Feeding Damage of the Introduced Leafhopper *Sophonia rufofascia* (Homoptera: Cicadellidae) to Plants in Forests and Watersheds of the Hawaiian Islands

VINCENT P. JONES, PUANANI ANDERSON-WONG, PETER A. FOLLETT, 1 PINGJUN YANG, DAPHNE M. WESTCOT, JOHN S. HI, 2 AND DIANE E. ULLMAN 3

Department of Entomology, University of Hawaii at Manoa, Honolulu, HI 96822


**ABSTRACT** Experiments were performed to determine the role of the leafhopper *Sophonia rufofascia* (Kuoh & Kuoh) in damage observed on forest and watershed plants in the Hawaiian Islands. Laboratory manipulation of leafhopper populations on fiddlewood, *Citharexylum spinosum* L., caused interveinal chlorosis and vein browning on young fully expanded leaves similar to that observed on leafhopper infested plants seen in the field and necrosis on older leaves. Field studies with caged "uluhe" fern, *Dicranopteris linearis* (Burman), demonstrated that frond veins turned brown within 2 d of leafhopper feeding; and by 141 d after feeding, an average of 85% of the surface area of the fronds were necrotic compared with only 12% necrosis in untreated cages. Field trials with stump-cut firetree, *Myrica faya* Aiton, were performed to determine the effect of leafhopper feeding on new growth. Our studies showed that the new growth in exclusion cages had significantly greater stem length and diameter, a higher number of nodes, fewer damaged leaves, and almost twice as much leaf area compared with plants caged but with the sides left open to permit leafhopper access. Microscopic examination of sections through damaged areas of several leafhopper host plants showed vascular bundle abnormalities similar to those associated with hopperburn caused by potato leafhopper, *Empoasca fabae* (Harris), feeding on alfalfa. On Hawaiian tree fern, *Cibotium splendens* (Gaudichaud), oviposition into the midvein also disrupted vascular bundle integrity and often caused death of the distal portions of the pinnule.

**KEY WORDS** *Sophonia rufofascia*, hopperburn, insect—plant interactions, insect feeding damage, *Dicranopteris linearis*, *Myrica faya*

*Sophonia rufofascia* (KUOH & KUOH) is an introduced leafhopper first discovered in Hawaii in 1988 on fiddle leaf fig, *Ficus lyrata* Warburg (Heu and Kumashiro 1989). It has since been recorded on >310 plant species in 83 families (Fukada 1996). Of these, 66 are endemic plant species and 15 of these 66 are on, or are candidates for, the federal endangered species list. The leafhopper has been found on all of the major Hawaiian Islands, from sea level to an elevation of 1,460 m (Fukada 1996).

Plant symptoms associated with leafhopper presence vary from no visible changes to leaf chlorosis and necrosis of varying severity. In extreme cases, plant death may result. One of the most severely affected plants is the "uluhe" or false staghorn fern, *Dicranopteris linearis* (Burman). This plant plays an important role in watershed and forest areas by stabilizing the soils in areas of steep slope and high rainfall, and discouraging the establishment of accidentally introduced weed species (Scott 1969, Kepler 1984). Uluhe grows in large thickets 0.5—2 m deep that can cover large portions of the forest and watershed areas in Hawaii (Cuddihy and Stone 1993). In 1993, large areas of dead and dying uluhe were reported and the suggestion was made that the problems were the result of *S. rufofascia* feeding (Palmer 1993). Our surveys showed that low populations of leafhopper were associated with these areas, but areas were also found where leafhoppers were present, but uluhe was relatively unaffected. In addition, our surveys showed areas where many large uluhe patches (2—4/ha covering >100 m²) had apparently died several years before our study began (because they were completely covered by other plant species). It was therefore impossible to determine what role, if any, *S. rufofascia* had played in the death of ferns in these areas.

