Does Early-Season Defoliation of Crabapple (*Malus* sp.) by Eastern Tent Caterpillar (Lepidoptera: Lasiocampidae) Induce Resistance to Japanese Beetles (Coleoptera: Scarabaeidae)?[1]

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Abstract We tested the hypothesis that early-season defoliation of flowering crabapple, *Malus* sp., by eastern tent caterpillars, *Malacosoma americanum* F., induces localized or systemic resistance to Japanese beetles, *Popillia japonica* Newman, feeding on the same trees in late June. 'Candymint Sargent' crabapple trees were inoculated with *M. americanum* egg masses, resulting in extensive defoliation during March and April. Second flush leaves of defoliated trees were smaller and thinner than those of control trees. In laboratory feeding assays with non-damaged foliage, beetles generally preferred fully expanded leaves over partially expanded ones, regardless of whether or not the source tree had been defoliated. Detached first flush leaves with caterpillar damage were fed upon less than comparable non-damaged leaves, suggesting that early-season wounding causes some within-leaf reduction in palatability to *P. japonica*. Other assays with detached first- and second-flush leaves, however, indicated absence of induced, systemic resistance. Previously-defoliated and control trees sustained comparable damage from natural beetle populations in the field. Our results suggest that defoliation of *Malus* sp. by tent caterpillars in early spring is unlikely to reduce feeding damage by Japanese beetles later in the same growing season.

Key Words *Popillia japonica,* Japanese beetle, *Malacosoma americanum,* Eastern tent caterpillar, induced resistance, *Malus* sp.

Herbivory by insects or related arthropods can affect the suitability of the damaged plant as food for phytophages that feed later (Green and Ryan 1972, Karban and Myers 1989, Tallamy and Raupp 1991, Baldwin 1994, Karban and Baldwin 1997). Wounding of leaves can induce localized or systemic changes in levels of secondary metabolites or nutrients (Karban and Myers 1989, Baldwin 1994, Stout et al. 1996), plant morphology such as density of prickles or hairs (Myers and Bazely 1990), and emission of plant volatiles that attract natural enemies (Vet and Dicke 1992). Changes induced by insect feeding are often stronger and more specific than plant responses to mechanical damage alone (Turlings et al. 1990, Mattiacci et al. 1994, Alborn et al. 1997). Induced resistance may be non-specific, e.g., cotton seedlings damaged by spider mites become more resistant to mites, caterpillars, and a fungal disease (Karban et al. 1987, Karban 1988). Mobile, polyphagous herbivores are thought to be

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more responsive to induced plant responses than are dietary specialists (Karban and Baldwin 1997).

When two or more herbivore species feed on the same plant, but at different times of the growing season, there may be indirect interactions between them mediated by induced changes in the shared host. Spring-active defoliators can affect the quality of both intact and damaged first-flush leaves, as well as regrowth foliage, for subsequent herbivores. Larvae of a lymantriid moth, for example, grew more slowly, and females attained lower pupal weights and produced fewer eggs, when they developed on leaves of bush lupine, *Lupinus arboreus* Sims, that had been damaged by an arctiid caterpillar earlier in the same year, as compared to larvae reared on leaves from non-damaged plants (Harrison and Karban 1986). Similarly, early-season herbivory triggered increased tannins and reduced protein content in damaged leaves of *Quercus emoryi* Torr., and lepidopteran leaf miners subsequently were less abundant and experienced higher parasitism rates on damaged than on non-damaged leaves (Faeth 1986).

Early-season defoliation sometimes has positive consequences for later-feeding species. Fall webworms, *Hyphantria cunea* (Drury), grew faster and attained higher pupal weights on leaves from red alder, *Alnus rubra* Bong., previously attacked by western tent caterpillars, *Malacosoma californicum* (Packard), than on leaves from non-damaged trees (Williams and Myers 1984). Hunter (1987) showed that some late-season caterpillar species feeding on spring-defoliated oaks suffered higher mortality on regrowth foliage or insect-damaged primary leaves than on intact primary leaves, whereas other caterpillar species were favored, evidently because the damaged leaves were better suited for construction of larval refuges.

