

Chlorosis, Photosynthesis, and Transpiration of Azalea Leaves After Azalea Lace Bug (Heteroptera: Tingidae) Feeding Injury

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ABSTRACT Feeding injury caused by nymphs, males and females of the azalea lace bug, *Stephanitis pyrioides* (Scott), reduced rates of photosynthesis and transpiration in 'Delaware Valley White' azalea, *Rhododendron mucronatum* leaves. Females caused substantially more leaf feeding injury than males or nymphs. *S. pyrioides* was observed to insert stylets through stomata on the lower leaf surface and to feed almost entirely on upper palisade parenchyma tissue by piercing and removing cell contents. Lace bug feeding increased leaf stomatal resistance which indicated that gas exchange was restricted by stomatal closure. Feeding injury also reduced leaf chlorophyll content and photosynthetic capacity of remaining chlorophyll, but did not consistently affect chlorophyll a:b or specific leaf weight. Net leaf photosynthesis was negatively correlated with stomatal resistance and positively correlated with both chlorophyll content per unit leaf area and photosynthetic rate of remaining chlorophyll. These results indicated that *S. pyrioides* reduced leaf photosynthesis in azalea by damaging palisade parenchyma which restricted gas exchange through stomata and reduced leaf chlorophyll content and photosynthetic capacity of remaining chlorophyll.

KEY WORDS *Stephanitis pyrioides*, photosynthesis, chlorosis, azalea

THE AZALEA LACE bug, *Stephanitis pyrioides* (Scott), although indigenous to Asia, currently has a wide geographic distribution, and has become the key pest of cultivated evergreen azaleas, *Rhododendron* spp., in the eastern United States. Host plant acceptance and injury vary between azalea cultivars and species with deciduous forms typically sustaining less damage than evergreen azaleas (Braman and Pendley 1992, Schultz 1993). Leaf damage can occur at any time except during the winter. *Stephanitis pyrioides* has 4 generations per year in Georgia (Braman et al. 1992) and 2-3 generations per year in the New England states (Bailey 1951).

Nymphs and adults colonize the underside of leaves, pierce the leaves and extract cell contents. Ishihara and Kawai (1981) found that *S. pyrioides* inserts stylets through stomates on the lower leaf surface and mostly feeds on the upper palisade parenchyma layer by piercing cells and removing their contents. Feeding injury causes leaves to have a stippled or bleached chlorotic appearance from above, with lower surfaces being disfigured with dark, varnish-like excrement and cast nymphal exuviae.

Insect and mite induced chlorosis has been found to impair photosynthesis and water relations in plants (e.g., Cockfield et al. 1987, Welter 1989, Buntin et al. 1993). However, the effect of feeding injury by tingids on photosynthesis and leaf gas exchange in plants has not been examined. Our objectives were to confirm the feeding habits of *S. pyrioides* reported by Ishihara and Kawai (1981) and examine the effect of feeding injury by nymphs, males, and females on leaf gas exchange and chlorosis in azalea.

Materials and Methods

Azalea cuttings, from 'Delaware Valley White', were transplanted into plastic pots (15 cm diameter) containing a pine bark sand mix during September 1992. Experiments were conducted in a greenhouse located at Griffin, GA. Pots were watered daily and were fertilized with slow release pellets (Osmocote 14-14-14, Sierra Chemical, Pittsburg, CA) and a liquid feed (Peters 20:20:20) *S. pyrioides* used during the study were obtained from a laboratory colony initiated with five selected adults and maintained as described by Braman et al. (1992). The effects of feeding by nymphs and adults were examined in 3

Trial 1. Ten plants were assigned to each of 8 treatments during November

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or 6 azalea lace bug nymphs, males or females, were confined to a single leaf on plant using a plastic sleeve cage ventilated with nylon screen at one end. Leaves of similar size and location on these even-aged plants were used. Pots with plants bearing caged leaves were arranged on a greenhouse bench in randomized complete block design. Plants were watered as usual during the infestation period. Treatments were no cage and no lace bugs, cage in place but no lace bugs added, 2 males, 2 females, 2 third-instars, 6 males, 6 females, and 6 third-instars. Cages and lace bugs were removed after 72 h and plants were allowed to recover from disturbance overnight. Leaf gas exchange measurements were then made on the injured or caged leaves. Leaves were photographed and computer-assisted TV image-capture (Imaging Technology, Woburn, MA) and analysis equipment (Microscience, Seattle, WA) was used to determine area injured as viewed from above. Number of frass spots on upper and lower surfaces was recorded. Leaf chlorophyll content was determined and leaves were dried and weighed.

