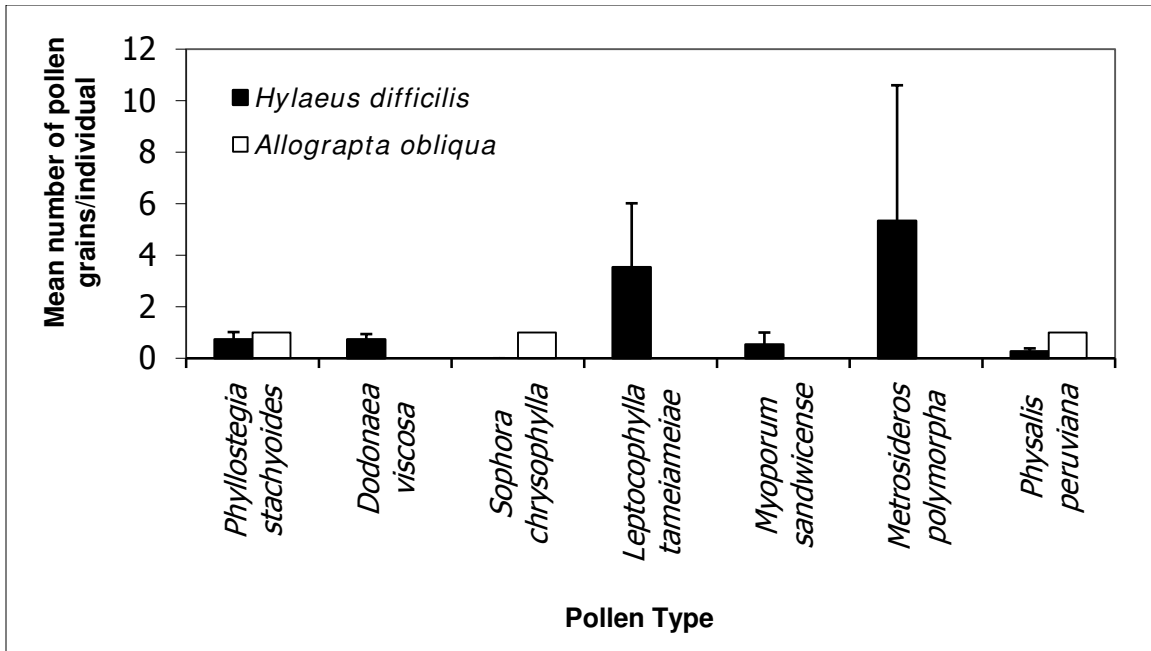


Figure 22. Pollen load composition of *Hylaeus difficilis* and *Allograpta obliqua* collected on flowers of *Phyllostegia stachyoides* in kīpuka of the western Mauna Loa Strip.

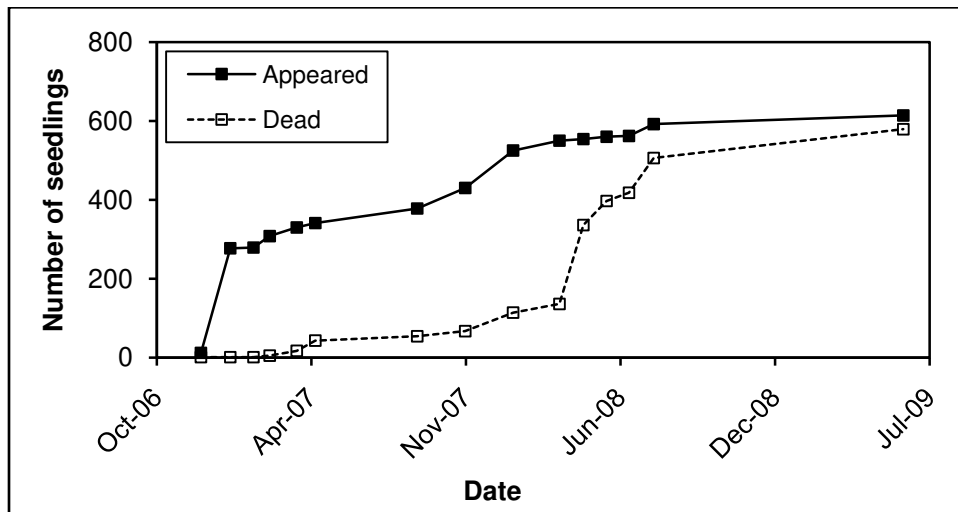


Figure 23. Cumulative appearance and death of *Phyllostegia stachyoides* seedlings at the natural population of kīpuka 4, 2006–2009.

Seeds and Seed Germination

Field seeding in grass and no-grass plots: Very low germination was observed in a direct seeding experiment in which an equal number of seeds was sowed in grass-covered and cleared plots near the natural population of *P. stachyoides* in kīpuka 4.

Cleaned, fresh, untreated seeds were sowed in September 2007. During 10 months of monitoring, only one seedling appeared in a single grass covered plot; this amounted to a

germination rate of 0.7% ($n = 150$). The grass plot seedling appeared four months after sowing and lived for five months before disappearing. Two seedlings were seen in grass-free plots for a germination rate of 1.3% ($n = 150$). Germination was noted in a grass-free plot seven months after sowing, and the second seedling appeared at a revisit in June 2009, 21 months after sowing. The first seedling lived for two months and grew to 6.5 cm in height before disappearing. The fate of the second seedling is unknown.

Seed germination in the greenhouse: Germination rates of *P. stachyoides* in the greenhouse trials were variable in six trials sowed over four years, ranging from a mean of 13.6% to 80.4% (Appendix II, Table 1). The first trial sown in May 2005, with variable numbers of seeds in replicates, had an overall germination rate of 32.3%. The August 2006 germination trial resulted in a mean of 31.3 of 50 seeds germinating for a rate of 62.6%. Three trials were carried out in summer 2008. In trial 6, a mean of 33.0 seeds of 63 sowed germinated for a germination rate of 52.5%. Trials 7 and 8, also sowed in June 2008, had the highest germination rates of all trials, with 72.6% and 80.4% of seeds germinating, respectively. The final trial sowed in June 2009 averaged only 3 germinants for 22 seeds per replicate pot, and had an overall germination rate of 13.6%. All trials used the same medium and were carried out at the same greenhouse. Seeds were freshly collected 8–12 days before sowing, except in trials 2 and 6, where seeds were stored for one to two months prior to planting.

Germination was not immediate in the trials; seedlings were first seen within 33 to 108 days. The shortest period of delay between sowing and germination was observed in trials sowed in August 2006. The mean number of days from sowing to first appearance of seedlings in all trials combined was 64.4 days. In the trials sown in June 2008, germination continued for 10 months after sowing; the last new seedlings were observed in April 2009.

***Silene hawaiiensis*, Hawaiian catchfly**

Stand Structure, Growth, and Mortality at Two Natural Populations

The natural population of *Silene hawaiiensis* at Three Trees Kīpuka on Mauna Loa exhibited a stable structure in both 2006 and 2008 (Figure 24). Most plants in the total sample of 200 were in the middle height classes between 20 and 50 cm. Small plants below 20 cm were rare in the sample, and plants larger than 60 cm were few, especially in 2006. Growth was detected on 66% of plants measured in both 2006 and 2008. The mean height of plants in 2006 was 38.4 cm (± 12.0 SD, $n = 200$), and that of the survivors in 2008 was 44.5 cm (± 16.4 SD, $n = 181$). Mean growth was 6.3 cm (± 5.7 SD) over the two-year period, and maximum growth observed for an individual was 30 cm.

Mortality within the Three Trees Kīpuka population of *S. hawaiiensis* was relatively low over the two-year monitoring period, where 13 of 200 plants (6.5%) died by 2008. Many of the plants that were lost during the monitoring period were in the 10–20 cm height class (40%), and a low percentage of losses was observed in the four size classes between 20 and 60 cm. No sampled plants >60 cm died. In a longer-term comparison of plants in 2008 with the same plants first observed in 2000, the mortality rate was 9.2% for 250 plants at the Three Trees Kīpuka.

At the second natural population of *S. hawaiiensis* south of Halema`uma`u Crater on Kīlauea, 50 randomly selected plants sampled for phenology displayed a relatively flat population structure in 2006 and the structure of a declining population in 2008 with pronounced losses of

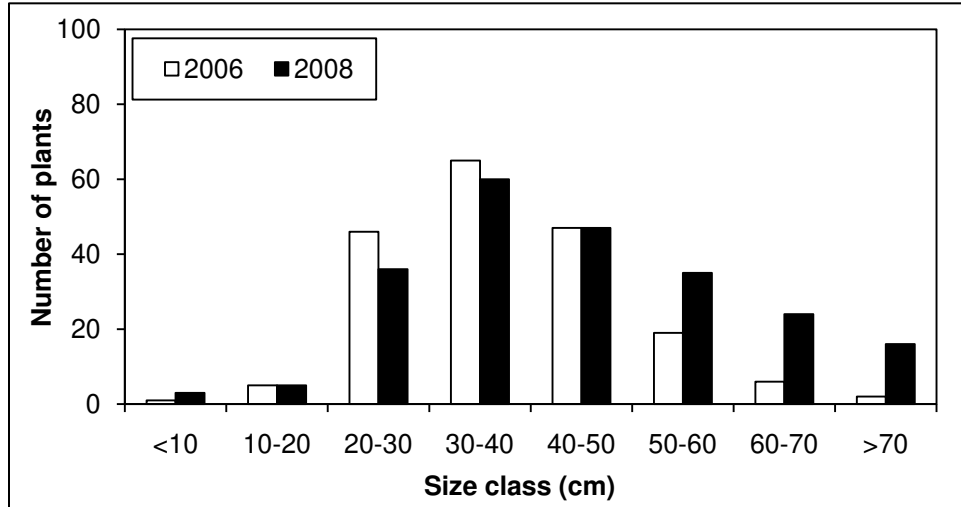


Figure 24. Height class structure of 200 *Silene hawaiiensis* plants at Three Trees Kīpuka, Mauna Loa, 2006 and 2008.

larger and presumably older plants. Most plants in 2008 fell into the smaller height classes of <10 cm and 10–20 cm, and few plants were observed in the 20–30 cm and >30 cm height classes (Figure 25). The mean height of sampled plants at Halema`uma`u was 19.3 cm (\pm 11.0 SD, $n = 50$) in 2006 and 16.8 cm (\pm 12.0 SD, $n = 36$) in 2008. Growth of the 33% of sampled plants that increased in height over the two-year period was 13.8 cm (\pm 14.0 SD). The mean height of plants at Halema`uma`u was significantly smaller than that of plants at Three Trees Kīpuka in 2006 ($t = 8.31$, $df = 98$, $p < 0.0001$). Mortality of *S. hawaiiensis* plants was relatively high at Halema`uma`u, with 30% of plants sampled for phenology ($n = 50$) dying between 2006 and 2008. In 2008 there were fewer plants at Halema`uma`u than had been present in 2006 in the two larger height classes >20 cm.

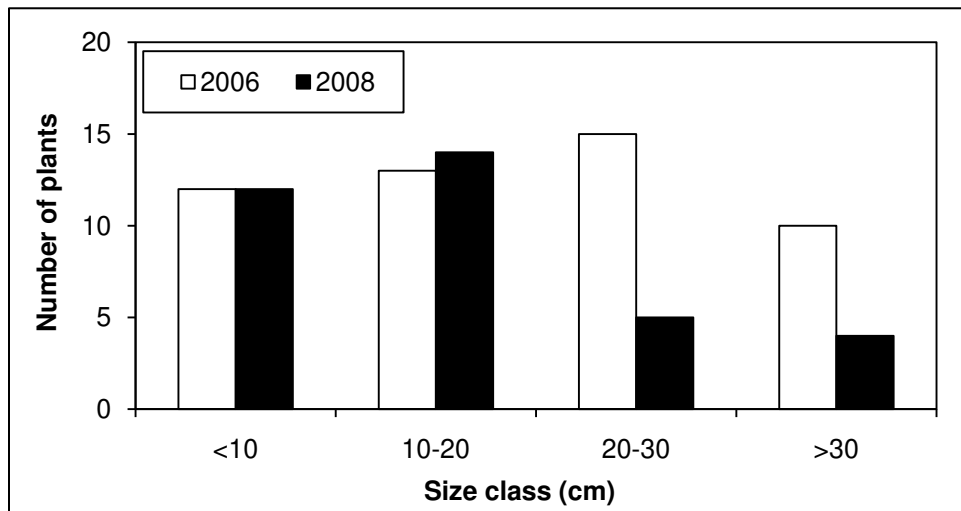


Figure 25. Height class structure of a sample of 50 *Silene hawaiiensis* plants south of Halema`uma`u, Kīlauea, 2006 and 2008.

