Oviposition of the invasive two-spotted leafhopper on an endemic tree: Effects of an alien weed, foliar pubescence, and habitat humidity

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Abstract

The two-spotted leafhopper, *Sophonia rufofascia* (Kuoh and Kuoh), is an exotic pest from South-East Asia that attacks a wide variety of plant species in Hawaii. *Myrica faya* Aiton is an aggressive exotic weed that displaces and excludes native plants in Hawaiian forests. It has been argued that because of the high nutritional quality of its foliage, *M. faya* might facilitate leafhopper invasion of native Hawaiian ecosystems that were originally dominated by the endemic tree *Metrosideros polymorpha* (Gaudichaud). In the present study, we quantified suitability of *M. faya* and *M. polymorpha* as ovipositional hosts for *S. rufofascia*. Overall, leafhoppers preferred to deposit their eggs into the foliage of *M. faya*. *M. faya* presence in the area did not affect leafhopper oviposition on *M. polymorpha*. Foliar pubescence provided good protection of hirsute morphotypes of *M. polymorpha*. At the same time, glabrous *M. polymorpha* morphotypes were quite suitable for leafhopper oviposition. There was no difference in the abundance of leafhopper eggs along a precipitation gradient. Our results confirm that invasion of native Hawaiian forests by the weed *M. faya* will facilitate their invasion by *S. rufofascia*. Because of the broad host range characteristic of the two-spotted leafhopper, this build-up may adversely affect a number of endemic plant species growing in native forests.

Introduction

The two-spotted leafhopper, *Sophonia rufofascia* (Kuoh and Kuoh), originally described from southern China (Kouh and Kouh 1983), was first discovered on Oahu in 1987 (Heu and Kumashiro 1989). Since then, it has spread to all of the major Hawaiian islands, where it has been reported to attack over 300 plant species in 83 families (Fukada 1996; Alyokhin *et al.* 2001). Leafhopper feeding and oviposition cause plant vascular bundle abnormalities, resulting in interveinal chlorosis, vein browning, retarded development of new growth, and even death of affected plants (Jones *et al.* 2000). In commercial guava, leafhopper injury reduces yields by ≈23% compared to pesticide-protected trees (Jones *et al.* 1998). Being a highly polyphagous insect, the two-spotted leafhopper poses a threat both to agricultural production and to natural habitat conservation in Hawaii. Among its recorded host plant species, 68% are economically important fruit, vegetable, and ornamental crops; and 22% are endemic to the Hawaiian islands, including 14 rare and endangered species (Fukada 1996). Two-spotted leafhopper damage has been implicated as a cause of severe dieback of several native Hawaiian plants, such as ohia-lehua tree *Metrosideros polymorpha* (Gaudichaud) and uluhe fern *Dicranopteris*

linearis Underwood (Palmer 1993; Lenz 2000). However, while proving that *S. rufofascia* feeding is indeed detrimental to *D. linearis* fern, Jones *et al.* (2000) failed to find a significant correlation between leafhopper presence and extensive uluhe death in natural habitats. Similarly, Alyokhin *et al.* (2001) observed wide spread symptoms of leafhopper damage but no significant dieback of surveyed plants. Nevertheless, the two-spotted leafhopper remains an important pest in Hawaii, applying a substantial stress on native and economically important vegetation (Lenz 2000; Lenz and Taylor 2001).

M. polymorpha is the endemic tree that used to dominate a wide variety of Hawaiian ecosystems (Walker and Vitousek 1991). It occurs over a wide ecological range from coast to high-elevation montane habitats, from desert to wet rainfall regions, and from recent lava flows to old, deeply weathered soils (Drake and Mueller-Dombois 1993; Kitayama and Mueller-Dombois 1995; Kitayama *et al.* 1997). Not surprisingly, this plant displays a high degree of morphological variation, with foliar pubescence being one of the major distinguishing characteristics among infraspecific varieties (Kitayama *et al.* 1997). This variation is clinal along elevational and rainfall gradients (Corn and Hiesey 1973; Kitayama *et al.* 1997). Hirsute trees are presumably better adapted to harsh environmental

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conditions that makes them the more abundant morphotype at higher elevations and in areas prone to drought. For the same reason, they are also predominant in pioneering situations, such as on young lava flows and in disturbed areas along roadsides. Hirsute morphotypes in such places are gradually replaced by glabrous morphotypes, similar to pioneer plant species being replaced by later successional plant species in more floristically diverse continental regions (Stemmermann 1983; Mueller-Dombois 1983; Kitayama *et al.* 1995; 1997).

