Relative Differences in Susceptibility of *Pieris* taxa (Ericaceae) to *Stephanitis* spp. Lace Bugs (Hemiptera: Tingidae)

SHAKUNTHALA NAIR,[1,2] S. KRISTINE BRAMAN,[1] AND D. A. KNAUFT[3]

Environ. Entomol. 41(5): 1145–1152 (2012); DOI: http://dx.doi.org/10.1603/EN11322

ABSTRACT Over 60 *Pieris* taxa (Ericaceae) were measured for their susceptibility to the Andromeda lace bug, *Stephanitis takeyai* Drake and Maa, and the azalea lace bug, *Stephanitis pyrioides* (Scott) (Hemiptera: Tingidae) based on leaf damage, adult survival on leaves, and emergence of nymphs in no-choice petri dish assays. *Pieris phillyreifolia* (Hook.) DC. and *P. japonica* (Thunb.) D.Don ex G.Don 'Variegata' were consistently resistant to both species of lace bugs, whereas *P. japonica* 'Cavatine' was consistently susceptible to both. *Pieris japonica* 'Temple Bells' was highly susceptible to *S. takeyai*, but resistant to *S. pyrioides*. Nymph emergence was noted only with *S. takeyai*, on 46 *Pieris* taxa, whereas *S. pyrioides* nymphs were not observed on any of the *Pieris* taxa. Choice assays (with 10 *Pieris* taxa) and whole plant assays (with five *Pieris* taxa) using *S. takeyai* alone also were conducted, confirming the resistance of *P. phillyreifolia* and susceptibility of *P. japonica* Temple Bells to lace bug feeding.

KEY WORDS *Pieris phillyreifolia*, *P. japonica*, *Stephanitis takeyai*, *S. pyrioides*, resistance

The ericaceous plant pieris (*Pieris* D. Don spp.) is a popular ornamental shrub used in landscape, foundation plantings, and shrub borders, or for incorporating with other evergreens. The plants are prized for their glossy green leaves; clusters of red, pink, or white urn-shaped flowers; and the striking colors displayed by new leaves. Foliage feeders like lace bugs and mites can cause severe damage to *Pieris.* They weaken the plant and also reduce the attractiveness of the foliage, which affects the esthetic value and marketability.

Stephanitis Stål is a genus of over 60 species that includes several pests of ornamental and fruit plants (Howard 2001). The three species occurring in North America, are the azalea lace bug, *Stephanitis pyrioides* (Scott); the Andromeda lace bug, *S. takeyai* Drake and Maa; and the rhododendron lace bug, *S. rhododendroni* Horváth. All three species attack woody ornamentals, especially those belonging to the family Ericaceae (Alverson et al. 1994). Although *S. rhododendroni* is native, *S. pyrioides* and *S. takeyai* are indigenous to Asia, as are many *Pieris* and azalea cultivars currently in production. Damage symptoms caused by all three lace bugs include yellowish white stipples or blotches on the upper leaf surfaces, and oily, black frass spots, on the lower surfaces. Lace bug damage may lead to premature leaf shedding, drying up of twigs, or even the whole plant (Schread 1968).

The azalea lace bug is the most widespread of the three species, and also the most important in terms of economic damage. Although its preferred hosts are azaleas (*Rhododendron* spp.), *S. pyrioides* is also known to infest other ericaceous plants such as kalmia (*Kalmia latifolia* L.) and pieris [*Pieris ovalifolia* (Wall.) D. Don] (Drake and Ruhoff 1965). The susceptibility of azalea cultivars to *S. pyrioides* has been measured earlier (Braman and Pendley 1992, Schultz 1993); however, information about the extent of its damage on kalmia and pieris is lacking. The Andromeda lace bug first was reported in North America in 1950 on *P. japonica* plants in Connecticut, and there were speculations even at that time that this recently introduced species may become a serious pest of *Pieris* and other ornamental Ericaceae (Bailey 1950). It has been reported from several other states (Dunbar 1974, Torres-Miller 1989, Nielsen 1997) and there have been unpublished reports of the pest from the southeastern United States recently. *Stephanitis takeyai* is an important pest of *Pieris* spp. (Johnson and Lyon 1991), but its ecology and management are not extensively studied (Johnson and Lyon 1991). Of the known *Pieris* taxa, *P. japonica* is reported to be the most preferred (Schread 1968), *P. floribunda* [(Pursh ex Simms) Benth. & Hook.] resistant, and *P. floribunda* × *japonica* hybrids less favorable to *S. takeyai* (Dunbar 1974). In Poland, severe damage was observed on cultivars 'Select', 'Debutante', and 'Cupido', and to a lesser degree on 'Flaming Silver', 'Variegata', and 'Redmill' (Labanowski and Soika 2000).

The genus *Pieris* includes 13 species (USDA–ARS 2011) of which the most common is the Japanese pieris, *P. japonica* (Thunb.) D.Don ex G.Don, native to Japan. It is also the most widely cultivated, and it is believed to have over 100 known cultivars (van Santvoort 2008). Mountain pieris, *P. floribunda,* native to North America, is an underutilized ornamental shrub

[1] Department of Entomology, University of Georgia, 1109 Experiment St., Griffin, GA 30223.
[2] Corresponding author, e-mail: nair.shaku@gmail.com.
[3] Department of Horticulture, University of Georgia, 1111 Plant Sciences Bldg., Athens, GA 30602.

indigenous to the Appalachian mountains of the United States (Starrett et al. 1996). *Pieris floribunda* is more tolerant to stresses such as alkaline soil and pests but is considered less attractive than *P. japonica* (Heriteau 2006). *Pieris phillyreifolia* (Hook.) DC. (climbing fetterbush), also native to North America, is common in the southeastern states of Alabama, Florida, Georgia, Mississippi, and South Carolina (USDA–ARS 2011). Lesser cultivated species of *Pieris* include *P. formosa* (Wall.) D. Don (Himalaya pieris), *P. taiwanensis* Hayata (dwarf pieris), *P. cubensis* (Grisebach) Small., and *P. swinhoei* Hemsley.

We measured cultivars of *P. japonica, P. phillyreifolia, P. taiwanensis,* and *P. formosa* for resistance against *S. takeyai* and *S. pyrioides.* The goals are to identify potential resistant *Pieris* germplasm to inform plant breeding efforts and understand management needs with respect to two adventive key pests.

