Pacific Island Ecosystems Research Center

Distribution and abundance of the two spotted leafhopper (*Sophonia rufofascia*) in relation to host plants in Hawaii Volcanoes National Park

By Linda Lenz, Jeffrey Taylor & David Foote

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ABSTRACT

The two-spotted leafhopper (TSLH) *Sophonia rufofascia* (Homoptera: Cicadellidae) (Kuoh and Kuoh), was first reported in the state of Hawai`i in 1987 and has since become a concern due to the wide range of plant damage that can result from this insect's feeding. Two-spotted leafhopper abundance was monitored on the native dominant Hawaiian tree, *Metrosideros polymorpha* (Gaud.), `ohi`a lehua, within three sites in Hawai`i Volcanoes National Park (HAVO). Monitoring was done within paired areas in each site: areas where the invasive, non-native *Morella (=Myrica) faya* (Aiton), faya tree, had been mechanically removed (referred to as Special Ecological Areas or SEAs) and in immediately adjacent areas, where faya tree had not been removed (referred to as control areas). In addition, TSLH abundance was monitored on co-occurring *M. faya* and *M. polymorpha* trees in each control area. The results demonstrate that population densities of the two-spotted leafhopper are higher in areas containing faya tree. These data indicate that numbers of this destructive insect pest can be reduced as a consequence of control of the invasive alien faya tree that serves as an important host plant.

Distribution and abundance of the two spotted leafhopper (*Sophonia rufofascia*) in relation to host plants in Hawaii Volcanoes National Park

By Linda Lenz, Jeffrey Taylor & David Foote[1]

INTRODUCTION

Of the 886 non-native plants, which have become naturalized in Hawai`i following human occupation, *M. faya* has been listed as one of the 12 most noxious (Smith 1985). Populations of this tree are currently found naturalized on the islands of Kaua`i, O`ahu, Lana`i, Maui, and Hawai`i (Whiteaker and Gardner 1985). The invasion of *M. faya* represents a great threat to conservation efforts in Hawai`i Volcanoes National Park (HAVO), on the island of Hawai`i (Loh, 2004). *Morella faya* cover has increased within HAVO from one tree in 1961 to over 18,000 ha as of the latest Park Service estimate (Camrath *et al.* 2000, Loh, 2004). The cause for concern lies in the ability of *M. faya* to form dense, monotypic stands on old soils, thereby effectively first replacing and then excluding native plants (Tunison *et al.* 2000, Loh, 2004). On newer soils, the nitrogen inputs from faya tree's actinorrhizal symbionts promote the invasion of non-native grasses (Adler *et al.* 1998) and thereby promote the frequency of fires.

Efforts to curb the further spread and increase in *M. faya* density have included mechanical removal, herbicide applications, and the release of biological control agents, the combined effects of which have had only limited success (Tunison 2000). Beginning in 1985, the HAVO's Resources Management Division began concentrating invasive plant control, most notably the control of *M. faya* in intensive management and research areas, referred to as Special Ecological Areas (SEAs) (Figure 1) (Tunison and Stone 1992). The idea of concentrating weed control efforts arose from the awareness that a total weed eradication program was not feasible. Rather, efforts would be most effective at meeting management goals by being concentrated in those areas that were the most intact, representative, and biologically rich. This management approach also allowed research to follow management actions, to assess the results of various strategies and manipulations. The present study aimed to investigate the effects of *M. faya* removal on the abundance of a noxious, non-native insect herbivore, the two-spotted leafhopper (TSLH), *Sophonia rufofascia* (Kuoh and Kuoh).

The TSLH, which is of Asian origin, was first collected in the state of Hawai`i at Waimanalo, on the island of O`ahu in June of 1987 (Heu and Kumashiro 1989) and was subsequently reported on the islands of Hawai`i (in 1989), Kaua`i (1990), Lana`i (1991), Moloka`i (1992), and Maui (1992) (Fukada 1996). A 1995 survey showed that the TSLH was widely distributed between sea level and 1,220 m on all the main islands and was detected at elevations of up to 1,463 m on the leeward side of the islands. Leafhoppers typically have restricted host plant ranges (Lamp *et al*. 1994); the TSLH, on the other hand, is polyphagous. *Sophonia*'s host plant range in Hawai`i is broad, encompassing at least 307 plant species from 87 different families (Fukada 1996). Of these host species, 21.8 %, or 67 species, are endemic or indigenous, and 4.6%, or 14 of these are either endangered or candidates for listing.

The symptoms associated with TSLH feeding include foliar chlorosis, changes in leaf morphology, and damage to leaf vascular tissue (Lenz, 2000; Yang *et al.*, 2002). Foliar chlorosis results from the breakdown of chlorophyll in the leaf mesophyll, and is most often seen as an interveinal-yellowing or yellowing along the leaf margins. The morphological effects of TSLH feeding include a reduction in leaf area, cupping of the leaf margins, and an increase in the number of auxiliary shoots and leaves (Jones *et al.* 2000, Yang *et al.* 2000). The tissue-level effects of TSLH feeding include disorganized phloem and severely distorted and shrunken xylem (Jones *et al*. 2000). The tissue-level effects are similar to those described by the feeding of the potato leafhopper, *Empoasca fabae* (Harris), on

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alfalfa (Ecale and Backus 1995). The potato leafhopper probes primarily into the phloem and only occasionally reaches the xylem. The observed leaf damage results from a combination of the mechanical action of the insect's stylet (feeding-tube mouth-part) and the injection of "toxic" saliva (Ecale and Backus 1995).

The present study aimed to investigate whether the presence of *M. faya* resulted in a larger abundance of the TSLH than would otherwise be present in an area. Because TSLH feeding has been associated with a wide range of plant damage and mortality, it is conceivable that native plants co-existing with *M. faya* in the mixed *M. faya – M. polymorpha* woodland experience higher levels of stress than those growing in the absence of *M. faya*.

MATERIALS AND METHODS

Study sites

Two-spotted leafhopper abundance was compared between areas in which *M. faya* had been cleared, referred to as SEAs, and immediately adjacent uncleared areas where faya tree was still present, referred to as control areas. This was done to address the hypothesis that the presence of *M. faya* results in a greater TSLH abundance than would otherwise be present in the absence of this host species. Study sites were selected from among those SEAs that met the following criterion: dominated by *M. polymorpha*, open-canopy in structure, and easily accessible. The following SEAs met these proposed criteria: Devastation, Hilina Pali, and Kipuka Kahali`i (Figure 1, Table 1).