Stand structure plots at Mauna Loa Three Trees Kīpuka: At the Three Trees Kīpuka population on Mauna Loa, the mean density of *S. hawaiiensis* plants in three stand structure plots (each 20 x 50 m) was relatively high in 2006 with 308.3 (\pm 246.4 SD) plants per plot counted. Extrapolating this density to the entire kīpuka, there were an estimated 1,027.7 plants/ha.

The height class structure of the population showed most plants in the middle ranges of 20–30, 30–40, and 40–50 cm tall (Figure 26). Small plants, including those <10 cm tall (presumably seedlings) were also well represented in the population within the plots. The larger height classes >50 cm had fewer plants than those of the middle classes with decreasing numbers of plants seen in the increasing height classes. When the same plots were re-monitored in 2007, the mean density of *S. hawaiiensis* had decreased to 286.0 (\pm 225.6 SD) plants per 1,000 m² plot. The mean number of plants that died in the three plots was 23.7 (\pm 19.4 SD). The percentage of plants that died was very similar in each of the plots, ranging from 7.4 to 7.8%. During the same time period, a total of 22 new seedlings appeared in the three plots, for a mean of 7.3 seedlings per plot (\pm 9.5 SD). Most seedlings (18) appeared in a single plot; 4 appeared in another; and the third had no new seedlings. Losses between 2006 and 2007 appeared to be primarily in the smaller height classes <40 cm; height classes above this gained individuals over the year of monitoring (Figure 26).

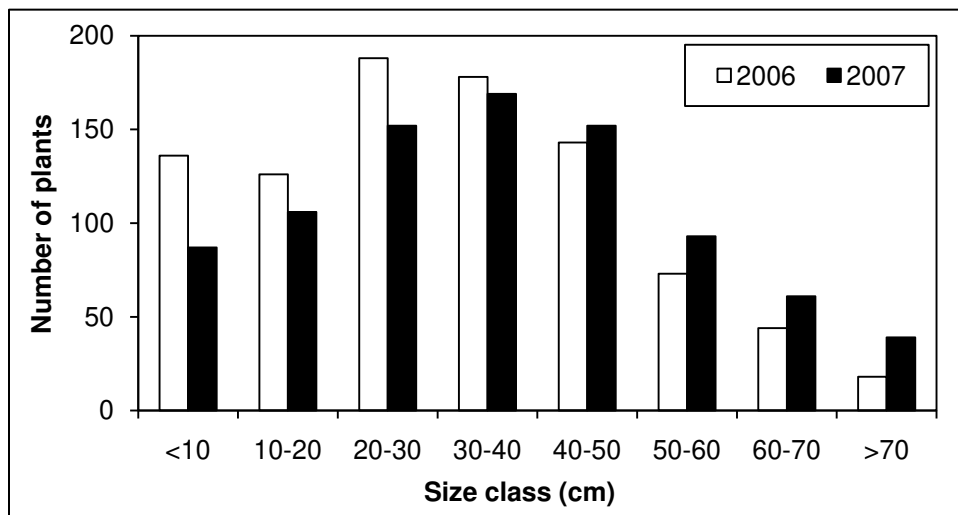


Figure 26. Height class structure of *Silene hawaiiensis* in three plots at Three Trees Kīpuka on Mauna Loa, 2006 and 2007.

Stand structure plots at Kīlauea Crater Rim south of Halema`ūma`u: The mean density of *S. hawaiiensis* in six plots on Kīlauea south of Halema`ūma`u was much lower than was seen at the Three Trees Kīpuka on Mauna Loa. In 2006, the mean number of plants per plot was 16.8 (\pm 12.5 SD), which may be extrapolated to a density of 168 plants/ha. The height class structure of the *S. hawaiiensis* population was biased toward the smallest height classes, with most plants seen in the <10 cm class and few plants >40 cm tall (Figure 27). When re-visited a year later in 2007, the mean number of *S. hawaiiensis* per plot had decreased to 14.8 (\pm 10.5 SD), or 148 plants/ha. The mean mortality in plots between 2006 and 2007 was 12.6 (\pm 7.3 SD) plants. Losses ranged from 0 to 19.1% of plants in the six plots. During the same time,

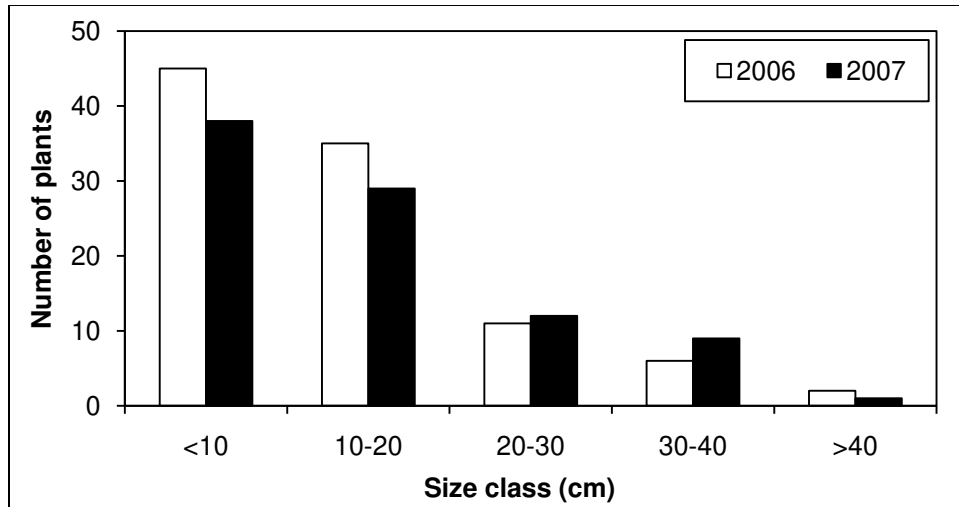


Figure 27. Height class structure of *Silene hawaiiensis* in six plots at the site south of Halema`uma`u on Kilauea, 2006 and 2007.

only 2 new seedlings appeared in all the plots combined, 1 in each of two plots (mean 0.3 ± 0.5 SD). Losses occurred in the two smallest height classes, and gains were noted in the 20–40 cm classes.

Reproductive Phenology at Two Natural Populations, 2006–2008

Mauna Loa Three Trees Kīpuka: At the *S. hawaiiensis* population in Three Trees Kīpuka, up to 80% of sampled plants produced buds during the summer. In two years of monitoring, July through September or November had the greatest percentage of monitored plants producing buds (Figure 28). Flower production followed a similar pattern, with peaks observed in July 2006 and November 2007 (Figure 29). Immature, green fruit had a more restricted seasonal appearance than did buds or flowers; July was the only month in 2006 in which young fruits were observed (Figure 30). During 2007, immature fruits were not restricted to July, but were also seen in November and to a lesser extent in January 2008. Old fruit capsules (dry and open at the top) were observed on almost half of monitored plants from August 2006 to January 2007 (Figure 31). Subsequently in 2007, few old fruits were noted until July 2007, after which low numbers of dry capsules were persistently present on a third of plants from summer 2007 through the end of monitoring in March 2008. At both the Ke`āmoku (below the Three Trees Kīpuka) and Mauna Loa weather stations (above the site), summer and late spring months were dry between May and September with June the driest month at both stations. November through March were months with the greatest rainfall (Appendix III, Figure 1 and Figure 2).

Kīlauea Crater Rim South of Halema`uma`u: As was seen at the Mauna Loa population, peak bud production at the Kīlauea site south of Halema`uma`u was seasonal with the greatest proportion of monitored plants producing buds in July 2006 and June 2007 (Figure 32). Buds were observed on 10 to 40% of plants throughout 2006, and a few plants had buds in every month monitored in 2007.

Flowers were observed on a lower proportion of *S. hawaiiensis* plants than those with buds. Flowers peaked in summer (July–August) in 2006, and more than 20% of plants had low

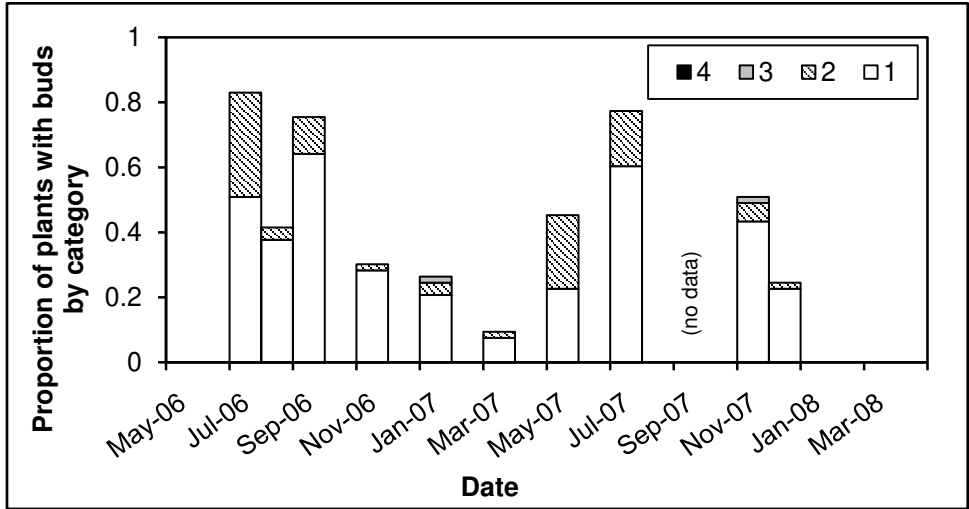


Figure 28. Proportion of *Silene hawaiiensis* plants producing buds at Three Trees Kīpuka, Mauna Loa, 2006–2008. (Categories are 1 = 1–10; 2 = 11–50; 3 = 51–100; 4 = >100 per plant.)

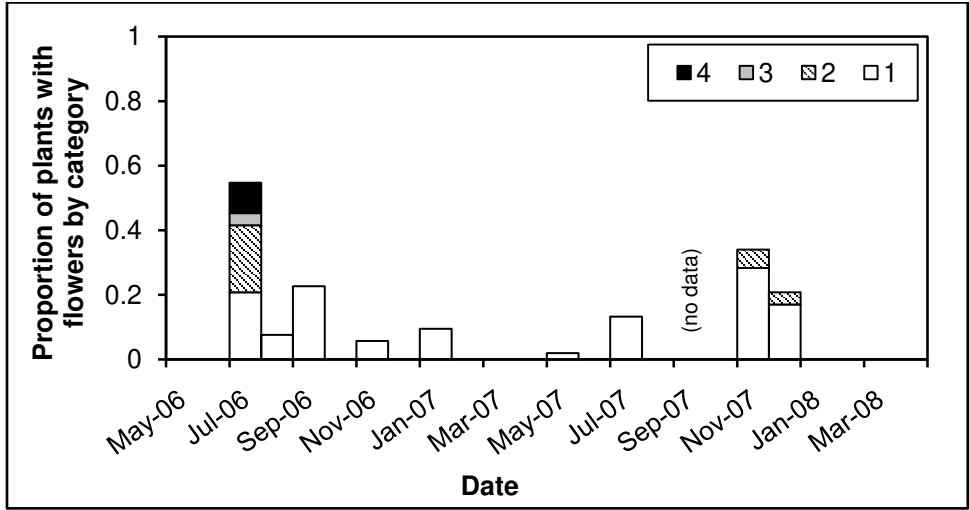


Figure 29. Proportion of *Silene hawaiiensis* plants producing flowers at Three Trees Kīpuka, Mauna Loa, 2006–2008. (Categories are 1 = 1–10; 2 = 11–50; 3 = 51–100; 4 = >100 per plant.)

numbers of flowers throughout the latter half of 2006 and the beginning of 2007 (Figure 33). Flowers were produced by fewer plants in 2007, although we have no data for July or September 2007. Production of immature fruit showed a pattern similar to that for flowers with almost 80% of plants bearing young, green fruits in August 2006, a month later than the peak for flowers (Figure 34). Bud and flower peaks occurred during the dry summer season at Halema`uma`u, when rainfall began to increase from the June minimum (Appendix III, Figure 3).