Materials and Methods

Plant Material. *Pieris* taxa (species or cultivars) were obtained from the Department of Horticulture *Pieris* collection located at the University of Georgia Horticulture Farm in Watkinsville, GA. These plants were obtained from various nurseries in 11.3-liter (3 gallon) and 3.7-liter (1 gallon) pots and maintained in a screen house with regular irrigation, but without additional pesticide and fertilizer inputs. For our experiments, leaves were collected from plants that had at least five branches.

Lace Bugs. *Stephanitis pyrioides* colonies were established and periodically replenished using adult azalea lace bugs collected from natural populations found near Griffin, GA. The colonies were housed in 1.0-m^3 screen cages in the Entomology Insect Rearing Facility at Griffin, GA. These colonies were reared on potted evergreen azaleas under conditions of 27 ± 1°C and a photoperiod of 14:10 (L:D) h. *Stephanitis takeyai* colonies were initiated from a population obtained from a landscape setting in New York in April 2009. The colonies were housed in plastic containers and maintained through the period of study at 27 ± 1°C and a photoperiod of 14:10 (L:D) h. *Pieris* cultivars *P. japonica* 'Dodd's Crystal Cascade Falls', 'Temple Bells' and 'Scarlett O'Hara' were used as hosts to maintain the colonies, and these were rotated to avoid selection by lace bugs. For the actual testing, 5–10-d-old adult lace bugs were first collected in plastic tubes by using an aspirator and then transferred into the testing petri dishes by using a brush.

No-Choice Petri Dish Assays (Single Species). Our first experiment was initiated using *S. pyrioides* in March 2008 with 61 *Pieris* cultivars, and repeated in May 2008. Each cultivar was replicated four times. For each replication, three mature leaves of a cultivar (fourth or fifth leaf from the bottom of a branch) were placed in a petri dish of 11 cm in diameter (VWR Scientific, Radnor, PA), with their petioles covered with sections of moist paper towels. Ten adult lace bugs were released into each petri dish and the dish covered with its friction-fitting lid. The dishes were arranged in a randomized complete block design and placed under 27 ± 1°C and a photoperiod of 14:10 (L:D) h. Observations on the number of bugs alive were taken at 48-h intervals. On day 13, the surviving adults were removed and the leaves were visually scored for the percent leaf area damaged using a scoring chart developed by Klingeman et al. (2000), in which damaged leaves were chosen to represent a range of lace bug feeding injury. After scoring, the leaves were maintained under the same environmental conditions and observed daily for emergence of nymphs. Nymphs were counted and removed when they were observed.

A similar assay was conducted using *S. takeyai* in July 2009 and repeated in August 2009. In these assays, two adult lace bugs were released into each petri dish. Observations on the number of bugs alive were taken at 2, 7, 9, and 13 d. Scoring of leaf damage and observations of nymph emergence were performed as described above in this section.

In another set of no-choice tests conducted in September and repeated in October 2009, we used 20 *Pieris* cultivars that represented the range in susceptibility. Both species of lace bugs were tested separately, with four replications and two adults per replication. Leaf damage and nymph emergence were assessed as described above in this section.

Multichoice Assay. Ten *Pieris* cultivars, including susceptible and tolerant cultivars, were selected based on the results of previous assays. Three mature leaves (fourth or fifth leaf from the bottom of a branch) of each cultivar were placed as a group with their bases covered with moist paper towels. Ten such groups of leaves from 10 *Pieris* cultivars, placed in a circular pattern inside a large 30-cm petri dish with a friction-fitting lid, constituted one replication and there were three such replications. The leaf groups were arranged randomly within the circular pattern in each replication. Twenty *S. takeyai* adults were released into each petri dish. All the petri dishes were placed inside a growth chamber maintained at 27 ± 1°C and a photoperiod of 14:10 (L:D) h. Observations on the number of bugs present on each of the leaves were recorded 1 hr after releasing the bugs, and then again at the start of each observation on the second, seventh, ninth, and thirteenth day. After the thirteenth day the surviving adults were removed and the leaves were assessed for leaf damage by counting the number of frass spots left by the bugs as an indicator of feeding, because frass spot numbers are highly correlated with leaf damage and served as an index for the amount of *S. pyrioides* feeding on azaleas (Ericaceae) (Buntin et al. 1996). After damage assessment, the leaves were placed back in their positions and maintained under the same conditions as during the exposure period and observed daily for emergence of nymphs. Nymphs were counted and removed when they were observed.

Whole Plant Assay. Five *Pieris* taxa, including susceptible and tolerant cultivars, were selected based on the results of previous assays. Six healthy potted plants of each cultivar, with at least five branches were chosen. One branch on each plant with at least 100 leaves

Table 1. No-choice assays with *S. pyrioides* and *S. takeyai* for adult survival, percent leaf area damaged, and nymph emergence on *Pieris* taxa

