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Natural Pest Resistance of *Prunus* Taxa to Feeding by Adult Japanese Beetles: Role of Endogenous Allelochemicals in Host Plant Resistance

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Abstract. **Feeding intensity of adult Japanese beetle (*Popillia japonica* Newm.) was compared among 27 taxa of *Prunus* host plants during 24-hour no-choice feeding trials conducted on individual leaves. Fecal dry mass per beetle, a measure of feeding intensity, varied from 0 mg·d^{-1} for *Prunus padus* L. to 20.4 mg·d^{-1} for *P. sargentii* Rehd. and *P. tomentosa* Thunb. *Prunus padus*, *P. laurocerasus* L., *P. mahaleb* L., *P. serotina* Ehrh., *P. virginiana* L., *P. americana* Marsh., *P.* ×*yedoensis* Matsum., and *P. besseyi* Bailey were resistant based on feeding intensities of <4.3 mg·d^{-1} (levels not significantly different from zero). Feeding intensity decreased exponentially as endogenous foliar cyanide potential increased. Evaluation of the cyanogenic glucoside prunasin in artificial diets showed a similar relationship with feeding being reduced by 50% (ED_{50}) at 4.9 mmol·kg^{-1} in the diet. *Prunus mahaleb* was highly resistant to Japanese beetles despite having low cyanide potential. Two coumarin compounds known to exist in *P. mahaleb*, herniarin and coumarin, were tested in artificial diets and were effective feeding deterrents with ED_{50} values of 5.9 and 2.5 mmol·kg^{-1} in the diet, respectively. This research demonstrated a wide range of host plant resistance to feeding by adult Japanese beetles and further indicates that prunasin, herniarin, and coumarin are important factors in host plant resistance to this pest.**

Since their introduction into the United States in 1916, Japanese beetles have spread rapidly throughout much of the eastern United States with isolated populations in the western United States and Canada (Hadley and Hawley, 1934; Johnson and Lyon, 1991). Climatological models have predicted other suitable habitats in much of Europe, Asia, and certain mountainous areas of Africa, Australia, Tasmania, New Zealand, and South America (Allsopp, 1996).

Although it is considered a minor pest in Japan, Japanese beetles are damaging pests in the United States (Fleming, 1972). Hawley and Metzger (1940) documented feeding on over 275 hosts species, including a wide diversity of agronomic crops and landscape plants. Despite the polyphagous nature of Japanese beetles, there is often a considerable range of susceptibility expressed among closely related plants. For example, Ranney and Walgenbach (1992) found that defoliation by adult Japanese beetles varied from 46% to 93% among eight taxa of *Prunus*. Hawley and Metzger (1940) documented several *Prunus* taxa including *P. cerasus* L., *P. domestica* Poir., and *P. salicina* Lindl. that were severely injured by beetle feeding and one taxa, *P. serrulata* Lindl. that was only moderately injured.

Variation in host-plant resistance can be due to many factors; however, differences in endogenous allelochemicals are often important in pest resistance (Reese, 1977; Waiss et al., 1977). Two potentially important groups of compounds found in species of *Prunus* include the cyanogenic glucosides and coumarins.

Many species of *Prunus* contain the L-phenylalanine-derived cyanogenic glucosides, prunasin and amygdalin (Conn and Butler, 1969). The cyanogenic diglucoside amygdalin is found only in seeds of *Prunus* species, while the monoglucoside prunasin has been found in all tissues including leaves (Mizutani et al., 1979). When damaged or ingested, catabolizing enzymes mix with these cyanogenic glycosides, ultimately resulting in release of cyanide gas (HCN) and the carbonyl compound benzaldehyde (Carvalho, 1981; Kuroki and Conn, 1989; Poulton, 1988; Xu et al., 1988). Once released, cyanide acts as an inhibitor of respiration and certain oxidation–reduction enzymes, such as nitrate reductase (Mizutani, 1980; Reilly and Edwards, 1982). Cyanide potential is an important factor in deterring the oblique-banded leafroller (*Choristoneura rosaceana* Harris) in peach and locust (*Locust migratoria* L.) on sorghum [*Sorghum bicolor* (L.) Moench] (Kaethler, et al. 1982; Woodhead and Bernays, 1978).