M. faya Aiton is an evergreen broad-leafed tree that is listed among the 12 most noxious weeds in the state of Hawaii (Smith 1985). *M. faya* forms monotypic stands that replace and exclude native vegetation, particularly *M. polymorpha*. In addition to direct competition with native plants, *M. faya* also alters ecosystem-level processes indirectly through association with a nitrogen-fixing actinorhizal symbiont (Vitousek *et al.* 1987; 1989). By increasing the nitrogen content of Hawaiian soils, it facilitates invasion by a broader range of exotic plant species, which are otherwise inadequately adapted to compete with endemic vegetation on nitrogen-poor volcanic soils (Gerrish and Mueller-Dombois 1980; Vitousek *et al.* 1987; Vitousek and Walker 1989). Furthermore, high nitrogen content in its foliage may favor development of herbivorous insect populations (Mattson 1980; Louda and Collinge 1992; Lenz and Taylor 2001).

An increase in leafhopper abundance on *M. faya* may result in their subsequent dispersal to other plant species in an area. Therefore, competitive stresses imposed on native vegetation by *M. faya* invasion might be further aggravated by increased leafhopper herbivory. In a recent survey conducted in Hawaii Volcano National Park, Lenz and Taylor (2001) captured up to 20 times more two-spotted leafhopper adults on traps hung on native plant species within sites invaded by *M. faya* than in sites where this weed was removed as a part of an ecosystem preservation effort. However, two-spotted leafhopper adults are highly mobile. Therefore, it was not clear if the observed increase in captures was due to the movement of adults that had completed their development on *M. faya*, to the establishment of higher leafhopper populations on native vegetation, or to the combination of these factors.

Unlike *M. polymorpha* leaves, *M. faya* leaves are never pubescent. Foliar pubescence is known to present a physical barrier to leafhopper colonization (Johnson 1975; Tingey 1985). Furthermore, in *M. polymorpha* pubescence is associated with a thicker cuticle layer (Kitayama *et al.* 1997), which can provide an additional challenge for both proboscis (especially in younger instars) and ovipositor penetration. Lee (1981) observed lower levels of herbivory on hirsute vs. glabrous trees prior to the leafhopper invasion. Jones *et al.* (2000) pointed out that feeding damage caused by the two-spotted leafhopper was also more severe on glabrous morphotypes of *M. polymorpha* and *D. linearis* when compared to hirsute morphotypes. However, they did not provide any data to quantify their observation. Nothing is known about effects of foliar pubescence on *S. rufofascia* oviposition. We hypothesized that two-spotted leafhopper eggs would be more abundant on *M. faya* and glabrous morphotypes of *M. polymorpha* than on hirsute morphotypes of *M. polymorpha*. As a result, *M. polymorpha* forests will be more prone to leafhopper invasion (1) in areas invaded by *M. faya*, and (2) during late successional stages dominated by glabrous *M.*

polymorpha morphotypes. To test our hypothesis, we quantified the rates of egg infestation of leaves on the two trees in different habitats on the islands of Hawaii and Kauai.

The two-spotted leafhopper has been recorded from a wide variety of habitats (Fukada 1996). In the survey by Alyokhin *et al.* (2001), leafhoppers appeared to have a preference for wetter, closed habitats rather than drier, open ones. However, the occurrence of different plant species in their survey was itself habitat-dependent. Therefore, it was not clear if the observed difference could be attributed to the humidity itself. Plants suffering from water-stress have been shown to be more prone to attack by phytophagous insects (Mattson and Haack 1987), and leafhopper herbivory by itself increases the level of moisture stress in affected trees (Lenz 2000). Therefore, knowing effects of humidity on leafhopper distribution is important for a better understanding of the consequences of its invasion in different habitats. In the present study, we surveyed the density of leafhopper eggs in floristically very similar habitats located along the precipitation gradient.