Pieris taxa 'cultivar' (source)	*S. pyrioides*		*S. takeyai*		
	No. of live adults	Leaf area damaged	No. of live adults	Leaf area damaged	No. of nymphs
P. phyllireifolia	0.00f	0.00k	0.29 h-j	0.10q	0.00 h
P. jx. 'Variegata'	0.00f	0.50 h-k	0.00j	1.33pq	0.43gh
P. j. 'Pygmaea' (FF)	0.00f	0.17jk	0.14ij	1.52pq	0.00 h
P. j. 'Valley Valentine' (B)	0.63b-f	1.75d-k	0.71e-j	2.00o-q	0.00 h
P. j. 'Bonsai'	0.25d-f	2.29c-j	0.29 h-j	2.67n-q	1.57f-h
P. j. 'Daisen'	0.00f	1.19f-k	0.43 g-j	2.71m-q	9.00b-g
P. j. 'Chaconne'	0.25d-f	1.04f-k	0.14ij	2.71m-q	2.43e-h
P. j. 'Crimson Compact'	0.13ef	2.09d-k	0.43 g-j	2.76m-q	0.00 h
P. j. 'Benihaja'	0.25d-f	1.13f-k	0.57f-j	3.10l-q	2.29e-h
P. j. 'Christmas Cheer'	0.25d-f	1.58d-k	0.86d-i	3.10l-q	2.57e-h
P. j. 'Valley Rose' (FF)	0.13ef	0.83 g-k	1.00c-h	3.15l-q	0.29gh
P. j. 'Flamingo'	0.00f	0.79 g-k	0.57f-j	3.24k-q	6.00b-h
P. j. 'Valley Rose' (B)	0.25d-f	0.83 g-k	1.14b-g	3.38j-p	5.86c-h
P. j. 'Nocturne'	0.00f	0.42i-k	0.43 g-j	3.62i-p	0.00 h
P. j. 'Debutante'	0.00f	1.29e-k	1.00c-h	3.76 h-p	6.71b-h
P. j. 'Dorothy Wycoff' (FF)	0.13ef	1.17f-k	0.71e-j	4.05 g-p	0.00 h
P. j. 'Shojo' (B)	1.25ab	4.29a-c	0.57f-j	4.14f-p	1.29f-h
P. j. 'PI 418 531'	0.25d-f	4.38a-c	0.86d-i	4.52e-p	3.00e-h
P. j. 'Little Heath' (B)	0.25d-f	1.25e-k	0.71e-j	4.76d-o	0.00 h
P. j. 'Compacta' (B)	0.75a-e	1.67d-k	0.57f-j	4.86d-o	4.14c-h
P. j. 'Mountain Fire' (B)	1.38a	4.29a-c	0.86d-i	4.95c-o	2.43e-h
P. j. 'Cupido'	0.25d-f	2.08d-k	0.86d-i	5.05c-o	7.29b-h
P. f. × *P. j.* 'Brower's Beauty' (B)	1.13a-c	2.33c-i	1.00c-h	5.05c-o	0.71f-h
P. j. 'Iseli Cream'	0.25d-f	1.83d-k	1.86ab	5.05c-o	7.14b-h
P. j. 'Wada'	0.00f	0.38i-k	1.43a-e	5.19c-o	3.86d-h
P. fo. var. *forestii*	0.25d-f	0.67 g-k	0.86d-i	5.24c-n	14.71ab
P. j. 'Coleman'	0.13ef	0.71 g-k	0.86d-i	5.29c-n	3.00e-h
P. t. 'Snow Drift' (FF)	0.13ef	0.63 g-k	1.14b-g	5.38c-n	1.14f-h
P. j. x *P. fo.* var. *forestii* 'Forest Flame'	0.25d-f	2.75b-g	1.14b-g	5.38c-n	9.00b-g
P. j. 'Stockman'	0.13ef	1.88d-k	1.29a-f	5.43b-n	3.86d-h
P. t. 'Snow Drift' (B)	0.88a-d	1.13f-k	1.14b-g	5.43b-n	8.86b-g
P. j. 'Red Mill'	0.13ef	1.21f-k	0.86d-i	5.43b-n	2.86e-h
P. j. 'Sarabonde' (B)	0.75a-e	1.96d-k	0.86d-i	5.48b-n	4.14c-h
P. j. 'White Caps'	0.13ef	2.00d-k	1.00c-h	5.67b-n	9.43b-f
P. j. 'Bolero'	0.13ef	1.75d-k	0.86d-i	5.71b-n	10.71b-e
P. j. 'Valley Fire' (FF)	0.13ef	0.92 g-k	0.86d-i	5.81b-n	2.86e-h
P. j. 'T44–82U'	0.00f	1.96d-k	1.00c-h	5.90b-n	2.14e-h
P. j. 'Dodd's Sugar Run Falls' (C)	0.13ef	0.84 g-k	1.29a-f	6.10b-l	4.86c-h
P. j. 'Sinfonia'	0.86a-d	3.38b-e	1.29a-f	6.10b-l	6.00b-h
P. j. × *P. f.* 'Spring Snow'	0.25d-f	1.25e-k	1.43a-e	6.10b-l	5.00c-h
P. j. 'La Rocaille'	0.88a-d	4.63ab	1.57a-d	6.43b-k	7.00b-h
P. j. 'Scarlett O'Hara' (B)	0.63b-f	1.71d-k	1.43a-e	6.52a-j	12.29a-d
P. j. 'Dodd's Crystal Cascade Falls' (C)	0.00f	0.42i-k	1.57a-d	6.62a-i	2.71e-h
P. j. 'Karenoma' (B)	0.75a-e	2.00d-k	1.29a-f	6.91a-h	2.14e-h
P. j. 'Flaming Silver' (FF)	0.88a-d	2.58b-h	1.71a-c	7.14a-g	1.57f-h
P. j. 'Valley Valentine' × 'Kubas'	0.00f	1.04f-k	2.00a	7.14a-g	2.29e-h
P. j. 'UNH'	0.63b-f	2.00d-k	1.86ab	7.19a-g	21.00a
P. j. 'Purity'	0.86a-d	2.24c-j	1.14b-g	7.29a-f	3.14e-h
P. j. var. *amamiana*	0.38d-f	1.58d-k	1.71a-c	7.71a-e	12.71a-c
P. j. 'Cavatine' (C)	0.13ef	1.29e-k	1.29a-f	7.76a-d	2.14e-h
P. j. 'Cavatine' (B)	0.00f	0.17jk	1.43a-e	8.14a-c	4.57c-h
P. j. 'Prelude' (B)	0.25d-f	0.00k	1.14b-g	8.62ab	3.00e-h
P. j. 'Temple Bells' (FF)	0.00f	1.00f-k	1.86ab	9.71a	1.86f-h
P. j. 'White Cascade'	0.71a-e	5.95a	–	–	–
P. j. 'Valentine's Day'	0.75a-e	3.71b-d	–	–	–
P. j. 'Firecrest'	0.88a-d	3.08b-f	–	–	–
P. j. 'Dodd's Pearl Falls' (C)	0.63b-f	1.00f-k	–	–	–
P. j. 'Havila'	0.13ef	1.67d-k	–	–	–
P. j. 'Flaming Silver' (B)	0.50c-f	1.42e-k	–	–	–
P. j. 'Bisbee Dwarf'	0.00f	1.29e-k	–	–	–
P. j. 'T40–82A'	0.14ef	0.90 g-k	–	–	–
F	2.03	2.42	3.17	2.85	1.83
P	<0.0001	<0.0001	<0.0001	<0.0001	0.0010
Overall model	$F = 1.94$ df = 63,419 $P < 0.0001$	$F = 2.32$ df = 63,419 $P < 0.0001$	$F = 3.07$ df = 55,315 $P < 0.0001$	$F = 3.14$ df = 55,315 $P < 0.0001$	$F = 1.87$ df = 55,315 $P = 0.0005$

Means in the same column bearing different letters are significantly different ($\alpha = 0.05$).
(B), (C), and (FF) indicate the source nurseries Briggs, Cofer's, and Forest Farm.
P.j.: *Pieris japonica*, *P.f.*: *Pieris floribunda*, *P.t.*: *Pieris taiwanensis*, *P.fo.*: *Pieris formosa*.