Besides uluhe, other plants commonly affected by *S. rufofascia* feeding include the endemic ohia-lehua tree, *Metrosideros polymorpha* Gaudich-Beaupre, which is the dominant hardwood tree in most Hawaiian forests, and several species of the Hawaiian tree ferns (hapu‘u), *Cibotium splendens* (Gaudichaud) and other species. Both ohia-lehua and hapu‘u are common and often dominant components of native forest...
stands and their presence is considered vital to the continued structural and functional integrity of native ecosystems in which they grow (Cuddihy and Stone 1993). Alien species in Hawaiian forests that are affected by leafhoppers include ti, Cordyline fruticosa (L.), which is an essential part of Hawaiian cultural practices; firetree, Myrica faya Aiton, an aggressive invader that is currently affecting plant succession in Hawaii Volcanoes National Park (Vitousek et al. 1987); guava, Psidium guajava L., a tropical fruit and invader in lowland forest and watershed areas; and fiddlewood, Citharexylum spinosum L. and C. caudatum L., which are common ornamental trees invading lowland forest and watershed areas (Cuddihy and Stone 1993).

The symptoms associated with S. rufofascia presence on these plants are similar to those observed in association with feeding of the potato leafhopper, Eupoaeca fabae (Harris), on alfalfa (Ecale and Backus 1995a). This similarity, as well as the ecological, cultural, and economic importance of the affected plants, led us to examine the role of S. rufofascia feeding in causing plant injury. The suggestion that a phytosystem transmitted by S. rufofascia might be involved in causing the damage observed on crops and plants in Hawaiian forests and watersheds was initially considered; however, studies to detect these organisms eliminated this possibility (Jones et al. 1998). The purpose of this study was to determine if leafhopper feeding can cause the type of damage observed on plants in Hawaiian forests and watersheds, to determine whether plant damage is localized to areas of leafhopper feeding or systemic, and to examine tissue damage in leafhopper host plants using light microscopy.

Materials and Methods

Fiddlewood Laboratory Studies. Laboratory experiments were set up to determine the effect of leafhopper feeding on leaves of different ages of fiddlewood, seedlings, whether there was any translocation of injury to leaves present on the plant but not exposed to leafhopper feeding, and whether leafhopper feeding on older growth affected new growth. Fiddlewood was chosen because it is easy to grow, has a leaf architecture consisting of 2 leaves per node that facilitates experimental manipulation, and exhibits severe symptoms of interveinal chlorosis in the field when leafhoppers are present. Plants used in the experiments were raised in the greenhouse until they were at least 30 cm tall and were as uniform as possible in terms of size and vigor, and undamaged by insect feeding. Seeds for the plants were collected from trees in the watershed area of Manoa Valley (Oahu, HI). Two leaves at a single node were caged separately using organdy cloth sleeve cages. Leafhoppers were introduced into one cage while the other cage received no leafhoppers. In the 1st experiment we caged the youngest pair of fully expanded leaves and introduced 18 late instar nymphs or adult leafhoppers into one of the cages. For a 7-d period, leafhoppers were counted daily, and replaced as necessary to maintain the initial number of leafhoppers. After 7 d, ~126 leafhopper days of feeding (where a leafhopper day is the equivalent of 1 leafhopper feeding for 1 d) had accumulated and all leafhoppers were removed. The 2nd experiment was identical to the 1st, except the caged leaves were at the 3rd node down from the 1st fully expanded leaf. The final experiment was identical to the other 2, except the oldest pair of leaves in good condition was caged.

The experiments were evaluated by examining each leaf on the plant for the presence or absence of damage symptoms. The leaves were evaluated at 22 and 58 d after the start of the experiment in experiment 1, at 14 and 50 d in experiment 2, and at 19 and 50 d in experiment 3. All new growth occurring during the experiment was also examined for any symptom development.

Data on presence/absence of damage versus type of treatment (control or leafhopper feeding) of the designated leaf node were tabulated in a 2 × 2 table and analyzed with a chi-square test to determine if damage was independent of leafhopper feeding (Ludwig and Reynolds 1988). Analyses were run separately for each of the 3 different experiments. Data for the presence or absence of damage on other nodes were simply tabulated to determine if any nodes above or below the treated node showed damage.