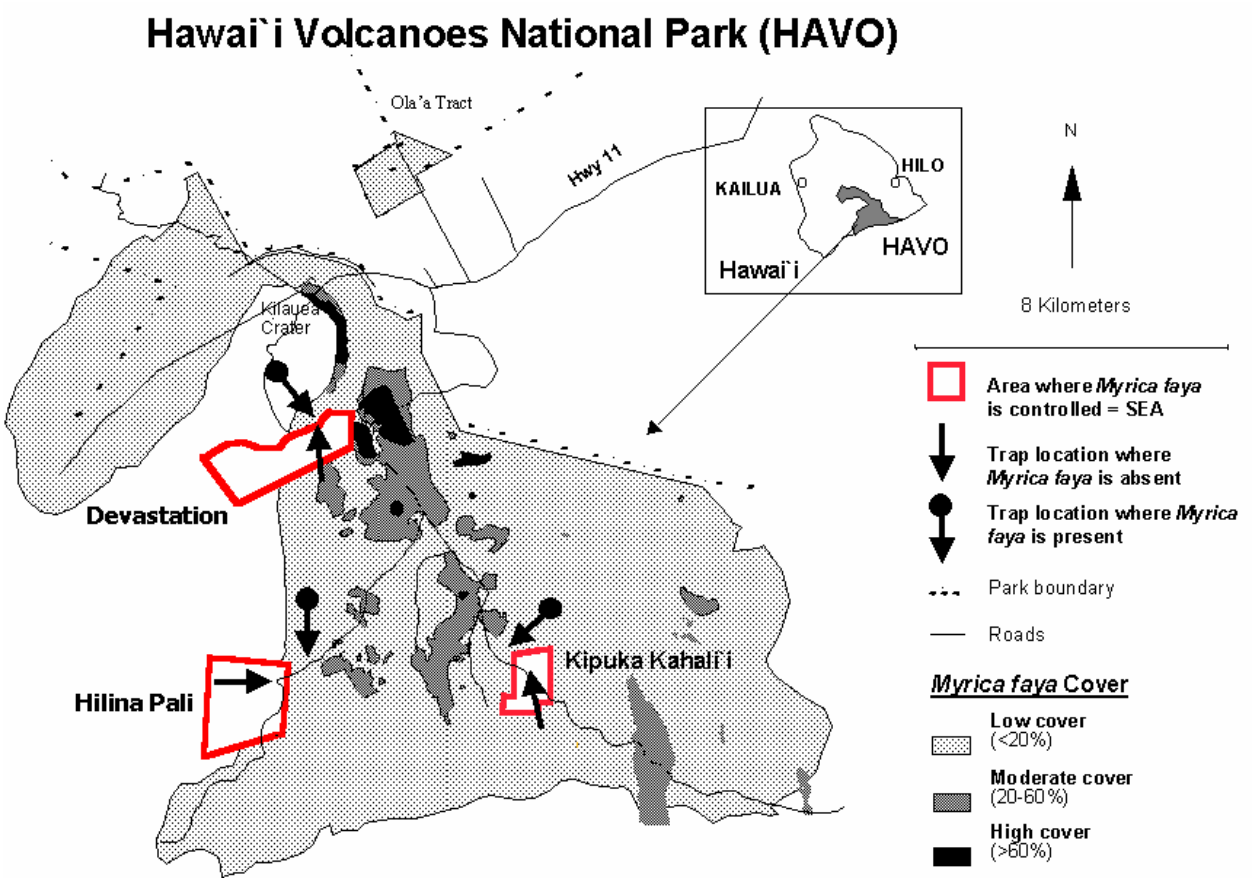


Figure 1. Diagram modified from Rhonda Loh (HAVO) showing the location of the paired control and Special Ecological Areas (SEA) used for this study.

Table 1. Elevation, precipitation, tree species, canopy-cover, dominant shrubs, and substrate found at the sites used for this study in Hawai`i Volcanoes National Park.

Site	Elevation (meters)	Precipitation (mm/yr.)	Tree species	Canopy-cover	Dominant shrubs	Substrate
Devastation	1,130	2,000	*Metrosideros polymorpha* *Morella faya*	Open	*Dodonaea viscosa* *Styphelia tameiameiae* *Vaccinium reticulatum* *Wikstroemia phillyreifolia* *Dubautia* sp. *Coprosma ernodeoides*	Cinder
Hilina Pali	990	1,500	*Metrosideros polymorpha* *Morella faya*	Open	*Dodonaea viscosa* *Styphelia tameiameiae* *Vaccinium reticulatum*	Pahoehoe lava flow
Kipuka Kahali`i	867	2,300	*Metrosideros polymorpha* *Morella faya*	Open	*Dodonaea viscosa* *Styphelia tameiameiae* *Vaccinium reticulatum* *Dubautia ciliolata* *Wikstroemia phillyreifolia* *Osteomeles anthyllidifolia* *Carex* sp.	Cinder

Abundance of TSLHs

The relative abundance of TSLH was determined following the methods of Yang *et al.* (2000). Two parallel trap-transects, separated by ≥ 20 m, with traps spaced at approximately 20 m intervals, were established within each SEA and control area. Seabright's (Emeryville, CA, product code SWFCSNT) sticky aphid/whitefly traps (with reverse folds to expose 10 X 35 cm of yellow surface coated with tanglefoot) were used to monitor insect abundance. Leafhoppers were attracted by the yellow color of the traps and the sticky surface worked successfully to trap insects under both dry and wet field conditions. Traps were placed on the southwest side of *M. polymorpha* trees that were not immediately adjacent to other living trees, at a height of between 1.5 and 2 m, over 8-day intervals. Traps were replaced once a month, from January through November 1999.

An additional study was conducted to address if *M. faya* supports, on average, a greater TSLH abundance than *M. polymorpha* does. To test this, a total of 20 cards were placed on *M. faya* in each control area. Concurrently 20 cards were placed on *M. polymorpha*. Trapping was repeated over a five month duration. Trap placement on *M. faya* followed the same protocol as placement on *M. polymorpha*, described above.

In a further study, the abundance of the TSLH on shrubs was assessed by placing ten traps on each of the two most abundant shrubs, *Dodonaea viscosa* (Jacq.) and *Styphelia tameiameiae* (Cham. & Schlechtend.), in each SEA and control site over one 8-day sampling period.