Few plants were observed bearing immature fruits in 2007, but peak production appeared to be in summer. Because of scheduling conflicts, we have no data from the summer months of July

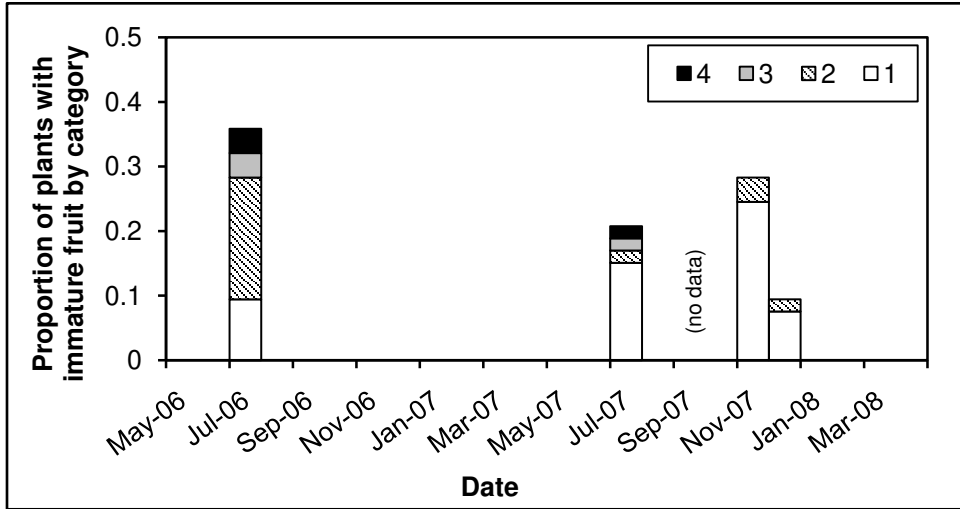


Figure 30. Proportion of *Silene hawaiiensis* plants producing immature fruit at Three Trees Kīpuka, Mauna Loa, 2006–2008. (Categories are 1 = 1–10; 2 = 11–50; 3 = 51–100; 4 = >100 per plant.)

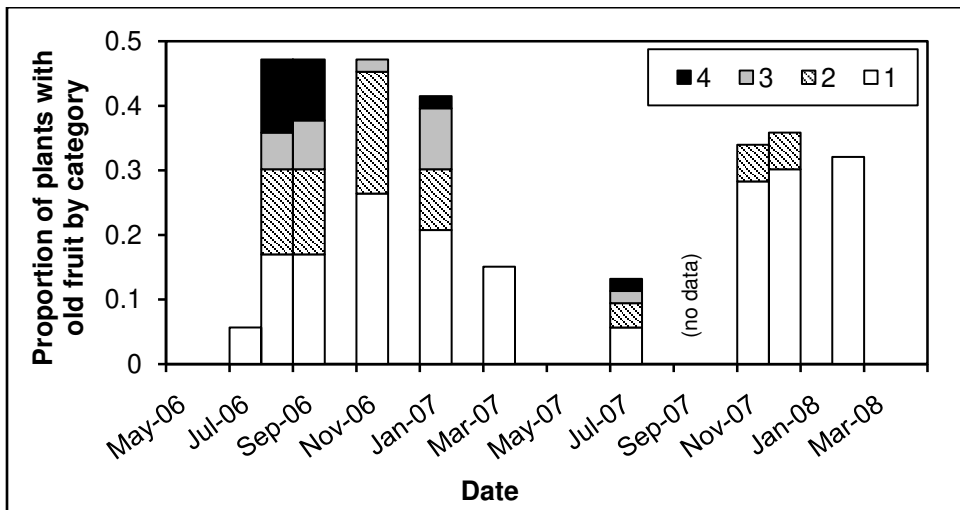


Figure 31. Proportion of *Silene hawaiiensis* plants bearing old dry fruit at Three Trees Kīpuka, Mauna Loa, 2006–2008. (Categories are 1 = 1–10; 2 = 11–50; 3 = 51–100; 4 = >100 per plant.)

or September. At Crater Rim, we observed old, dry fruit capsules mixed with mature, but unopened fruit capsules; old fruits were borne by approximately 80% of plants from September through December 2006 and on approximately 40% of plants from August through November 2007 (Figure 35). The fall and winter months from October through March were months with higher than average rainfall at the NPS weather station near Halema`uma`u (Appendix III, Figure 3).

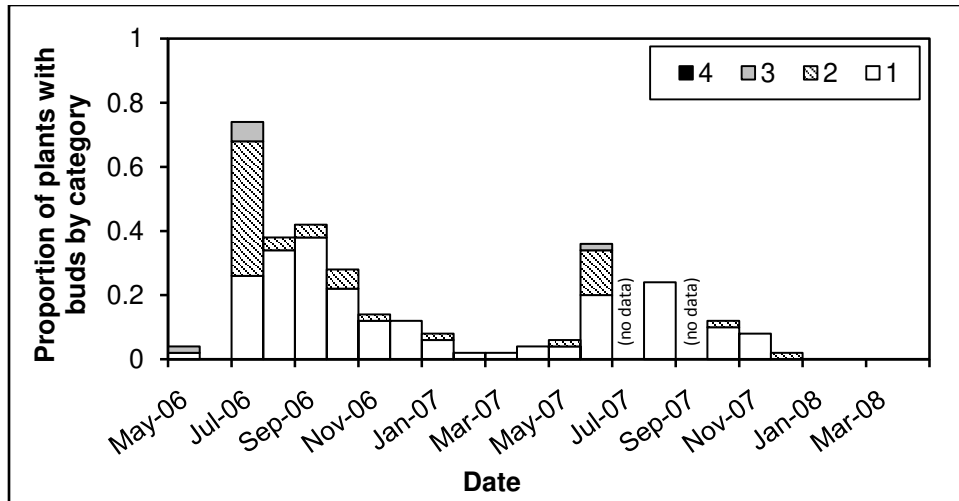


Figure 32. Proportion of *Silene hawaiiensis* plants producing buds at Halema`uma`u, Kilauea, 2006–2008. (Categories are 1 = 1–10; 2 = 11–50; 3 = 51–100; 4 = >100 per plant.)

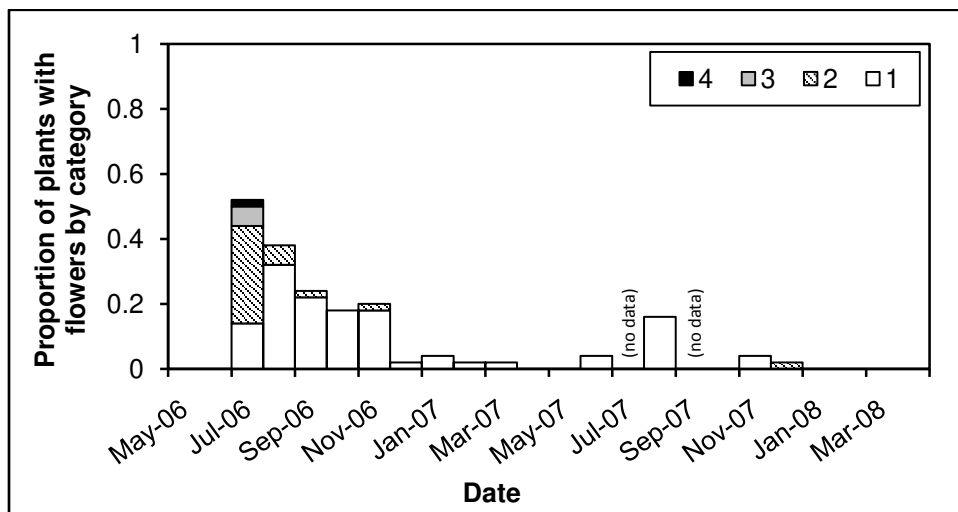


Figure 33. Proportion of *Silene hawaiiensis* plants producing flowers at Halema`uma`u, Kilauea, 2006–2008. (Categories are 1 = 1–10; 2 = 11–50; 3 = 51–100; 4 = >100 per plant.)

Success of Fruit Production

At the *Silene hawaiiensis* population south of Halema`uma`u, tagged buds successfully formed open flowers at a rate of 33.3% (n = 30). Buds required on average 2.8 days (\pm 2.0 SD) to mature into flowers. Flowers (including flowers originally tagged as buds) became green, immature fruit at a rate of 52.5% (n = 40); the mean transition time from flower to young fruit capsules was 7.4 days (\pm 3.1 SD). Immature fruit ripened to mature fruit at a rate of 66.7% (n = 18); we did not have enough data to determine the mean transition time from green to mature fruit, but it was less than three weeks. The mean number of seeds in dry but unopened capsules was 60.7 (\pm 23.6 SD, n = 22).

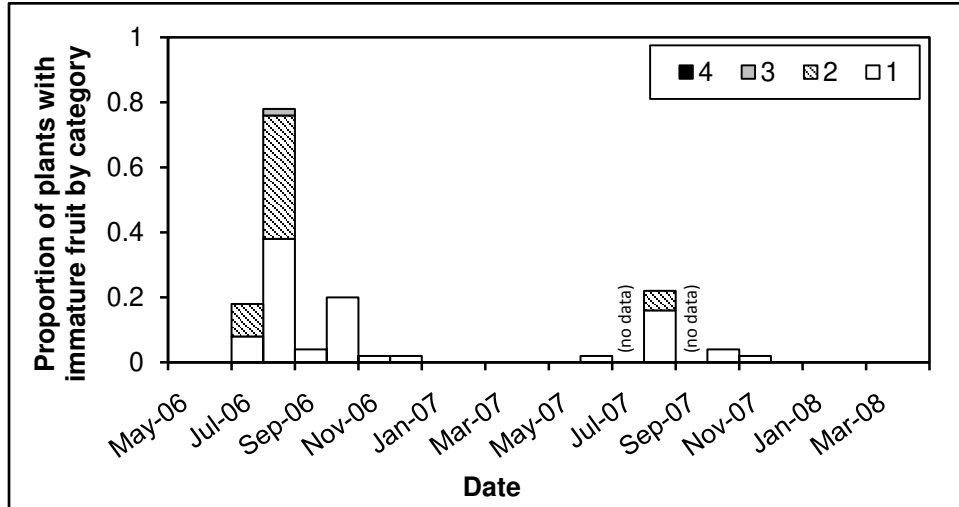


Figure 34. Proportion of *Silene hawaiiensis* plants producing immature fruit at Halema`uma`u, Kīlauea, 2006–2008. (Categories are 1 = 1–10; 2 = 11–50; 3 = 51–100; 4 = >100 per plant.)

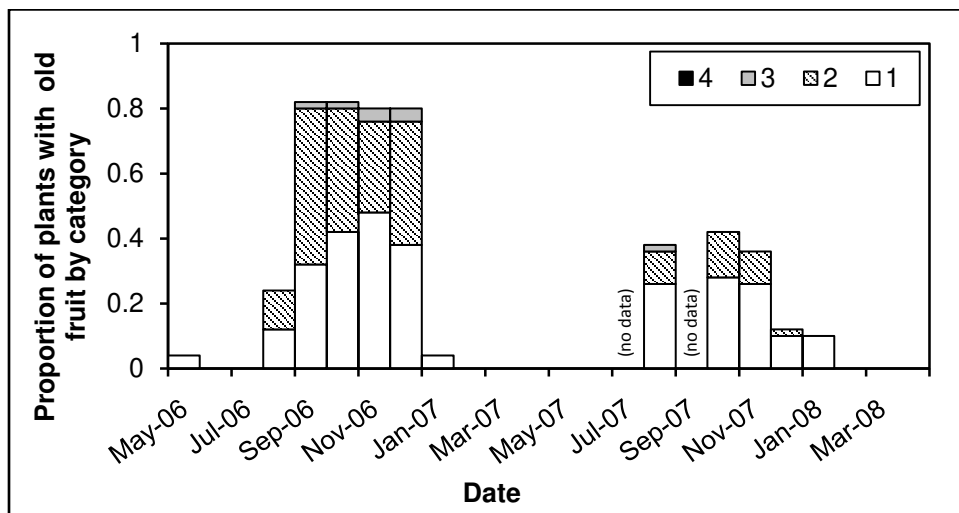


Figure 35. Proportion of *Silene hawaiiensis* plants bearing old dry fruit at Halema`uma`u, Kīlauea, 2006–2008. (Categories are 1 = 1–10; 2 = 11–50; 3 = 51–100; 4 = >100 per plant.)