Uluhe Response of Leafhopper Feeding. Observations of several areas with uluhe dieback suggested that symptoms were more severe on sunny slopes than on shaded slopes. We performed 2 field experiments to help understand the effect of leafhopper feeding on uluhe and to determine whether rate of dieback was affected by sun/shade. The 1st field experiment was performed on the island of Oahu at a site in the Maunawili Valley, just off the Maunawili hiking trail at an elevation of ~200 m. One plot was established in a 0.25-ha shaded site. Uluhe in the center of the shaded plot was healthy, but damage was present at the outer edge. A 1-ha plot of uluhe in full sun ~150 m from the 1st plot was established at the same time. Treatments began on 26 March 1995 and the experiment was terminated 15 August 1995. The fronds treated were almost fully expanded, undamaged, and occurred near the center of the patches. In uluhe, 2 fronds arise from each branching point along the rachis of the fern; thus, they are approximately the same age. We caged both fronds arising from a branching point using organdy sleeve cages, and introduced leafhoppers into 1 of the 2 cages. Voucher specimens of the leafhoppers used are in the University of Hawaii Insect Museum. A total of 10 such paired caged fronds was used in each plot. Adult and late instar leafhoppers were collected from nearby host plants using aspirators, and 10 leafhoppers were placed in each cage. Leafhopper numbers in the cages were checked daily and newly collected leafhoppers were added to replace those dead or missing until ~55 leafhopper-days worth of damage had accumulated on the treated fronds. Frond necrosis was measured using 2 methods on days 1, 1.5, 2, 3, 13, 18, 24, 28, 34, 39, 44, 49, 54, 59, 77, 93, 114, 127, and 141 d after the start of the experiment. The 1st method was a visual
determination of the percentage of surface area of the frond that was necrotic, and the 2nd method determined the proportion of the pinnule tips that were necrotic. The 1st method gives an indication of the overall effect of leafhopper feeding, and the 2nd method is more sensitive to signs of early damage.

Because examining the fronds required removal of the organdy cages, we gave particular attention to handling the fronds gently. Even so, occasionally a frond was damaged, and it was removed from the analysis at that point. We also reexamined the data from the previous sampling occasions to determine if the damage increased dramatically on the date immediately before we found the damage. If so, that data were also eliminated from the analysis.

Statistical analysis was performed using the Wilcoxon sign test (SAS Institute 1994) on data from day 13 (1st d after the 85 leafhopper days had accumulated) and day 141 (the final day of the experiment). The analysis was performed separately for fronds from the sun and shade plots. Regression analyses (SAS Institute 1994) were performed separately on the mean percentage of the frond necrosis versus time for both the sun and shade plots. The rate of necrosis (i.e., the slopes) in the sun and shade was compared using covariance analysis (Zar 1996).

The 2nd field experiment was conducted from 7 July 1995 to 12 December 1995 at Puuimau in Hawaii Volcanoes National Park (referred to as Volcanoes) on the island of Hawaii at =1,000 m elevation. The 3 trees in each group were chosen for their physical proximity (1.5-m radius) and their similarity in basal trunk diameter. Trunk diameters across all trees ranged from 25 to 50 mm. Each tree in a group of 3 were assigned randomly to 1 of 3 treatments: (1) closed cage (cage completely enclosed in screen), (2) open cages (cage tops screened but sides left open), and (3) uncaged. All trees were stump cut to soil level on 13 September 1995 and allowed to regenerate with or without cages. Cage frames were constructed of wood (2.5 by 5 cm); dimensions were 60 cm square at the base with 50 cm
long A-frames. Gray window screen (6 × 6 holes per square centimeter) was used to cover the frame.

On 22 February 1996, cages were removed and various measures of firetree regeneration were taken. Regrowth consisted of multiple shoots growing up from above- and below-ground portions of cut stumps. For each stump, the 3 longest stems were selected and harvested. Leaf area was measured for the 3 terminal leaves (typically the largest leaves on the stem) using leaf length (L) and width (W) and the formula for the area of an ellipse, (W/2) × (L/2) × π. For each of the 3 stems, data were taken on length, basal diameter, number of plant nodes, primary leaves, damaged primary leaves, axillary shoots, and axillary leaves. Analysis of the different parameters was performed using a randomized block design analysis of variance (ANOVA) (with group of 3 trees being a block), followed with 2 single degree of freedom orthogonal comparisons for the separation of the cage effect (no cage versus open cage) and the effect of leafhoppers (open cage versus closed cage). Leaf size was analyzed separately using a one-way ANOVA and the same 2 single degree of freedom orthogonal comparisons described above (SAS Institute 1994). Before ANOVA, all data were checked for normality and homogeneity of variance using the Minitab (1995) version of the Ryan—Joiner test (1976), and Bartlett’s test (Bartlett 1937), respectively.