Vegetation sampling

Vegetation was sampled to compare the relative abundance of potential TSLH host-plant material between each paired SEA and control area. Plots for vegetation sampling were drawn from a 200 × 50 m field that encompassed the sticky-trap transects. Coordinates for plot corners were generated using a random number table and kept in-line with the aid of a compass. Ten 10 × 20 m plots were sampled in each SEA and control area. Within each plot, the basal diameter of all trees was measured with either a dial caliper or diameter tape. Basal areas were then calculated from basal diameters, followed by a calculation for basal area/ha. All trees were categorized as either living or dead, and each *M. faya* tree was assessed for defoliation class. Defoliation class (Figure 2), which served as an indication of health/vigor, was agreed upon by two surveyors and was recorded as follows: 0= completely foliated; 1= > 2/3 foliated; 2=1/3 to 2/3 foliated; 3= <1/3 foliated; 4= no foliage. For comparisons of *M. faya* health between study sites, trees in classes 0 and 1 were considered healthy, trees in classes 2 and 3 were considered unhealthy, and trees in class 4 were considered dead.

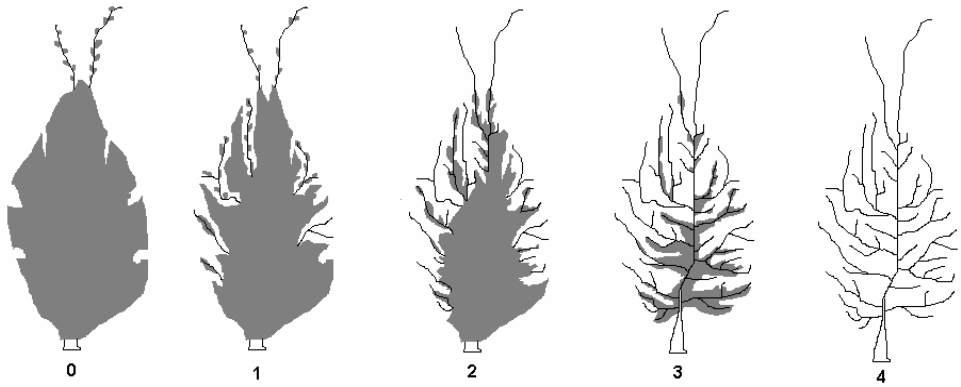


Figure 2. *Morella faya* defoliation class as scored during the vegetation surveys: 0= completely foliated; 1= > 2/3 foliated; 2=1/3 to 2/3 foliated; 3= <1/3 foliated; 4= no foliage.

In addition to trees, shrubs were sampled in each plot. All shrubs were separated according to genus and/or species and given both a height and crown width classification as follows: Width: 1=seedling; 2= ≤ 0.5 m; 3= ≤ 1.0 m; 4= ≤

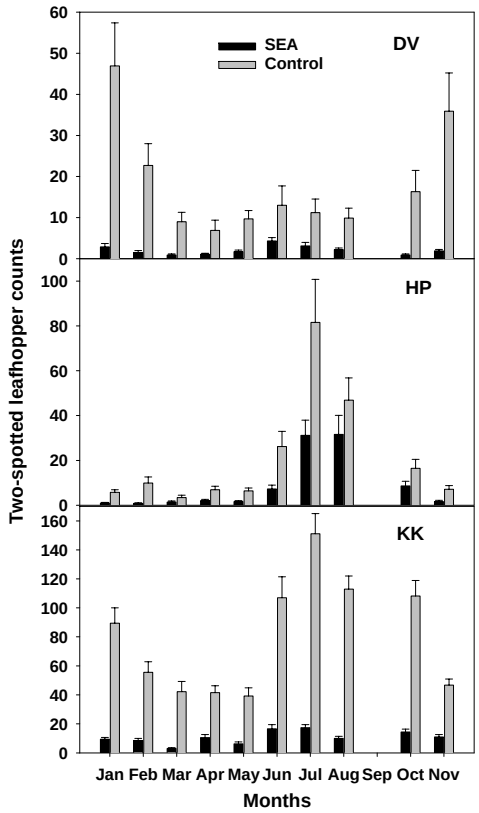
1.5 m; 5= >1.5 m. Height: 1=≤ 20 cm; 2= 21-40 cm; 3= 41-60 cm; 4= 61-80 cm; 5= >80 cm. The height and width classifications were then averaged for each individual shrub, which does not accurately reflect biomass, but does allow for a comparison of relative frequency and size class distribution between each paired SEA and control area. Presented here are only those shrub species that occurred in five or more of the ten plots sampled in each study area. Grasses were not included during the vegetation sampling because the TSLH was not found when grasses were sampled with a sweep-net (P. Yang pers. comm.), and secondly, grasses are not listed among the plants utilized by the TSLH (Fukada 1996).

Statistical analysis

The statistical package MINITAB® (for Windows, Release 12.1, copyright1998, Minitab Inc.) was used for the statistical analysis. Mean abundance values were determined for each SEA and control area by averaging the TSLH counts from each set of sticky-traps that were placed in each monitoring location, over each month. These mean abundance values were then compared using analysis of variance on log-transformed values. Bonferroni adjusted t-tests were made to compare TSLH abundance between SEAs and control areas and between study sites. To compare TSLH abundance between *M. polymorpha* and *M. faya* within and between sites, and TSLH abundance on shrubs, Bonferroni adjusted t-tests were performed on log-transformed values for each individual sample month's TSLH counts.

RESULTS

TSLH abundance: SEAs/control areas



Two-spotted leafhopper abundance was significantly greater in each control area when compared with that of each respective SEA (Figure 3). It is important, however, to notice the difference in the values of the y-axes in comparing the graphs in Figure 3. Averaged over the 10-month sampling period, the TSLH abundance at Devastation, Hilina Pali, and Kipuka Kahali`i control areas was eight, two, and eight times greater than that which was found in each respective SEA. There were also location differences in TSLH abundance over the 10-month sampling period. Two-spotted leafhopper abundance was significantly greater at Kipuka Kahali`i than at either Devastation or Hilina Pali, but there was no significant difference in the abundance between Devastation and Hilina Pali.

Figure 3. Two-spotted leafhopper abundance in three paired control and Special Ecological Area (SEA) study sites in Hawai`i Volcanoes National Park between January and November 1999. The study sites are Devastation (DV), Hilina Pali (HP), and Kipuka Kahali`i. (KK).

The relationship between season and TSLH abundance at each site can be seen in Figure 4. In all the control areas, TSLH abundance decreased between January and February and remained low throughout the spring. Between May and June, however, TSLH abundance increased greatly at both Hilina Pali and Kipuka Kahali`i (by about eight and three times greater than that which was found for each respective location over the spring months). In the fall TSLH abundance began to decline at both Hilina Pali and Kipuka Kahali`i. TSLH abundance at Devastation remained relatively low throughout the summer, only increasing slightly in the fall. In the SEAs, TSLH abundance remained more or less constant at Devastation. At Kipuka Kahali`i, TSLH abundance was sporadic over the sampling period. TSLH abundance at Hilina Pali SEA had a pattern similar to that, which was found in its control area counterpart.