Materials and Methods

Site characterization

Natural plant communities were categorized using descriptions and vegetation maps developed by Ripperton and Hosaka (1942), Mueller-Dombois and Fosberg (1974), and Sohmer and Gustafson (1987). Mean annual precipitation for each of the surveyed sites was interpolated from published isohyets based on 67-year rainfall data (Giambelluca *et al.* 1986). Accordingly, sites were classified as dry if annual precipitation was < 1200 mm, mesic if between 1200 and 2500 mm, and wet if > 2500 mm. Also, sites with canopy cover > 60% were classified as closed, and sites with canopy cover between 25 and 60% were classified as open.

Sampling procedures

Leaves were sampled haphazardly from *M. faya* and *M. polymorpha* trees within each survey site in January, March, and April, 2000 (a total of three collection dates). The leaves were sampled at a height of 0.5 – 2 m above the ground from both inner and outer parts of the canopy. No attempt was made to distinguish between sun vs. shade leaves, nor among leaves at different stages of maturity. Collected leaves were brought to the laboratory and checked for the presence of leafhopper eggs using backlighting, as described by Yang *et al.* (2000). Two-spotted leafhopper eggs were identified using descriptions provided by Culliney (1998). To confirm identification, collected eggs were reared to the nymphal stage by incubating infested leaves at $24 \pm 2°$ C and natural lighting in 1 gallon Ziploc® plastic bags. Voucher leafhopper specimens are stored in the Entomology Museum of the University of Hawaii at Manoa.

The total area of collected leaf material was estimated by measuring 35 leaves of each species with a leaf area meter (LiCor-3100, Lincoln, Nebraska), and then multiplying the mean area of measured leaves by the total number of leaves in a sample (Alyokhin *et al.* 2001).

Egg abundance in different habitats

In the first study, we surveyed two-spotted leafhopper egg

Table 1. Ecological characteristics of the *Myrica faya* and *Metrosideros polymorpha* habitats sampled on the islands of Hawaii and Kauai.

Island	Site	Elevation (m)	Habitat type	Rainfall (mm/year)	Canopy cover	Dominant tree species	Understory
Hawaii	Puhimau Crater	1150	mesic	2500	closed	*Metrosideros polymorpha* *Myrica faya*	native shrub*
	Escape Road	1020	wet	3000	open	*Metrosideros polymorpha* *Myrica faya*	*Dicranopteris linearis* native shrub
	Halemaumau Crater	1130	mesic	2000	open	*Metrosideros polymorpha* *Myrica faya*	native shrub
	Kulanaokuaiki Camp	990	mesic	1500	open	*Metrosideros polymorpha* *Myrica faya*	native shrub
	Kipuka Kahalii	867	mesic	2300	open	*Metrosideros polymorpha* *Myrica faya*	native shrub
Kauai	Alakai Trailhead	1200	mesic	2322	open	*Metrosideros polymorpha* *Myrica faya*	*Dicranopteris linearis* *Rubus* spp.
	Kokee State Park	1200	mesic	1765	open	*Metrosideros polymorpha* *Myrica faya*	*Dicranopteris linearis* *Rubus* spp.
	Makaha Ridge	600-900	dry	982-1106	closed	*Pinus* spp. *Grevillea robusta*	*Psidium* spp. *Lantana camara*
	Waimea Canyon	1000	mesic	1300	closed	*Pinus* spp. *Grevillea robusta*	*Psidium* spp. *Lantana camara*

* *Vaccinium reticulatum*, *Dodonaea viscosa*, *Styphelia tameiameiae*, *Coprosma ernodeoides*, *Dubautia* spp.

infestation levels in *M. faya* and *M. polymorpha* leaves at 9 different sites on the islands of Hawaii and Kauai. A more detailed description of the study sites is provided in Table 1. On Hawaii, which is the youngest Hawaiian island, the sites were located on relatively recent lava flows and represented early stages of plant succession. Therefore, the majority of *M. polymorpha* trees growing within those sites were hirsute (≈75 : 1 hirsute to glabrous tree ratio). On the geologically and ecologically older island of Kauai, all *M. polymorpha* trees were glabrous. A total of 23,816 leaves were collected from *M. faya* trees, and a total of 12,600 leaves were collected from *M. polymorpha* trees.

