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Plant–Insect Interactions

Short-Term Physiological Response of a Native Hawaiian Plant, *Hibiscus arnottianus*, to Injury by the Exotic Leafhopper, *Sophonia orientalis* (Hemiptera: Cicadellidae)

Alina Avanesyan,[1,3] Kirsten A. Snook,[2] Peter A. Follett,[2] and William O. Lamp[1]

[1]Department of Entomology, University of Maryland, College Park, MD 20742, [2]U.S. Pacific Basin Agricultural Research Center, USDA-ARS, 64 Nowelo Street, Hilo, Hawaii 96720, and [3]Corresponding author, e-mail: alina@umd.edu

Abstract

Sophonia orientalis (Matsumura), also known as the two-spotted leafhopper, is a widespread exotic pest of many economically important crop plants and ornamental plants in Hawaii. *Sophonia orientalis* is highly polyphagous and is a major threat to some of the native endemic plants. Despite the successful establishment in Hawaii, interactions of *S. orientalis* with its host plants remain poorly understood. Previous studies primarily focused on distribution, parasitism, and oviposition of *S. orientalis* in Hawaii, whereas plant physiological responses to the leafhopper's injury, and, specifically, gas exchange rates in plants, have not yet been described. In this study, we examined a short-term physiological response of a native Hawaiian plant, *Hibiscus arnottianus* (A. Gray), to injury by *S. orientalis*. We also explored whether *Camellia sinensis* (L.) Kuntze, a native host plant of *S. orientalis* in Asia, exhibits a similar response. We found that *H. arnottianus* plants demonstrated a rapid (2-d) physiological response to injury accompanied by 40% reduction in rate of photosynthesis and 42% reduction in rate of transpiration, whereas *C. sinensis* did not exhibit any reduction in gas exchange rates. We did not record any changes in plant chlorophyll levels after plant injury in either species. Our results suggest that *H. arnottianus* is responding to the leafhopper feeding with a generalized wound response predicted for novel plant–insect herbivore associations. We discuss potential future directions for studies which might focus on host plant responses to *S. orientalis* in its native versus introduced range.

Key words: novel association, plant gas exchange, *Hibiscus*, insect–plant interaction, wound response

Through co-evolution, plants adapt to their native herbivores using a diversity of mechanisms including physical structures, such as trichomes and waxes (Levin 1973), leaf toughness (Price et al. 2011), constitutive plant toxins (Wittstock and Gershenzon 2002), and mutualisms with natural enemies (Janzen 1966). Accidental introduction of an exotic herbivorous insect can have significant effects on a native plant community (Nuñez et al. 2010, Kempel et al. 2015). Without previous association and adaptation, herbivore introductions create novel plant-herbivore interactions. Following Saul and Jeschke (2015), by novel species association we consider any association between native and non-native (exotic) species in which species do not have previous experience of interacting with each other's traits due to lack of their co-evolutionary history. In such novel associations, native plants, which do not have previous co-evolutionary history with exotic insects, may lack specific defenses needed for protection. Such plants may resort to a generalized wound response to injury—i.e., the activation of an array of systemic defense responses regulated by specific genes and focused on both healing of the damaged tissue and preventing further damage

(León et al. 2001, Schilmiller and Howe 2005). Here, we report on such a response of a native Hawaiian plant, *Hibiscus arnottianus* A. Gray, or koki'o ke'oke'o, to injury by an introduced leafhopper, *Sophonia orientalis* (Matsumura, 1912).

Sophonia orientalis, also known as the two-spotted leafhopper as well as the synonym, *Sophonia rufofascia* (Kuoh and Kuoh), is a widespread pest of many economically important plants in Hawaii (Aguin-Pombo et al. 2007). Native to Asia, it was first described from southern China (Kuoh and Kuoh 1983). It was discovered in Hawaii on the island of Oahu in 1987 (Heu and Kumashiro 1989), and within 5 yr it had spread to all major islands of the Hawaiian archipelago (Culliney 1998). A decade later, *S. orientalis* was also detected in Tahiti (Polhemus 2001) and the Macaronesian archipelagos (Aguin-Pombo et al. 2007). More recently, the presence of *S. orientalis* was reported from Gibraltar where this species is likely well established, as well as from a nearby region in southern Spain (San Roque; Wilson et al. 2011).

