RESPONSE OF LEAF PHOTOSYNTHESIS AND WATER RELATIONS OF IMPATIENS AND PEACH TO THRIPS' INJURY

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Abstract: The effect of injury by a leaf-feeding thrips, Echinothrips americanus Morgan, on leaf photosynthesis and water relations of impatiens, Impatiens wallerana Hook f., and peach, Prunus persica L. Batsch, was investigated. These plants differ in growth characteristics and leaf morphology. Thrips injury reduced leaf photosynthetic rates, but increased stomatal conductance of impatiens. Impatiens leaf water potential was not affected by thrips injury. Echinothrips americanus adults fed primarily on the upper leaf surface of peach. Feeding injury reduced leaf photosynthesis, but had no effect on stomatal conductance and transpiration rates of peach leaves. These findings suggest possible mechanisms by which thrips injury reduces leaf photosynthesis.

Key Words: Thrips, Echinothrips americanus, photosynthesis, stomatal conductance, water relations, impatiens, peach.

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Injury by leaf-feeding thrips causes direct leaf damage and has been found to reduce growth and yield of a number of plants (Lewis 1973). Thrips possess highly modified, asymmetrical mouthparts consisting of a single mandibular stylet and paired axillary stylets surrounded by a mouthcone, thus allowing thrips to pierce and suck fluids from plant cells. In a histological study with wheat, Chisholm and Lewis (1984) found that Limothrips cerealium (Halliday) completely removed the contents of mesophyll cells while feeding which resulted in the collapse of surrounding epidermal cells. More extensive injury completely disrupted leaf cell structure causing desiccation of mesophyll and epidermal cells. They further postulated that this feeding behavior was representative of injury by terebrantian thrips.

Although feeding behavior and the resulting injury of leaf-feeding thrips have been studied (Chisholm and Doncaster 1982; Chisholm and Lewis 1984; Heming 1978), the impact of injury by leaf-feeding thrips on host leaf photosynthesis and water relations has not been investigated. Echinothrips americanus Morgan is a polyphagous, leaf-feeding thrips with a host range that includes many broadleaved foliage and woody ornamental plant species. This terebrantian thrips has been recognized recently as a pest of numerous ornamental and greenhouse plants. We investigated the impact of leaf feeding by E. americanus on leaf photosynthesis and water relations of two plant species that vary in growth characteristics and leaf morphology. The two plants selected for study were impatiens, Impatiens
wallera Hook f., and peach, *Prunus persica* L. Batsch. Both species are dicotyledons and possess a leaf structure with distinct spongy mesophyll and palisade layers. *Impatiens*, however, is an annual, foliage plant with succulent leaves, whereas peach is a perennial, woody species with relatively firm leaves.

**MATERIALS AND METHODS**

*Echinothrips americanus* were obtained from a stock colony that had been maintained in the greenhouse for 1 year. The stock colony was reared on Irish shamrock, *Oxalis acetosella* L.

**Impatiens Study**

Impatiens were seeded in pots containing a potting mix (2:2:2:1 by volume of peat, pine bark, perlite, sand) and were grown in the greenhouse for 2 months. Pots were watered daily, and a complete nutrient solution (200 ppm of N:P:K) was supplied twice per week. Four randomly selected plants of uniform size were placed in screen cages within the greenhouse. Four treatments were established by infesting cages with 0, 10, 20, and 40 adult *E. americanus* per plant. Thrips were allowed to feed and reproduce for 25 days. At that time, leaves of similar size, age, and position within the canopy were selected and categorized by damage severity. A scale of damage severity based on the percentage of discolored leaf area caused by feeding punctures was used, where (0) = no visible damage, (1) = 1 to 33%, (2) = 34 to 67%, and (3) = 68 to 100%. Leaves were randomly selected and rated for damage by one person. Selected continued until 15 leaves in each damage category were chosen. Final thrips density was determined for each leaf by counting immature and adult thrips under a 2X magnification.