Egg abundance in relation to M. faya removal

In the second study, we compared two-spotted leafhopper egg abundance between areas in which *M. faya* had been mechanically removed, and immediately adjacent areas where the tree was still present. *M. faya* removal took place from 1986-1988 as part of weed eradication effort within intensively managed special ecological areas of Hawaii Volcano National Park. Presently, these areas remain free of *M. faya* that has been naturally replaced by *M. polymorpha*. Our survey was conducted at three sites that were initially covered by an open *M. polymorpha-M. faya* forest with native shrub understory. The sites were located at Halemaumau, Kulanaokuaiki, and Kipuka Kahalii areas (Table 1). Special ecological areas size varied between 272 and 401 ha. Within each site, an approximately 6 m wide paved road separated special ecological areas from other areas. Samples were taken at least 50 m

away from the area border. A total of 8,217 leaves were collected from *M. faya* trees, 3,517 from *M. polymorpha* trees growing together with *M. faya*, and 3,663 leaves from *M. polymorpha* trees growing in the areas where *M. faya* had been removed.

Egg abundance in relation to foliar pubescence

In the third study, we compared the infestation rates of leafhopper eggs on glabrous and hirsute *M. polymorpha* morphotypes. Foliage was collected twice, in May and July of 2000, from glabrous and hirsute *M. polymorpha* trees growing along Hilina Pali Road (975 – 1067 m elevation, 1500 – 2500 mm annual precipitation), near Pauahi crater (975 m elevation, 2300 mm annual precipitation), and at Kipuka Kahalii area (867 m elevation, 2300 mm annual precipitation) in Hawaii Volcano National Park. Both morphotypes were interspersed in an apparently random manner within each of the three sites. All the sites were covered by an open *M. polymorpha-M. faya* forest with native shrub understory. A total of 2,611 leaves were collected from glabrous *M. polymorpha* trees, and a total of 2,882 leaves from hirsute *M. polymorpha* trees. This time no data on the proportion of leaves infested with leafhopper eggs were taken.

Egg abundance in relation to mean annual precipitation

In the fourth study, we surveyed two-spotted leafhopper egg abundance along a precipitation gradient at ≈1000 m elevation between Mauna Ulu lava shield and Kulanaokuaiki Camp in Hawaii Volcano National Park. Four sites were selected based on their mean

annual precipitation, equal to 3000, 2500, 2000, and 1700 mm/year, respectively (Giambelluca *et al.* 1986). All four sites were covered by an open *M. polymorpha-M. faya* forest with native shrub understory and separated from each other by a distance of between 1.7 - 3.4 km. A total of 9,850 leaves were collected from *M. faya* trees, and a total of 4,586 leaves from *M. polymorpha* trees.

Statistical analysis

Variations in the proportion of sampled leaves containing leafhopper eggs and egg density per m² of leaf surface area were analyzed by two-way ANOVA (PROC GLM, SAS Institute 1999). Tree species and site of leaf collection were used as the main effects, and all leaves collected at a given site during a given month were considered to comprise a single unit of replication. Prior to the analysis, the data on proportions of infested leaves were transformed using arcsine-square root transformations (Zar 1999). The normality of egg density data was checked using the Wilk-Shapiro test at the 0.05 level of significance (PROC UNIVARIATE, SAS Institute 1999). When necessary, those data were transformed using rank transformations (Conover and Iman 1981). Means and standard errors were calculated from the non-transformed data only. When analyzing impacts of *M. faya* removal, we used the tree context (e.g., *M. faya*, *M. polymorpha* growing together with *M. faya*, or *M. polymorpha* growing in the areas where *M. faya* had been eradicated) instead of tree species as the main effect in ANOVA tests. Those tests were followed by orthogonal multiple contrasts that were designed *a priori* (Zar 1999) to test the differences between *M. faya* and *M. polymorpha*, as well as between *M. polymorpha* growing together with *M. faya* and *M. polymorpha* growing separately from *M. faya*. The variation between the leaf infestation of glabrous and hirsute *M. polymorpha* was analyzed by a two-sample t-test (PROC TTEST, SAS Institute 1999).