Table 2. Analysis of variance in assays showing differences between *Pieris* taxa and between lace bug species

	Day 2		Day 7		Day 9		Day 13	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Adult survival								
Between *Pieris* taxa	1.39	0.1302	4.33	<0.0001	3.19	<0.0001	2.58	0.0004
Between lace bug sp.	0.56	0.4567	30.91	<0.0001	60.42	<0.0001	105.60	<0.0001
Pieris taxa × lace bug sp.	0.98	0.4789	0.40	0.9884	0.93	0.5505	1.73	0.0307
Overall model	$F = 1.28$, df = 42,277, $P = 0.1246$		$F = 3.04$, df = 42,277, $P < 0.0001$		$F = 3.44$, df = 42,277, $P < 0.0001$		$F = 4.53$, df = 42,277, $P < 0.0001$	
Leaf damage							*F*	*P*
Between *Pieris* taxa	–	–	–	–	–	–	5.11	<0.0001
Between lace bug sp.	–	–	–	–	–	–	101.79	<0.0001
Pieris taxa × lace bug sp.	–	–	–	–	–	–	2.21	0.0030
Overall model							$F = 5.78$, df = 42,277, $P < 0.0001$	

was enclosed in a 20 by 40 cm sleeve cage (BugDorm, BioQuip Products Inc., Rancho Dominguez, CA). Ten *S. takeyai* adults (five males and five females) were released into the sleeve cage and this constituted one replication. Each cultivar was thus replicated six times from July to August 2010. The plants were placed in the laboratory at 27 ± 1°C and a photoperiod of 14:10 (L:D) h. They were irrigated as needed and observed on the second, seventh, ninth and thirteenth day after release, for survival of the lace bugs. After the thirteenth day, the branches were cut at the base beyond the cage and the leaf damage was assessed. A 'damaged' leaf was one with frass spots left by the lace bugs (Buntin et al. 1996). The number of leaves that were damaged out of 100 leaves was counted in each of the sleeve cages. Of the damaged leaves, five leaves were selected at random and the average number of frass spots was recorded. After this, each of the entire cut branches (with their cut ends covered in sections of moist paper towels) was placed inside a large petri dish or container and maintained under conditions of 27 ± 1°C and a photoperiod of 14:10 (L:D) h to observe for nymph emergence. Nymphs were counted and removed when they were observed.

Statistical Procedures. The experiments used a randomized complete block design. The replications were considered as the block factor. Treatment means were analyzed separately for each kind of assay. Means of the variables (adult survival, leaf damage and nymph emergence in no-choice assays; adult presence on leaves, leaf damage and nymph emergence in choice assays; and adult survival, number of damaged

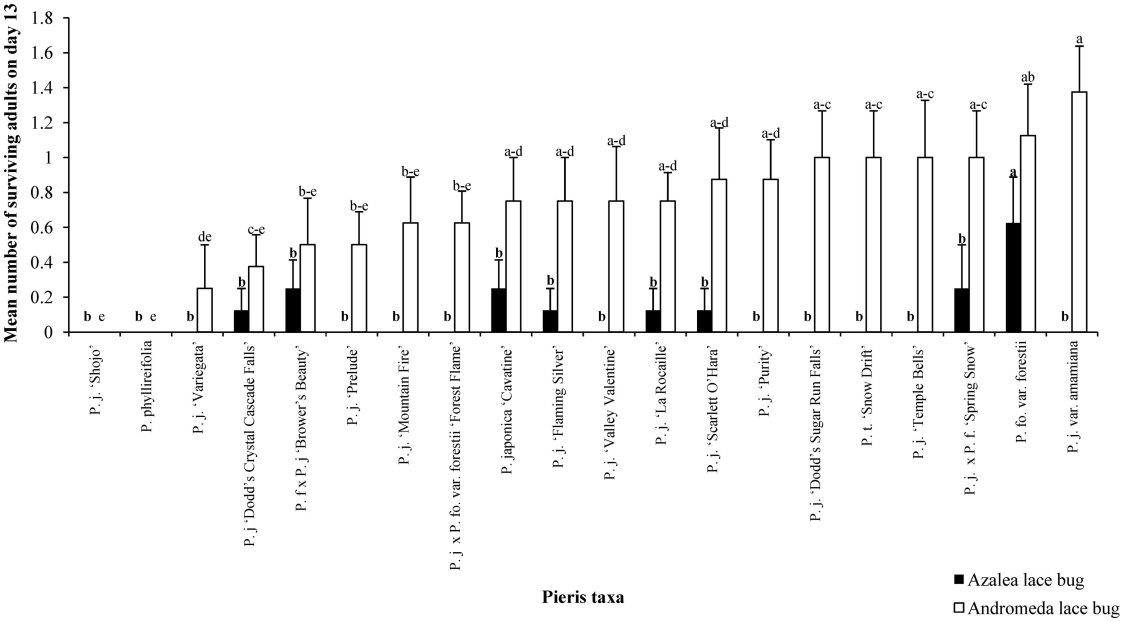

Fig. 1. Differences in adult *S. pyrioides* and *S. takeyai* survival (mean ± SEM, $N = 8$) on 20 *Pieris* taxa. Data are averages of two trials conducted in September 2009 and October 2009.—- Bars of the same fill color bearing different letters are significantly different ($\alpha = 0.05$, LSD). *P.j.*: *Pieris japonica*, *P.f.*: *Pieris floribunda*, *P.t.*: *Pieris taiwanensis*, *P.fo.*: *Pieris formosa*.