Sophonia orientalis is an extremely polyphagous agricultural pest in Hawaii which feeds on many important crop plants, as

well as ornamental plants (Duan and Messing 2000). It is a phloem-feeder; it has been reported from more than 300 plant species (both introduced and native to Hawaii) in 83 families (Fukada 1996). These host plants, in particular, include 66 species which are endemic to Hawaii; and of these, 16 species are listed as rare or endangered native plants (Follett et al. 2000). This pest has become a concern due to the severe damage it may cause to its host plants (Lenz and Taylor 2001). One of the most critically damaged crop plants is guava, *Psidium guajava*. Jones et al. (1998) provided evidence that damage to guava was the result of direct feeding injury by the two-spotted leafhopper, and not by phytoplasmas, which may be transmitted by leafhoppers.

As with other phloem feeders, leafhopper feeding has an important effect on host plant physiology. In Hawaii, *S. orientalis* injury to plants has been described as a typical hopperburn response (Backus et al. 2005). Such response includes symptoms of foliar chlorosis and yellowing, changes in leaf morphology, and reduced stem length and leaf area, as well as tissue effects such as disorganized phloem and distorted xylem (Jones et al. 2000). Plant injury from *S. orientalis* results in reduced plant growth and, in extreme cases, death of endemic plants, such as uluhe, or false staghorn fern (*Dicranopteris linearis*), the tree ōhi'a-lehua (*Metrosideros polymorpha*), hāpu'u fern (*Cibotium splendens*), and the endangered *Polyscias racemosa* (Follett et al. 2000, Jones et al. 2000). Successful establishment and spread of *S. orientalis* in Hawaii is apparently promoted by the introduced plant *Morella faya* (syn. *Myrica faya*) (Lenz and Taylor 2001, Yang et al. 2002): the high nitrogen content of *M. faya* leaves most likely facilitates development of insect populations and their subsequent dispersal to other plant species (Lenz 2000).

The introduction of *S. orientalis* in Hawaii resulted in novel associations with Hawaiian endemic plants, such as *H. arnottianus*. Considering that many endemic plant species in Hawaii have lost the defensive adaptations which their ancestors retain on a continent (Messing et al. 2007), such endemic plants are especially vulnerable to additional exploitation by invasive species (Howarth and Ramsay 1991). While distribution, parasitism, and oviposition of *S. orientalis* on native plants (including endemics) have been quite well explored in Hawaii (Duan and Messing 2000; Alyokhin et al. 2001, 2004), only a few studies have focused on feeding damage of *S. orientalis* to plants (Jones et al. 1998, 2000). Also, little is known of host range of this pest in its native range. First described (as *Pseudonirvana rufofascia*) from tea plant, *Camellia sinensis*, one of its hosts in Asia (Kuoh and Kuoh 1983), *S. orientalis* has also been collected on other plants, such as rice (*Oryza sativa*), mulberry (*Morus* spp.), oak (*Quercus spp.*), apricot (*Prunus* spp.), and fig (*Ficus* spp.) (Johnson et al. 2001). However, information about the effect of *S. orientalis* on plant physiology (in both native and introduced range) is limited; in particular, changes in gas exchange rates in plants (if any), as a response to the leafhopper's injury, have not been described. A better understanding of plant physiological response to injury by the two-spotted leafhopper may allow us not only to prevent damage to agriculturally important plants, but also develop effective management strategies to protect rare and endangered plants in Hawaii.