Leaf photosynthesis and stomatal conductance measurements were made in a growth chamber under conditions of 25.5°C, 46 to 56% RH, and photosynthetically-active-radiation levels of 55 μE m⁻² s⁻¹. Measurements were made with LI-6000 (LI-COR, Lincoln, NE) closed gas-exchange photosynthesis system equipped with a 1.0-liter leaf chamber. Ten measurements were taken at 5-sec intervals over a 1-min period to calculate mean photosynthetic rates and stomatal conductance. Each leaf was excised, and leaf water potential was measured using a Scholander pressure bomb (Scholander et al. 1965). Leaf area of each leaf also was measured using a LI-3000 (LI-COR, Lincoln, NE) leaf area meter. Photosynthesis, stomatal conductance, and leaf water potential values (y) were regressed against final thrips density (x) using the linear model \( y = a + bx \) (SAS Institute 1985). Plant physiological measurements also were analyzed by damage rating category using an analysis of variance and Duncan’s (1955) multiple range test (Steel and Torrie 1960).

**Peach Study**

‘Lovell’ peach seedlings were established in 2.5-liter pots containing a 2:1 soil:sand mixture. Seedlings were grown in the greenhouse for six months before selecting ten uniformly-sized plants for experimentation. All plants were watered throughout the study to maintain soil water potential near field capacity. A complete nutrient solution (200 ppm of N:P:K plus soluble trace element (fertilizer) was supplied weekly to each plant.
Six leaves of similar size, age, and height from the soil surface were selected on each plant. The center portion of five leaves was covered with a thrips cage that consisted of a 5 × 5-cm piece of foam (0.3 cm thick) with the center 3 × 3 cm area removed. A piece of foam with the center removed was placed on the upper and lower leaf surfaces and were covered with plexiglass to form a cage around the leaf. The cage was clipped together and attached to a support stake. Cages were wider than the peach leaves, thus thrips could move freely between leaf surfaces. Cages were infested with either 0, 5, 10, 20, or 40 adult *E. americanus*. A sixth leaf served as an uncaged control. Adult thrips fed for seven days after which cages and thrips were removed.

Photosynthesis, stomatal conductance, and transpiration of the leaf section that was caged were measured following cage removal. Measurements were made with an LI-6000 portable, closed gas-exchange photosynthesis system equipped with a 1.0-liter leaf chamber. Measurements were taken as described in the impatiens study in the greenhouse at 27 to 30°C, 50 to 70% RH and photosynthetically-active-radiation levels of 700 to 900 μE m⁻² s⁻¹. The leaf was excised, and leaf area of the caged portion was measured with a LI-3000 portable leaf area meter. Leaf water potential was not measured because thrips injury was confined to only a portion of the leaf.

Leaf damage was rated using the 0 to 30 scale described in the impatiens study. Although thrips mortality within the cages was not determined, it was apparent that differential amounts of feeding injury occurred within the same treatment. Therefore, the amount of feeding activity was estimated by counting the final number of fecal droppings on both surfaces of each leaf. Daily fecal production of an adult *E. americanus* was determined in a companion study that was conducted in a growth chamber using the same environmental conditions as described in the impatiens study. Five adult thrips were placed on an excised peach leaf within each of twelve petri dishes. Petri dishes were lined with moistened filter paper and fecal production was monitored daily for four days. One adult *E. americanus* produced ($x \pm SE$) 11.9 ± 2.7 fecal droppings per day. Fecal dropping counts were used to calculate the number of thrips feeding days (thrips-days) where, thrips-days = the number of fecal droppings per leaf ÷ the mean daily rate of fecal production per adult.

Photosynthetic and transpiration rates and stomatal conductance (y) were regressed on the number of thrips-days (x) using a linear model of $y = a + bx$ (SAS Institute 1985). Plant physiological measurements also were analyzed by initial thrips density and damage rating category using an analysis of variance, with means being separated using Duncan’s (1955) multiple range test (Steel and Torrie 1960).