Trial 2. Cages and procedures were the same as in trial one except that lace bug densities were control with no cage, control with cage, 3 males, 12 males, 3 females, 6 females, 12 females, and 18 females per leaf. The trial was conducted during February 1993. Plant parameters measured were the same throughout all trials.

Trial 3. Azaleas were transplanted to 3.7-liter pots and housed in an outdoor screenhouse. Pots were returned to the greenhouse in September 1993. Leaves were infested with azalea lace bugs in a manner and densities equivalent to those used in trial 2.

Examination of Adult Feeding and Chlorotic Tissue. Adults feeding on azalea leaves were examined using scanning electron microscopy. Twenty leaves with actively feeding females were frozen in liquid nitrogen (-70°C) and then freeze-dried under a vacuum. After critical point drying, leaves with adults were sputter-coated with 35 nm of gold and examined on a Phillips 505 scanning electron microscope.

Injured leaves were examined histologically by cutting pieces of leaf tissue cut from uninjured leaves and leaves with injury by females in trial 2. Leaf pieces were fixed with glutaraldehyde, post-fixed in osmium tetroxide, and embedded in Spurr's medium. Sections were cut 1 μm thick, stained with toluidine blue, and mounted on microscope slides. Prepared sections were examined under a light microscope (400 \times).

Plant Measurements. In all trials, net CO_2 exchange rate (net photosynthesis), leaf stomatal resistance, and transpiration were measured with a LI-6200 portable closed-gas-exchange photosynthesis system equipped with a 1-liter leaf chamber and the LI-6250 CO_2 analyzer (LiCor, Lincoln, NE). Measurements were conducted a greenhouse equipped with high-intensity lights between 1000

and 1600 hours (EDT). Average levels of photosynthetically active radiation were 706, 701 and 810 $\mu\text{mol photon/m}^2/\text{s}$ for each respective trial. Air temperatures varied from 25 to 34 $^{\circ}\text{C}$. Leaflets were removed from the plant and leaf area measured with a LI-3000 portable leaf area meter (LiCor).

In all trials, four disks of tissue were removed from each leaf for chlorophyll analysis. Fresh weights of leaves were determined before and after removal of the disks. Leaves were dried at 50 $^{\circ}\text{C}$ for 48 h and dry weight was measured. Leaf disks were immersed in N,N-dimethyl formamide for at least 48 h. Concentrations of chlorophyll a and b were determined spectrophotometrically from absorbance at 647 and 664 nm with a Spectronic 401 (Milton Roy, Rochester, NY) and using the equations of Moran (1982). Total chlorophyll content was calculated as the sum of chlorophyll a and b and was expressed on the basis of leaf area and dry weight. The ratio of chlorophyll a:b and specific leaf weight (mg/cm^2) of leaves also were calculated.

Statistical Analyses. Leaf area injured and number of frass spots per square centimeter of leaf were analyzed by trial with an analysis of variance for a randomized complete block design. Treatment means were separated using a protected least significant difference procedure, and selected treatment comparisons were made using single degree-of-freedom contrasts (PROC GLM, SAS Institute 1985). Net leaf photosynthetic rate, leaf stomatal resistance, transpiration rate, chlorophyll content per unit area and per unit of leaf dry weight, photosynthetic rate per unit of chlorophyll, chlorophyll a:b, and specific leaf weight were regressed on leaf area injured or number of frass spots using a linear regression model (PROC REG, SAS Institute 1985). Pearson correlation coefficients of all parameters also were calculated (PROC CORR, SAS Institute 1985).

Results

Feeding Activity, Leaf Damage, and Frass Production. *S. pyrioides* adults and nymphs fed almost exclusively on the abaxial leaf surface. However, females at the highest density (18 per leaf) in trials 2 and 3 became increasingly active during the caging interval and were often noted on the upper surface of leaves. Frass spots were usually confined to lower surfaces of leaves, but were occasionally noted and counted on upper surfaces of leaves which supported high numbers of lace bugs. Frass spot numbers provided an index of the amount of feeding by nymphs and adults in each treatment. The number of frass spots increased with increasing density for nymphs, males and females (Table 1 and 2). Females usually produced more spots than males or nymphs at the same density.