Coumarin compounds are not widely present in *Prunus* spp., but herniarin and coumarin have been reported in foliage of *Prunus* species in the subgenus *Cerasus*, section Phyllomahaleb (Koehne) Rehd., including *P. mahaleb, P. pensylvanica, P. maximowiczii,* and *P. maackii* (Fung and Herrebout, 1987; Krüssmann, 1986; Santamour and Riedel, 1994). Coumarins are known to be feeding deterrents to many insect pests including the gypsy moth (*Porthetria dispar* L.), cotton leafworm (*Alabama argillarea* Hubner), and cowpea aphid (*Aphis craccivora* Koch) (Mansour, 1981; Mansour et al., 1982; Meisner and Skatulla, 1977).

Identification and development of taxa with natural pest resistance can minimize the need for pesticide usage and aid in the development of more sustainable landscapes and cropping systems. The genus *Prunus* is diverse and includes six subgenera and ≈430 species (Krussman, 1986). Preliminary work (unpublished)

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indicated considerable variation in host plant resistance to feeding by adult Japanese beetles among *Prunus* taxa, suggesting the possibility for selection and improvement of these plants for pest resistance. Thus, our objectives were to 1) document variation in host plant resistance to Japanese beetles among diverse taxa of *Prunus* and 2) to evaluate the role of cyanogenic glycosides and coumarins in host plant resistance.

Materials and Methods

INSECTS. Adult Japanese beetles were collected in the morning from smartweed (*Polygonum* spp.) plants at the Mountain Horticultural Crops Research Station, N.C., 1 day before feeding trials. Female beetles were used because they tend to feed for a longer time and are disturbed less easily during feeding than males (Smith, 1923). The beetles were kept on moist paper towels at 25 °C without food for 24 h in a continuously lighted growth chamber with 75 to 85 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation.

PLANT MATERIAL. Twenty-seven taxa of *Prunus* were tested in this study. They included *P. americana* Marsh, *P. armeniaca* L.; *P. avium* L.; *P. besseyi* Bailey; *P. cerasifera* Ehrh.; *P. cerasus* L. 'North Star'; *P. ×cistena* (Hansen) Koehne; *P. domestica* L. 'Stanley'; *P. dulcis* D.A. Webb; *P. laurocerasus* L.; *P. mahaleb* L.; *P. mume* S. & Z.; *P. padus* L.; *P. pennsylvanica* L.; *P. persica* (L.) Batsch 'Redhaven', 'Saharanpur', 'Ta Tao #6', 'PI 134401', and 'Quetta'; *P. salicina* Lindl.; *P. sargentii* Rehd.; *P. serotina* Ehrh.; *P. serrulata* Lindl.; *P. subhirtella* Miq. 'Autumnalis'; *P. tomentosa* Thunb.; *P. virginiana* L. 'Canada Red'; and *P. ×yedoensis* Matsum. Taxa without cultivar names were of seedling origin. All plants were grown in 18.9-L containers using a medium of 3 milled pine bark : 1 sphagnum peat (v/v) amended with Micro-Start (Sta-Green Corp., Sylacauga, Ala.) at 1.8 $kg \cdot m^{-3}$ and dolomitic lime at 2.2 $kg \cdot m^{-3}$. Plants were maintained on an outdoor gravel container pad in a randomized complete-block design with 10 replications of each taxon. About 1 month after potting, each plant was fertilized with 7 g of 17N–2.6P–6.6K Nutricote fertilizer (Florikan ESA, Sarasota, Fla.).

Table 1. Feeding intensity (fecal dry mass) of Japanese beetles and foliar cyanide potential (fresh mass basis) for 27 taxa of *Prunus*.