Eastern tent caterpillars, *Malacosoma americanum* F. (Lepidoptera: Lasiocampidae), and Japanese beetles, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), are common, leaf-chewing pests of deciduous trees in the eastern United States. Both species are univoltine, dietary generalists whose host plants include various species within the Rosaceae (e.g., *Prunus* and *Malus* spp.). Eastern tent caterpillar, a native species, defoliates trees in early spring (Fitzgerald 1995). In central Kentucky, the larvae typically emerge from egg masses in mid-March and are active until early May. Adult Japanese beetles begin emerging from the soil about mid-June and are active into August (Potter and Held 2002).

Flowering crabapples, *Malus* spp., are among the most widely-planted ornamental trees in urban landscapes (Fiala 1994). They typically produce two, or sometimes three, flushes of leaves during a growing season. In Kentucky, the first flush of leaves often is severely damaged by *M. americanum,* and then first- and second-flush leaves may be subsequently attacked by *P. japonica.* The present study was motivated, in part, by testimonials from some local growers that trees that had been defoliated by tent caterpillars seemed to be less heavily damaged by Japanese beetles. We sought to test this hypothesis in the context of induced resistance.

Materials and Methods

Defoliation by eastern tent caterpillar. The main study site was a block of mature, 3-m tall 'Candymint Sargent' crabapple trees that had been planted in 1989 at Hillenmeyer Nurseries, Lexington, KY. The trees were spaced about 3.5 m apart in an open, weedy field. They had not been irrigated or fertilized, nor had they been treated with any insecticides for several years prior to our study. Eight pairs of trees were blocked by nearest neighbors, with one receiving eastern tent caterpillar egg masses ("caterpillar-defoliated" trees) and the other receiving no egg masses (control trees).

Twigs with eastern tent caterpillar egg masses were collected between 27 February and 5 March 1998 from wild cherry, *Prunus serotina* Ehrh., and crabapple trees in central Kentucky. Egg masses were placed in paper bags and held at 4.4°C. On 13 March 1998, one egg mass per branch was secured with a wire twist-tie to five different branches of each caterpillar-defoliated tree. A few branches were lightly pruned as necessary to avoid contact and prevent between-tree movement of tent caterpillars. By 16 March, all egg masses had hatched and larvae had begun to build nests. The caterpillar-defoliated trees were heavily (>75%) damaged by 1 May, and the tent caterpillars had pupated. There, nonetheless, were some first-flush leaves that had escaped damage. Several hundred such leaves were marked for use in subsequent feeding trials by tagging the twig basal to the leaf petiole.

Leaf physical characteristics. On 16 June 1998, early in the Japanese beetle seasonal flight period, samples of first- and second-flush leaves were collected for analysis of physical characteristics that might be affected by eastern tent caterpillar defoliation. Three different age classes of leaves were collected from both caterpillar-defoliated and control trees: (1) first flush, fully expanded, non-damaged leaves that had been present during the caterpillar feeding period, (2) second flush, fully expanded (>6 cm long) non-damaged leaves, and (3) second flush, partially expanded (<6 cm) non-damaged leaves. Excised leaves were placed in plastic bags and brought to the laboratory in a cooler. Leaf thickness and relative toughness were measured for five leaves of each type per tree. Leaf thickness was measured with an electronic thickness indicator (Mititoyo Corp., Tokyo, Japan), and relative toughness was measured with a digital force gauge with a pointed punch (Mark-10 Corp., Hicksville, NY). Leaf area measurements (Li-Cor, Lincoln, NE) and percentage water content (based on difference between wet and dry leaf weights) were also determined using three replicates of five leaves of each type per tree. Data were tested by analysis of variance (ANOVA) for main effects and interaction of tree type (caterpillar-defoliated or control), tree (replicate), and leaf age class (see above). Single degree of freedom orthogonal contrasts were used to compare leaf age classes, and between second flush leaves from caterpillar-defoliated versus control trees. All analyses were done with Statistix for Windows (Analytical Software 1998).

No-choice feeding tests. Foliage samples were collected from caterpillar-defoliated and control trees during the last week of June. The excised leaves were brought to the laboratory in coolers as before and used in assays within a few hours after collection. Seven types of leaves were used. These included first flush, fully expanded, non-damaged leaves from either caterpillar-defoliated or control trees; first flush, fully expanded, caterpillar-damaged leaves from defoliated trees; second flush, fully expanded, non-damaged leaves from either defoliated or control trees; and second flush, partially expanded, non-damaged leaves from either defoliated or control trees. These comparisons were used to test for within-leaf (localized) change in palatability resulting from eastern tent caterpillar feeding damage, systemic changes in second flush leaves that had not been present at the time of early-season defoliation, and comparisons between fully- and partially-expanded foliage.