The range of percentage of leaf injury was lower in trial 1 than the other trials and only exceeded

Table 1. Mean \pm SD percentage of leaf injury and number of frass spots products by *S. pyrioides* nymphs and adults in trial 1

Treatment	% leaf injury	Frass spots per cm ²
0—No cage	0.0 \pm 0.0a	0.0 \pm 0.0a
0—Cage	0.0 \pm 0.0a	0.0 \pm 0.0a
2 nymphs	12.0 \pm 6.0b	4.9 \pm 2.9b
6 nymphs	20.2 \pm 9.4bc	10.8 \pm 3.2c
2 males	10.9 \pm 4.3b	5.1 \pm 2.1b
6 males	24.4 \pm 14.5c	7.4 \pm 4.6b
2 females	15.9 \pm 13.3bc	4.9 \pm 2.8b
6 females	64.6 \pm 22.7d	17.0 \pm 2.3d
Contrasts		
Nymphs vs adults	17.40**	1.25
Male vs female	40.62**	26.07**
2 vs 6 bugs	65.57**	76.09**
2 vs 6 females	94.26**	84.12**

Means within columns followed by the same letter are not significantly different ($P < 0.05$, LSD). **, Significant contrast F value ($P < 0.001$).

25% in the treatment with 6 females per leaf (Table 1). Females caused significantly more injury than males and nymphs at the same density in all trials (Table 1 and 2). Third-instar nymphs and males produced similar levels of injury at the same densities in trial 1 (Table 1). Leaf injury also increased with increasing numbers for nymphs, males, and females in all trials. Females produced more frass spots than males in 2 trials, and frass production increased with bug numbers in all trials (Tables 1 and 2). Percentage of leaf injury and number of frass spots were highly correlated in all trials (1: $r = 0.90$, $N = 66$; 2: $r = 0.93$, $N = 76$; 3: $r = 0.89$, $N = 72$; $P < 0.0001$).

Histological Examination of *S. pyrioides* Feeding Injury. *S. pyrioides* feeding causes noticeable leaf chlorosis that is best described as a stippling type injury. Examination of leaf cross sections revealed that palisade parenchyma tissue of

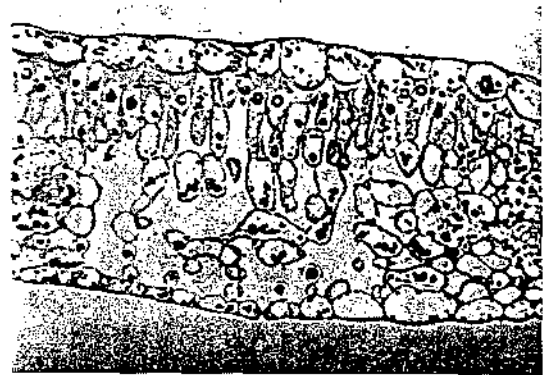


Fig. 1. Cross sections of a healthy leaf (top) and a leaf with *S. pyrioides* feeding injury (bottom).

injured leaves was almost completely devoid of cell contents including chloroplasts (Fig. 1). Spongy mesophyll parenchyma and epidermal tissues of injured leaves generally were intact with cells containing chloroplasts, although some spongy mesophyll cells were devoid of chloroplasts. In all instances where adults were captured while feed-

Table 2. Mean \pm SD percentage of leaf injury and number of frass spots produced by various densities of *S. pyrioides* adults in trials 2 and 3