**RESULTS**

**Impatiens Study**

Thrips caused extensive damage to impatiens leaves with some leaves in the highest density treatment abscising before the end of the feeding period. Leaf photosynthetic rate declined linearly ($F = 11.15; P = 0.0015; df = 1.58$) with increasing final thrips density (Fig. 1). Inclusion of a quadratic term into the model was not significant ($F = 2.50; P = 0.12; df = 1.57$). Conversely, stomatal conductance increased linearly ($F = 24.72; P < 0.0001; df = 1.58$) with increasingly
greater thrips density (Fig. 2). Leaf water potential was not significantly \( (F = 2.74; P = 0.10; R^2 = 0.05; \text{df} = 1,58) \) related to thrips density.

\[
Y = 0.52292 - 0.00240(x), \\
R^2 = 0.16
\]

Fig. 1. Response of impatiens leaf photosynthesis to thrips feeding injury as measured by number of thrips per leaf.

Final mean \( (\pm \text{SE}) \) thrips densities on leaves with damage ratings of 0, 1, 2, and 3 were 0, 17.0 ± 2.3, 38.3 ± 4.3, and 60.6 ± 7.8 thrips per leaf, respectively. Leaf photosynthesis declined and stomatal conductance increased with increasingly severe damage (Table 1). Leaf water potential was not affected by damage rating \( (F = 1.15; P = 0.34, \text{df} = 3,56) \).
Peach Study

The cages used in this study did not cause noticeable leaf damage nor did they significantly (P > 0.05) affect leaf photosynthesis, transpiration and stomatal conductance. Adult *E. americanus* feeding caused visible injury to peach leaves after seven days. Densities of 0, 5, 10, 20, and 40 thrips per cage caused an average damage rating of 0.2, 0.3, 0.7, 1.9, and 2.0, respectively. Fecal production and thrips-days increased with increasingly severe damage (Table 2). When averaged across all treatments, 74.6% of fecal droppings occurred on the upper leaf surface which suggests that adults fed primarily on the upper leaf surface. However, we have observed that larvae feed primarily on the lower leaf surface.

Leaf photosynthesis declined with increasingly severe damage levels (Table 2). Leaf photosynthesis also declined linearly with increasing number of thrips-day (F = 11.69; P = 0.0002; df = 1,58) (Fig. 3), with the greatest decline in photosynthesis tending to occur between 0 to 15 thrips-day. Photosynthesis did not decline as
sharply at greater levels of feeding injury. Addition of a quadratic term, however, did not significantly ($F = 3.56; P = 0.06; df = 1,58$) improve the linear model of photosynthesis and thrips-days. Leaf transpiration rates and stomatal conductance were not different between leaf damage ratings (Table 2). Likewise, thrips-days was not linearly related to leaf transpiration ($F = 0.18; P = 0.67; df = 1,58$) or stomatal conductance ($F = 0.43; P = 0.51; df = 1,58$).

Table 1. Leaf photosynthesis (PN) and stomatal conductance (SC) of impatiens leaves with various degrees of damage by *E. americanus*.

<table>
<thead>
<tr>
<th>Damage rating*</th>
<th>PN (mg/m²/sec)</th>
<th>SC (cm/sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0.59a</td>
<td>0.13a</td>
</tr>
<tr>
<td>1</td>
<td>0.47b</td>
<td>0.29b</td>
</tr>
<tr>
<td>2</td>
<td>0.46b</td>
<td>0.31b</td>
</tr>
<tr>
<td>3</td>
<td>0.31c</td>
<td>0.59c</td>
</tr>
</tbody>
</table>

Means followed by the same letter are not significantly different ($P = 0.05$, Duncan's (1955) multiple range test).

* Damage rating based on percentage of leaf area discolored by feeding injury, where (0) = no visible discoloration, (1) = 1-33%, (2) = 34-67%, and (3) = 68-100%.

Table 2. Thrips-days, thrips fecal production, and leaf photosynthesis (PN), transpiration (E), and stomatal conductance (SC) of peach leaves with various degrees of damage by *E. americanus* adults.