Results

Egg abundance in different habitats

Overall, 6.0±0.5% (mean ± 1SE) of *M. faya* leaves and 3.3±0.5% of *M. polymorpha* leaves contained two-spotted leafhopper eggs. Egg density was equal to 118.1 ± 9.1 eggs/m² of leaf area for *M. faya* and 63.9 ± 10.4 eggs/m² for *M. polymorpha*. Both proportion of infested leaves and egg density were significantly higher for *M. faya* than for *M. polymorpha* ($F_{1,36}$ = 42.47, P < 0.0001 and $F_{1,36}$ = 31.21, P < 0.0001, respectively).

Sampling site had a significant effect on the proportion of infested leaves ($F_{8,36}$ = 2.51, P = 0.0280), but not on egg density ($F_{8,36}$ = 2.07, P = 0.0654). The interaction between plant species and sampling site was significant for both proportion of infested leaves ($F_{8,36}$ = 3.84, P = 0.0023), as well as for egg density ($F_{8,36}$ = 2.74, P = 0.0179). At all Hawaii sites, leaf infestation was higher for *M. faya* than for *M. polymorpha* trees (Table 2). The same was true for two of the Kauai sites, although the difference was not as great as at the Hawaii sites. At the remaining two Kauai sites, *M. polymorpha* foliage harbored slightly more eggs than *M. faya* foliage (Table 2).

Egg abundance in relation to M. faya removal

Leafhopper eggs infested 6.1 ± 0.7% of *M. faya* leaves, 1.4 ± 0.5% of *M. polymorpha* leaves collected from the trees growing together with *M. faya*, and 1.4 ± 0.4% of *M. polymorpha* leaves collected from the trees growing in the areas where *M. faya* had been removed. The proportion of infested leaves was significantly different among Halemaumau, Kulanaokuaiki, and

Table 2. Infestation of *Myrica faya* and *Metrosideros polymorpha* leaves with the two-spotted leafhopper eggs at the habitats sampled on the islands of Hawaii and Kauai.