Treatment	Trial 2		Trial 3	
	% leaf injury	Frass spots per cm ²	% leaf injury	Frass spots per cm ²
0—No cage	0.0 \pm 0.0a	0.0 \pm 0.0a	0.0 \pm 0.0a	0.0 \pm 0.0a
0—Cage	0.0 \pm 0.0a	0.0 \pm 0.0a	0.0 \pm 0.0a	0.0 \pm 0.0a
3 Males	7.7 \pm 1.5a	2.7 \pm 1.9a	14.0 \pm 5.7b	7.8 \pm 3.5b
12 Males	26.9 \pm 7.1bc	12.2 \pm 5.3c	51.2 \pm 21.9c	24.0 \pm 4.6de
3 Females	19.7 \pm 5.0b	7.8 \pm 2.9b	19.7 \pm 8.9b	6.6 \pm 1.9b
6 Females	32.0 \pm 11.9c	14.1 \pm 4.6c	49.6 \pm 30.7c	16.7 \pm 11.6c
12 Females	72.3 \pm 22.3d	20.0 \pm 6.7d	70.2 \pm 19.0d	20.1 \pm 4.1cd
18 Females	81.0 \pm 15.9d	22.4 \pm 3.7d	93.7 \pm 5.4e	26.6 \pm 10.0e
Contrasts				
Male vs female	72.89**	25.13**	5.61*	2.94
3 vs 12 bugs	113.73**	71.80**	76.62**	63.23**
3 vs 12 males	18.04**	30.72**	26.21**	36.98**
3 vs 12 females	110.55**	41.10**	52.79**	26.43**

Means within columns followed by the same letter are not significantly different ($P < 0.05$, LSD). *, ** Indicate significant contrast F value at $P < 0.05$ and $P < 0.001$, respectively.

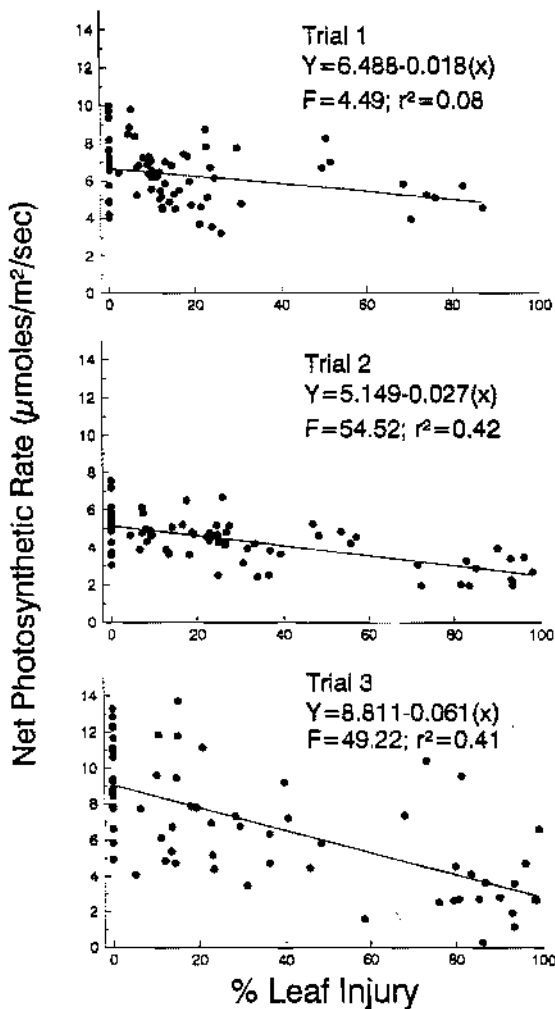


Fig. 2. Relationship between azalea net leaf photosynthetic rate and percentage of leaf area injured by *S. pyrioides* in 3 trials.

ing, stylets were inserted into the leaf through a stoma on the lower leaf surface.

Feeding Injury and Leaf Gas Exchange. Photosynthetic rate declined linearly with increasing level of percentage of leaf injury by *S. pyrioides* in all trials (Fig. 2). However, because of the variability in photosynthetic rate measurements and

the relatively low level of leaf injury in most treatments, the association was poor ($r^2 = 0.08$) in trial 1. Leaf transpiration rate also declined linearly with increasing injury in trial 2 (Table 3). Conversely, stomatal resistance increased as the percentage of injured leaf area increased in trials 2 and 3 (Table 3). Stomatal resistance and leaf transpiration were not significantly affected by *S. pyrioides* injury in trial 1 where lace bug numbers were comparatively low.

Chlorophyll content per unit leaf area and per unit leaf weight declined significantly with increasing percentage of leaf injury in trials 2 and 3 (Table 4). Feeding injury also caused highly significant linear reductions in net photosynthetic rate per unit of chlorophyll in trials 2 and 3 (Table 4). Chlorophyll a:b and specific leaf weight declined significantly with increasing leaf injury in trial 3 but were not associated with leaf injury in trial 2. These parameters in trial 1 (Table 4) also exhibited the same trend of declining with increasing leaf injury as in the other trials, but regressions of these parameters were not significant ($P > 0.05$) for any parameter in trial 1.