To address these issues, we examined a short-term physiological response of a native Hawaiian plant, *H. arnottianus* (novel host plant), to injury by *S. orientalis* and explored whether *C. sinensis* (a host plant from the native range of *S. orientalis*) exhibits a similar response. We hypothesized that the *H. arnottianus* plant, which has not co-evolved with *S. orientalis* would defend itself using a generalized wound response characterized by a rapid reduction in rates of photosynthesis and transpiration through the closing of its stomata. In contrast, we hypothesized that *C. sinensis*, which should be adapted to its insect herbivores in its native range in Asia, would not respond to leafhopper feeding injury by reducing gas exchange rates.

Materials and Methods

Experiments were conducted in a screenhouse located at the USDA-ARS U.S. Pacific Basin Agricultural Research Center, Hilo, Hawaii, during two periods: January 2011 and January 2012. *Hibiscus arnottianus* plants (obtained from Lehua Lena Nursery, Keaau, HI) and *C. sinensis* plants (provided by Dr. Jon Suzuki; USDA-ARS, U.S. Pacific Basin Agricultural Research Center, Hilo, HI) had been grown in 15-cm-diameter plastic pots with standard greenhouse potting mixture. The leafhoppers were collected in Volcano, Hawaii (approximately 19.439563°N, 155.280527°W) from firetree, *M. faya*.

Gas Exchange Response, *H. arnottianus*

To measure the short-term response of plants to exposure to the leafhoppers, three experimental trials were run. In all trials, two adjacent leaves (one served as a control and one received a treatment) were paired on the same plant to represent a block. Plants of a sufficient size were used in all the trials (three plants per trial; two to three blocks per plant).

Clear plastic boxes, 12 × 9 × 3.5 cm, that could be opened from the side served as whole-leaf cages. On the top and bottom faces, holes were cut into the plastic boxes and covered with mesh to allow ventilation. On one of the front faces, a 2.1-cm-diameter hole in the middle was created for the stem of the leaf, while a 0.8-cm-diameter hole off center on the other side was created to introduce the leafhoppers. Each of the side holes was covered with a piece of foam. Each leaf in all the blocks received a cage; within each block, one randomly selected cage served as a healthy control while the other cage served as the injured treatment with the insertion of leafhoppers.

In trial 1, conducted in 2011, three adults were introduced to each treatment cage on seven blocks. In trial 2, conducted in 2012, two adults were introduced to each treatment cage on eight blocks. In trial 3, also conducted in 2012, three adults were introduced to each treatment cage on six blocks. In all three trials, after 2 d, cages and leafhoppers were removed and measurements were taken on each caged leaf using the LI-6400 Photosynthesis Measurement System (LICOR, Lincoln, NE). The LI-6400 was set for standard levels of light (1500 μmol m^{-2} s^{-1}), CO_2 concentration (400 μmol CO_2 mol^{-1}), and block temperature (25°C).

To assess differences in gas exchange response between healthy and injured leaves the following measurements were taken: 1) chlorophyll levels (SPAD); 2) net photosynthesis (PHOTO); 3) transpiration (TRMMOL); and 4) internal CO_2 levels (C_i). Two measurements were taken on each leaf, then averaged before analysis. Chlorophyll levels in each leaf were measured using a SPAD meter (SPAD 502 chlorophyll meter, Spectrum Technologies, Plainfield, IL). Ten SPAD measurements were averaged for each leaf.

In addition, the A/C_i curve analysis (photosynthetic assimilation rate, A, vs internal CO_2 level) from the 2011 and 2012 experiments estimated respiration rates on healthy and injured leaves. For A/C_i curve analysis, using software provided by LICOR and following Long and Bernacchi (2003), we estimated: 1) the maximum carboxylation rate of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (V_{cmax}); 2) maximum electron transport rate (J_{max});

and 3) triose phosphate utilization (V_{tpu}). In 2011, from the seven blocks described above for trial 1, we selected three blocks to relate net photosynthesis rates (=assimilation, A) to internal CO_2 levels (C_i). The LI-6400 was set for the same level of light, with CO_2 concentration setting changing in the following sequence: 400, 300, 200, 100, 50, 400, 400, 600, 800 μmol CO_2 mol^{-1}, with the first two measurements of 400 deleted from the analysis. In 2012, five blocks were selected from trial 2 for a second but similar A/C_i curve analysis. Measurements and analysis were identical to those in trial 1.