| Island	Location	Plant	No. of leaves examined	% leaves infested Mean	SE	Egg density per 1 m2 Mean	SE
Hawaii	Puhimau Crater	*M. faya*	2869	6.95	0.67	130.65	14.05
		M. polymorpha	926	0.72	0.17	12.55	3.02
	Escape Road	*M. faya*	2870	8.79	2.40	165.64	43.00
		M. polymorpha	1002	2.14	1.36	45.37	31.74
	Halemaumau Crater	*M. faya*	2438	5.16	0.71	95.78	13.25
		M. polymorpha	1025	0.39	0.20	6.80	3.57
	Kulanaokuaiki Camp	*M. faya*	3812	5.86	1.67	111.41	29.76
		M. polymorpha	1403	1.49	0.84	27.21	15.80
	Kipuka Kahalii	*M. faya*	1967	7.21	0.92	132.34	16.81
		M. polymorpha	1089	2.28	0.58	41.15	10.78
Kauai	Alakai Trailhead	*M. faya*	2954	3.52	0.32	75.36	12.25
		M. polymorpha	1598	4.41	0.95	80.03	17.39
	Kokee State Park	*M. faya*	2244	6.52	2.24	138.98	50.18
		M. polymorpha	1403	3.32	1.30	68.20	24.25
	Makaha Ridge	*M. faya*	2406	5.65	0.62	110.20	11.68
		M. polymorpha	1248	7.86	1.14	156.83	31.94
	Waimea Canyon	*M. faya*	2256	4.72	1.02	102.23	22.66
		M. polymorpha	1811	3.05	0.99	56.69	17.77
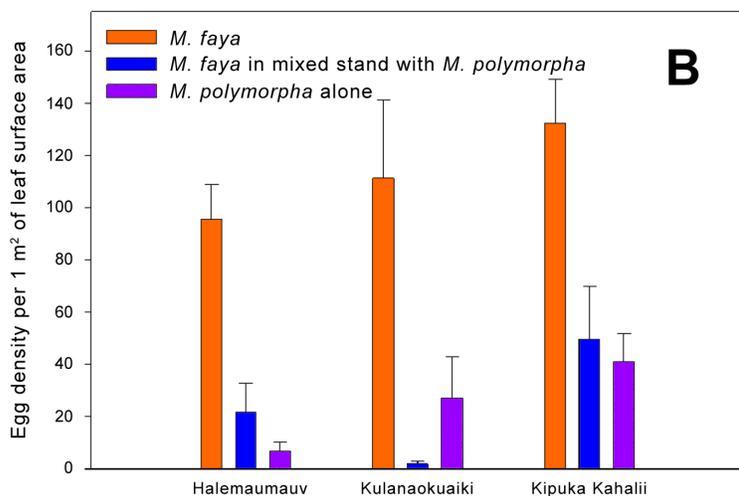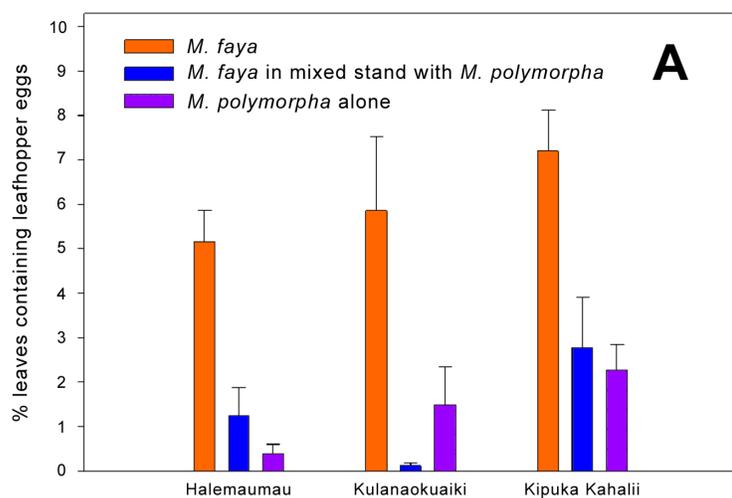
Figure 1. Abundance of *Sophonia rufofascia* leafhopper eggs in relation to *Myrica faya* removal in Hawaii Volcano National Park. **A** – percent leaves containing leafhopper eggs; **B** – leafhopper egg density/m² of leaf surface.

between those two factors was not statistically significant ($F_{4,18} = 1.08$, P = 0.3963). Egg density was higher on *M. faya* leaves than on *M. polymorpha* leaves (orthogonal contrast, F = 55.01, P < 0.0001), but *M. faya* presence had no impact on leafhopper egg density in *M. polymorpha* leaves (orthogonal contrast, F = 0.01, P = 0.9574).