Taxa	Feeding intensity (mg)	Cyanide potential ($mmol \cdot kg^{-1}$)
P. padus	0.0	9.2
P. laurocerasus	0.2	7.0
P. mahaleb	0.3	0.2
P. serotina	0.5	5.9
P. virginiana 'Canada Red'	1.1	3.1
P. ×yedoensis	3.7	2.4
P. americana	4.0	3.0
P. besseyi	4.1	2.6
P. pennsylvanica	4.4	1.3
P. persica 'Redhaven'	4.8	1.2
P. persica 'Saharanpur'	5.2	1.3
P. persica 'Ta Tao #6'	5.3	1.3
P. armeniaca	6.5	0.3
P. serrulata	7.3	0.9
P. mume	7.7	0.2
P. cerasifera	8.6	1.4
P. persica '134401'	9.4	1.2
P. persica 'Quetta'	10.2	1.2
P. subhirtella 'Autumnalis'	12.2	1.6
P. ×cistena	12.5	1.1
P. domestica 'Stanley'	14.2	0.3
P. cerasus 'North Star'	15.4	0.3
P. avium	17.4	0.3
P. salicina	18.3	0.5
P. dulcis	18.8	1.1
P. sargentii	20.4	0.3
P. tomentosa	20.4	0.3
$LSD_{0.05}$	4.3	0.5

FEEDING TRIALS. Individual branches were collected from each of the 27 taxa of *Prunus* the morning of a feeding trial. Cut stems were kept in water to minimize dehydration and subsequent decompartmentalization of the cyanogenic system. A single, recently matured leaf was later cut from each branch. The petiole of each leaf was inserted into a hole made in the top of a microfuge tube. The tubes were filled with distilled water and the tops snapped closed. Each leaf plus microfuge tube apparatus was placed into a petri dish (15 cm in diameter). One starved beetle was placed into each dish in contact with the leaf.

Dishes were put into a growth chamber identical to the one described previously. Beetles were allowed to feed for 24 h. Fecal matter was collected, dried at 70 °C for ≈24 h, and weighed. The experiment was arranged as a randomized complete block with 10 replications of each taxa. Feeding trials were blocked over time with one leaf from each plant in a given block being tested on a given day.

DETERMINATION OF CYANIDE POTENTIAL. About 10 of the most recently matured leaves were collected from each taxa in the morning concurrently with those collected for feeding trials. Leaf tissue was weighed, freeze-dried, ground, and stored at –80 °C. Cyanide potential was determined by an enzymatic cyanide assay procedure similar to that of Lambert et al. (1975). A 25-mg sample of tissue was homogenized in 3 mL phosphate buffer, centrifuged, and decanted. This process was repeated with an additional 3 mL of buffer. Meanwhile, enzymes capable of catabolizing cyanogenic glycosides were extracted by combining 2.03 g sweet almond meal with 27 mL distilled water. This mixture was bubbled with N and filtered through a glass fiber filter circle (4.25 cm in diameter) using an aspirator.

Sodium hydroxide (2.5 mL) was pipetted into the center well of a Conway diffusion dish (Bel-Art, Pequannock, N.J.). Sample supernatant (2.6 mL) and almond extract (1.25 mL) were pipetted into the outer well. Amygdalin was also tested at 0.0165, 0.231, and 0.990 $mg \cdot L^{-1}$ as a calibration. A NaCN standard was also tested at 0.220 $mg \cdot L^{-1}$. Dish lids were coated with a thick layer of petroleum jelly that formed an airtight seal and allowed for entrapment of hydrogen cyanide gas in the NaOH. The reaction was incubated at 35 °C for ≈4 h.

After incubation, the NaOH was pipetted from the center well into a 50-mL volumetric flask. The reaction site was rinsed two times into the flask with 1.25 mL distilled water. Phosphate buffer (2.5 mL) and N-chlorosuccinimide reagent (2.5 mL) plus barbituric acid (2.5 mL) reagent were added. The flasks were inverted to mix the contents and then allowed to stand for 15 min, after which

the volume was adjusted to 50 mL with distilled water. Absorbance was measured at 580 nm.

ARTIFICIAL DIETS. Prunasin, coumarin, and herniarian (7-methoxycoumarin) were incorporated into artificial diets similar to that used by Hsiao and Fraenkel (1968). Agar (4 g) and cellulose (4 g) were added to 100 mL boiling distilled water while stirring vigorously. Sucrose (3.42 g) as well as the appropriate amount of test compound then were added to the cooling media. Each compound was added to the standard diet described previously to yield concentrations of 1, 5, 10, 20, and 40 mM.