Respiration Rates, *H. arnottianus*

Two methods were used to compare leaf respiration rates in healthy and injured plants. First, in 2011, from the seven blocks described above for trial 1, we selected four blocks to measure respiration rates of injured and healthy leaves. LI-6400 measurements were made as described above, except light level was set at zero (i.e., the measurements were taken in the dark). To assess differences in respiration rates, the same measurements except SPAD were compared. Second, the A/C_i curve analysis experiment described above provided an estimate of respiration rates.

Gas Exchange Response, *C. sinensis*

While cages with *H. arnottianus* leaves included the whole-leaf blade by placing the petiole in the foam plug at the base of the cage, *C. sinensis* leaves have a short petiole and the cage base covered the base of the leaf blade. As above, two leaves per individual plant (three *C. sinensis* plants total) served as one of six blocks, each block with one of two treatments randomly assigned to each leaf in the pair: healthy, with no leafhoppers; or injured, with three adults. After 2 d, gas exchange measurements were taken as described above.

Oviposition, *S. orientalis*

Additionally, to examine whether oviposition was a factor of injury in our experiments, we searched for eggs in leaf tissue used for experiments in 2012. We searched for eggs in 28 *H. arnottianus* leaves, and in 12 *C. sinensis* leaves, in which half of the leaves had been exposed to adult leafhoppers. Clearing leaves and staining eggs were performed following the methods of Carlson and Hibbs (1962).

Statistical Analysis

To compare gas exchange responses and respiration rates between non-injured leaves and leaves with feeding injury from *S. orientalis*

leafhoppers (in both *H. arnottianus* and *C. sinensis* plants), separate two-sample paired *t* tests were used for each measurement, including parameters in the A/C_i curve analysis. To test normality and homoscedasticity of all data, the Shapiro–Wilk test and Bartlett's test were used respectively at α = 0.05. To estimate the relationship between net photosynthesis (PHOTO) and chlorophyll content (SPAD), regression analysis was used separately for each treatment. All data analyses were conducted using R (v.3.1.1); package *lme4* was used for regression analysis.

Results

Gas Exchange Response, *H. arnottianus*

Comparison of gas exchange response between non-injured leaves of *Hibiscus* plants and leaves with feeding injury from *S. orientalis* demonstrated significantly lower rates of photosynthesis and transpiration in injured leaves, whereas chlorophyll levels were not significantly different between healthy and injured leaves. These results were consistent across three trials. On average, injury resulted in 40% reduction in net photosynthesis and 42% reduction in transpiration (Table 1).

Results of regression analysis differed between trial 2 and trials 1 and 3. In trial 2, net photosynthesis was significantly correlated with chlorophyll content in healthy leaves ($r^2 = 0.75$; $P = 0.003$); however, it was not significantly correlated with chlorophyll content in injured leaves ($r^2 = 0.11$; $P = 0.49$). In trials 1 and 3 we did not observe a significant relationship between net photosynthesis and chlorophyll content in both healthy and injured leaves (trial 1: $r^2 = 0.37$; $P = 0.09$ [healthy]; $r^2 = 0.42$; $P = 0.07$ [injured]; trial 3: $r^2 = 0.17$; $P = 0.23$ [healthy], $r^2 = 0.02$, $P = 0.35$ [injured]; Fig. 1).

The A/C_i curve analysis demonstrated significantly lower V_{tpu} values for *Hibiscus* injured leaves in trial 1, whereas V_{cmax} and J_{max} measurements did not differ between healthy and injured leaves. In trial 2, we did not record any significant changes in the A/C_i response after leaf injury (Table 2).