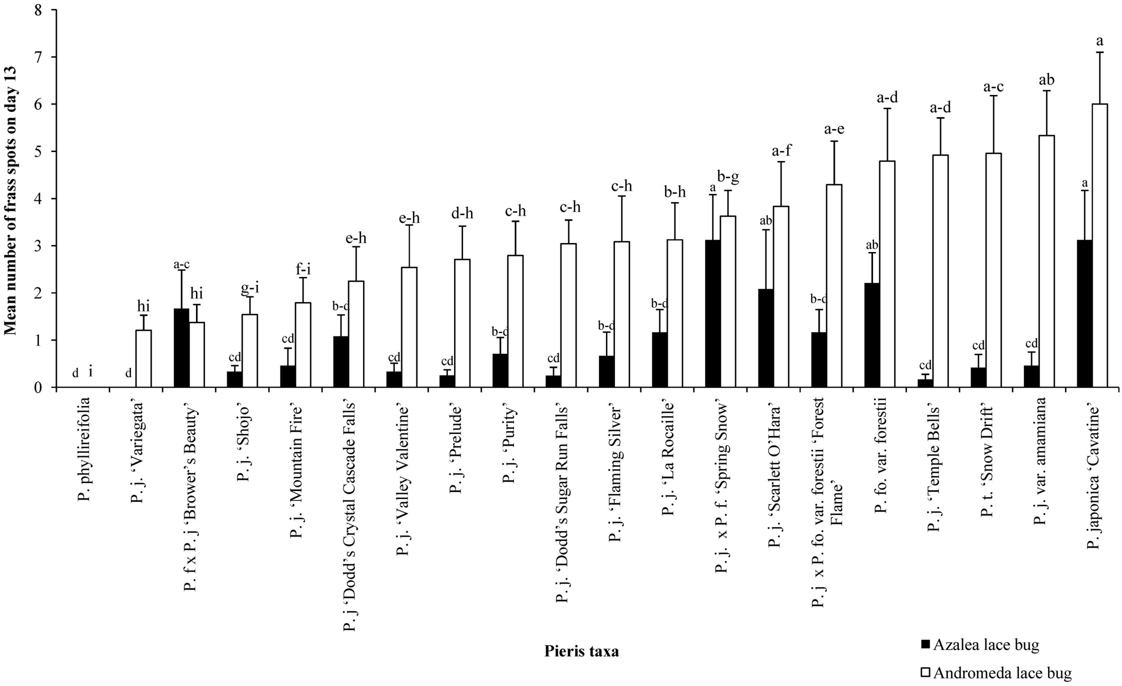

Fig. 2. Differences in leaf damage caused by *S. pyrioides* and *S. takeyai* (mean ± SEM, $N = 8$) on 20 *Pieris* taxa. Data are averages of two trials conducted in September 2009 and October 2009.—- Bars of the same fill color bearing different letters are significantly different ($\alpha = 0.05$, LSD). *P.j.*: *Pieris japonica*, *P.f.*: *Pieris floribunda*, *P.t.*: *Pieris taiwanensis*, *P.fo.*: *Pieris formosa*.

leaves, average leaf damage and nymph emergence in whole plant assays) were subjected to analysis of variance (ANOVA) using the general linear model procedure (PROC GLM) (SAS Institute 2003). Means were separated with Fisher protected least significant difference (LSD) test.

Results

No-Choice Petri Dish Assays. *Pieris* cultivars varied with respect to adult lace bug survival and leaf damage. The cultivars that showed 3% or more damaged leaf area by *S. pyrioides* were the *P. japonica* 'White Cascade', 'La Rocaille', 'P 1418531′', 'Mountain Fire', 'Shojo', 'Valentine's Day', 'Sinfonia', and 'Firecrest' (Table 1). The highest adult survival was seen on 'Mountain Fire' and 'Shojo' (Table 1). The cultivars that showed the least damage (0.5–0%) were *P. phillyreifollia* and *P. japonica* cultivars 'Prelude', 'Pygmaea', 'Wada', 'Nocturne', 'Dodd's Crystal Cascade Falls', and 'Variegata'. These cultivars also showed no surviving adults on the final day of observation.

Table 3. Mean number of *S. takeyai* frass spots on leaves and nymphs emerged in choice trials with *Pieris* taxa

Pieris taxa	Mean frass spots				Mean nymphs
	Day 2	Day 7	Day 9	Day 13	Day 17
P. p. 'Little Leaf'	0.22 ± 0.11cd	0.22 ± 0.11c	0.22 ± 0.11e	0.22 ± 0.11e	0.00c
P. p. 'Baldwin'	0.00d	0.67 ± 0.38c	0.22 ± 0.22e	0.22 ± 0.22e	0.00c
P. j. 'Temple Bells'	8.33 ± 2.61a	17.11 ± 3.27a	21.89 ± 1.31ab	31.0 ± 0.58a	19.78 ± 9.78a
P. j. 'Dodd's Sugar Run Falls'	7.89 ± 2.78ab	10.11 ± 3.64b	10.78 ± 3.91c	18.67 ± 2.41b	1.56 ± 1.24c
P. j. 'Dorothy Wycoff'	4.33 ± 1.35a-c	9.89 ± 1.72b	16.78 ± 4.05b	18.89 ± 4.89b	11.0 ± 0.51b
P. j. 'Valley Rose'	0.22 ± 0.22cd	4.89 ± 2.11bc	5.22 ± 2.3de	5.78 ± 2.59c-e	0.56 ± 0.56c
P. j. 'Cavatine'	8.22 ± 0.22a	18.33 ± 3.42a	23.67 ± 2.7a	28.11 ± 3.23a	10.78 ± 3.49b
P. t. 'Snow Drift'	0.22 ± 0.11cd	0.44 ± 0.22c	0.89 ± 0.59e	1.78 ± 1.18de	0.00c
P. j. 'Dodd's Crystal Cascade Falls'	1.22 ± 0.22cd	6.89 ± 0.78b	8.22 ± 0.78cd	9.22 ± 1.28cd	2.11 ± 0.73c
P. j. 'Prelude'	3.67 ± 0.33b-d	7.0 ± 0.58b	10.56 ± 0.87cd	12.44 ± 1.18bc	4.78 ± 2.38bc
F	5.44	12.14	19.98	15.91	4.89
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Overall model	$F = 4.17$	$F = 9.66$	$F = 15.43$	$F = 12.03$	$F = 4.17$
	df = 13,76	df = 13,76	df = 13,76	df = 13,76	df = 13,76
	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$