Individual, starved beetles were placed into plastic petri dishes (100 × 15 mm) with 1.5 × 1 cm plugs of cooled diet media. Dishes were placed into a continuously lighted growth chamber, and beetles were allowed to feed for 24 h. Fecal material was dried and weighed. Each treatment (diet) concentration was replicated 10 times. Control treatments containing the basic diet were included during each test. Individual treatments were arranged in a completely randomized design. Data were subjected to regression analysis. The effective dose of a compound that reduced feeding by 50% (ED_{50}) was calculated from regression equations for each compound.

Results and Discussion

Feeding intensity of beetles, as indicated by fecal production per beetle, varied from 0 mg·day^{-1} for *Prunus padus* to 20.4 mg·day^{-1} for *P. sargentii* and *P. tomentosa* (Table 1). *Prunus padus*, *P. laurocerasus*, *P. mahaleb*, *P. serotina*, *P. virginiana* 'Canada Red', *P.* ×*yedoensis*, *P. americana*, and *P. besseyi* all were resistant with feeding intensities of <4.3 mg (levels not significantly different from 0). Endogenous cyanide potential varied considerably among *Prunus* taxa (Table 1). Cyanide potentials ranged from 0.2 mmol·kg^{-1} (fresh mass basis) for *P. mahaleb* and *P. mume* to 9.2 mmol·kg^{-1} (fresh mass basis) for *P. padus*. Feeding intensity showed a significant ($P < 0.05$) exponential decrease with increasing endogenous cyanide potential (Fig. 1). Taxa with cyanide potentials ≥2.4 mmol·kg^{-1} (fresh mass basis) had reduced feeding at levels not significantly different from 0 (Table 1). In general, taxa with cyanide potentials <2.4 mmol·kg^{-1} (fresh mass basis) were fed on more intensely and in a more random fashion. *Prunus mahaleb*, however, was a noticeable outlier with a high level of resistance, despite having a low cyanide potential. These data suggest an apparent threshold level of ≈2.4 mmol·kg^{-1} (fresh mass basis) is needed to effectively deter feeding and further indicated that the resistance of *P. mahaleb* appeared to result from other factors.

As the dose of prunasin increased in an artificial diet, feeding intensity of adult Japanese beetle decreased exponentially (Fig. 2). The effective dose of prunasin, which reduced feeding by 50% (ED_{50}), was 4.9 mmol·kg^{-1} of diet. This concentration was higher than the concentration found to reduce feeding by the same amount in leaf tissue. The greater efficacy in the plant may be due to localization of cyanogenic glycosides near the leaf surface. Although a common compartmentation strategy has not been recognized (Poulton, 1988), the cyanogenic glycoside dhurrin occurs in the vacuole of epidermal cells in sorghum seedlings (Kojima et al., 1979; Saunders and Conn, 1978). Gruhnert et al. (1994), working with *Hevea brasiliensis* M.A. (rubber tree), found the cyanogenic glycoside linamarin to be localized exclusively in the central vacuole of protoplasts of epidermal and mesophyll cells. Thus, herbivores that feed initially on the leaf surface, such as the Japanese beetle, may be exposed to higher concentrations of cyanogenic glycosides than would be indicated by a measure of