Japanese beetles were field-collected using standard traps baited with food-type lures, a 3:7:3 mixture of geraniol, eugenol, and phenthyl propionate (Trécé Inc., Garwood, NJ). Sexes were separated using foretibial characters (Fleming 1972).

Females were confined with moist soil for oviposition, but without food, for 24 h before use in feeding trials.

The assays were conducted in an environmental chamber at 24° ± 0.5°C with a photoperiod of 14:10 (L:D). Test arenas were 470-mL plastic cups containing a 1-cm layer of moist sand. One freshly-excised leaf was inserted by its petiole into the sand, one female beetle was added to the arena, and the cup then was covered with clear plastic wrap. Four leaves of each type were tested from each of the eight caterpillar-defoliated or control trees (448 total leaves). Beetles were allowed to feed for 20 h. The leaves were then removed and the area eaten was traced onto sheets of clear acetate film with a black marker and measured by an electronic area meter. Area eaten was converted to fresh weight consumed by using a mg/cm conversion factor for each leaf type, determined by weighing and measuring the area of 10 freshly-harvested leaves of that type. Feeding on the four leaves of each type was averaged to provide a single value per leaf type for each true replicate (i.e., tree). Data were analyzed by two-way ANOVA for main effects of leaf type and tree, followed by single degree of freedom orthogonal contrasts to compare amount of feeding on leaves from caterpillar-defoliated versus control trees, and between age classes of leaves.

Choice tests. To further evaluate whether systemic or localized changes resulting from defoliation by eastern tent caterpillars would alter Japanese beetle feeding response to *Malus* foliage, three series of choice tests were conducted during the last week of June. The first series compared beetle preference for non-damaged leaves from caterpillar-defoliated versus control trees. These between-tree comparisons were done separately for fully expanded first flush leaves; fully expanded second flush leaves; and partially expanded second flush leaves.

To test for localized induced resistance, caterpillar-damaged, fully expanded first flush leaves from caterpillar-defoliated trees were paired with similarly-aged, non-damaged leaves from either caterpillar-defoliated or control trees. A third series of tests, comparing beetle response to leaves of varying age, included all possible paired comparisons of first flush, fully expanded non-damaged leaves, second flush, fully expanded non-damaged leaves, and second flush, partially expanded leaves. These leaf-age comparisons were within the same tree type, either caterpillar-defoliated or control trees.

There were eight true replicates (trees) for each comparison, each based on the average of five beetles and leaves of a particular type per tree. The tests were conducted in the same type of arenas described for the no-choice tests. Each cup contained two leaves, one of each type being compared, inserted into the moist sand about 1 cm apart. Three starved female beetles were placed on the sand in each cup. Beetles were allowed to feed for 18 h in the first two sets of comparisons, or for 12 h in the last set. The arenas were kept in an environmental chamber under the same conditions as previously described. Beetles never consumed all of any choice. Area eaten was converted to mass (mg) as previously described. Data were analyzed by Wilcoxon signed rank tests ($\alpha = 0.05$) using Statistix for Windows (Analytical Software 1998).

Field evaluation. Four branches were randomly removed from each tree on 27 August 1998, at the end of Japanese beetle seasonal flight. All leaves were removed from these branches and pooled. A sample of 100 leaves was randomly selected to determine the degree of feeding damage from *P. japonica* that each tree had sustained. Japanese beetle feeding results in characteristic skeletonization that can be readily distinguished from caterpillar damage (i.e., missing sections of leaf). Each leaf was ranked as having no feeding, light feeding (20% of leaf area skeletonized), or substantial feeding (>20% skeletonized) by beetles. Numbers of leaves within each damage category were compared between caterpillar-defoliated and control trees by the Wilcoxon rank sum test (Analytical Software 1998).

Results

Leaf physical characteristics. There was no overall difference in thickness, toughness, or water content of leaves from caterpillar-defoliated versus control trees, but the main effect of defoliation was significant for leaf area (Table 1). There were, however, significant differences between types of leaves, as well as interaction between defoliation and leaf type (Table 1). Notably, fully-expanded, second flush leaves from defoliated trees were smaller (orthogonal contrasts; $t = 3.30$; $P < 0.01$) and thinner ($t = 3.68$; $P < 0.001$) than corresponding leaves from control trees, although comparable in toughness ($t = 0.80$; $P = 0.43$).