Correlation of Leaf Net Photosynthetic Rate with Leaf Parameters. Azalea leaf net photosynthetic rate was positively correlated with chlorophyll content per unit leaf area in all trials but was only correlated with chlorophyll content per unit leaf dry weight in trial 2 (Table 5). Leaf photosynthetic rate and photosynthetic rate per unit of chlorophyll also were highly positively correlated in all trials. Chlorophyll a:b was not correlated with leaf photosynthetic rate in trial 1 and 2 but was weakly associated with leaf photosynthetic rate in trial 3. Specific leaf weight was positively correlated with photosynthetic rate in trials 1 and 3 but was not correlated in trial 2. Stomatal resistance was highly negatively correlated with net photosynthetic rate in all trials (Table 5).

Discussion

Feeding injury by *S. pyrioides* reduced chlorophyll content and adversely affected net leaf photosynthesis and transpiration in azalea. Females fed more, as indicated by numbers of frass spots, and caused substantially more leaf injury than males and third instar nymphs. Although only com-

Table 3. Intercept and slope of linear regression between leaf stomatal resistance or transpiration and percentage of leaf area damaged by *S. pyrioides* in azalea

Parameter	Trial	Intercept a	Slope b	r^2	F	$P > F$
Transpiration (mmol/m ² /s)	1	4.6522	-0.0092	0.02	1.47	0.23
	2	3.0597	-0.0158	0.22	20.51	0.0001
Stomatal resistance (s/cm)	1	2.4589	0.0046	0.01	0.53	0.47
	2	3.3461	0.0477	0.24	23.28	0.0001
	3	4.8474	0.0443	0.10	7.35	0.0084

Table 4. Intercept and slope of linear regression between leaf parameters to percentage of damaged leaf area by *S. pyrioides* in 3 trials in azalea

Parameter	Trial	Intercept a	Slope b	r ²	F	P > F
Chlorophyll per unit leaf area (mg/m ²)	1	44.890	-0.105	0.07	3.97	0.0520
	2	55.021	-0.113	0.15	12.85	0.0006
	3	95.284	-0.059	0.09	6.60	0.012
Chlorophyll per unit leaf dry wt (mg/g)	1	7.7236	-0.0139	0.05	3.28	0.075
	2	9.7441	-0.0140	0.05	4.01	0.049
	3	13.3513	-0.0319	0.07	5.58	0.021
Photosynthetic rate per unit of chlorophyll ($\mu\text{mol CO}_2/\text{s}/\text{mg}$)	1	0.1533	-0.0002	0.01	0.93	0.34
	2	0.0953	-0.0004	0.26	25.69	0.0001
	3	0.0932	-0.0006	0.39	44.62	0.0001
Chlorophyll a:b	1	2.8571	-0.0015	0.05	3.43	0.069
	2	2.5815	-0.0001	<0.01	0.07	0.79
	3	2.0386	-0.0011	0.10	8.07	0.006
Specific leaf weight (mg/cm ²)	1	5.7852	-0.0002	<0.01	0.11	0.74
	2	5.7792	-0.0050	0.03	2.00	0.16
	3	7.6125	-0.0209	0.16	13.54	0.0005

pared in trial 1, males and nymphs generally caused similar levels of leaf injury. Relatively low levels of leaf injury ($\leq 25\%$) in most treatments resulted in few significant associations between azalea leaf parameters and *S. pyrioides* leaf injury in trial 1. Nevertheless, trends in slope values for regressions in trial 1 were similar to trends in slopes in trials 2 and 3 for all leaf parameters.

Our observations are consistent with those of Ishihara and Kawai (1981) that *S. pyrioides* feed on azalea by inserting stylets through stomata on the lower leaf surface and pierce and completely remove cell contents including chloroplasts mostly from the palisade layer of leaf parenchyma tissue. Selective destruction of the palisade parenchyma, which is located below the upper epidermal layer, would explain the silvery chlorotic appearance of leaves injured by *S. pyrioides*. Although, spongy mesophyll parenchyma mostly remained intact and probably continued to function photosynthetically, damage to palisade parenchyma presumably would disrupt the photosynthetic efficiency of remaining mesophyll tissue. This would account for reduced photosynthetic capacity of remaining chlorophyll, although it also is possible that the photosynthetic capacity chlorophyll inately varies between different leaf parenchyma tissues in azalea. Furthermore, the selective loss of palisade cell contents may partly explain why leaf photosynthetic rates

were more consistently associated with chlorophyll content per unit leaf area than per unit of leaf dry weight. In short, *S. pyrioides* inserts stylets through stomata, penetrates spongy mesophyll parenchyma intercellularly and selectively pierces and removes palisade cell contents.