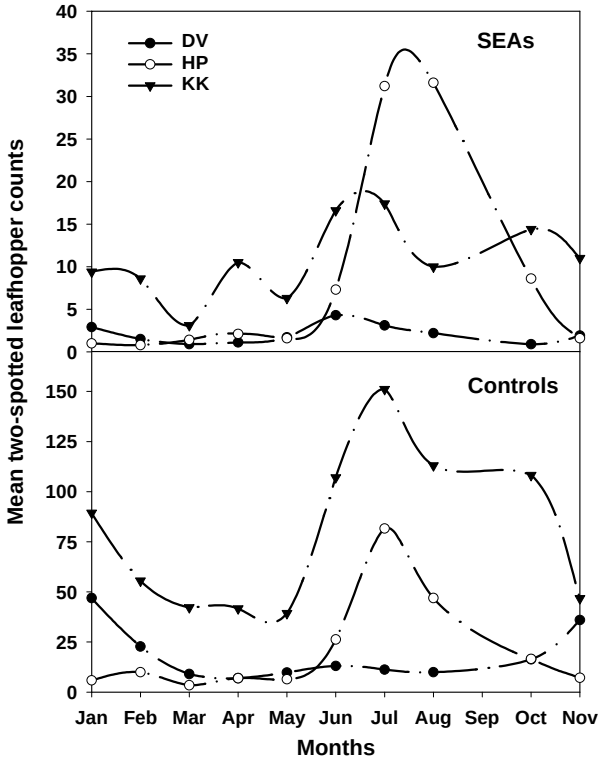
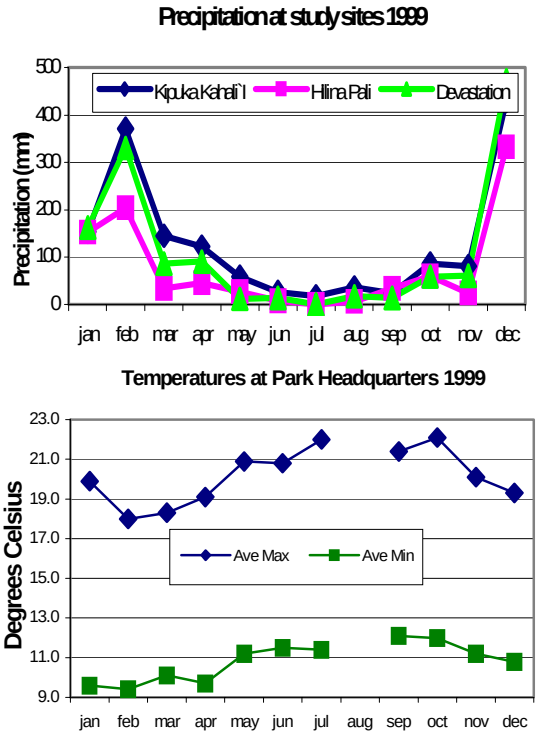


Figure 4 (a-b). The relationship between time (months) and mean two-spotted leafhopper counts in three Special Ecological Areas (SEA; top panel), compared with three control areas (lower panel), in Hawai`i Volcanoes National Park between January and November 1999. The study sites are Devastation (DV), Hilina Pali (HP), and Kipuka Kahali`i.

Seasonal precipitation and temperature patterns



Precipitation data, available from Park Service monitoring locations near the study sites, showed extreme seasonal fluctuations in rainfall (Figure 5a), which is the typical pattern for the area (Rainfall Atlas of Hawai`i 1986). All three study sites showed a similar trend in precipitation, with wet conditions in the fall and winter and drier conditions in the spring through the summer. Over the year of study, the sites were from wettest to driest: Kipuka Kahali`i with an average precipitation of 1,553 mm, Devastation with an average precipitation of 1,323 mm, and Hilina Pali with an average precipitation of 928 mm. Temperature data, available from the Park Service only at Park Headquarters, showed very little fluctuation throughout the year (only about 3°C) (Figure 4b). Although this data was not recorded at the individual study sites, previous weather data indicates that little seasonal variation in temperature is typical for a number of diverse locations within HAVO (Bridges 1981).

Figure 5 (a-b). Figure a shows the precipitation between January and December 1999 at the Park Service monitoring locations nearest to the three study sites. Figure b shows average minimum and maximum temperatures at Park Headquarters between January and December 1999.

TSLH abundance: M. polymorpha/M. faya

Two-spotted leafhopper abundance was significantly higher on *M. faya* trap-trees than on co-occurring *M. polymorpha* trap-trees, over each of the five months sampled at each control area (Figure 6). When averaged over the five month sampling period, the TSLH abundance on *M. faya* at Devastation, Hilina Pali, and Kipuka Kahali`i was 20.0, 3.4, and 2.3 times greater than the abundance found on *M. polymorpha* in each respective study site. There were significant site differences in the TSLH abundance on *M. polymorpha*. The abundance at both Hilina Pali and Kipuka Kahali`i was significantly greater than that found at the Devastation site. The abundance at Kipuka Kahali`i was significantly greater than that found at Hilina Pali.

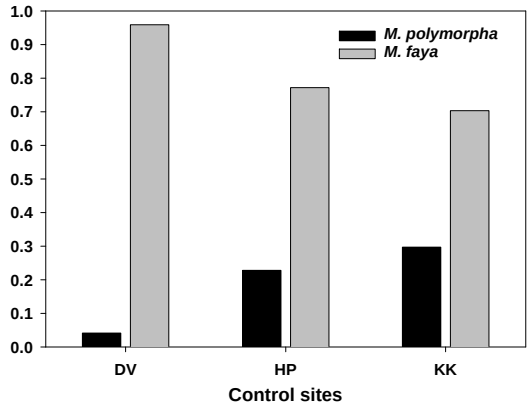


Figure 6. The mean (from five sample months) proportion of two-spotted leafhoppers trapped on Metrosideros polymorpha and Morella faya trees in each of three control areas within Hawai`i Volcanoes National Park: Devastation (DV), Hilina Pali (HP), and Kipuka Kahali`i (KK), during the summer and fall of 1999.