Pollination—Floral Visitor Observations

A total of 70.2 hours of video record was obtained, during which native yellow-faced bees *Hylaeus difficilis* and *H. volcanicus* (Colletidae) and the introduced hover fly *Allograpta exotica* (Syrphidae) visited flowers of *S. hawaiiensis*, resulting in 8 total floral visits. Both the yellow-faced bees and hover flies landed on the edge of the corolla and inserted their heads into the corolla opening to harvest a floral resource. Limitations of the video resolution made it difficult to discern *Hylaeus* to species level, which floral resource (nectar or pollen) was obtained, and whether the flower’s anthers or stigma were incidentally contacted. Duration of a visit by *Hylaeus* spp. varied between 1 and 6 seconds, with an average duration of 2.8 seconds (SD = 2.2, n = 6). Visits by Syrphid hover flies ranged from 1 and 2 seconds with an average duration of 1.5 seconds (SD = 0.7, n = 2).

Growth and Mortality of Plantings Inside and Outside Exclosures at Kahuku

Plantings of *Silene hawaiiensis* inside and outside ungulate exclosures at Kahuku survived at a similar rate. Seedlings planted within exclosures in 2006 had a mortality rate of 48% (n = 25) 2.5 years after planting, and a similar number of unprotected seedlings planted outside the same exclosures had a mortality rate of 54.2% (n = 24; Figure 36). This small difference in survival was not statistically significant ($\chi^2 = 0.19$, df = 1, p = 0.666). A second group of seedlings planted in equal numbers inside (n = 9) and outside (n = 9) the same exclosures in May 2007 had a mortality rate of 88.9% after two years in both protected exclosures and immediately outside (Figure 37). All seedlings planted outside exclosures in November 2006 showed evidence of animal browsing within four months of planting; no plants inside exclosures were browsed. All unprotected seedlings planted in May 2007 showed browsing damage within six months of planting, and protected seedlings inside exclosures were unaffected.

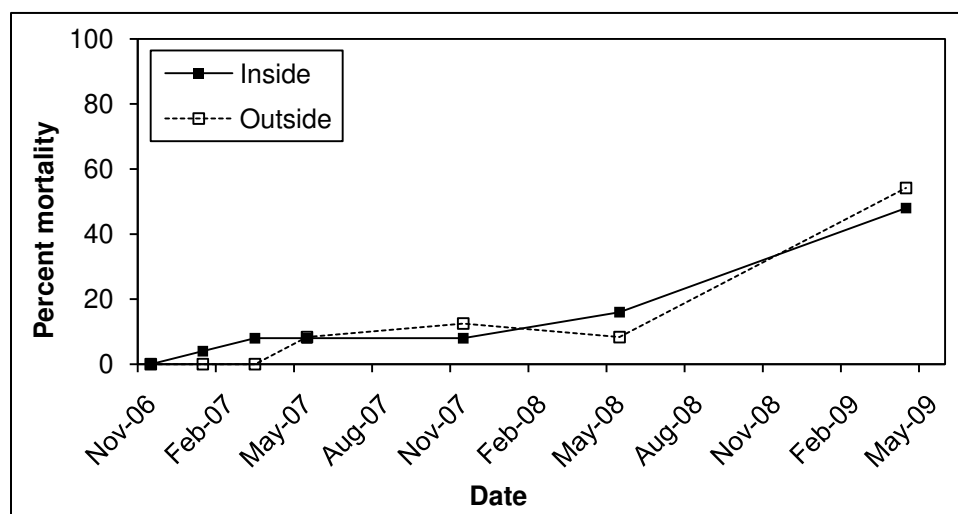


Figure 36. Mortality (%) of *Silene hawaiiensis* planted in 2006 inside (n = 25) and outside (n = 24) ungulate exclosures at Kahuku Unit, HAVO.

Browsing by mouflon sheep did not result in greater mortality of *S. hawaiiensis*, but did affect the height and reproduction of unprotected plants. In the 2006 planting, 32% of seedlings inside exclosures increased in height, and the mean growth of plants was 12.7 cm (± 8.4 SD) between 2006 and 2009. Seedlings planted outside exclosures in 2006 grew at first and then decreased in size throughout the monitoring period of 2007–2009 (Figure 38), losing an average of 29.4 cm in height (± 9.1 SD). Although there was no statistical difference ($t = 1.5$, df = 44, p = 0.151) in the original mean height of plants inside (27.2 cm ± 12.1 SD) and outside (31.5 cm ± 9.0 SD) exclosures, the final mean height after 2.5 years of monitoring was significantly larger inside exclosures (28.0 cm ± 10.0 SD) than outside, where plants were only 4.6 cm (± 2.3 SD) tall due to repeated bouts of browsing ($t = 8.2$, df = 13, p < 0.0001). Reproduction of the 2006 plantings also differed inside and outside the exclosures ($\chi^2 = 6.12$, df = 1, p = 0.013). While 92% of seedlings inside exclosures produced buds, flowers, or fruit capsules during the 2.5 years of monitoring, only 62% of plants outside exclosures did so.

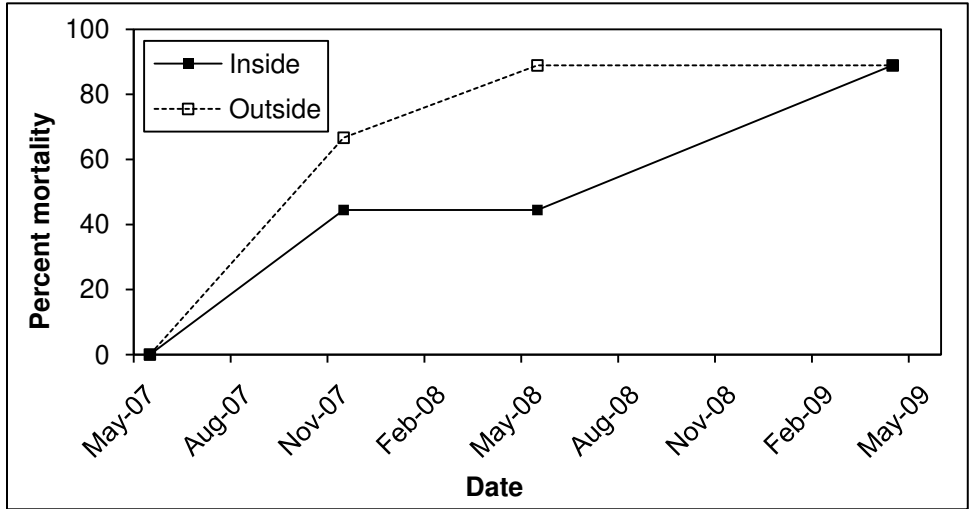


Figure 37. Mortality (%) of *Silene hawaiiensis* planted in 2007 inside (n = 9) and outside (n = 9) ungulate exclosures at Kahuku Unit, HAVO.

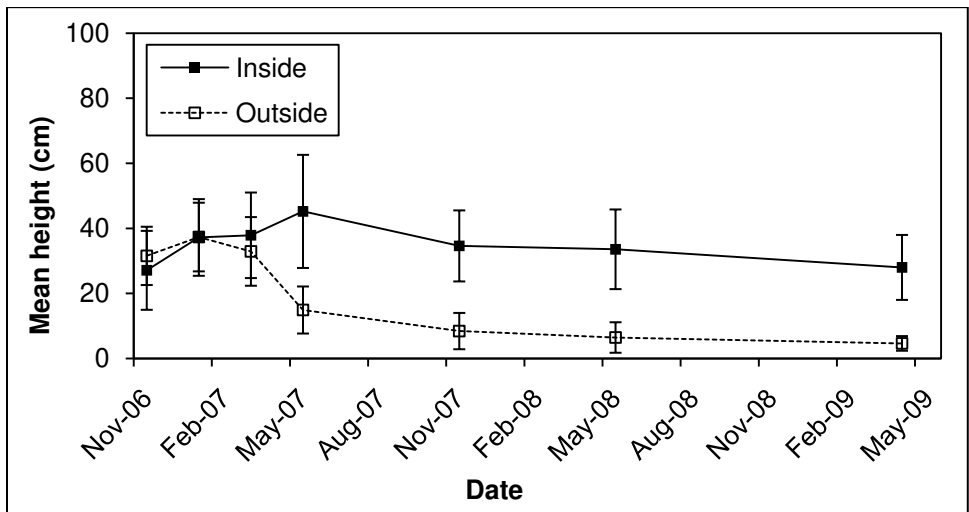


Figure 38. Mean height (\pm SD) of *Silene hawaiiensis* planted in 2006 inside (n = 25) and outside (n = 24) ungulate exclosures at Kahuku Unit, HAVO.

Seeds and Seed Germination

Seed dispersal at the Kilauea site south of Halema`uma`u. Dispersal of seeds from open capsules of *S. hawaiiensis* plants at the Crater Rim study site south of Halema`uma`u was predictably greater near the seed-bearing plants than at distances of up to 40 m (Figure 39). A total of 41 *S. hawaiiensis* seeds was counted on 30 sticky cards placed in groups of five at six distances away from the edge of the dense population of plants at the boundary of the study site with the 1971 lava flow. Five cards (on five different transects) a meter distant from the edge of the *S. hawaiiensis* population had a mean of 6.0 seeds per card (\pm 6.4 SD). The five cards set at a distance of 5 m from the source of the seeds had a mean of 1.2 seeds per card (\pm 1.2 SD). At a distance of 10 m from *S. hawaiiensis* plants, the mean number of seeds per

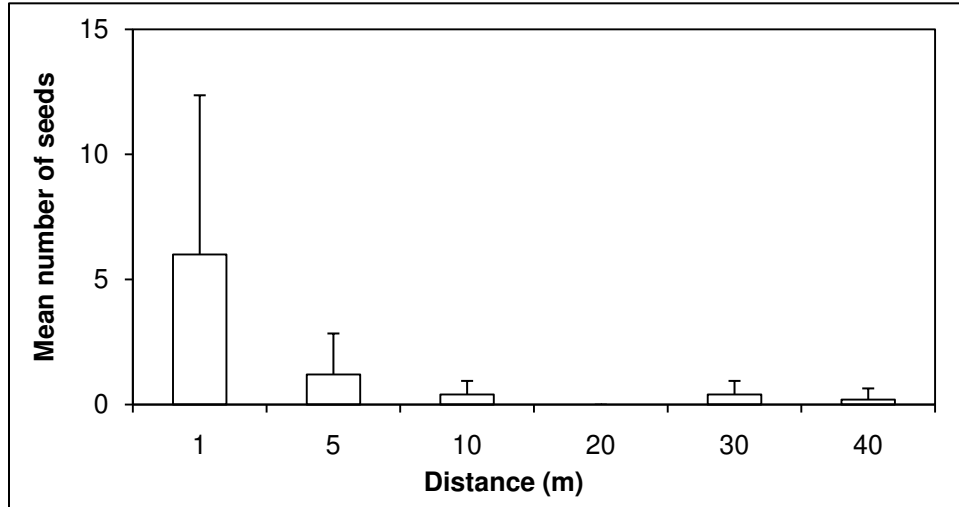


Figure 39. Mean number (\pm SD) of *Silene hawaiiensis* seeds counted on 30 sticky cards placed at six distances (1–40 m) away from plants at the natural population south of Halema`uma`u, Kilauea, HAVO.

card fell below 1 (0.4 ± 0.6 SD). At 20 m, there were no seeds on any of the sticky cards, and at a distance of 30 m the mean number of seeds per card was $0.4 (\pm 0.6$ SD). At the farthest distance from the edge of the *S. hawaiiensis* population (40 m), there were on average only 0.2 seeds per card (± 0.5 SD).