Means (±SEM) in the same column bearing different letters are significantly different ($\alpha = 0.05$; LSD).
P.j.: *Pieris japonica*, *P.t.*: *Pieris taiwanensis*, *P.p.*: *Pieris phillyreifolia.*

Table 4. Mean number of *S. takeyai* adults present on leaves in choice trials with *Pieris* taxa (averages from three replications)

Pieris taxa	Day 0	Day 2	Day 7	Day 9	Day 13
P. p. 'Little Leaf'	0.22 ± 0.11a	0.33 ± 0.19a	0.00c	0.11 ± 0.11c	0.00c
P. p. 'Baldwin'	0.44 ± 0.22a	0.33 ± 0.19a	0.11 ± 0.11c	0.00c	0.00c
P. j. 'Temple Bells'	0.67 ± 0.00a	1.00 ± 0.38a	1.22 ± 0.22a	1.67 ± 0.19a	1.56 ± 0.41a
P. j. 'Dodd's Sugar Run Falls'	0.11 ± 0.11a	0.33 ± 0.00a	0.56 ± 0.11bc	0.33 ± 0.19c	0.44 ± 0.41bc
P. j. 'Dorothy Wycoff'	0.89 ± 0.22a	0.78 ± 0.22a	0.56 ± 0.29bc	0.67 ± 0.19bc	0.44 ± 0.29bc
P. j. 'Valley Rose'	0.67 ± 0.19a	0.22 ± 0.11a	0.11 ± 0.11c	0.00c	0.00c
P. j. 'Cavatine'	0.89 ± 0.29a	0.89 ± 0.22a	1.0 ± 0.19ab	1.33 ± 0.38ab	1.0 ± 0.19ab
P. t. 'Snow Drift'	0.22 ± 0.11a	0.22 ± 0.22a	0.00c	0.00c	0.00c
P. j. 'Dodd's Crystal Cascade Falls'	0.22 ± 0.11a	0.44 ± 0.22a	0.56 ± 0.11bc	0.11 ± 0.11c	0.00c
P. j. 'Prelude'	0.44 ± 0.23a	0.78 ± 0.22a	0.11 ± 0.11c	0.22 ± 0.11c	0.00c
F	1.62	1.18	4.54	5.72	6.28
P	0.1236	0.3204	<0.0001	<0.0001	<0.0001
Overall model	$F = 1.64$	$F = 0.90$	$F = 3.32$	$F = 4.06$	$F = 4.50$
	df = 13,76	df = 13,76	df = 13,76	df = 13,76	df = 13,76
	$P = 0.0936$	$P = 0.5555$	$P = 0.0005$	$P < 0.0001$	$P < 0.0001$

Means (±SEM) in the same column bearing different letters are significantly different ($\alpha = 0.05$; LSD).
P.j.: *Pieris japonica*, *P.t.*: *Pieris taiwanensis*, *P.p.*: *Pieris phillyreifolia*.

Leaf damage caused by *S. takeyai* was visibly much higher than that caused by *S. pyrioides.* The most notable difference seen in the assays with *S. takeyai* was the high susceptibility of *P. japonica* 'Temple Bells' as indicated by the higher leaf damage, and adult survival; whereas this cultivar had shown low adult survival and leaf damage by *S. pyrioides. P. japonica* 'Temple Bells' was statistically similar to *P. japonica* 'Cavatine', 'Flaming Silver', and *P. japonica* var. *amamiana,* all of which showed leaf area damage of 7% or higher. *Pieris* cultivars resistant to *S. takeyai* feeding activity included *P. phillyreifolia*, *P. japonica* 'Variegata' and 'Pygmaea', which was consistent with the previous assays using *S. pyrioides.*

Stephanitis pyrioides nymphs were not observed in the leaves of any *Pieris* cultivar, whereas *S. takeyai* oviposited in the majority of *Pieris* cultivars (Table 1). Counts of emerged nymphs appeared related to adult survival and leaf damage. The highest number of nymphs was observed on *P. japonica* 'UNH', and *P. japonica* var. *amamiana,* while the lowest numbers were observed on *P. phillyreifolia*, *P. japonica* 'Variegata' and *P. japonica* 'Pygmaea'.

In the no-choice assays with 20 cultivars (Table 2; Figs. 1 and 2), *Pieris phillyreifolia* and *P. japonica* 'Variegata' were consistently resistant to both species of lace bugs, *P. japonica* 'Cavatine' was susceptible to both, whereas 'Temple Bells' was notable in being highly susceptible to *S. takeyai,* but resistant to *S. pyrioides.*

Multichoice Assay. Of the 10 *Pieris* cultivars used in the multichoice assays with *S. takeyai*, *P. japonica* 'Temple Bells' exhibited the highest number of frass spots on all four days of observation (Table 3). *Pieris japonica* 'Cavatine' was also highly susceptible and was statistically similar in the number of frass spots to *P. japonica* 'Temple Bells'. *Pieris phillyreifolia* 'Little Leaf' and 'Baldwin' showed the least amount of damage but were similar to *P. taiwanensis* 'Snow Drift' and *P. japonica* 'Valley Rose', the other least-preferred cultivars. A higher number of nymphs was observed on *P. japonica* 'Temple Bells' than on all the other cultivars. This was followed by *P. japonica* 'Dorothy Wycoff' and *P. japonica* 'Cavatine' which were not different from each other statistically.

Observations on presence of adults on the leaves (Table 4) show that the lace bugs did not exhibit a marked preference for any cultivar at the beginning of the experiment (1 h after release) or even on the second day. However, from the seventh day onwards there were clear indications of the adults' preferences, and the highest number of adults was seen on *P. japonica* 'Temple Bells' on the seventh, ninth, and thirteenth day.