The physical damage of the palisade tissue by *S. pyrioides* would explain the observed leaf chlorosis and suggests several possible mechanisms by which feeding injury reduced leaf photosynthetic rates in azalea. Feeding impaired photosynthetic capacity of remaining chlorophyll (i.e., assimilation per unit of chlorophyll) and reduced chlorophyll content per unit leaf area both of which were highly correlated with leaf net photosynthetic rates. However the association between leaf injury, chlorophyll content per unit leaf dry weight and leaf photosynthetic rate was more variable. Although cause and effect were not determined, it seems likely that *S. pyrioides* reduced leaf photosynthesis by reducing both leaf chlorophyll content and photosynthetic capacity of remaining chlorophyll. Feeding injury also increased leaf stomatal resistance, and stomatal resistance was highly negatively correlated with photosynthetic rates in all trials. Increased stomatal resistance indicates closure of stomata. Other studies of arthropod feeding injury have associated increased stomatal resistance with leaf moisture stress which impairs normal function

Table 5. Pearson's correlation coefficients of leaf net photosynthetic rate and selected leaf parameters for *S. pyrioides* injury trials in azalea

Parameter	Trial 1 (N = 70)	Trial 2 (N = 76)	Trial 3 (N = 72)
Chlorophyll per unit leaf area	0.459**	0.527**	0.289*
Chlorophyll per unit leaf dry wt	0.051 NS	0.413**	-0.123 NS
Photosynthetic rate per unit of chlorophyll	0.643**	0.804**	0.981**
Chlorophyll a:b	0.063 NS	0.103 NS	0.272*
Specific leaf weight	0.489**	0.079 NS	0.299*
Stomatal resistance	-0.738**	-0.712**	-0.337**

*, ** Significance at $P < 0.05$ and $P < 0.001$, respectively; NS = not significant.

of guard cells causing stomatal closure (Sances et al. 1979a, b; Anderson and Mizell 1987; Royalty and Perring 1989; Welter 1989). The cause of increased stomatal resistance was not determined, but stomatal closure might be expected to reduce exchange of CO₂ thereby reducing leaf photosynthesis. Nevertheless, we hypothesize that chlorophyll loss and non-stomatal limitations are primarily responsible for photosynthetic rate reductions by *S. pyrioides*.

Feeding injury by *S. pyrioides* is similar to the model of feeding injury outlined for the diaspid scale *Unaspis euonymi* (Comstock) which produces chlorotic halos on scale-infested euonymus leaves (Sadof et al. 1993). Important differences are that diaspid scales feed throughout the leaf with stylets penetrating epidermal and mesophyll cells intracellularly, and removing cell contents, before stylets usually terminate in the upper palisade parenchyma. Furthermore, reductions in CO₂ assimilation in euonymus by *U. euonymi* and in scots pine, *Pinus sylvestris* L., by the pine needle scale, *Phenacaspis pinifoliae* (Fitch), have been attributed primarily to chlorophyll loss, although reductions in photosynthetic capacity of remaining chlorophyll were noted in euonymus damaged by *U. euonymi* (Walstad et al. 1973, Cockfield et al. 1987). *U. euonymi* feeding also increases stomatal resistance in euonymus which might inhibit CO₂ assimilation (Cockfield and Potter 1986). The effects of leaf feeding injury on leaf physiological processes reported for these diaspid scales generally are similar to the effects we found for *S. pyrioides* on azalea.

The effect of *S. pyrioides* feeding injury on azalea growth has not been examined, but the resulting chlorosis from even moderate levels of injury clearly reduces the aesthetic value of azalea. Reduced CO₂ assimilation presumably would reduce the amount of photosynthates available for plant growth, flowering and possibly survival. Leaf injury caused by other tingids resembles the injury caused by *S. pyrioides* on azalea. The feeding injury of other tingids should be examined to determine if the mechanism outlined for *S. pyrioides* on azalea is typical of tingids on other plants.

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