Seed germination in the greenhouse: Germination rates of *S. hawaiiensis* in the greenhouse were high in three trials and relatively low in two others (Appendix II, Table 2). The first trial sown in May 2006 had a mean germination rate of 73.0%. This was followed in August 2006 by a second trial with a mean of only 7.0% germination in six replicated pots. The third and fourth trials were sown in June and July 2007 and differed greatly in mean germination rates; the third trial had 60.7% germination and the fourth only 13.3%. In the final fifth trial seeds were sown in January 2008, and a mean of 62.4 of 100 seeds in each replicate germinated (62.4%). The source of the seeds was the Three Trees Kipuka, except for the third trial, in which seeds were collected at the population south of Halema`uma`u. The planting medium was the same for all trials (perlite, vermiculite, cinder mix with fine sifted cinder on top), and all trials were carried out at the same greenhouse near 1,170 m elevation. Elapsed time between seed collection and sowing did not seem to explain the differences in trials, as the seeds used in the three trials with high germination rates varied from seeds freshly collected within eight days of sowing to seeds stored for 2 to 11 months before sowing.

Time from sowing to first germination varied from 7 to 27 days; the mean of all trials was 14.6 days for the appearance of the first seedlings. The most rapid germination was observed in summer 2007, but the longest period from sowing to germination was observed in summer 2006. Time of year did not seem to affect the rapidity of germination in our trials. In the four trials for which we have weekly seedling counts, germination continued for three to five months from sowing.

Potential Limiting Factors of Rare Plant Species Investigated in This Study

A comparison of stand structure at the beginning and end of a two-to-three-year period indicated relatively stable populations at the *P. stachyoides* population and one of the *S. hawaiiensis* study sites. Adult mortality ranged from relatively low (<10%) to moderately high (20–30%), and natural seedlings were observed at populations of both species (Table 3). Longevity of either species is unknown. Even though natural seedling mortality was high at the populations studied, the duration of the study was short, and survival may be better in years with higher summer rainfall. Fruit production was high in both species, and the success rate of transition from bud or flower to fruit was also high. Floral visitors, including native yellow-faced bees (*Hylaeus* spp.), were identified for both plant species. Pollen washing on insects collected at the *P. stachyoides* population revealed that both the native yellow-faced bees *H. difficilis* and the alien hover fly *Allograpta obliqua* were carrying pollen of the rare mint.

Table 3. Potential limiting factors of two rare plant species investigated in this study.

Factor	<i>Phyllostegia stachyoides</i>	<i>Silene hawaiiensis</i>
Stand structure	Stable	Stable—declining
Adult mortality	19.1% ¹	6.5–30.0% ²
Flower/fruit phenology	Annual	Annual
Fruit production	High	High
Percent bud/flower to green fruit	45% ³	51.2% ⁴
Percent green fruit to mature	17.8% ³	66.7% ⁴
Number of species of floral visitors identified	5	3
Seed germination (greenhouse)	13.6–80.4%	7.0–73.0%
Ungulate browsing of unprotected plants	n/a	100%
Natural seedlings observed	Yes	Yes
Natural seedling mortality	97.7%	n/a
Planted seedling mortality	89.9% ⁵	48.0–54.2% ⁶
Impact of grass on seedling mortality	No	n/a

n/a Not tested or not observed

¹ Mortality of plants in kīpuka 3 and 4 between 2005 and 2008

² One population stable and second declining; mortality of 200 plants at Three Trees Kīpuka and 50 plants sampled south of Halema`uma`u from 2006 to 2008

³ At the natural population of kīpuka 3 and 4

⁴ At the Kīlauea study site south of Halema`uma`u

⁵ At all four planting sites along the Mauna Loa Road combined, 2007–2010

⁶ Inside/outside ungulate exclosures at Kahuku Unit, 2006–2009

Seed germination was high in at least some of the germination trials carried out for both species. The viability of seeds was not studied, but is clearly high based on the high germination rates achieved in the greenhouse. The soil seed bank was not investigated for either species, but the presence of natural seedlings at studied populations after the peak fruiting season indicated that at least a transitory seed bank was likely present. Both natural

and planted seedlings of *P. stachyoides* had high mortality, but this trend was less pronounced for *S. hawaiiensis*. Grass cover, a combination of native and alien species, appeared to have no effect on the survival of planted seedlings of *P. stachyoides*; *S. hawaiiensis* did not occur in grassy habitats. Ungulates, most likely mouflon sheep, browsed 100% of unprotected plantings of *S. hawaiiensis* outside exclosures. Browsing was shown to have an impact on the plants' height and reproduction, although it did not increase the mortality rate, at least in the short-term. Plants of *P. stachyoides* were not subjected to ungulate damage in this study. The impacts of rodents were not specifically studied for either species, but no sign of flower or fruit/seed predation by rodents was noted in two to three years of monitoring.

DISCUSSION

Population Structure, Growth, and Mortality

The natural population of *Phyllostegia stachyoides* appeared to be relatively stable in the two kīpuka monitored, with low to moderate mortality of adult plants and the recruitment and persistence of natural seedlings. The two populations of *Silene hawaiiensis* studied did not display the same population structure; the Mauna Loa population (Three Trees Kīpuka) appeared to be relatively stable with low adult mortality and low seedling recruitment. Both the group of 200 sampled plants and those in the three stand structure plots at Three Trees Kīpuka displayed nearly bell-shaped population structures, indicating stability (Barbour *et al.* 1980). However, the Kīlauea *S. hawaiiensis* population south of Halema`uma`u appeared to be declining with pronounced losses of larger plants, at least in the subset of plants monitored for phenology. The more geographically dispersed stand structure plots at Kīlauea showed a slightly different pattern with larger size classes remaining stable and smaller classes exhibiting small losses. The population structure of the Kīlauea *S. hawaiiensis* within the stand structure plots was a reverse J-curve, indicating a potentially growing population (Barbour *et al.* 1980).

For both species, there was a loss of adult plants in the natural populations between 2006 and 2008. In one of the monitored kīpuka that supported *P. stachyoides*, seedling recruitment compensated for the loss of adult plants, at least in the final year of the study, since there were almost twice as many surviving seedlings present as there were dead adults. Longevity is unknown for most rare species of Hawaiian *Phyllostegia* (U.S. Fish and Wildlife Service 1998), but the species is presumed to be a short-lived perennial (U.S. Fish and Wildlife Service 2008).

The adult plant mortality was very low for *S. hawaiiensis* at the natural population on Mauna Loa; the mortality rate between 2000 and 2008 was less than half that reported for *S. hawaiiensis* in 1992–1998 at a slightly lower-elevation site on Mauna Loa (Belfield and Pratt 2002). Mortality was considerably higher at the population south of Halema`uma`u on Kīlauea, amounting to almost a third of monitored plants. Losses at the Kīlauea site did not appear to be related to exceptionally dry conditions, as the years immediately preceding and during the study (2005–2007) had higher than average yearly rainfall totals, amounting to >300–400 mm greater than the seven-year mean annual precipitation of 1,317 mm (HAVO Fire Cache, unpublished data). On Mauna Loa, seedling recruitment of *S. hawaiiensis* was detected in 2 of 3 stand structure plots, but this did not completely compensate for the loss of adult plants in the plots. It is unclear if seedling recruitment offset the high losses of adult plants at the regularly monitored population south of Halema`uma`u, since it was not possible to accurately detect seedlings during monitoring of the scattered plants. A few seedlings were detected within the six stand structure plots, but their low number did not compensate for the losses of adult plants

in the same plots. Little is known about the life history or longevity of *S. hawaiiensis* (U.S. Fish and Wildlife Service 1996), but the presence of an enlarged fleshy tap root (Wagner *et al.* 1999) indicates that the species is relatively long-lived and capable of withstanding dry conditions. The current study showed that most individuals on Mauna Loa were older than eight years, and a few plants at the Kīlauea site south of Halema`uma`u still had numbered tags dating from 1994, indicating age greater than 14 years (L. Pratt, unpublished data).

Growth in height was detected among sampled individuals in the natural *Phyllostegia stachyoides* population, but height was not a particularly useful tool to determine population structure in this species. There was little variation in heights of adult plants, and it is likely that number of stems may be a better gauge of size and age in this shrubby, semi-woody species. *Silene hawaiiensis* at the Mauna Loa Three Trees Kīpuka site tended to be taller and more robust than those at the Kīlauea population south of Halema`uma`u. *Silene hawaiiensis* monitored at the Mauna Loa population increased in height during the study, while those at the Kīlauea population decreased. This may be another indication of the decline in the population at this site. These multi-branched shrubs are likely decreasing in height by the death of the larger branches.

When *Silene hawaiiensis* was listed as a threatened species in 1994, it was thought to have approximately 3,000 plants on the island of Hawai`i. Subsequently, more than 11,000 plants were reported within 11 populations on the island (U.S. Fish and Wildlife Service 1996), including more than 5,000 plants in HAVO and more than 3,000 at Pōhakuloa Training Area (PTA). More recent surveys for this threatened species on the island have led to the mapping of more than 6,400 plants over 13% of the island, with estimates of as many as 25,000 plants present (Center for Ecological Management of Military Lands [CEMML] 2006). However, except for the plants protected within fenced exclosures at HAVO, most other Hawai`i Island plants are subject to browsing by feral ungulates. While PTA supports a population of several thousand *S. hawaiiensis* plants, few of them occur within existing ungulate-proof exclosures (CEMML 2006).

The results of the Kahuku plantings inside and outside exclosures in the current study, as well as results from previous studies in HAVO (Belfield and Pratt 2002), indicate that exposure to browsing ungulates reduces the size of *S. hawaiiensis* plants and prevents them from flowering and reproducing by seeds. While the plants appear to be able to survive repeated browsing events and persist, at least in the short term, the ultimate impact of continuous ungulate pressure on populations of *S. hawaiiensis* is likely reduction and eventual loss, as old plants succumb and are not replaced by recruited seedlings. This scenario is indeed what was observed at Kahuku Unit of HAVO (Benitez *et al.* 2008), where very few scattered individual *S. hawaiiensis* were found in extensive subalpine areas that appeared to be suitable habitat for the plant but were infested with a large population of mouflon sheep (Hess *et al.* 2006). The *S. hawaiiensis* populations protected within fenced management units and SEAs at HAVO receive the highest level of protection afforded the species anywhere on the island, and HAVO continues to represent a significant part of this threatened species' designated critical habitat (U.S. Fish and Wildlife 2002).

Patterns of Reproductive Phenology

Both of the rare plant species monitored in this study had annual patterns of flower and fruit production. *Phyllostegia stachyoides* plants at the natural population showed consistent peaks for buds, flowers, and immature fruit in the spring and summer and a slightly later peak in fall for mature fruit. Flowering phenology was similar at three of the planting sites on the Mauna

Loa Road, although the pattern was less pronounced as data were collected for a shorter time period. Fruit production was more truncated at the planting sites, and the peak was earlier in the summer as compared to the natural population.

Silene hawaiiensis reproductive phenology at the Mauna Loa population was strongly seasonal with buds and flowers seen primarily in the summer and fall, although some budding and flowering was noted in all months except March. Immature fruits were produced during fewer months, primarily in the summer and fall, but old dry fruit capsules were present in all months except May and occurred in high abundance for an extended period from August to January in one year. The pattern of bud and flower production at the Kilauea Crater Rim site was similar to that seen at the Mauna Loa site with the seasonal lows in spring even more pronounced. Immature fruits were seen during few months in the summer and fall, as was noted at the Mauna Loa site. Mature and old fruits were observed on most plants in fall and winter from September to January; the mature category of fruits was more ephemeral at the Mauna Loa site (which was visited bimonthly), and most fruits were categorized there as either immature or old dry capsules. Previous studies of HAVO *Silene hawaiiensis* on Mauna Loa reported that approximately half of plants bore buds, flowers or young fruit in the fall and winter; most of the observed fertile plants were in the large size class >30 m in height (Belfield and Pratt 2002). The persistence of dry fruit capsules for up to a year was also noted in the previous study on Mauna Loa.