No-choice feeding tests. Beetles consumed similar amounts of all seven types of leaves ($F = 2.16$; df = 6, 42; $P = 0.21$) (Fig. 1). When caterpillar-damaged first flush leaves were omitted to produce a balanced treatment structure, main effects and interaction of tree type (defoliated or control) and leaf type were non-significant. Orthogonal single degree of freedom comparisons also suggested absence of induced resistance from early-season defoliation. Contrasts between first flush, non-damaged versus caterpillar-damaged leaves from within defoliated trees ($t = -1.22$; $P = 0.23$), and between first flush, non-damaged leaves from either caterpillar-defoliated or control trees ($t = 0.09$; $P = 0.93$) suggested absence of short-term, local or systemic induced resistance relevant to *P. japonica*. Contrasts between caterpillar-defoliated and control trees for fully-expanded second flush leaves also were non-significant ($t = -1.79, -1.01$; $P = 0.08, 0.32$; respectively) suggesting absence of delayed, systemic induced resistance. Second flush, partially expanded leaves were fed upon less than first flush leaves ($t = -2.42$; $P < 0.02$), but the contrast between partially and fully expanded second flush leaves was not significant ($t = -1.64$; $P = 0.11$).

Choice tests. Choice tests comparing Japanese beetle feeding response to intact leaves from caterpillar-defoliated versus control trees showed no significant differences, suggesting absence of systemic, induced resistance within age classes of leaves (Fig. 2). However, first flush leaves that had been damaged by caterpillars were fed upon less than intact leaves, regardless of whether the latter came from defoliated or control trees (Fig. 3A). This suggests a localized, within-leaf reduction in palatability resulting from early-season wounding.

Within-tree comparisons suggested some differences in beetle feeding response to different age classes of intact leaves. Fully expanded first or second flush leaves from caterpillar-defoliated trees were preferred over second flush partially expanded leaves (Fig. 3C,D). The same pattern occurred within control trees, but was significant only for the contrast between fully-versus partially-expanded second flush leaves (Fig. 3D).

Field evaluation. Caterpillar-defoliated and control trees sustained similar amounts of Japanese beetle injury in the field. Both sets of trees had similar proportions of leaves with no feeding, light feeding, or substantial feeding (Table 2), suggesting absence of delayed induced resistance.

Table 1. Physical characteristics of intact crabapple leaves sampled in June from trees that had, or had not, been defoliated by eastern tent caterpillars in early spring

Defoliation treatment	Leaf type	Mean (±SE) leaf Thickness (μm)	Toughness (g)	Water (%)	Area (cm^2)
ETC-defoliated	1st flush, fully expanded	152.8 ± 5.4	71.8 ± 4.6	54.8 ± 0.3	10.8 ± 0.7
	2nd flush, fully expanded	162.8 ± 4.5	72.0 ± 4.6	52.9 ± 0.4	24.6 ± 1.2
	2nd flush, partially expanded	174.9 ± 5.0	69.7 ± 5.2	54.2 ± 0.5	12.6 ± 0.7
Control	1st flush, fully expanded	148.9 ± 4.1	90.3 ± 4.4	54.2 ± 0.5	10.6 ± 0.7
	2nd flush, fully expanded	197.5 ± 4.6	77.7 ± 5.5	52.9 ± 0.6	28.7 ± 1.4
	2nd flush, partially expanded	171.4 ± 5.4	64.8 ± 4.3	54.4 ± 0.5	14.1 ± 0.4

Defoliation main effect was significant for leaf area ($F = 6.20$; df = 1, 35; $P < 0.05$), but non-significant for other leaf parameters. Leaf-type main effect was significant for all leaf parameters: thickness ($F = 10.55$; df = 3, 35; $P < 0.001$), toughness ($F = 3.84$; df = 3, 35; $P < 0.05$), water content ($F = 7.92$; df = 3, 35; $P < 0.01$), and leaf area ($F = 195.8$; df = 3, 35; $P < 0.001$).

Defoliation × Leaf type interaction was significant for leaf thickness ($F = 5.51$; df = 2,35; $P < 0.01$); marginal for area ($F = 3.11$; df = 2, 35; $P = 0.06$), and non-significant for toughness and water content.