Respiration Rates, *H. arnottianus*

We observed no significant changes in rate of photosynthesis (under no light conditions) and respiration values in leaves from *H. arnottianus* plants after the injury. The results for the respiration values were consistent across trials 1 and 2 (trial 1: mean value for healthy leaves 0.97 ± 0.35 μmol CO_2 m^{-2} s^{-1}, mean value for injured leaves 0.94 ± 0.23 μmol CO_2 m^{-2} s^{-1} ($t = -0.05$; df = 2; $P = 0.96$); trial 2:

Table 1. Gas exchange response in injured and healthy *H. arnottianus* leaves: comparisons of chlorophyll levels (SPAD), net photosynthesis, and transpiration

Trial	Parameter	Mean ±SE		*t*-test		
		Healthy	Injured	*t*	df	*P*
Trial 1	chlorophyll levels (SPAD units)	32.8 ± 2.0	31.5 ± 2.3	−0.95	6	0.38
	net photosynthesis (μmol CO_2 m^{-2} s^{-1})	9.4 ± 1.2	5.6 ± 1.6	−3.04	6	0.02*
	transpiration (mol H_2O m^{-2} s^{-1})	3.7 ± 0.8	2.5 ± 1.0	−2.96	6	0.025*
Trial 2	chlorophyll levels (SPAD units)	25.5 ± 2.0	23.0 ± 2.0	1	7	0.35
	net photosynthesis (μmol CO_2 m^{-2} s^{-1})	9.8 ± 0.9	7.1 ± 0.8	3.98	7	0.005*
	transpiration (mol H_2O m^{-2} s^{-1})	4.7 ± 0.5	3.0 ± 0.5	4.45	7	0.003*
Trial 3	chlorophyll levels (SPAD units)	26.0 ± 1.0	26.0 ± 2.29	−0.01	5	0.99
	net photosynthesis (μmol CO_2 m^{-2} s^{-1})	10.1 ± 0.9	4.9 ± 0.8	7.22	5	0.0008*
	transpiration (mol H_2O m^{-2} s^{-1})	3.6 ± 0.4	1.5 ± 0.4	7.73	5	0.0006*

*Significant differences ($P < 0.05$) between gas exchange response measurements in healthy and injured leaves.
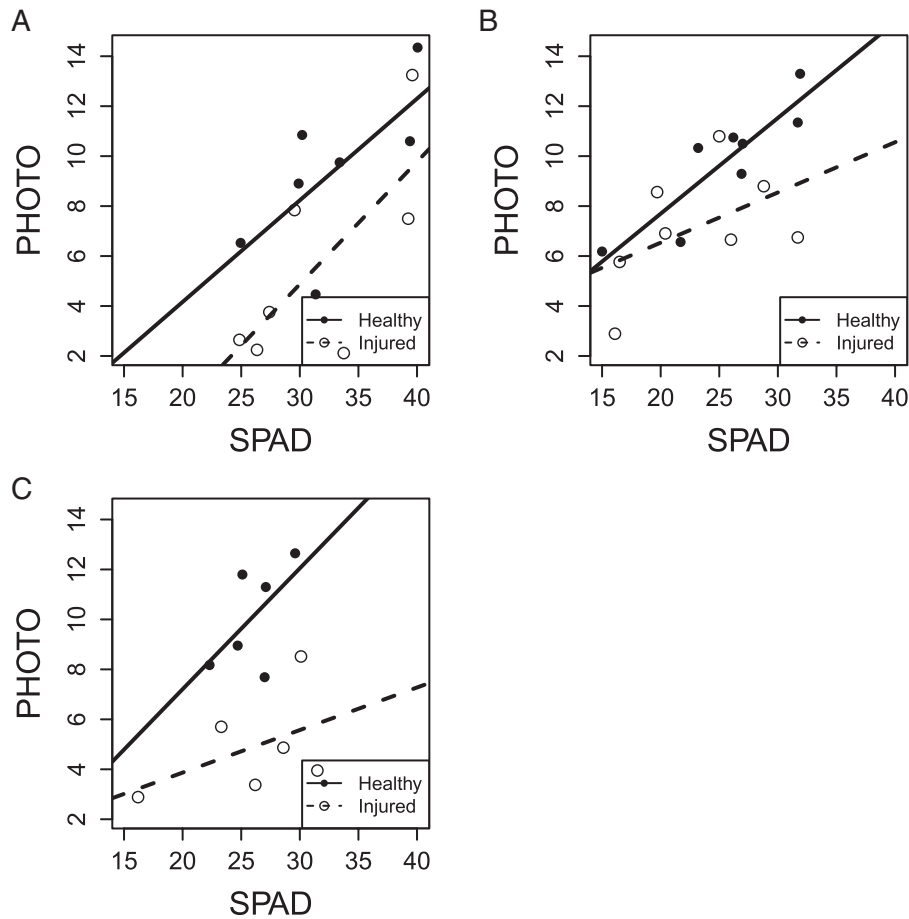
Fig. 1. Relationships between net photosynthesis (PHOTO, µmol CO_2 m^{-2} s^{-1}) and chlorophyll levels (SPAD, SPAD units) in healthy (control) and injured *H. arnottianus* plants in three trials (A: trial 1; B: trial 2; and C: trial 3).