Host Sectioning. To determine the effect of S. rufofascia feeding on a wide variety of forest and watershed plants, we collected leaves fromiddlewood, guava, firetree, and Hawaiian tree fern showing yellowing in the presence of leafhoppers. When possible, undamaged leaves were collected at the same site; but

**Fig. 2.** Mean percentage of pinnule tips necrotic on fronds exposed to 84 leafhopper days in either the sun or shade and control plants in the same location at the Maunawili site.

![Graph showing mean percentage of pinnule tips necrotic](image)

**Fig. 3.** Control (left) and frond exposed to 84 leafhopper days (right) in sun portion of Maunawili site. Veins on the control frond are clear, those on treated fronds are brown. Necrosis occurs first at the tip then moves down toward the midvein of the frond.
for guava, greenhouse-grown controls were used because undamaged leaves were rare in field situations. Cross sections of the leaves were cut through the midvein and fixed for 2–3 h using a 4% glutaraldehyde in 0.05 M cacodylate buffer and 2% formaldehyde solution and evacuated at 10 psi for 30 min. Samples were then washed in 0.05 M cacodylate buffer and fixed with 2% osmium tetroxide in 0.05 M cacodylate buffer for 1.5 h. Samples were then washed and stained with 5% uranyl acetate in double distilled water for 15 min, washed, run through a dehydration series of ETOH (50–100% in 10% increments), and embedded in Spurr’s plastic (Spurr 1969) (Ted Pella, Redding CA) for sectioning (Westcot et al. 1993). Leaves were sectioned using an ultramicrotome and cut to 0.5- to 1-μ thickness, stained in toluidine blue-O (0.25 g in a 1% sodium borate solution for 1 min), and examined using a compound microscope for gross structural abnormalities.

Results

Fiddlewood Laboratory Studies. Damage to fiddlewood in all 3 experiments occurred on all the leaves exposed to leafhoppers and only on those leaves. The leaf on the opposite node showed no damage, nor did any other leaf on the plant or any subsequent new growth. Because the results were the same in all experiments, the chi-square tests were all identical and all showed that the damage was not independent of leafhopper feeding ($\chi^2 = 8.0$, df = 1, $P = 0.0047$).

The severity of the damage increased as the age of the leaf exposed to leafhoppers increased. In the 1st experiment, browning of tertiary veins and chlorosis on the treated leaves were the only symptoms, and damage looked very similar to that seen in the field. However, leafhopper feeding in the 2nd and 3rd experiments resulted in necrosis of the older, but still vigorous leaves. Necrosis was not a symptom noticed in the field on leafhopper infested trees. Tertiary veins were also brown and chlorosis was very noticeable in leaves fed upon.

Uluhe Response of Leafhopper Feeding. At the Maunawili site, damage to uluhe was virtually negligible on the caged control fronds over the study period (Fig. 1). For fronds exposed to leafhoppers, percentage of frond necrosis rose in an approximately linear fashion until frond necrosis averaged 85.4% on day 141 (Fig. 1). The Wilcoxon tests indicated significant differences in percentage of frond necrosis between the control and leafhopper treatments at both 13 and 141 d ($T = 22.5$, df = 8, $P = 0.004$; the results for all 4 comparisons are the same because the sign of the differences is always the same in these 4 data sets). Similar trends were seen with the percentage of necrotic tips index, but because of its greater sensitivity, showed a much quicker response and leveled out after April 2000

Fig. 4. Normal pattern of senescence of glabrous uluhe fern. Necrosis occurs randomly along the length of the frond.

Fig. 5. Mean percentage of pinnule tips necrotic on fronds exposed to 84 leafhopper days in either the sun or shade and control fronds in the same location at the Hawaii Volcanoes National Park site.
70 d between 90 and 100% (Fig. 2). As with the percentage frond necrosis, the percentage of necrotic tips was significantly higher on fronds exposed to leafhoppers at both 13 and 141 d \((t = 22.5, df = 8, P = 0.004)\).

Linear regression of the percentage of fronds necrotic in the sun and shade treatments were highly significant (sun \% frond necrosis \(= 5.7 + 2.16 \times (\text{days after treatment}) \) \(r^2 = 0.97, F = 432.6, df = 15, P < 0.001\); shade \% frond necrosis \(= 0.43 + 0.62 \times (\text{days after treatment}) \) \(r^2 = 0.97, F = 531.7, df = 17, P < 0.0001\). Covariance analysis indicated that there were no significant differences in the slope (rate of increase in necrosis) between the sun and the shade plots \((t = 0.85, df = 32, P = 0.79)\), suggesting any differences between damage observed in sun and shaded areas are a result of differential feeding or insect abundance.