Egg abundance in relation to foliar pubescence

Glabrous *M. polymorpha* trees harbored an average of 298.2 ± 59.9 leafhopper eggs/m² of leaf surface area, while hirsute trees harbored only 11.3 ± 4.2 eggs/m². The difference between morphotypes was highly significant (t-test, $T_{10} = -4.78$, P = 0.0008).
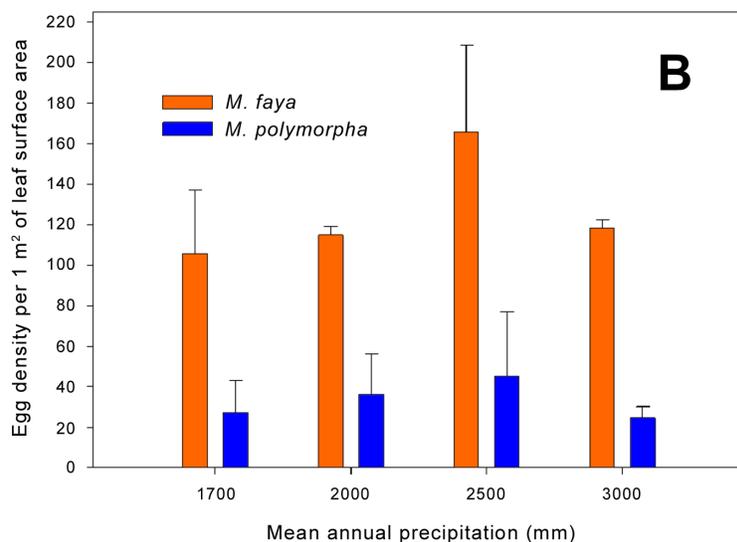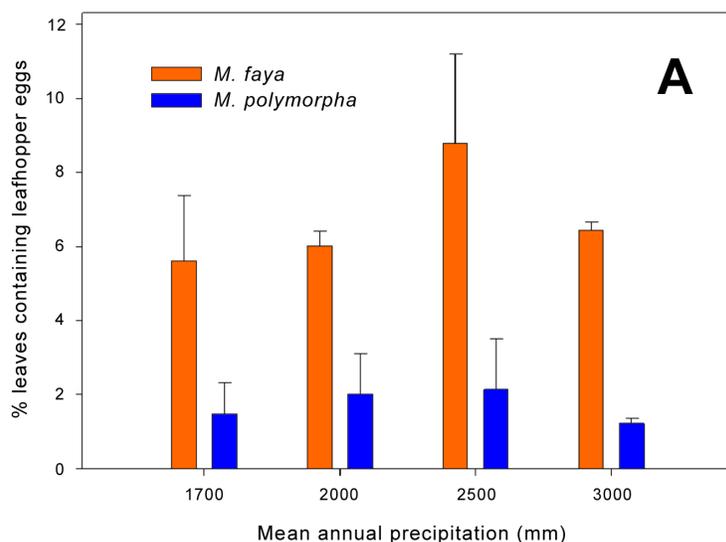
Egg abundance in relation to mean annual precipitation

Figure 2. Abundance of *Sophonia rufofascia* leafhopper eggs in relation to habitat humidity along a precipitation gradient in Hawaii Volcano National Park. **A** – percent leaves containing leafhopper eggs; **B** – leafhopper egg density/m² of leaf surface.

Kipuka Kahalii ($F_{2,18} = 4.61$, P = 0.0241). It was also influenced by the tree context ($F_{2,18} = 21.66$, P < 0.0001) (Fig. 1A). However, orthogonal contrasts revealed that while a higher proportion of *M. faya* leaves contained two-spotted leafhopper eggs compared to *M. polymorpha* leaves (F = 43.24, P < 0.0001), *M. faya* presence had no impact on the infestation of *M. polymorpha* leaves themselves (F = 0.08, P = 0.7774). The interaction between the site and the tree context was not statistically significant ($F_{4,18} = 1.08$, P = 0.3947).

Leafhopper egg density was equal to 113.2 ± 11.8 eggs/m² in *M. faya* leaves, 24.4 ± 9.6 eggs/m² in *M. polymorpha* leaves collected from the trees growing together with *M. faya*, and 25.1 ± 7.5 eggs/m² in *M. polymorpha* leaves collected from the trees growing in the areas where *M. faya* had been removed. Similar to the proportion of infested leaves, egg density was significantly influenced by sampling site ($F_{2,18} = 4.52$, P = 0.0257) and by tree context ($F_{2,18} = 27.51$, P < 0.0001) (Fig. 1B). Again, the interaction

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Over all leaves collected along the precipitation gradient, approximately $6.7 \pm 0.7\%$ of *M. faya* leaves and $1.7 \pm 0.4\%$ of *M. polymorpha* leaves contained two-spotted leafhopper eggs. Egg density was 126.2 ± 13.4 eggs/m^2 for *M. faya* and 33.4 ± 10.1 eggs/m^2 for *M. polymorpha*. As in the other two surveys, both proportion of infested leaves and egg density were significantly higher for *M. faya* than for *M. polymorpha* ($F_{1,16} = 34.02$, P < 0.0001 and $F_{1,16} = 35.57$, P < 0.0001, respectively) (Fig. 2). However, site location along the precipitation gradient influenced neither proportion of infested leaves ($F_{3,16} = 0.69$, P = 0.5624), nor egg density ($F_{3,16} = 0.34$, P = 0.7942). Also, none of the interactions was statistically significant ($F_{3,16} = 0.18$, P = 0.9113 for proportion of infested leaves, and $F_{3,16} = 0.16$, P = 0.9223 for egg density).