mean value for healthy leaves 0.99 ± 0.13 µmol CO_2 m^{-2} s^{-1}, mean value for injured leaves 0.93 ± 0.08 µmol CO_2 m^{-2} s^{-1}; $t = 1.32$; df = 4; $P = 0.26$). Rate of photosynthesis was measured for trial 1 only (mean value for healthy leaves -0.88 ± 0.08 µmol CO_2 m^{-2} s^{-1}, mean value for injured leaves -1.03 ± 0.12 µmol CO_2 m^{-2} s^{-1}; $t = -0.99$; df = 4; $P = 0.4$).

The A/C_i curve analysis also demonstrated no significant changes in respiration rates between healthy and injured leaves in both trials (trial 1: $t = -0.05$; df = 2; $P = 0.96$; trial 2: $t = 1.32$; df = 4; $P = 0.26$).

Gas Exchange Response, *C. sinensis*

Comparison of gas exchange response between healthy and injured leaves from *C. sinensis* plants showed significant increase (15%) in chlorophyll levels after leaf injury (mean SPAD value for healthy leaves 23.9 ± 1.65, mean SPAD value for injured leaves 28.05 ± 1.36; $t = -5.46$, df = 5; $P = 0.003$). Differences in net photosynthesis, as well as transpiration were not significant (PHOTO: mean value for healthy leaves 6.60 ± 1.04 µmol CO_2 m^{-2} s^{-1}, mean value for injured leaves 6.20 ± 1.08 µmol CO_2 m^{-2} s^{-1} ($t = 0.75$, df = 5; $P = 0.49$); TRMMOL: mean value for healthy leaves 2.99 ± 0.65 mol H_2O m^{-2} s^{-1}, mean value for injured leaves 2.90 ± 0.72 mol H_2O m^{-2} s^{-1}; $t = 0.20$, df = 5; $P = 0.84$).

Oviposition, *S. orientalis*

We did not observe any eggs on *H. arnottianus* plants and only one egg on *C. sinensis* plants.

Discussion

Overall, our results demonstrated a rapid physiological response of native *H. arnottianus* plants to injury by the introduced leafhopper, *S. orientalis*; we observed approximately 40% reduction in rate of photosynthesis and 42% reduction in rate of transpiration after 2 d of exposure. We did not record any changes in leaf chlorophyll levels after leaf injury, nor any visible symptoms of leaf injury through time. Our two assimilation-internal CO_2 (A/C_i) experiments differed in results, but suggest that the leafhopper does affect both stomatal behavior and mesophyll biochemical limitations in photosynthesis, although additional studies are needed to compare these mechanisms of injury. Our expectation of lack of such rapid response to injury in *C. sinensis* leaves was also confirmed: although we observed an increase in chlorophyll levels in injured leaves, rate of photosynthesis and transpiration did not change after leaf injury.