TSLH abundance: Shrubs

Two-spotted leafhopper abundance, sampled from *D. viscosa* and *S. tameiameiae*, was significantly higher in each control area than in each respective SEA (Figure 7). Two-spotted leafhopper abundance on shrubs at the Devastation control area was approximately 19 times greater than that of the SEA. In Hilina Pali and Kipuka Kahali`i control areas, the TSLH abundance on shrubs was approximately four times greater than that found in each respective SEA. Site differences for TSLH abundance showed a significantly greater abundance at Kipuka Kahali`i when compared with that at Hilina Pali. Hilina Pali had a greater abundance (p= 0.084) than that found at Devastation.

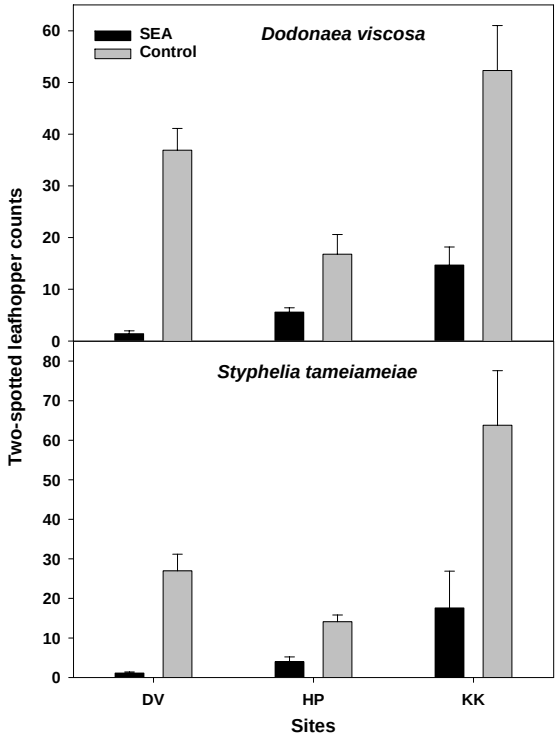
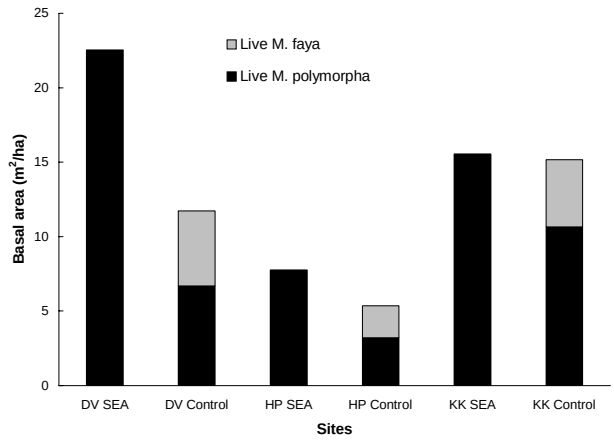


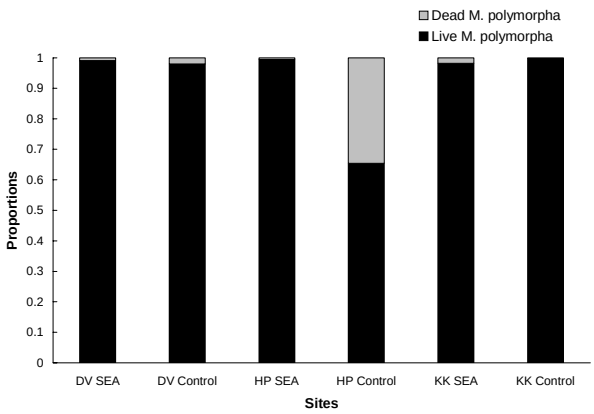
Figure 7. Two-spotted leafhopper abundance in October 1999 on the shrubs Dodonaea viscosa and Styphelia tameiameiae in three paired control and Special Ecological Area (SEA) study sites in Hawai`i Volcanoes National Park. The sites are Devastation (DV), Hilina Pali (HP), and Kipuka Kahali`i (KK).

Woody vegetation health and abundance: SEAs/control areas



The total amount of live woody basal area was similar between the SEA and control areas at Kipuka Kahali`i and was greater in the SEAs than in the control areas at both the Hilina Pali and Devastation sites (Figure 8). The Devastation SEA had the highest live basal area, at 22.5 $m^2$/ha, followed by the Kipuka Kahali`i SEA, at 15.6 m^2/ha, the Kipuka Kahali`i control area at 15.2 m^2/ha, the Devastation control area at 11.7 m^2/ha, the Hilina Pali SEA at+ 7.8 m^2/ha, and the lowest basal area was recorded at the Hilina Pali control area, at 5.3 m^2/ha.

Figure 8. Total live woody basal area of *Metrosideros polymorpha* and *Morella faya* in three paired control and Special Ecological Area (SEA) study sites in Hawai`i Volcanoes National Park.



There was a greater proportion of dead to live *M. polymorpha* in the control areas than in the SEAs at both the Devastation and Hilina Pali study sites, 2% and 35% as compared to 1% and 0.5% (Figure 9). However, at Kipuka Kahali`i, there was a greater, though still small, proportion of dead to live *M. polymorpha* in the SEA than in the control area, with 2% as compared to 0%. Overall, the site with the highest proportion of dead to live *M. polymorpha* was Hilina Pali.

Figure 9. The proportion of dead and live *Metrosideros polymorpha* in three paired control and Special Ecological Area (SEA) study sites in Hawai`i Volcanoes National Park.

The site with the highest proportion of healthy *M. faya* was Devastation, where all individuals where classified as healthy (Figure 10). Kipuka Kahali`i had a slightly higher proportion of healthy *M. faya*, with 9%, than did Hilina Pali, with 1%; however, both sites had healthy trees as a very small proportion of total. Kipuka Kahali`i had the highest proportion of unhealthy *M. faya*, at 91%, but no dead trees. Hilina Pali, on the other hand, had dead *M. faya* making up approximately 40% of the total.

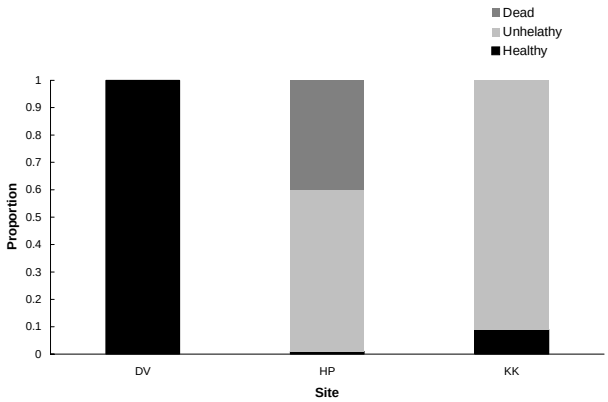


Figure 10. The proportion of *Morella faya* in healthy, unhealthy, and dead categories within three control areas in Hawai`i Volcanoes National Park.