Examination of the fronds during the early part of the test indicated that veins turned orange-brown within 2 d after being exposed to leafhoppers, whereas veins in the unexposed cages remained clear for the entire period of the test. The damage on fronds exposed to leafhoppers also did not follow the pattern of normal senescence observed in other fronds in the same patch. Necrotic areas on the fronds exposed to leafhoppers typically started at the tip of the pinnules and moved toward the midvein (Fig. 3), whereas in normal senescence, necrotic areas appeared randomly along the length of the pinnules (Fig. 4). In addition, leafhopper damaged fronds had a reduced pinnule size compared with control fronds (Fig. 3), whereas normally senescent pinnules were normal size.

The results of the 2nd feeding study, performed at Hawaii Volcanoes National Park, showed a marked decrease in the percentage of tips becoming necrotic and a lower rate at which necrosis occurred compared with that observed in the Maunawili experiment (Fig. 5). For example, at Maunawili, >80% of the tips were

![Fig. 6. Control (left) and frond exposed to 84 leafhopper days (right) in Hawaii Volcanoes National Park site. Control frond is dark green with clear veins, treated frond is yellow with brown veins.](image)

![Fig. 7. Mean percentage of pinnules yellow on fronds exposed to 84 leafhopper days in either the sun or shade and control plants in the same location at the Hawaii Volcanoes National Park site.](image)

\begin{table}[h]
\centering
\begin{tabular}{|l|c|c|c|c|c|}
\hline
\textbf{Measurement} & \textbf{Mean Per Stem ± SEM} & \textbf{P > |t|} for Single DF Comparisons & \textbf{P > |t|} for Single DF Comparisons \tabularnewline & \textbf{Closed Cage} & \textbf{Open Cage} & \textbf{No Cage} & \textbf{Closed Cage versus Open Cage} & \textbf{No Cage versus Open Cage} \tabularnewline \hline
\text{Stem length (cm)} & 31.4 ± 1.6 & 18.7 ± 1.0 & 25.2 ± 2.0 & >0.0001 & 0.0002 \tabularnewline \text{Stem diameter (mm)} & 3.0 ± 0.1 & 2.3 ± 0.1 & 2.6 ± 0.2 & >0.0001 & 0.034 \tabularnewline \# Plant nodes & 26.8 ± 0.9 & 22.3 ± 1.0 & 25.1 ± 1.3 & 0.0003 & 0.017 \tabularnewline \# Primary leaves & 18.8 ± 1.2 & 17.0 ± 0.9 & 19.6 ± 1.3 & 0.20 & 0.083 \tabularnewline \# Damaged leaves & 3.2 ± 0.7 & 15.7 ± 1.0 & 19.6 ± 1.3 & >0.0001 & 0.003 \tabularnewline \# Axillary shoots & 0.7 ± 0.4 & 1.3 ± 0.5 & 3.1 ± 0.6 & 0.38 & 0.013 \tabularnewline \# Axillary leaves & 2.6 ± 1.2 & 7.9 ± 1.0 & 11.6 ± 3.3 & 0.21 & 0.24 \tabularnewline Leaf area (mm$^2$) & 1385.1 ± 81.3 & 790.2 ± 45.0 & 620.5 ± 80.1 & >0.0001 & 0.027 \tabularnewline Stem dry weight (g) & 2.0 ± 0.3 & 0.8 ± 0.2 & 1.4 ± 0.3 & 0.0006 & 0.007 \tabularnewline Leaf dry weight (g) & 3.6 ± 0.7 & 2.4 ± 0.6 & 2.8 ± 0.6 & 0.075 & 0.13 \tabularnewline \hline
\end{tabular}
\caption{Response of firetree to caging conditions in the presence of Sophonia rufofascia}
\end{table}