The annual pattern of reproductive phenology displayed by the two rare plant species investigated in this study is typical in neotropical shrubs of both wet and dry forests (Opler *et al.* 1980), as well as for tropical tree species in general (van Schaik *et al.* 1993). The annual pattern of flowering has also been reported for most plant species studied in Hawai`i. All nine wet forest species for which phenology was studied on Maui were found to have annual flower peaks (Berlin *et al.* 2000). The dominant tree of wet forests and most other vegetation types in Hawai`i, *Metrosideros polymorpha*, was found to have a strongly annual flowering and fruiting phenology in several studies (Carpenter and MacMillan 1973, Porter 1973, Berlin *et al.* 2000). Dry and mesic forest trees of Hawai`i, such as *Sophora chrysophylla* and *Acacia koa*, have also been observed to have annual patterns of flowering and fruiting (Lanner 1965, van Riper 1980, Pratt *et al.* 1997, Banko *et al.* 2002). By contrast, four of five rare mesic forest plant species recently studied in HAVO had continuous patterns of flowering and fruiting and only the rare vine *Sicyos macrophyllus* displayed an annual phenological pattern (Pratt *et al.* 2010).

The pattern of seasonal flowering in the summer and fall observed for *Silene hawaiiensis* on Mauna Loa in the current study was in contrast to the winter flowering peak reported for both *Acacia koa* and *Sophora chrysophylla* on Mauna Loa (Lamoureux *et al.* 1981). However, the flowering season of *S. hawaiiensis* was shared by three other mesic forest tree species studied on Mauna Loa: *Santalum* sp.; *Myoporum sandwicense*; and *Sapindus saponaria* (mānele; Lamoureux *et al.* 1981). The annual seasonal pattern of spring and summer bud and flower production observed for *P. stachyoides* in the current study was also displayed by the rare wet forest mint *P. floribunda* in a recent study of plants in `Ōla`a Forest, HAVO (VanDeMark *et al.* 2010).

Success of Fruit Production

Both rare plant species investigated in this study demonstrated high rates of successful fruit production. Flowers and buds of *P. stachyoides* transitioned to immature fruit at a rate of 45% at the natural population and similarly at 46% at the planting sites. These rates of fruit

production are on a par with the 55% fruit set reported for red-flowered *Metrosideros polymorpha* (Carpenter 1976), the dominant native tree species of most Hawaiian forests. The rates of fruit set determined in the current study were much higher than those reported for other common native Hawaiian trees, such as *Acacia koa* with 15% fruit set (Lanner 1965) or *Sophora chrysophylla* with 17% pod production from flowers (van Riper 1980). The rate of transition of *P. stachyoides* buds and flowers to immature fruit was similar to the 51% fruit set determined for its rare congener in the park's `Ōla`a wet forest, *P. floribunda*, and the 17.8% transition of immature to mature fruit demonstrated for *P. stachyoides* at its natural population was only slightly higher than that reported for *P. floribunda* (VanDeMark *et al.* 2010). In both mint species, the transformation from immature to mature fruit was relatively rapid, and the monitoring interval may not have been short enough to detect all mature fruits before they were dispersed.

The higher rate of mature fruit formation from immature fruit observed at the planting sites of *P. stachyoides* (36.7%), as compared to that at the natural population, is not understood, but may relate to a lower number of natural dispersal agents at the planting site. Dispersal of *P. stachyoides* was not examined in the current study, but the dispersal agents for the fleshy-fruited Hawaiian mints are presumed to be birds (Lindqvist and Albert 2002, Price and Wagner 2004). The endemic fruit-eating `ōma`o or Hawaiian Thrush (*Myadestes obscurus*) is present on Mauna Loa in the general area of both the natural *P. stachyoides* population and planting sites (Conant 1976), but the relative abundance of the bird at different sites is unknown. While the fruits of Hawaiian mints are not listed as major food items for the `ōma`o (Wakelee and Fancy 1999), the size of the fleshy nutlets of this *Phyllostegia* (ca. 3 mm according to Wagner *et al.* 1999) is within the range of diameters of fruit consumed by the thrush (mean size 8.3 mm), and the species is known to feed on a wide variety of available fruits within its habitat (Wakelee and Fancy 1999).

The success rate of immature, green fruit formation for *S. hawaiiensis* at the Kīlauea study site, 52.5%, was even higher than that for *P. stachyoides*. The formation of mature fruit, which are dry, straw-colored capsules, was very high with 66.7% of immature *Silene* fruit successfully maturing on the plant. This high fruit set means that the threatened species *S. hawaiiensis* is more successful at producing seeds than are most common Hawaiian plants studied. Each mature *S. hawaiiensis* capsule contained a large number of tiny seeds (>60), which were presumably dispersed over short distances by wind, through an opening at the top of the mature, dry fruit. *Silene* in general have no adaptations for long-distance dispersal (Eggens *et al.* 2007). Because animals were not dispersing the dry fruit, they were retained on the plant for several months.

Pollination

Flowers of *P. stachyoides* were visited by a limited number of insect taxa. The hover fly *Allograpta obliqua* was by far the most frequent visitor. Adult Syrphids or hover flies are flower specialists that require nectar for energy and pollen for proper egg development (Schneider 1969). The second most abundant visitor, *Hylaeus difficilis*, has been recorded as a floral visitor of a variety of other Hawaiian plant species (Daly and Magnacca 2003). The white petals of *P. stachyoides* are fused into a tubular corolla that flares out to form a smaller lower and larger upper lip. The floral visitors were observed landing on the lower lip and then probing the anthers for pollen. Pollen-load analyses of insects collected near the natural population of *P. stachyoides* indicated that *A. obliqua* and *H. difficilis* were both carriers of pollen of *P. stachyoides*. The pollen of other plant species found in the pollen loads suggested that neither

insect species restricted visits to the flowers of *P. stachyoides*. Further studies are needed to determine if *P. stachyoides* is self-compatible and is capable of self-fertilization.

Flowers of *S. hawaiiensis* were visited by three different insect taxa, including two species of *Hylaeus* yellow-faced bees and a species of hover fly, each with extremely low visitation rates. The exposed habitat of the Ka`ū *S. hawaiiensis* population is characterized by moderately high wind speeds, which may be an important variable influencing the low floral visitation rates. High winds have been documented to constrain pollinator floral visitation (Totland 1994). Even though the flowers of *S. hawaiiensis* exhibit several characteristics of a moth-pollinated syndrome (white petals, tubular corollas, and nocturnal anthesis; Faegri and van der Pijl 1966), no nocturnal floral visitors were observed. Since access to the study area was closed due to an eruption in Halema`uma`u Crater in early 2008, the number of floral visitation observations was limited. A greater number of observations hours are needed to attain a better understanding of the composition of the floral visitor assemblage and their visitation rates.

Seed Germination, Dispersal, and Natural Seedlings

Seed germination rates from greenhouse trials were variable for *Phyllostegia stachyoides* and *Silene hawaiiensis*, but in both species more than half of the germination trials achieved >50% germination. Germination as high as 80% was observed for *P. stachyoides*, and the highest rate achieved by *S. hawaiiensis* in the study was 73%. Germination rates this high indicate that seed viability and germinability are not serious problems for the two species. In a previous study of another rare *Phyllostegia* native to the `Ōla`a Forest in HAVO, greenhouse seed germination rates were typically >80% and some trials had 100% germination (VanDeMark *et al.* 2010). Plant propagators at HAVO Natural Resources Management Division have also reported high germination rates for several other species of wet forest *Phyllostegia* (S. McDaniel, pers. comm.).

Seeds of *Phyllostegia stachyoides* have been reported to have physiological dormancy (Baskin *et al.* 2004), which is a physiological mechanism within the seed embryo that prevents the embryonic root from emerging (Baskin and Baskin 1998). This type of dormancy is typically broken by a certain length of time at high or low temperatures. The relatively long period between seed sowing and germination observed in the current study may be evidence for this type of dormancy. Lilleeng-Rosenberger (2005) reported that two weeks to three months were required for germination of Hawaiian members of the genus *Phyllostegia*. The low end of this range is shorter than the emergence time we observed, but three months was the typical emergence time in several trials of our study. Lilleeng-Rosenberger's work was carried out at low elevation on Kaua`i, under conditions considerably warmer than those of the HAVO greenhouse. Dormancy that delays germination of *P. stachyoides* seeds from the time they are produced in the dry summer and fall until the arrival of greater rainfall during the winter months would likely be an advantage for this species of the dry to mesic montane forests of its natural habitat.

No seed dormancy studies have been carried out on *Silene hawaiiensis*, although seeds of a related Hawaiian species, *S. lanceolata*, have physiological dormancy (Baskin *et al.* 2004). Seeds of several other species of *Silene* from temperate sclerophyllous woodlands in North America and Europe also display physiological dormancy (Baskin and Baskin 1998). The relative rapidity with which *S. hawaiiensis* seeds germinated in the current study is evidence for the lack of dormancy in seeds of this species, although the fact that seeds continued to germinate for up to five months may relate to some aspect of physical dormancy. Lilleeng-Rosenberger

(2005) found that Hawaiian members of the family that includes *Silene* (Caryophyllaceae) required from three weeks to three months for germination, a considerably longer emergence time than the two-week average we observed for *S. hawaiiensis*.

The seed dispersal experiment with *Silene hawaiiensis* at the Kilauea Crater Rim population demonstrated that the tiny seeds of the species could be dispersed by wind to a distance of 40 m. Presumably, wind can disperse *Silene* seeds even farther, but we have no data to support this. However, the pattern of wide distribution in the Ka`ū Desert of HAVO, as well as that of the species over enormous areas of Hawai`i Island (CEMML 2006) indicates that the species is capable of dispersing far into suitable dry habitat. The dry straw-colored capsules of *S. hawaiiensis* do not have the characteristics of a bird-dispersed fruit (Carlquist 1980, Howe and Smallwood 1982), and the small seeds have no obvious adaptation for long-distance seed dispersal such as wings or plumes. The ancestor of the species is presumed to have been dispersed to the Hawaiian Islands by birds externally on feathers or muddy feet (Eggens *et al.* 2007). Within the dry open habitat of the Kilauea Crater Rim and Ka`ū Desert, the seeds of *S. hawaiiensis* may be spread over short distances by wind, as demonstrated in the current experiment, or by water; adult plants in the study area were often seen on the edge of intermittent flow channels cut through the ash and cinder substrate.

Phyllostegia stachyoides dispersal was not investigated in the current study, but the fleshy fruits in this genus and other members of the mint family are considered to be an adaptation for dispersal by birds (Carlquist 1980, Price and Wagner 2004), and the endemic frugivorous thrush, the `ōma`o, is present within the mint's habitat on Mauna Loa (Wakelee and Fancy 1999; see previous section).

Natural seedlings appeared in large numbers near many of the monitored plants at a single monitored kīpuka supporting a natural population of *P. stachyoides*. Over two years, seedlings appeared in the late fall and winter; most seedlings were first observed during the month of January, which typically had >150 mm mean monthly rainfall at a nearby weather station on Mauna Loa (HAVO Fire Cache, unpublished; Appendix III, Figure 2). Seedling survival was very low (2.3%) for the entire study, but because of the large number of seedlings that appeared, the number of new plants that recruited into the population was greater than the number of adult plants that were lost, and the population had a net gain of individuals. We did not carry out soil seed bank studies for this species, but the appearance of seedlings several months after the last production of mature fruit indicated that at least a transitory seed bank formed. Lack of seed banks or transitory seed banks are typical of most native plant species in Hawaiian wet forests that have been studied (Drake 1998, Loh and Daehler 2008). The cause of the disappearance of natural seedlings is unknown, but may be related to dry conditions. Most seedlings were lost during the months of April through July, which correspond to the driest months, on average, at two nearby weather stations on Mauna Loa (HAVO Fire Cache, unpublished; Appendix III, Figure 1 and Figure 2). No sign of slugs was noted at the study site, so these aliens do not appear to be the cause of seedling disappearance. Slugs have been demonstrated to be serious seedling predators in Hawaiian wet forests (Joe and Daehler 2008).