Shrub abundance: SEAs/control areas

The most abundant shrubs, listed in their order of abundance, in the Kipuka Kahali`i SEA and control area were: *D. viscosa, S. tameiameiae,* and *V. reticulatum* (Figure 11a). The most abundant shrubs, listed in their order of abundance in the Devastation SEA were: *Vaccinium reticulatum* (Sm.), *S. tameiameiae*, *Coprosma ernodeoides* (A. Gray), *Dubautia* sp., and *Wikstroemia phillyreifolia* (A.Gray). The most abundant shrubs, listed in their order of abundance, in the Devastation control area were: *V. reticulatum*, *Dubautia scabra* (D. Keck), *D. viscosa*, and *S. tameiameiae* (Figure 11b). The most abundant shrubs, listed in their order of abundance, in the Hilina Pali SEA were: *D. viscosa, S. tameiameiae, Dubautia ciliolata* (D. Keck), *Osteomeles anthyllidifolia* (Sm. Lindl.), and *W. phillyreifolia*. The most abundant shrubs, listed in their order of abundance in the Hilina Pali control area were: *D. viscosa, S. tameiameiae, D. ciliolata, Carex* sp., *V. reticulatum, O. anthyllidifolia,* and *W. phillyreifolia* (Figure 11c).

There was greater than two times the amount of total shrub material in the Devastation SEA when compared with the control area. The abundance of shrub material was slightly greater in both the Kipuka Kahali`i and Hilina Pali control areas when compared with that of each respective SEA.

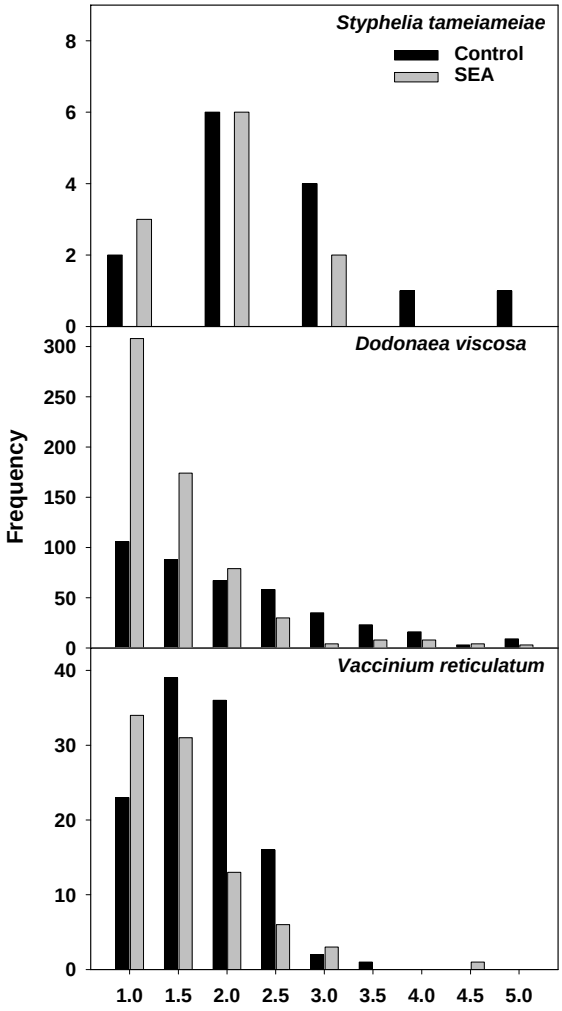


Figure 11a. The frequency and size class distribution of the shrubs present in five or more of the ten vegetation plots sampled in the paired control and Special Ecological Area (SEA) at the Kipuka Kahali`i study site in Hawai`i Volcanoes National Park.