<table>
<thead>
<tr>
<th>Damage Rating</th>
<th>No. of Thrips-days</th>
<th>Fecal Spots per leaf</th>
<th>PN (mg/m²/sec)</th>
<th>E (mg/m²/sec)</th>
<th>SC (cm/sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>28</td>
<td>1.9a</td>
<td>0.741a</td>
<td>181.8a</td>
<td>1.51a</td>
</tr>
<tr>
<td>1</td>
<td>20</td>
<td>7.7b</td>
<td>0.620b</td>
<td>183.8a</td>
<td>1.30a</td>
</tr>
<tr>
<td>2</td>
<td>4</td>
<td>27.1c</td>
<td>0.581b</td>
<td>168.9a</td>
<td>1.20a</td>
</tr>
<tr>
<td>3</td>
<td>8</td>
<td>30.9c</td>
<td>0.532b</td>
<td>189.2a</td>
<td>1.30a</td>
</tr>
</tbody>
</table>

Means followed by the same letter are not significantly different ($P = 0.05$, Duncan's (1955) multiple range test).

* Damage rating based on percentage of leaf area discolored by feeding injury, where (0) = no visible discoloration, (1) = 1-33%, (2) = 34-67%, and (3) = 68-100%.

**DISCUSSION**

Reduction in leaf photosynthesis as a result of injury by *E. americanus* was demonstrated for both impatiens and peach. Thrips feeding also increased stomatal conductance of impatiens, which implies an increase in leaf transpiration (Nobel 1974), but had no effect on stomatal conductance and transpiration of peach leaves.

Leaf injury by thrips is superficially similar to leaf injury caused by spider mites (Chisholm and Lewis 1984; Sances et al. 1979b). Spider mite injury has been found to reduce leaf photosynthesis, conductance, and transpiration of strawberries (Sances et al. 1979a, b), peppermint (DeAnglis et al. 1982, 1983), almonds (Andrews and LaPre 1979), and peach (Mizell et al. 1986) with the greatest reductions occurring at low infestation levels. The initial reduction in photosynthesis and transpiration seems to be caused by stomatal closure which inhibits the exchange of carbon dioxide and water (Sances et al. 1979a; DeAnglis et al. 1983). Stomatal
closure, which is measured as a decrease in stomatal conductance, occurs in response to mite-induced water stress caused by mechanical disruption of the leaf epidermis and cuticle. This injury, however, enhanced cuticular transpiration in peppermint (DeAnglis et al. 1982). Additional reductions in photosynthesis occur as a result of mechanical damage of mesophyll cells (Sances et al. 1979a).

\[ PN = 0.71328 - 0.00548(x), \]
\[ R^2 = 0.22 \]

![Graph showing photosynthesis vs. thrips-days/leaf](image)

Fig. 3. Response of peach leaf photosynthesis to thrips feeding injury as measured by thrips-days.

Thrips injury reduced the leaf photosynthetic rate of impatiens and peach leaves in a manner similar to the reduction reported for spider mite injury. The mechanism of stomatal closure inhibiting gas exchange is not supported by our data in that stomatal conductance increased in impatiens, and stomatal conductance and transpiration were not affected by thrips injury in peach. It is possible that mechanical disruption of chlorophyll-containing mesophyll cells by thrips is more severe than with spider mites and that this damage is the primary mechanism whereby thrips reduce leaf photosynthesis. The lack of effect of thrips injury on
leaf water potential in impatiens suggest that leaves were not under moisture stress. However, the impatiens measurements were made under conditions of very low evaporative demand. Consequently, stomata may have remained open and the increase in leaf conductance could reflect cuticular gas exchange as a result of epidermal damage. The lack of change in stomatal conductance and transpiration in peach leaves may be due, in part, to adult *E. americanus* feeding mostly on the upper leaf surface, whereas peach stomata occur entirely on the lower leaf surface (Mizell et al. 1986). Damage to mesophyll cells near the upper leaf surface could have reduced photosynthesis without extensively disrupting water movement through the leaf and stomatal function on the lower leaf surface. Results of our study suggest that this reduction probably is caused by mechanical damage of mesophyll cells, but more detailed information will be needed to determine conclusively the mechanism of photosynthesis reduction by thrips feeding. The reduction in leaf photosynthesis by thrips undoubtedly would lower photosynthate production by infested plants which eventually could be expected to reduce plant growth and productivity.

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