Although it has been suggested that oviposition may cause damage to plants, Alyokhin et al. (2001) surveyed the oviposition occurrence of *S. orientalis* and suggested that the density of eggs was not high enough to cause significant plant damage. Exploring oviposition of *S. orientalis* was not the primary focus in our study; however, the results of our search for eggs on *H. arnottianus* and *C. sinensis* plants also suggested that plant damage in our study was caused primarily by feeding.

Our observation of rapid changes in gas exchange response in *H. arnottianus* plants is consistent with the results of previous

Table 2. A/Ci curve analysis of injured and healthy *H. arnottianus* leaves: comparisons of V_{cmax}, J_{max}, and V_{tpu}

Trial	Parameter	Mean ±SE		*t*-test		
		Healthy	Injured	*t*	df	*P*
Trial 1 (2011)	V_{cmax} (µmol CO_2 m^{-2} s^{-1})	40.3 ± 7.3	14.5 ± 1.5	−2.92	2	0.1
	J_{max} (µmol electrons m^{-2} s^{-1})	44.0 ± 8.7	15.3 ± 1.1	−2.94	2	0.1
	V_{tpu} (µmol CO_2 m^{-2} s^{-1})	4.0 ± 0.3	1.7 ± 0.2	−4.41	2	0.047*
Trial 2 (2012)	V_{cmax} (µmol CO_2 m^{-2} s^{-1})	29.4 ± 4.7	18.0 ± 2.0	0.53	4	0.63
	J_{max} (µmol electrons m^{-2} s^{-1})	30.0 ± 5.5	17.5 ± 1.7	0.53	4	0.62
	V_{tpu} (µmol CO_2 m^{-2} s^{-1})	3.9 ± 0.4	2.7 ± 0.4	0.54	4	0.61

*Significant differences ($P < 0.05$) between measurements in healthy and injured leaves.

studies on other novel interactions between leafhoppers and their host plants, and specifically on physiological response of introduced crop plants (non-native, novel host plants) to leafhoppers, native to North America, such as *Empoasca fabae* Harris (e.g., Flinn et al. 1990; Lamp et al. 2004, 2007, 2011). In these studies, feeding injury by native *E. fabae* resulted in approximately 50% reduction in the photosynthesis rate (Lamp et al. 2004) and 66.9% reduction in transpiration rates in alfalfa, *Medicago sativa* (Lamp et al. 2007), introduced to North America from South-Central Asia (Brough et al. 1973). Flinn et al. (1990) observed 60 and 80% reduction in alfalfa photosynthesis after feeding by 4 or 8 *E. fabae*, respectively. Similarly, *E. fabae* caused rapid declines in photosynthesis and transpiration rates (ranging between 22 and 52%) in non-native grapevine, *Vitis vinifera* L. in greenhouse tests (Lamp et al. 2011).

Reduction of photosynthetic rates in plants as a response to injury by arthropods has also been commonly observed in non-novel associations between plants and other hemipteran (such as aphids) and non-hemipteran piercing herbivores. For example, significant reduction of photosynthetic rates in wheat, *Triticum eastivum*, in response to feeding by the Russian wheat aphid, *Diuraphis noxia* Kurdjumov, has been demonstrated by Haile et al. (1999); these results were consistent across three lines of wheat with different levels of resistance to this aphid. Shannag et al. (1998) also found that overall photosynthetic rates in leaves of cotton, *Gossypium hirsutum*, were significantly reduced after infestation by aphid, *Aphis gossypii* Glover; however, in contrast to our observations of gas exchange response in *Camellia* plants, transpiration rates increased in the infested cotton leaves. Similar to our results, de Bueno et al. (2009) showed no changes in chlorophyll levels and significant photosynthetic rate reduction in soybean, *Glycine max*, after injury by the two-spotted spider mite, *Tetranychus urticae* Koch, due to stomatal closure.