*All means based on 3 stems from 8 replicates, except for the no cage treatment where one of the replicates died.*
necrotic by 50 d after introduction of leafhoppers; whereas, at Volcanoes, <10% of the tips were necrotic by the same time. Comparison of the damage at 17 d at Volcanoes showed no significant difference in damage between fronds exposed to leafhoppers and control fronds (shade $T = 4$, df = 9, $P = 0.125$; sun $t = 2$, df = 9, $P = 0.25$). However, at 151 d the trends of fronds being exposed to leafhoppers showing significantly greater tip necrosis were repeated (shade $t = 22.5$, df = 8, $P > 0.002$; sun $t = 27.5$, df = 9, $P > 0.001$). Comparison of the slope of plant damage over time for the sun and shade areas revealed that the rate of necrosis was significantly faster in the shaded area ($t = 3.42$, df = 12, $P = 0.002$) (sun: $\%$ tips necrotic $= 0.65$ (SE = 0.74) + 0.022 $\times$ (days after treatment) (SE = 0.001); $F = 313.8$, df = 7, $P < 0.0001$; shade: $\%$ tips necrotic $= 0.54$ (SE = 0.34) + 0.05 $\times$ (days after treatment) (SE = 0.006); $F = 77.1$, df = 7, $P < 0.0001$).

Necrosis was a common symptom at the Maunawili Valley site (Fig. 3). However, at the Volcanoes site, we noticed that by 60 d, the fronds in the sun exposed to

Fig. 8. Cross-section through the midvein of (A) healthy fiddlewood leaf and (B) midvein of fiddlewood showing chlorosis.
leafhoppers were noticeably more chlorotic and spindly than the untreated fronds and necrosis was more confined to the pinnule tips (Fig. 6). This led us to determine the percentage of pinnules that were chlorotic from 60 d onward. At 60 d, we found that fronds in the sun were significantly more chlorotic when exposed to leafhoppers ($t = 10.5, df = 9, P = 0.31$), but there were no significant differences in chlorosis in the shaded areas between fronds exposed to leafhoppers and unexposed fronds ($t = 0.5, df = 9, P = 1.0$).

At the termination of the experiment (day 151), fronds in both the sun and shade showed significantly higher percentage of chlorotic pinnules on leafhopper fed upon pinnules (sun, $t = 27.5, df = 9, P = 0.002$; shade, $t = 10.5, df = 8, P = 0.031$). In a reversal of the effect seen by examining percentage of necrotic tips, the treatments in the sun showed more damage than those from the shade (Fig. 7).

**Effect of Leafhoppers on Firetree Growth Patterns.** Significant differences among treatments were observed for stem length ($F = 25.0; df = 2, 68; P < 0.001$), stem diameter ($F = 8.7; df = 2, 68; P < 0.0005$), number of nodes ($F = 7.6; df = 2, 68; P < 0.001$), number of damaged leaves ($F = 97.1; df = 2, 68; P < 0.0001$), number of axillary shoots ($F = 6.2; df = 2, 68; P < 0.004$), dry stem weight ($F = 11.1; df = 2, 22; P = 0.002$), and leaf surface area ($F = 46.5; df = 2, 68; P < 0.0001$) (Table 1).

Orthogonal comparison tests indicated there was a cage effect for all measures but the number of axillary leaves, and leaf dry weight (Table 1). Therefore, the effect of *S. rufofascia* exposure can be estimated best by comparing the closed cage (exclusion) and open cage treatments. Firetree in the exclusion cages had significantly greater mean stem length and diameter, a higher number of nodes, fewer damaged leaves, almost double the leaf area, and greater stem dry weight than plants in the open cage treatment (Table 1). These data are consistent with the general observation that firetree attacked by *S. rufofascia* has a rosette appearance as a result of smaller leaf size and an increase in the number of axillary shoots and leaves, and decreased stem length compared with undamaged plants.

**Leaf Sections.** Damaged sections revealed that these sections consistently stained darker than the control sections and cellular membranes and structures within the cells were less well defined. Examination of the fiddlewood and firetree sections showed similar injury with the vascular bundle distorted compared with the undamaged leaves (Figs. 8 and 9). Under light microscopy, the vascular bundle of guava leaves injured by leafhopper feeding was identical to uninjured leaves.

The sections of Hawaiian tree ferns were confined to areas where oviposition scars were detected. A single egg blocks up to one-third of the vascular bundle and disrupts both the phloem and xylem (Fig. 10). On Hawaiian tree fern, the oviposition of a single egg can cause death of the pinnule distal to the oviposition site. Although *S. rufofascia* lays its eggs singly, we have observed multiple eggs laid into the midrib within 12...
mm of each other. Thus, vascular tissue in smaller stems could be completely disrupted by egg deposition alone in certain plant species.