Planting Survival and Potential Restoration Strategies

The two rare plant species examined in the current study have been propagated and planted in several restoration projects in HAVO over the last six years (McDaniel *et al.* 2008, McDaniel and Anderson 2010, Belfield *et al.* 2011), but they were not the subject of earlier restoration efforts (Morris 1967, Smith 1977). *Phyllostegia stachyoides* was only recently recognized as a

component of the park's natural flora (Pratt *et al.* 2011), and the natural populations in the Mauna Loa Strip were located or relocated just seven years ago. *Silene hawaiiensis* was previously considered to be a variety of the more common and widespread species *S. struthiolooides* (Sherff 1946, Fosberg 1966), and the species did not appear on HAVO vascular plant checklists until 1976 (Fosberg 1976). The vulnerability of the species to feral ungulate browsing in HAVO was only recently documented (Belfield and Pratt 2002).

The results of the current study indicated that accessible sites along the Mauna Loa Road were capable of supporting plantings of *P. stachyoides*, but survival over three years was very low. The comparison of ground cover among a natural population and three planting sites demonstrated that there were subtle differences in plant species composition in the two areas. The presence of 10–30% cover of the native grass *Deschampsia nubigena* at all planting sites and its near absence at kīpuka 4 may indicate that these areas on the Mauna Loa Road were drier than was the natural site supporting *P. stachyoides*. Total grass cover was higher than that at the natural population at one of the planting sites (site 4, grass), similar in percentage at site 2, and much lower at site 3 and site 4, low grass areas. Although the low-grass planting sites had a greater percentage of live plants at the end of three years than did the high grass planting sites at the same elevation, survival was not significantly higher there.

Alien grasses are generally considered to be detrimental to native species in tropical ecosystems worldwide (D'Antonio and Vitousek 1992) and in seasonal ecosystems in Hawai'i (Hughes *et al.* 1991), largely because of their alteration of the natural fire cycle. However, in a grass removal experiment in a HAVO woodland near Kīpuka Nēnē, grass removal plots had lower soil moisture and greater mortality of some shrub species than did untreated control plots (D'Antonio *et al.* 1998). Only shrub seedlings responded positively to the grass removal and appeared in greater numbers than in untreated plots with heavy alien grass cover. The results of the current study indicate that the amount of grass cover and the relative proportion of native to alien grasses may not significantly influence the survival of planted *P. stachyoides*. Further work selecting appropriate planting sites is warranted, based on the low survival rates of planted seedlings. On west Maui and Moloka'i, *P. stachyoides* is known from elevations lower (to 880 m) than the Kona and Ka'ū populations on Hawai'i Island (Sherff 1935, Wagner *et al.* 1999), and many collections are from wet forest sites (Bishop Museum *Herbarium Pacificum* n.d.) indicating that somewhat wetter habitats at lower elevations within the park might be appropriate planting sites for this rare mint. Additional plantings of the species are planned at several park sites (McDaniel and Anderson 2010), and the results of these efforts may guide the selection of future restoration sites.

Based on the limited work we did with seeding *P. stachyoides* at the natural population in kīpuka 4, there appears to be little benefit gained for seedling recruitment by removing grasses. This experiment may be considered inconclusive, as it was carried out in only one season, and results might differ in other seasons or in times of greater rainfall. Direct seeding did not appear to be a useful management tool for restoration of the species, at least at the tested site. In *Metrosideros polymorpha* woodlands of HAVO, direct seeding into burned sites has been shown to be effective at recruiting seedlings for several common tree and shrub species, such as *Acacia koa*, *Dodonaea viscosa*, and *Sophora chrysophylla* (Loh *et al.* 2007). Seeding was feasible at the burned sites because the target native plant species were abundant and large quantities of seeds were readily available. The technique has not been used in recent rare plant restoration projects (Belfield *et al.* 2011) because of the paucity of available seeds and the

lower rate of establishment from seeding when compared to the planting of propagated seedlings or saplings.

In the current study, *Silene hawaiiensis* was planted only at Kahuku to evaluate the differential survival, size, and reproduction of plants in the presence and absence of feral ungulates. The results of this planting indicated that *S. hawaiiensis* was severely browsed by mouflon sheep, and restoration efforts would be most effective within ungulate-proof exclosures.

CONCLUSIONS

Phyllostegia stachyoides has small known populations in several kīpuka of the Mauna Loa Strip. It is unknown whether these populations have declined in the recent past, since they were discovered only a few years ago, and intensive monitoring began with the current study. The mortality rate of adult plants in the natural population was relatively low, and natural seedling recruitment exceeded the loss of adult plants during the course of the study, despite the high percentage of mortality of seedlings. The phenology of flowering and fruiting was annual and strongly seasonal, and the successful formation of fruit from flowers was very high. Both native and alien insect species were observed visiting flowers and carrying pollen of the rare mint. Seed germination rates were high, indicating that floral visitors were acting as effective pollinators of the species. Mortality of planted seedlings was very high after two-to-three years, and the presence of a high cover of grass did not significantly affect seedling mortality rates. Planted seedling survival was approximately the same at pairs of sites at two elevations (1,710 and 1,830 m). The most important limiting factor recognized for this rare mint species was low seedling recruitment.

Silene hawaiiensis had large populations within HAVO, both on Mauna Loa and on Kīlauea Crater Rim south of Halema`ūma`u. The population structure of the species at Three Trees Kīpuka on Mauna Loa indicated a relatively stable population, but the structure of the population at the Kīlauea site suggested a declining population. Mortality rates of adult plants were also very high (>30%) at the Kīlauea site and much lower (<10%) at the Mauna Loa study site. Heights of adult plants were greater on Mauna Loa than at the Kīlauea study site. Randomly selected stand structure plots indicated a much higher density of *S. hawaiiensis* plants in the study area on Mauna Loa as compared to the general area of the natural population on the Crater Rim and Ka`ū Desert of Kīlauea. Natural seedling recruitment was detected in stand structure plots at both sites, but in both cases, numbers of new seedlings did not exceed the number of adult plants lost over the year between sampling and re-sampling.

Reproductive phenology of *S. hawaiiensis* was annual at both study sites, and most plants bore buds and flowers in the summer and fall and fruit in the fall and winter. The successful formation of immature fruit from buds and flowers was high, and most immature fruit became mature fruit. The transitions from bud to flower and flower to immature fruit capsule were rapid. Floral visitation rates for insects at the Kīlauea site were low, but observations were curtailed by an eruption. Seed germination rates were high in some trials, although variable in others. Seed dispersal was detected from the edge of the Kīlauea population south of Halema`ūma`u to a distance of 40 m across a recent lava flow. Mortality of *S. hawaiiensis* seedlings planted at Kahuku was not significantly greater outside ungulate exclosures than inside, but the growth in height and production of reproductive structures was significantly greater inside the exclosures. Similarly to *P. stachyoides*, the seedling stage seemed to be the

most vulnerable part of the life cycle of *S. hawaiiensis*, and low seedling recruitment appeared to be the most important limiting factor for this species.

Suggestions for Future Work

The natural populations of *P. stachyoides* currently inhabit very small kīpuka within a larger region of potentially suitable habitat on the Mauna Loa Strip. Further exploration of the many small kīpuka and dense vegetation on the edge of the large Kīpuka Mauna`iu of the western half of the Mauna Loa Strip might lead to the discovery of additional populations of the rare species.

Additional natural populations of *S. hawaiiensis* might be sought in suitable habitat on old pāhoehoe flows at Kahuku in the vicinity of previous sightings of the threatened plant (Benitez *et al.* 2008). Any new populations or individuals of *S. hawaiiensis* at Kahuku would be important seed donors for future propagation and planting at the Kahuku Unit of HAVO.

Since pollination observations on *S. hawaiiensis* were curtailed by the current summit eruption, further investigation of potential pollinators is warranted for this rare species. Floral visitor observations at the park's Mauna Loa population of *S. hawaiiensis* might identify additional potential pollinators of the plant.

Management Recommendations

- To enhance seedling survival, additional sites for planting *P. stachyoides* could be sought at lower elevations than the current natural HAVO population and recent planting sites. Because of the historical record of the past occurrence of the species in Kīpuka Puauulu, that site, the adjacent Kīpuka Kī, and nearby small boundary kīpuka are likely planting sites.
- While *S. hawaiiensis* plants were abundant in the original section of the park on both Mauna Loa and Kīlauea, seedling recruitment appeared to be low and planting sites might be established in suitable open areas to extend the populations to the east and into the natural gap between the two HAVO populations. Potential sites for planting *S. hawaiiensis* are the area between the base of Kalanokuaiki Pali and Hilina Pali Road north of Kīpuka Nēnē and the areas bare of other vegetation within the Ke`āmoku Special Ecological Area west/southwest of Kīlauea Caldera.
- Because *S. hawaiiensis* is vulnerable to browsing pressure by mouflon sheep, and these ungulates remain a disturbance factor in the Kahuku addition, planting sites for the species at Kahuku are most logically ungulate-free exclosures in suitable open subalpine habitat. Exclosures exist that are currently being used for planting *Argyroxiphium kauense*, the Mauna Loa silversword, and these are also appropriate habitat for *S. hawaiiensis*. Additional plantings in the silversword exclosures (excluding the exclosure protecting the wild silversword plants) would help increase the numbers of *S. hawaiiensis*, which have been severely depleted at Kahuku.
- Removal of common mullein (*Verbascum thapsus*) from the habitat of *S. hawaiiensis* at the Three Trees Kīpuka would be prudent to prevent this aggressive alien biennial from becoming well established at the site and competing for seedling recruitment sites with *S. hawaiiensis*.

- Removal of the invasive alien plants *Physalis peruviana*, *Solanum pseudocapsicum*, and *Bidens pilosa* from the Mauna Loa habitat of *P. stachyoides* in kīpuka 4 might enhance the rare species reproduction by providing additional area for seedling recruitment near adult plants.
- Enhancement of the native vegetation in kīpuka that currently support few *P. stachyoides* (kīpuka 3 and 5) with plantings of native fruit-bearing tree species might help support the population of `ōma`o or Hawaiian thrush, the putative dispersal agent for the rare mint. Possible species to consider for this planting are *Myoporum sandwicense*, *Santalum paniculatum* (sandalwood), *Myrsine lessertiana* (kōlea lau nui), *Cheirodendron trigynum* (`ōlapa), *Pittosporum confertiflorum* (hō`awa), and *Rubus hawaiensis* (`ākala). All these suggested tree and shrub species currently exist in the area in depleted numbers.
- It would be prudent to consider the impacts to insect pollinators of rare plants when pesticides are used in the vicinity of rare plant populations or plantings.

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APPENDIX I

Descriptions of the Flowers of Two Rare Plant Species in This Study

Phyllostegia stachyoides—Flowers are borne in whorls of 10–14 on compound inflorescences (racemes) composed of the main stem and at least two lateral branches. (A raceme is an inflorescence with stalked flowers maturing from the bottom up.) Individual flowers have pedicels (flower stalks) 2–7 mm long, which are villous with long soft hairs. The bracts are lanceolate (lance-shaped) and 7–17 mm long, with the lowermost pair larger at 25–40 mm. The calyx of the flower is campanulate (bell-shaped), 3.5–8 mm long; it is covered with short fine hairs and gland dots. Calyx teeth are linear or linear-deltate, 2–4 mm long, hairy primarily along margins, evenly gland-dotted, with a tapered, pointed tip. The corolla is white, sometimes with a pink-tinged upper lip. The corolla tube is straight, 6–12 mm long and pubescent; the small upper lip is 3 mm; and the lower lip is 7–8 mm long with a margin either entire or notched. There are four stamens with the upper pair slightly longer than the other but still within the corolla. Stamen filaments are finely hairy and bear anthers with two cells. The pistil (female part of flower) has a two-lobed style included within the corolla and a terminal stigma (Wagner *et al.* 1999). Flowers may be slightly fragrant.