Our results also suggest that this response, as well as recognition of *H. arnottianus* as a potential host plant by *S. orientalis*, may be potentially attributed to a new association between an invasive leafhopper and an endemic plant. Such a plant response in novel plant–insect associations is predicted by several commonly accepted invasion hypotheses. These hypotheses predict that insect herbivores will actively utilize novel host plants, and plants can be well defended against novel herbivores due to a variety of factors (the 'biotic resistance hypothesis', Parker and Hay 2005; the 'Darwin's naturalization hypothesis', Lambdon and Hulme 2006; the 'novel weapons hypothesis', Callaway and Ridenour 2004; but see Lankau et al. 2004). From an exotic insect perspective, strong physiological/molecular plant responses may potentially result in preventing the establishment of such insect association with a novel host plant, and may ultimately provide

biotic resistance of native plant communities to insect invaders. In our experiments, we focused on immediate gas exchange response in plants to feeding injury by *S. orientalis* and did not monitor plant physiological response after removing cages with leafhoppers. Other studies on *E. fabae*, however, showed that, e.g., injured grapevine leaves were able to repair themselves within 5 d (Lamp et al. 2011); such ability is presumably associated with certain carbohydrate source-sink relationships in grapevines (Mercader and Isaacs 2003), as well as age of leaves (Lenz et al. 2009). It would be helpful for future studies to explore whether endemic *Hibiscus* plants are capable of such recovery after injury from leafhopper feeding, and whether plant phenology has any effect on plant tolerance to herbivory. Future studies might also focus on the *Hibiscus* plant responses to injury by native phloem feeders, such as native leafhoppers, to better understand whether the observed short physiological response can be fully attributed to the lack of co-evolutionary history.

The Hawaiian Islands have one of the highest rates of plant endemicity in the world and 44% of all the endangered plants in the United States (Messing et al. 2007). At least 12 taxa within the Hawaiian flora are represented by a single individual, and many endemic plants occur in a single location (Gemmill et al. 1998). Continuous impact of non-native species (both animals and plants) is one of the main explanations for plant endangerment in Hawaii (Gemmill et al. 1998). Alien invertebrate herbivores, in particular, affect native plant communities through repeated defoliation and subsequent plant mortality, or indirectly, by affecting plant seeds and seedlings, reducing plant populations, and shifting species composition in a community (Kenis et al. 2009).

As oceanic islands are extremely vulnerable to such consequences of species invasions, it is of great importance to develop an effective management program and preserve endemic biota (Loope et al. 1988). Given that biological conservation on islands is a challenging and expensive activity (Loope et al. 1988), one step toward preservation of native species can be thorough exploration of the biology of exotic insect herbivores and their interactions with different host plants, particularly, endemic plants. Many previous studies on introduced insects have focused on crop protection, and their results might be difficult to apply in natural ecosystems (Causton et al. 2006). Also, comparative studies of exotic insects, such as *S. orientalis*, in different introduced ranges, including environmental conditions which facilitate insect invasiveness, would be extremely helpful (Causton et al. 2006).

Additionally, future studies on comparison of interactions of *S. orientalis* with host plants in its native range (such as *Camellia*) and novel host plants can also help investigate 1) feeding behavior *S. orientalis* and determining whether it uses cell rupture or sheath feeding method, or both, similar to *E. fabae* (DeLay et al. 2012); and 2)

the range of genes involved in a generalized wound response as observed in *H. arnottianus* plants. Previous studies on alfalfa suggest wound-induced gene activation in the jasmonic pathway, leading to a generalized wound response by the plant to injury by potato leafhopper, *E. fabae* (DeLay 2013). As for *C. sinensis* responses to herbivory, to date, only a few studies have explored interactions of *C. sinensis* with other leafhoppers, such as, *Empoasca vitis* (Göthe) (Miao et al. 2014, Zhang and Chen 2015), and defense mechanisms of *C. sinensis* plants remain largely unexplored.

Acknowledgments

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