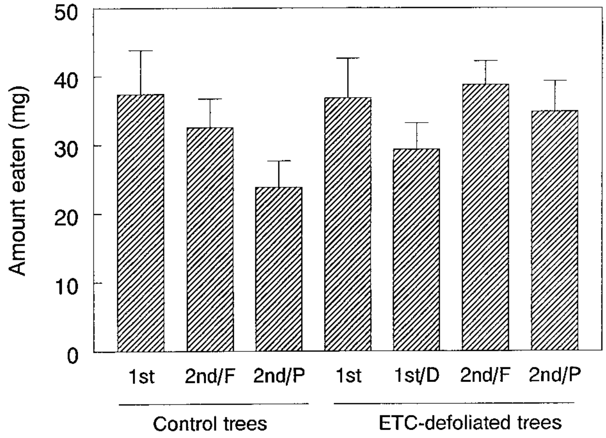

Fig. 1. Japanese beetle feeding on different age classes of leaves in no-choice tests. 1st = first flush, fully expanded; 1st/D = first flush, fully expanded, with Eastern tent caterpillar (ETC) feeding damage; 2nd/F = second flush, fully expanded; 2nd/P = second flush, partially expanded. See text for statistical comparisons.

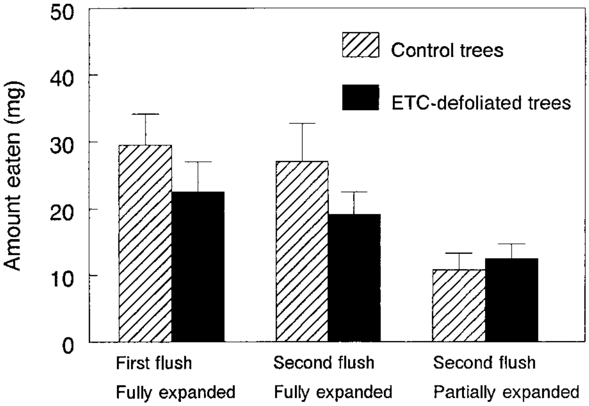

Fig. 2. Japanese beetle feeding response to intact leaves from trees defoliated by eastern tent caterpillar (ETC) versus control trees in choice tests. There were no significant differences within leaf age classes, suggesting absence of systemic, induced resistance.

Discussion

Damage-induced responses, often enhancing resistance, have been demonstrated for at least 300 plant species representing 34 families, but there are also studies in which no induced response, or even induced susceptibility, was found (Williams and Myers 1984, Hunter 1987, Karban and Baldwin 1997). Our results