**Discussion**

Our results show that *S. rufofascia* feeding and oviposition cause serious damage to plants in Hawaiian forests and watersheds. On all the plant hosts studied, damage from feeding was localized to those leaves exposed to *S. rufofascia* and was not apparent on other leaves of the same plant, even those on the opposite side of a node. This finding suggests that the factor causing damage (i.e., toxins present in leafhopper salivary secretions) is not translocated far from the feeding site. In laboratory manipulations of leafhoppers on young fiddlewood leaves, symptoms indistinguishable from those observed in the field were observed. Symptoms on middle aged and old leaves were more severe than what is normally observed in the field. However, in the field the leafhoppers tend to feed almost exclusively on new growth (V.P.J., unpublished data), so the type of symptoms we were able to generate by caging leafhoppers on older leaves would rarely occur.

Overall, the damage symptoms and the sections through damaged leaves show that the disruption of tissue structure is consistent with the damage associated with *E. fabae* feeding on alfalfa (Ecale 1995a, 1995b). The damage caused by *E. fabae* has been attributed to mechanical damage caused by movement of their stylets and injection of salivary enzymes during feeding. Nothing is known regarding the feeding behavior of *S. rufofascia*; however, it is likely they cause damage in a manner similar to that reported for *E. fabae*. Although the factor causing plant damage is not apparently systemic, the localized damage to the vascular tissues may result in reduced vigor of affected plants. In our firetree field tests, plants had significantly reduced stem length, diameter and leaf area. Field studies with uluhe also showed that leafhopper feeding caused decreased plant vigor and an increased rate of senescence. These studies agree well with the reduced yield of guava associated with leafhopper damage reported by Jones et al. (1998). In addition, our sections through Hawaiian tree fern show that oviposition into the midvein may disrupt vascular bundle integrity. Yang et al. (1998) found that *S. rufofascia* uses the midvein as an oviposition site on many host plants and suggesting that oviposition may be damaging for many hosts other than Hawaiian tree fern. Because the distortion of the vascular bundle caused by leafhopper feeding and oviposition observed, the symptoms of plant death or decline are probably enhanced when plants are under water stress because of reduced water transport. These effects may become clearer in the next few years because high rainfall occurred during the winter of 1997, and the current (1998) El Nino effects on Hawaii caused a drought throughout much of the island of Oahu where uluhe dieback areas are common.

The field studies with uluhe fern confirmed that leafhopper feeding causes decreased plant vigor and an increased rate of senescence. However, the rate of necrosis expression was much slower at the Volcanoes site compared with the Maunawili site. Much of the difference can probably be attributed to the differences in feeding on glabrous versus pubescent forms of uluhe. We have seen the same damage differential on glabrous and pubescent forms of ohia-lehua, which can be commonly found growing with branches in-
tertwined; the damage is always more severe on the glabrous leaves (V.P.J. and P.A.F., unpublished data). We also found that damage expression on the 2 forms of uluhe was different, with yellowing commonly found on the pubescent form and necrosis common on the glabrous form. In addition to the differences in uluhe, there are environmental and elevation differences that may account for the reduced rate of damage expression. For example, the Maunawili site is warmer and has higher rainfall than the Volcanoes site.

The field tests with firetree show that S. rufofascia feeding can also cause severe distortion and changes in plant growth patterns. However, in the case of firetree, the effect is probably not enough for S. rufofascia to act as a useful biological control agent for this invasive alien weed, even if its host range were restricted solely to firetree.

Our experiments show that S. rufofascia feeding can severely affect plant health. Combined with its broad host range and its affect on many of the dominant plants in Hawaiian forests and watershed areas, S. rufofascia provides an excellent opportunity to examine community structure and stability in what are typically thought of as fragile ecosystems.

Acknowledgments

We thank D. Foote (USGS, HI, Volcanoes National Park) for providing the use of facilities, field sites, and for discussions on the effect of Sophonia on firetree. We also thank V. Tanimoto (Hawaii Department of Land and Natural Resources) for financial and operational support in this project. C. Lamoureux (Department of Botany, University of Hawaii at Manoa) and C. Imada (Bishop Museum) graciously provided confirmation of plant identifications. This work was supported by a McIntire-Stennis grant and grants from the Hawaii Department of Agriculture and the Hawaii Department of Land and Natural Resources to V.P.J., D.E.U., and J.S.H. This is journal series number 4463 of the College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu.

References Cited


Received for publication 30 December 1999; accepted 30 September 1999.