Table 5. *S. takeyai* adult survival in whole plant assays with *Pieris* taxa

Pieris taxa	Day 2	Day 7	Day 9	Day 13
P. j. 'Prelude'	7.5 ± 0.76b	6.33 ± 0.8b	4.67 ± 1.05bc	3.5 ± 1.06bc
P. j. 'Cavatine'	9.33 ± 0.49a	8.5 ± 0.76a	8.17 ± 0.75a	6.0 ± 1.55a
P. j. 'Dodd's Sugar Run Falls'	7.33 ± 0.49b	6.0 ± 0.82b	4.5 ± 0.67c	2.83 ± 0.70cd
P. j. 'Temple Bells'	8.67 ± 0.42ab	7.67 ± 0.42ab	6.17 ± 0.87b	5.5 ± 1.15ab
Pieris phillyreifolia	5.33 ± 0.56c	2.50 ± 0.99c	1.83 ± 0.91d	1.17 ± 0.75d
F	7.91	13.92	18.00	6.94
P	0.0005	<0.0001	<0.0001	0.0011
Overall model	$F = 4.23$	$F = 8.42$	$F = 12.60$	$F = 6.64$
	df = 9,20	df = 9,20	df = 9,20	df = 9,20
	$P = 0.0035$	$P < 0.0001$	$P < 0.0001$	$P = 0.0002$

Means (±SEM) in the same column bearing different letters are significantly different ($\alpha = 0.05$; LSD).
P.j.: *Pieris japonica.*

Table 6. Leaf damage by *S. takeyai* and nymph emergence in whole plant assays with *Pieris* taxa

Pieris taxa	Damaged leaves out of 100	Average damage on five leaves	Number of nymphs
P. j. 'Prelude'	34.33 ± 4.1c	30.17 ± 4.07b	30.67 ± 8.33bc
P. j. 'Cavatine'	54.0 ± 7.65b	74.5 ± 11.08a	73.50 ± 14.17a
P. j. 'Dodd's Sugar Run Falls'	20.67 ± 3.53cd	16.17 ± 2.95b	11.0 ± 2.88cd
P. j. 'Temple Bells'	75.67 ± 5.01a	78.67 ± 10.39a	55.33 ± 17.94ab
Pieris phillyreifolia	12.33 ± 2.42d	9.83 ± 3.16b	0.00d
F	26.71	18.28	10.15
P	<0.0001	<0.0001	0.0001
Overall model	$F = 12.32$ df = 9,20 $P < 0.0001$	$F = 8.45$ df = 9,20 $P < 0.0001$	$F = 5.94$ df = 9,20 $P = 0.0005$

Means (± SEM) in the same column bearing different letters are significantly different ($\alpha = 0.05$; LSD).
P.j.: *Pieris japonica.*

Whole Plant Assay. Highest survival of *S. takeyai* adults was noted on *P. japonica* 'Cavatine' with an average of six adults surviving on the thirteenth day (Table 5), similar to 'Temple Bells' which had an average of 5.5 adults. The lowest adult survival was recorded on *P. phillyreifolia.* The highest number of damaged leaves was noted in *P. japonica* 'Temple Bells', which was higher than all the other cultivars (Table 6). The highest average leaf damage (indicated by frass spots) was also noted in *P. japonica* 'Temple Bells', which was similar to that on *P. japonica* 'Cavatine'. Nymph emergence was the highest in *P. japonica* 'Cavatine', and similar to 'Temple Bells'.

Discussion

The results of this study provide information on susceptibility of cultivated *Pieris* taxa to *S. pyrioides* and *S. takeyai,* which has not been reported previously. Our experimental design was similar to that used in previous studies that examined susceptibility of host plants to lace bugs (Wang et al. 1998). We used two methods (Buntin et al. 1996, Klingeman et al. 2000) for assessing lace bug damage, both of which gave consistent results. In the initial no-choice assays with the larger number of cultivars, we used damage scoring (Klingeman et al. 2000) for better feasibility and also to account for the consumer's perception. However, in the multichoice and whole plant assays where fewer cultivars representing the range in susceptibility, we used the more objective method, frass spots (Buntin et al. 1996), to quantify leaf damage.

Survival of adult lace bugs was higher on the whole plants, as compared with incised leaves inside petri dishes. Also, there was indication of feeding in the form of frass spots on leaves of *P. phillyreifolia,* which was never noticed in the petri dish assays. This could be because of higher moisture content and longer maintenance of turgor in leaves on whole plants, as compared with excised leaves. This may have prompted the lace bugs to explore the leaves for a longer time and make more attempts to feed than they would have done in a petri dish situation. However *P. phillyreifolia* still ranked as the most resistant selection to lace bug feeding and exhibited negligible injury, consistent with detached leaf studies.

In the no-choice assays, the number of adults used was different (10 *S. pyrioides* and two *S. takeyai*) because of differences in availability of adults. Even so, a higher number of adults of *S. pyrioides* did not cause as much damage as a lower number of *S. takeyai.* Therefore, it was clear that *S. takeyai* favored *Pieris* as its host, as indicated by its better adult survival, higher leaf damage and most importantly, nymph emergence, whereas *Pieris* was not a suitable host for *S. pyrioides.* Among the different *Pieris* species, the greatest preference was for *P. japonica* as reported earlier (Schread 1968). *Pieris taiwanesis* and *P. formosa* were less preferred and *P. phillyreifolia,* was the least preferred among the four species. We measured 51 *P. japonica* taxa in our assays. *Stephanitis takeyai* showed clear preference for certain *P. japonica* taxa viz., 'Temple Bells', and 'Cavatine', whereas others like 'Variegata' and 'Prelude' were less preferred. The lower preference of 'Variegata' has been mentioned earlier (Labanowski and Soika 2000), but in our assays 'Flaming Silver' and 'Red Mill' were more damaged than 'Debutante' and 'Cupido', whereas Labanowski and Soika (2000) observed severe damage on cultivars 'Select', 'Debutante', 'Cupido', and to a lesser degree on 'Flaming Silver', 'Variegata', and 'Redmill'. In further screening experiments, it might be useful to ascertain the identity of the taxa being tested to ensure uniformity of results. We could not include *P. floribunda* which is reported to be resistant to *S. takeyai* in our screening because of lack of plants. However, the hybrid *P. floribunda* × *P. japonica* 'Brower's Beauty' seemed to be less preferred, as mentioned in an earlier report (Dunbar 1974), and so did the hybrids *P. japonica* × *P. floribunda* 'Spring Snow' and *P. japonica* × *P. formosa* variety *forestii* 'Forest Flame'. This may indicate that *P. floribunda* and *P. formosa* may be sources of resistant genes. The resistance shown by *P. phillyreifolia* in all screening experiments also suggests that it may be a source of resistance, although there is no mention of successful hybridization between *P. phillyreifolia* with other *Pieris* species in the literature.