Silene hawaiiensis—Flowers are borne in a narrow, paniculate cyme (a round-topped determinate inflorescence, in which the terminal flowers blooms first), and there are usually short, sticky hairs throughout the inflorescence. Individual flowers have pedicels (flower stalks) 3–6 mm long. The calyx of the flower is purple, five-toothed, 11–14 mm long, covered with short, sometimes sticky hairs, with 10 faint nerves or veins. The calyx lobes are pointed and have hairs on the margins (ciliate). The flower petals are greenish white or white above and maroon below and are structurally in two parts: a cleft blade 4.5–5.5 mm long, exserted beyond the calyx, and a base with a two-lobed appendage exserted 3 mm beyond the calyx. There are 10 stamens included or barely exserted beyond the corolla and fused to the petals at the base. Anthers are two-celled and open by longitudinal slits. The pistil has three styles and a one-celled ovary (Wagner *et al.* 1999). Flowers do not appear to have any fragrance.

APPENDIX II

Data From Greenhouse Germination Trials

Table 1. Germination of *Phyllostegia stachyoides* in the greenhouse.

Trial/ replicate #	# seeds	Date sown	Date 1st germination	# seeds germinated	% germinated	Date terminated
1/1	24	5/15/2005	8/8/2005	11	45.8	4/4/2006
1/2	25	5/15/2005	8/8/2005	3	12.0	4/4/2006
1/3	50	5/15/2005	8/8/2005	18	36.0	4/4/2006
Mean				10.7	32.3	
2/1	50	8/10/2006	9/13/2006	30	60.0	6/18/2007
2/2	50	8/10/2006	9/13/2006	30	60.0	6/18/2007
2/3	50	8/10/2006	9/13/2006	34	68.0	6/18/2007
Mean				31.3	62.6	
6/1	63	6/12/2008	9/16/2008	44	69.8	6/8/2009
6/2	63	6/12/2008	9/29/2008	35	55.6	6/8/2009
6/3	63	6/12/2008	9/29/2008	20	31.7	6/8/2009
Mean				33	52.4	
7/1	28	6/24/2008	9/2/2008	17	60.7	6/8/2009
7/2	28	6/24/2008	9/2/2008	23	82.1	6/8/2009
7/3	28	6/24/2008	9/10/2008	21	75.0	6/8/2009
Mean				20.3	72.6	
8/1	50	6/24/2008	9/2/2008	42	84.0	6/8/2009
8/2	50	6/24/2008	9/2/2008	38	76.0	6/8/2009
8/3	50	6/24/2008	9/2/2008	49	98.0	6/8/2009
8/4	50	6/24/2008	9/2/2008	34	68.0	6/8/2009
8/5	50	6/24/2008	9/10/2008	38	76.0	6/8/2009
Mean				40.2	80.4	
9/1	22	6/24/2009	8/28/2009	3	13.6	6/1/2010
9/2	22	6/24/2009	8/3/2009	4	18.2	6/1/2010
9/3	22	6/24/2009	8/3/2009	2	9.1	6/1/2010
Mean				3.0	13.6	

Table 2. Germination of *Silene hawaiiensis* in the greenhouse.

Trial/ replicate #	# seeds	Date sown	Date 1st germination	# seeds germinated	% germinated	Date terminated
1/1	50	5/11/2006	5/23/2006	38	76.0	8/29/2006
1/2	50	5/11/2006	5/23/2006	35	70.0	8/29/2006
Mean				36.5	73.0	
2/1	50	8/24/2006	9/20/2006	4	8.0	3/6/2007
2/2	50	8/24/2006	9/20/2006	5	10.0	3/6/2007
2/3	50	8/24/2006	9/20/2006	2	4.0	3/6/2007
2/4	50	8/24/2006	9/20/2006	2	4.0	3/6/2007
2/5	50	8/24/2006	9/20/2006	4	8.0	3/6/2007
2/6	50	8/24/2006	9/20/2006	4	8.0	3/6/2007
Mean				3.5	7.0	
3/1	50	6/27/2007	7/5/2007	18	36.0	1/8/2008
3/2	50	6/27/2007	7/5/2007	37	74.0	1/8/2008
3/3	50	6/27/2007	7/5/2007	36	72.0	1/8/2008
Mean				30.3	60.7	
4/1	50	7/2/2007	7/9/2007	6	12.0	1/8/2008
4/2	50	7/2/2007	7/9/2007	9	18.0	1/8/2008
4/3	50	7/2/2007	7/9/2007	5	10.0	1/8/2008
Mean				6.7	13.3	
5/1	100	1/17/2008	2/5/2008	59	59.0	8/6/2008
5/2	100	1/17/2008	2/5/2008	79	79.0	8/6/2008
5/3	100	1/17/2008	2/5/2008	48	48.0	8/6/2008
5/4	100	1/17/2008	2/5/2008	58	58.0	8/6/2008
5/5	100	1/17/2008	2/5/2008	68	68.0	8/6/2008
Mean				62.4	62.4	

APPENDIX III

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

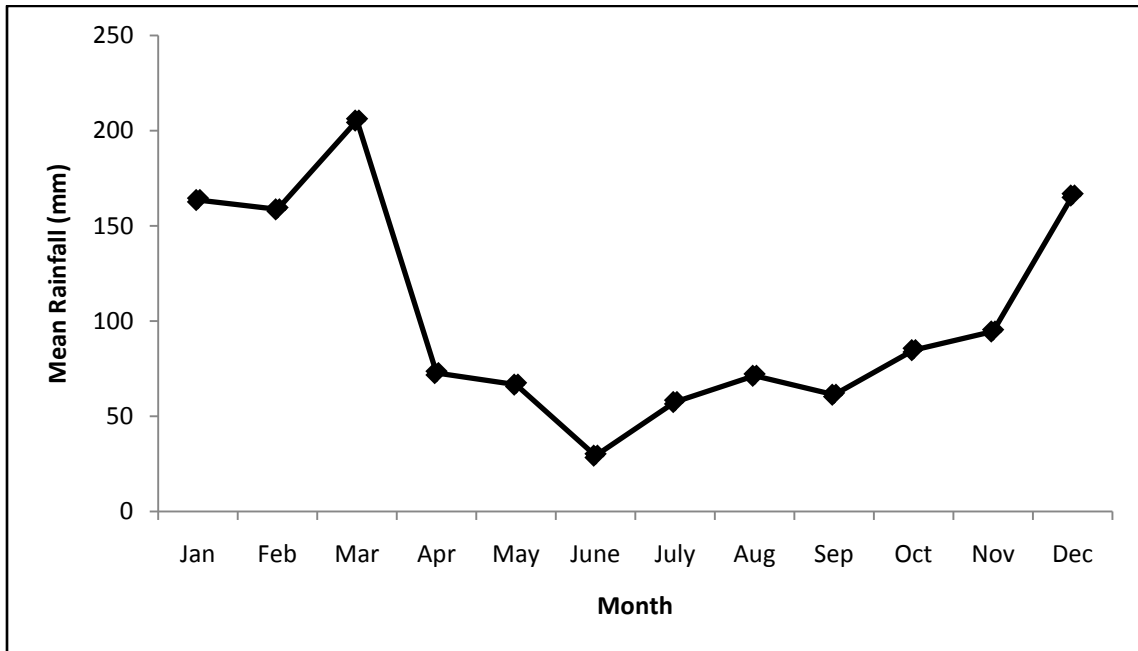


Figure 1. Mean monthly rainfall at the Ke`āmoku weather station in HAVO (1,680 m elevation).

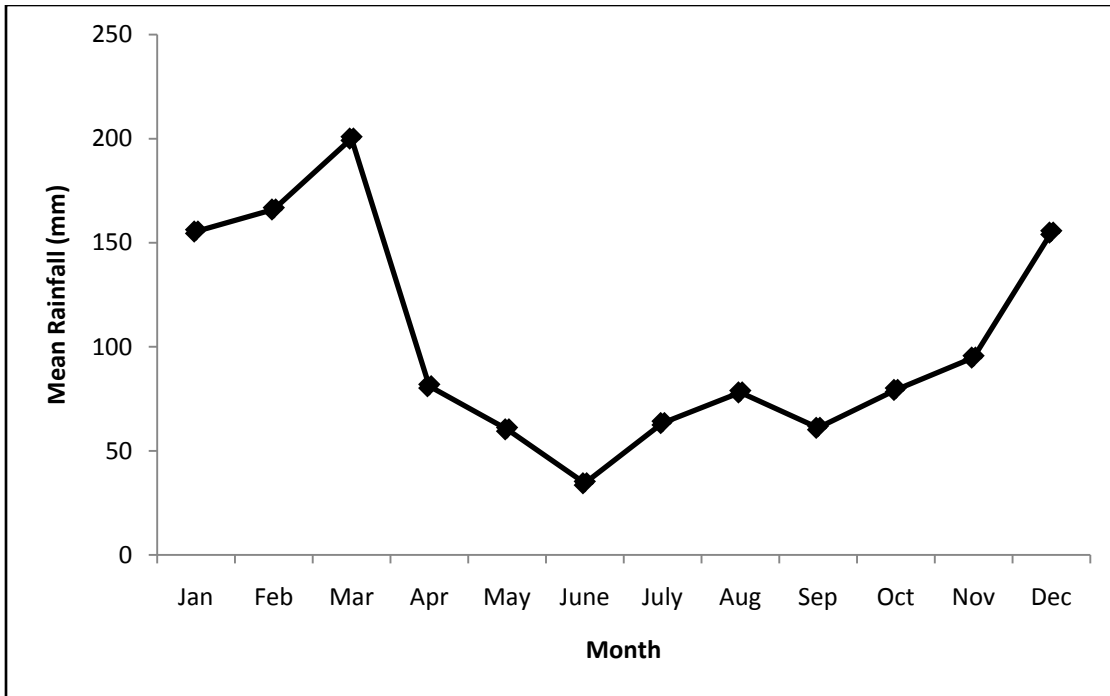


Figure 2. Mean monthly rainfall at the Mauna Loa weather station in HAVO (2,040 m elevation).

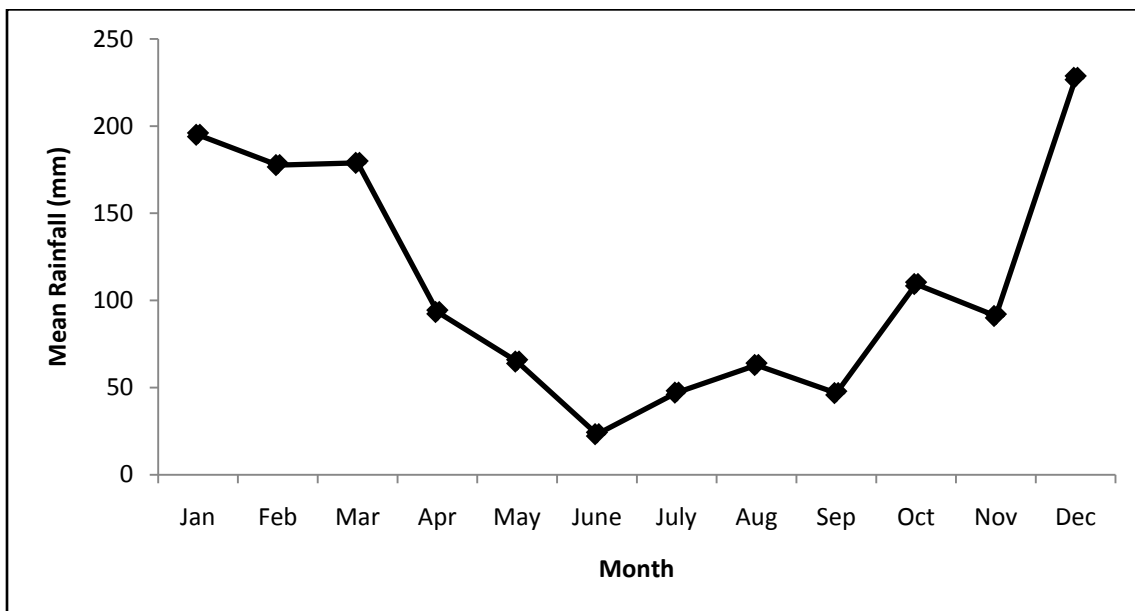


Figure 3. Mean monthly rainfall at the Halema`uma`u weather station in HAVO (1,200 m elevation).