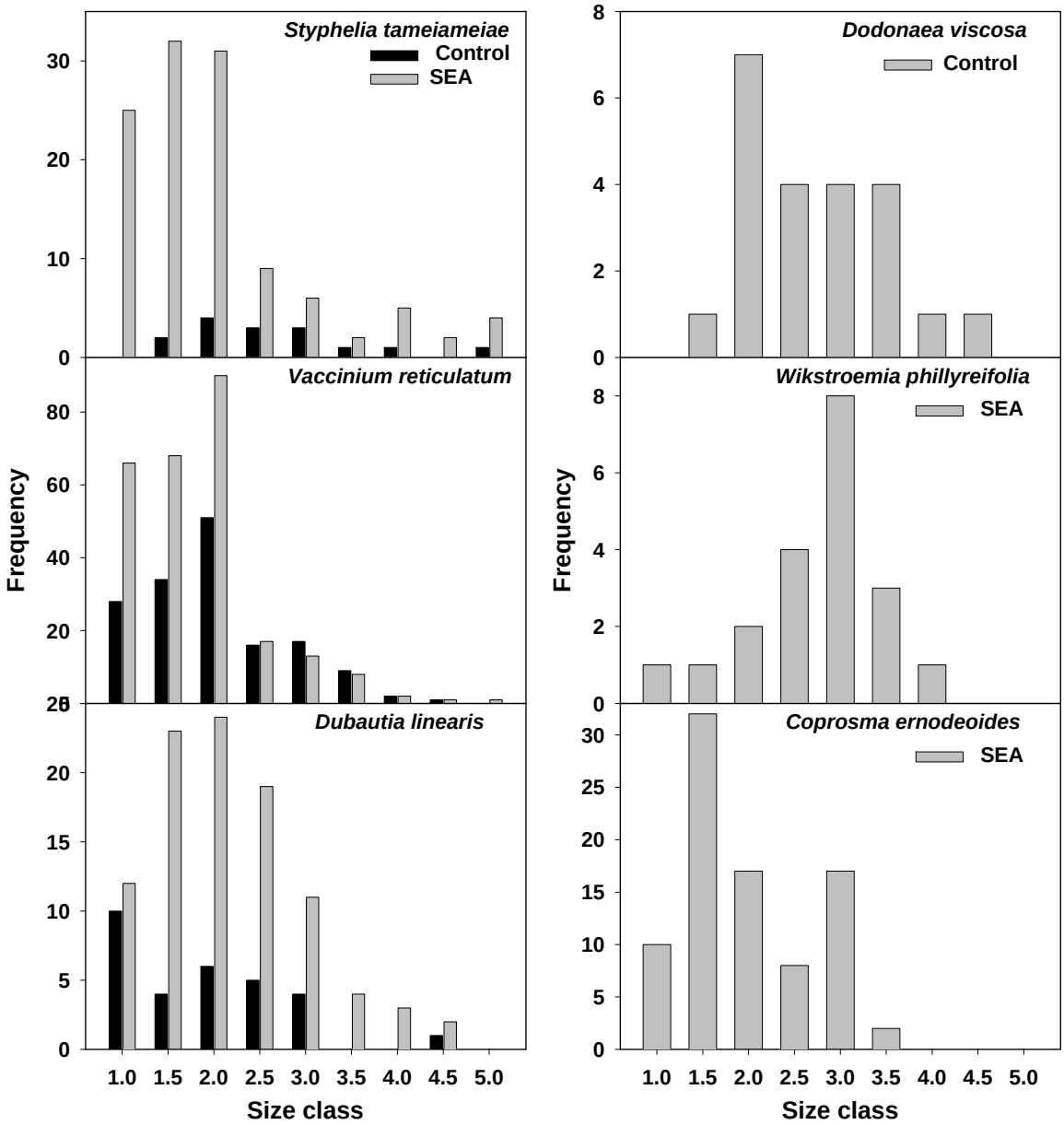


Figure 11b. The frequency and size class distribution of the shrubs present in five or more of the ten vegetation plots sampled in the paired control and Special Ecological Area (SEA) at the Devastation study site in Hawai`i Volcanoes National Park.

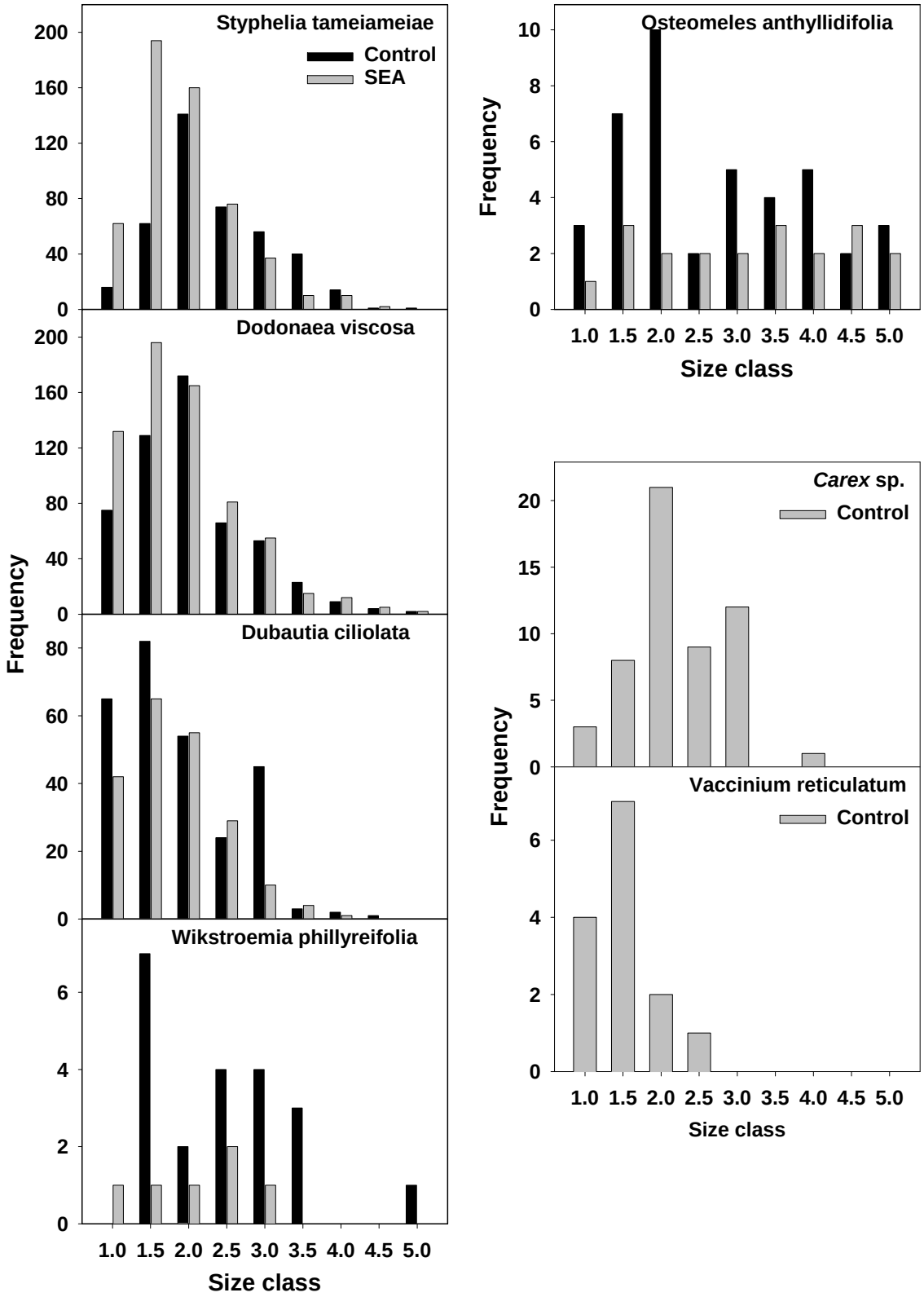


Figure 11c. The frequency and size class distribution of the shrubs present in five or more of the ten vegetation plots sampled in the paired control and Special Ecological Area (SEA) Hilina Pali study site in Hawai`i Volcanoes National Park.

DISCUSSION

TSLH abundance in relation to two host plants

Two-spotted leafhopper abundance was significantly greater in areas where *M. faya* was present, referred to as control areas, when compared with those areas where faya tree had been removed, referred to as Special Ecological Areas (SEAs). Yet the amount of live woody vegetation and shrub material, available to the TSLH, was comparable between each paired SEA and control area. If TSLH abundance were simply proportional to the total amount of available host material, without regard to host species similar TSLH numbers in both SEA and control areas would be expected. However, the much larger TSLH abundance found among control areas (eight, two, and eight times greater) when compared with that found in the SEAs, supports the hypothesis that the presence of *M. faya* facilitates an increase in the abundance of the TSLH. This hypothesis was further substantiated by the finding that TSLH abundance was much greater on *M. faya* than on the co-occurring *M. polymorpha*.

Morella faya may be a host-plant preferred by the TSLH, in part, due to the high nitrogen content of its foliage: 1.76 %, as compared to 0.95% for *M. polymorpha* (Vitousek and Walker 1989). Insect herbivores have been shown to prolong their feeding, have increased fecundity, and improved survival when they feed on nutrient rich substrates (House 1965, Mattson 1980). The performance of sap-feeding insects in particular, such as leafhoppers, is usually correlated with the availability of host-plant nitrogen (Louda and Collinge 1992). It is unlikely, however, that secondary compounds have a large effect on plant preference. Secondary compounds are thought to be less influential on vascular feeders than on any other guild of herbivorous insects (Brodbeck *et al.* 1995), because secondary compounds are either absent or found in such low concentrations in leaf vascular tissues.