Our studies have revealed the gradients in susceptibility of cultivated *Pieris* taxa to the two species of lace bugs, *S. pyrioides* and *S. takeyai,* and also that *S. takeyai* is capable of causing significant damage to several *Pieris* cultivars. Although *S. takeyai* was introduced in 1950, very little information is available regarding its potential host range among Ericaceae and other related families and therefore it would be worthwhile to conduct further studies on these aspects. The exact reasons for the preferences exhibited by *S. takeyai* are not understood, but the wide variability in leaf shape, size, texture, color, and growth habit among the *Pieris* taxa, even within the *japonica* cultivars suggest that different mechanisms may be involved.

Acknowledgments

We greatly appreciate the technical assistance provided by Jim Quick and Ryan McNeill. We are indebted to Dan Gilrein for providing adult *S. takeyai* lace bugs, and Jerry Davis for valuable advice on data analysis. We thank two anonymous reviewers for critical reviews of an earlier draft of this manuscript. Partial funding for this project was provided by the Southern SARE program.

References Cited

Alverson, D. R., S. K. Braman, F. A. Hale, W. G. Hudron, R. F. Mizell III, B. Sparks, and M. L. Williams. 1994. Update on management of the top seven landscape pest groups, pp. 180–184. *In* B. L. James (ed.), November 1994. Proceedings, 39th Southern Nursery Association Research Conference, Southern Nursery Association Inc., Acworth, GA.

Bailey, N. S. 1950. An Asiatic tingid new to North America (Heteroptera). Psyche 57: 143–145.

Braman, S. K., and A. F. Pendley. 1992. Evidence for resistance of deciduous azaleas to azalea lace bug. J. Environ. Hortic. 10: 40–43.

Buntin, G. D., S. K. Braman, D. A. Gilbertz, and D. V. Phillips. 1996. Chlorosis, photosynthesis, and transpiration of azalea leaves after azalea lace bug (Heteroptera: Tingidae) feeding injury. J. Econ. Entomol. 89: 990–995.

Drake, C. J., and F. A. Ruhoff. 1965. Lacebugs of the world: a catalog (Hemiptera: Tingidae). Chinches de encaje del mundo: un catálogo (Hemiptera: Tingitidae). U.S. Natl. Mus. Bull. 243: 1–634.

Dunbar, D. M. 1974. Bionomics of the andromeda lacebug, *Stephanitis takeyai*, pp. 277–289. *In* R. L. Beard (ed.), 25th Anniversary Memoirs, Connecticut Entomological Society, New Haven, CT.

Heriteau, J. 2006. Complete trees, shrubs & hedges. Creative Homeowner, Upper Saddle River, NJ.

Howard, F. W. 2001. Insects on palms. CABI Publishers, New York.

Johnson, W. T., and H. H. Lyon. 1991. Lace bugs of broad-leaved evergreens and sages, pp. 424–429. *In* W. T. Johnson and H. H. Lyon (eds.), Insects that feed on trees and shrubs, 2nd ed. Comstock Publ. Associates, Ithaca, NY.

Klingeman, W. E., S. K. Braman, and G. D. Buntin. 2000. Evaluating grower, landscape manager, and consumer perceptions of azalea lace bug (Heteroptera: Tingidae) feeding injury. J. Econ. Entomol. 93: 141–148.

Labanowski, G. S., and G. M. Soika. 2000. *Stephanitis takeyai* Drake & Maa and other lace bugs (Tingidae) as pests of ornamental plants from Ericaceae family in Poland, pp. 690, (abstr.) No. 2731, XXI International Congress of Entomology, 20–26 August 2000, Iguassu, Brazil. Sociedade Entomológica do Brasil, Ministério da Agricultura e do Abastecimento, Embrapa Soja, Londrina, PR, Brazil.

Nielsen, G. R. 1997. Lace bugs, entomology leafl. 153. University of Vermont Extension, Burlington, VT.

SAS Institute. 2003. SAS system version 9.1 for Windows. SAS Institute, Cary, NC.

Schread, J. C. 1968. Control of lace bugs on broadleaf evergreens. Bull. Conn. Agric. Exp. Stn. 684: 1–7.

Schultz, P. B. 1993. Host plant acceptance of azalea lace bug (Heteroptera: Tingidae) for selected azalea cultivars. J. Entomol. Sci. 28: 230–235.

Starrett, M. C., F. A. Blazich, L. F. Grand, and S. R. Shafer. 1996. Response of microshoots of mountain andromeda to *in vitro* ericoid mycorrhizal inoculation, pp. 239–242. *In* B. L. James (ed.), November 1996. Proceedings, 41st Southern Nursery Association Research Conference, Southern Nursery Association Inc., Acworth, GA.

Torres-Miller, L. 1989. New records of lace bugs from West Virginia (Hemiptera: Tingidae). Insecta Mundi 3: 10.

[USDA–ARS] US Department of Agriculture, Agricultural Research Service. 2011. Species records of *Pieris*. National Genetic Resources Program. *Germplasm Resources Information Network - (GRIN)* [Online Database]. National Germplasm Resources Laboratory, Beltsville, MD. (http://www.ars-grin.gov/cgi-bin/npgs/html/splist.pl?9380).

van Santvoort, B. 2008. *Pieris japonica* information. Nursery G. van Santvoort BV, North Brabant, the Netherlands (http://www.pieris.eu/pieris-japonica).

Wang, Y., C. D. Robacker, and S. K. Braman. 1998. Identification of resistance to azalea lace bug among deciduous *Azalea* taxa. J. Am. Soc. Hortic. Sci. 123: 592–597.

Received 14 December 2011; accepted 5 July 2012.