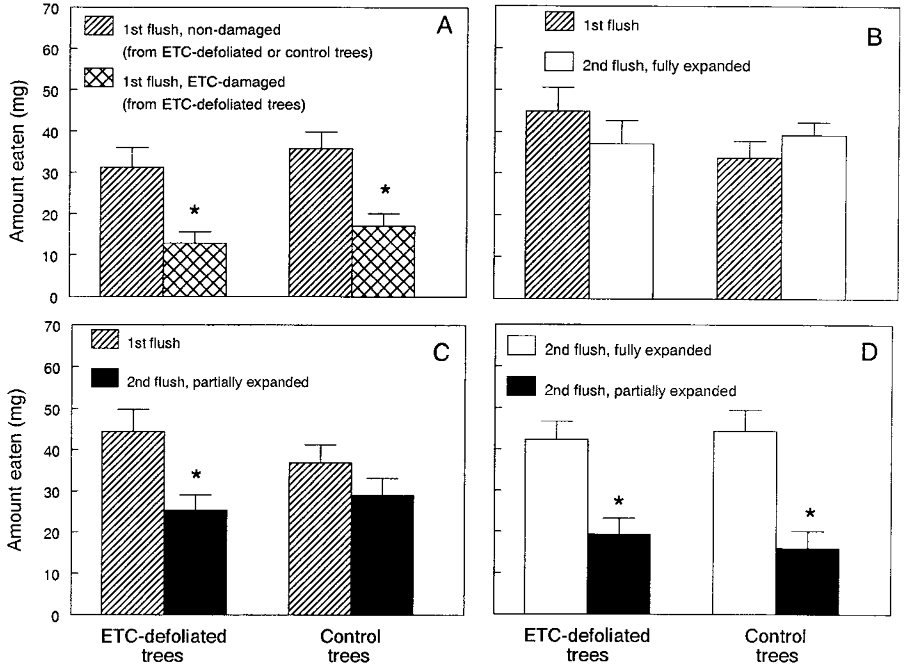

Fig. 3. Japanese beetle feeding response to various leaf types from eastern tent caterpillar (ETC) defoliated or control trees in choice tests. A) ETC-damaged first flush leaves (from ETC-defoliated trees) versus intact leaves from either ETC-defoliated or control trees; B,C,D) within-tree comparisons between different age classes of leaves. Asterisks denote a significant difference within pairs (Wilcoxon signed rank tests, $\alpha = 0.05$).

generally failed to support the hypothesis that 'Candymint Sargent' crabapple trees that are heavily defoliated by eastern tent caterpillars in early spring are less heavily fed upon by Japanese beetles later in the same growing season.

Testing methodology can affect the outcome of assays examining insect feeding preference among different species or varieties of plants, or to previously-damaged leaves in studies on induced resistance (Barnes 1963, Risch 1985, Jones and Coleman 1988). Whole, detached leaves may be more representative of whole plants than are leaf discs (Risch 1985). Risch (1985) suggested using several methodologies for feeding studies from which ecological inferences are to be drawn. Our laboratory and field tests both suggested absence of systemic induced resistance to Japanese beetles in non-damaged leaves from caterpillar-defoliated trees.

Beetles tended to feed sparingly on partially expanded, second flush foliage irrespective of whether or not the source tree had been defoliated. Phenologically young apple foliage (*Malus domestica* L.) contains relatively high concentrations of two phenolic compounds, phloridzin and its hydrolysis product, phloretin (Hunter and Hull 1993). Phloretin deterred Japanese beetle feeding on artificial medium (Fulcher et al. 1998). Partially expanded, second flush leaves were less preferred than first flush

Table 2. Lack of effect of early-season defoliation of crabapple trees by eastern tent caterpillars on subsequent feeding damage by naturally-occurring Japanese beetle populations in the field

	Number of leaves (out of 100) with*		
Defoliation treatment	No feeding	Light feeding	Substantial feeding
ETC-defoliated	77.0 ± 5.2	17.8 ± 3.5	5.3 ± 1.9
Control	68.1 ± 5.1	23.5 ± 3.2	8.4 ± 2.1
P-value**	0.142	0.156	0.294

* Based on 100-leaf samples randomly drawn from four branches per tree. No, light, and substantial feeding correspond to 0, ≤20, and >20% of leaf area with characteristic feeding damage (i.e., skeletonization) by Japanese beetles.

** Based on Wilcoxon rank sum test.

leaves regardless of whether or not trees had been defoliated by tent caterpillars, so this is not evidence for an induced response.

We found some subtle differences in leaf physical characteristics, e.g., fully expanded second-flush leaves from caterpillar-defoliated trees were relatively smaller than comparable leaves from control trees. Although no chemical assays were done, any delayed, systemic changes in nutrients or secondary chemistry that may have resulted from the earlier defoliation did not measurably affect beetle feeding response. Small phytochemical changes in a preferred host, even if they did occur, likely would not deter a dietary generalist (>300 host plant species; Fleming 1972) that has a rapidly-inducible polysubstrate monooxygenase system (Ahmad 1983).

Regarding *P. japonica,* Fleming (1972) states that "diseased plants and those injured by other insects are more susceptible to attack by the beetle than healthy plants." As evidence, he cites several anecdotal accounts, e.g., that elms (*Ulmus* spp.) with feeding damage from elm leaf beetle, *Pyrrahalta luteola* (Muller), and Norway maples, *Acer platanoides* L., infested with aphids, reportedly were more attractive to the beetles than non-infested trees. Loughrin et al. (1995) found that crabapple leaves that had been damaged overnight by *P. japonica* or fall webworms, *Hyphantria cunea* Drury, attracted more Japanese beetles than did non-damaged leaves. Beetles' aggregation in response to feeding-induced plant volatiles also was shown in the field (Loughrin et al. 1996). Thus, the aforementioned accounts likely represent beetle attraction to freshly-wounded leaves rather than long-term, systemic, induced preference.

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