A further factor, which might confer a greater herbivore load on *M. faya* compared with *M. polymorpha*, is the lack of foliar pubescence (leaf hairs) in the former. In the areas where this study took place, the majority of *M. polymorpha* trees had foliar pubescence, particularly concentrated on the abaxial leaf surface, which is also the surface of the leaf from which the TSLH feeds. Foliar pubescence has been demonstrated to act as a physical barrier for herbivores, a barrier which is particularly important in deterring feeding by probing insects, such as leafhoppers (Tingey 1985). A number of studies with leafhoppers have demonstrated avoidance of pubescent leaves. For example, glabrous (lacking leaf hairs) germ plasm lines of crop plants have been shown to be more susceptible to the potato leafhopper, *Empoasca fabae* (Harris), than pubescent forms (Lamp *et al*. 1994). And more severe TSLH damage has been observed among glabrous than among pubescent leaves of *M. polymorpha*, in situations where the two varieties were seen growing with intertwined branches (Jones unpubl. data). Also associated with pubescence in *M. polymorpha* is a thicker cuticle layer (Kitayama *et al.* 1997), which can also act as a barrier to insect herbivory.

It could be argued that the observed difference in TSLH abundance, based on host species, is due to a difference in the total leaf surface area between the two species. For trees of the same size, *M. faya* has a larger total leaf surface area than does *M. polymorpha*; therefore, *M. faya* would be expected to support a greater herbivore load when compared with *M. polymorpha*. This is, however, an unlikely possibility with at least two of the three study sites, where *M. faya* were classified as severely defoliated. The largest TSLH abundance was supported at Kipuka Kahali`i, where 95% of the *M. faya* trees were classified as unhealthy (severely defoliated). Devastation, where 100% of the *M. faya* were classified as healthy (fully or near fully foliated), was a site that had an overall low TSLH abundance. Factors other than total leaf surface area may be more important in influencing TSLH abundance.

Seasonal TSLH abundance patterns

In addition to documenting the relationship between TSLH abundance in the presence and absence of a preferred host plant, this study also revealed seasonal and site-specific patterns in TSLH abundance. These patterns most likely reflect temporal differences in a combination of biotic and abiotic factors that influence insect life history traits, most notably precipitation and the availability of newly flushed foliage. Overall, TSLH abundance was the lowest during the wet winter and early spring months. Following a substantial decrease in precipitation over the spring months, abundance peaked between June and July. Although conditions remained dry throughout the summer and into the early fall, TSLH abundance declined. This decline in abundance was likely in response to

depleted food resources, because the TSLH feeds almost exclusively on newly flushed foliage (Fukada 1996, Jones *et al*. submitted). In the areas where the study took place, the rate of *M. faya* flushing decreased markedly after June, and by July or August, most leaves had fully matured (L. Lenz unpublished data).

Temperature fluctuated seasonally by between 3 and 5º C at Park Headquarters and other temperature data indicate that such low seasonal fluctuations are common for diverse locations within HAVO (Bridges 1981). Although this degree of difference may not be expected to affect TSLH population trends within a site, temperature may nonetheless be an important abiotic factor affecting leafhopper population dynamics between sites. Lower elevation and thus warmer sites may be favored over higher elevation, cooler sites. For example, Kipuka Kahali`i and Devastation had similar levels of precipitation, and yet the lower elevation site (Kipuka Kahali`i) supported by far a greater overall TSLH abundance than the higher elevation site.

TSLH abundance and host plant health

Two-spotted leafhopper herbivory has been shown to result in plant damage including foliar chlorosis, leaf cupping and necrosis, and damage to vascular tissue (Jones *et al.* 1998, Jones *et al.* submitted, Yang *et al.* 2000). TSLH has been implicated as being involved with the dieback phenomenon in HAVO. The current study demonstrated a higher proportion of dead to live *M. polymorpha* in two of the three control areas when compared with each respective SEA. The difference was the most extreme at Hilina Pali, where 35% of the *M. polymorpha* in the control area were dead, while only 1% was dead in the SEA. Control areas also had significantly more TSLHs than SEAs, and therefore, plants in the control areas experienced greater herbivory stress when compared with that experienced by plants in the SEAs. Furthermore, among control areas, there was little difference between the proportion of dead to live *M. polymorpha* and *M. faya*, suggesting that even though *M. faya* appears to be a preferred host plant of the TSLH, the risk of mortality is similar for *M. polymorpha*.

As expected, *M. faya* was the healthiest at Devastation, the site with the lowest overall TSLH abundance; while at Kipuka Kahali`i, the site with the highest TSLH abundance, 91% of the basal area was classified as unhealthy. Surprisingly, however, there were no dead trees recorded as yet at Kipuka Kahali`i. The majority of *M. faya* were severely defoliated, however, suggesting that dieback may occur at this site in the near future. It may not have occurred sooner because the relatively high precipitation (2,300 mm/yr.) this site receives may have helped to mitigate TSLH-induced plant water-stress. The high degree of dieback of both tree species as seen at Hilina Pali, a site with comparatively low numbers of the TSLH, may be the result of historically high TSLH densities. Alternatively, the combination of TSLH-induced plant water-stress, seasonal drought and high temperatures and exposure, may have acted to hasten the dieback process at the Hilina Pali site.

CONCLUSIONS

When averaged over the entire 10-month monitoring period, TSLH abundance was between two and eight times greater in each control area when compared with that found in each respective SEA. Yet the amount of live woody vegetation and shrub material available to the TSLH between paired SEA and control areas could not explain the difference in TSLH abundance. In addition, TSLH abundance was between 2.3 and 20.0 times greater on the invasive *M. faya* when compared with that found on the co-occurring native dominant tree, *M. polymorpha*. The striking difference in TSLH abundance, based on the *M. faya* removal treatment, as well as the larger TSLH abundance found on *M. faya* than on co-occurring *M. polymorpha*, substantiates the hypothesis that *M. faya* promotes an increase in TSLH abundance. These findings suggest that native plants co-occurring with *M. faya* in these mixed woodlands are exposed to greater herbivory stress than they would experience in the absence of *M. faya*. The results from the current study also suggest that the removal of *M. faya* can serve as a management approach to decrease a local abundance of the TSLH.

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