Discussion

Both *M. faya* and *M. polymorpha* were suitable oviposition hosts for two-spotted leafhoppers. However, within most surveyed sites leafhoppers laid significantly more eggs on the foliage of *M. faya* than on *M. polymorpha*. Therefore, it is probable that invasion of native Hawaiian forests by *M. faya* creates a more favorable habitat for the two-spotted leafhopper. Our results support the suggestion that damage caused by exotic pests often entails positive interactions, either one-way or two-way, among the introduced species (Howarth 1985; Simberloff and Von Holle 1999). Indeed, in their recent review of the published literature, Simberloff and Von Holle (1999) reported that of 190 pairwise interactions between the alien species tested, 82% consisted of +/- interactions similar to the one described in the present study, 5.3% consisted of +/+ interactions, and only 6.3% consisted of mutually negative -/- interactions.

Oviposition preference of the leafhoppers was strongly influenced by the presence of foliar pubescence on *M. polymorpha* trees. In all habitats where *M. polymorpha* trees were mostly hirsute, the number of leafhopper eggs was lower on the endemic tree than on *M. faya*. Furthermore, *M. faya* presence did not affect infestation of hirsute *M. polymorpha* with leafhopper eggs in mixed tree stands. Therefore, we suggest that increased captures of adult leafhoppers on *M. polymorpha* trees in the areas invaded by *M. faya* (Lenz and Taylor 2001) probably indicate a general build-up of the leafhopper populations in those areas, not their increase specifically on *M. polymorpha* trees. In other words, the invasive plant provided a reservoir for the pest to build up upon, but its direct association with the native plant did not appear to be particularly important.

The glabrous morphotype of *M. polymorpha* was more suitable for leafhopper oviposition than the hirsute morphotype. All *M. polymorpha* trees surveyed on the island of Kauai lacked foliar pubescence. Accordingly, their infestation with leafhopper eggs was comparable to that of *M. faya* at two of the Kauai sites. At the remaining two Kauai sites, *M. polymorpha* harbored fewer eggs than *M. faya*, possibly because the high nitrogen content of *M. faya* foliage favored leafhopper development under particular local conditions (Mattson 1980; Louda and Collinge 1992). However, the difference was far less dramatic than at the hirsute morphotype-dominated sites surveyed on the island of Hawaii. When growing within the same geographic area, hirsute morphotypes of *M. polymorpha* harbored 30 times less eggs than glabrous morphotypes.

Also, visible symptoms of leafhopper damage (chlorosis, vein browning) were always more severe on the glabrous trees (Alyokhin, unpublished data). This confirms anecdotal observations of Jones *et al.* (2000), who reported higher levels of leafhopper damage to the glabrous morphotypes of *M. polymorpha* and *D. linearis* when compared to the hirsute morphotypes of the same species.

Foliar trichomes create a mechanical barrier, limiting leafhopper access to the leaf surface, interfering with locomotion and attachment to a plant, and often causing death of entrapped individuals (Broersma *et al.* 1972; Pillemer and Tingey 1976; Tingey 1985; Elden and Elgin 1992). Therefore, it is not surprising that hirsute *M. polymorpha* made a poor ovipositional host for two-spotted leafhoppers. Its replacement by glabrous *M. faya* will result in build-up of leafhopper populations that are otherwise tolerant of dry conditions dominated by the hirsute morphotype. Because of the broad host range characteristic of the two-spotted leafhopper, this build-up may adversely affect a number of endemic plant species growing in native forests.

Acknowledgements

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