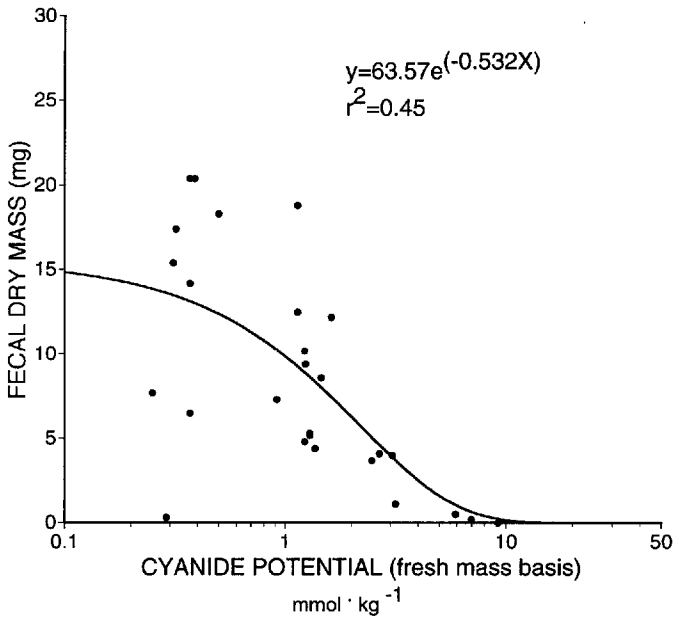

Fig. 1. Relationship between feeding intensity (fecal dry mass) and cyanide potential measured in leaf tissue of 27 *Prunus* taxa. Each symbol represents the means for a given taxa of *Prunus*, n = 10.

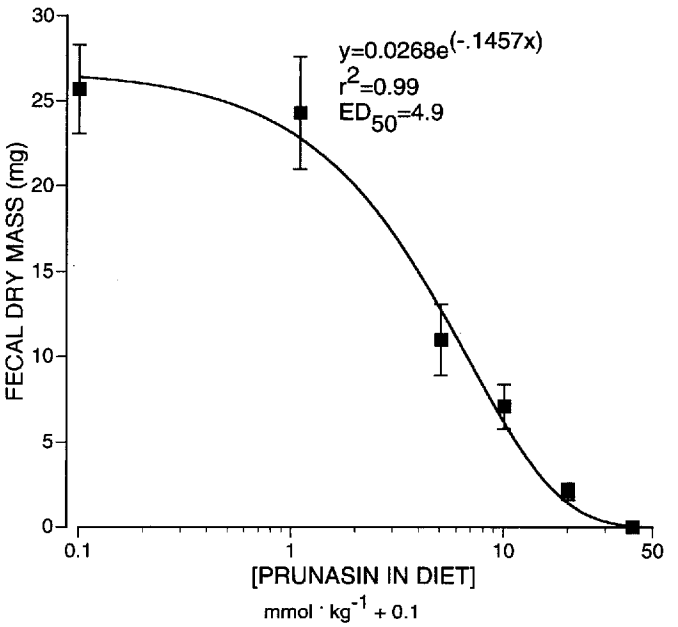

Fig. 2. Feeding intensity (fecal dry mass) as a function of prunasin content in an artificial diet. Each symbol represents a mean of 10 observations.

bulk leaf cyanide potential.

Another possible explanation of the higher activity of cyanogenic glycosides in leaf tissue as opposed to artificial diet is the presence of catabolizing enzymes in the plant. These enzymes, which consist of β -glucosidase and an α-hydroxynitrile lyase, often occur in conjunction with, but not in the same cellular location as, the cyanogenic glycoside. In sorghum, for example, the catabolizing enzymes are located in the underlying mesophyll tissue (Kojima et al., 1979; Saunders and Conn, 1978).

Following correlation of endogenous cyanide potential of *Pru-*

nus taxa with feeding intensity, the strong resistance of *P. mahaleb* was not explained by cyanide content. This taxon exhibited a low level of cyanide potential but was highly resistant to beetle feeding. Resistance of *P. mahaleb* to feeding by Japanese beetle, therefore, was due to a mechanism other than cyanide potential. Although endogenous levels of coumarins were not measured in this study, *P. mahaleb* is know to contain high levels of coumarins. As the dose of herniarin and coumarin was increased in artificial diets, feeding of Japanese beetle decreased significantly (Figs. 3 and 4). The effective dose of herniarin, which reduced feeding by 50% (ED_{50}), was 5.93 mmol·kg^{-1} of diet. Coumarin reduced feeding by the same amount at a diet concentration of 2.48 mmol·kg^{-1}. Yu and Carlson (1975) found concentrations of herniarin and coumarin in leaves of *P. mahaleb* to be equivalent to 2.5 and 5.2 mmol·kg^{-1} (fresh mass basis), respectively, indicating sufficient coumarins present in leaf tissue of *P. mahaleb* to deter beetle feeding. Prior reports of coumarins in the foliage of *P. pensylvanica* (Santamour and Riedel, 1994) and the levels of cyanide potential measured in this study suggest that both types of compounds may be involved in the resistance of this plant to Japanese beetles.

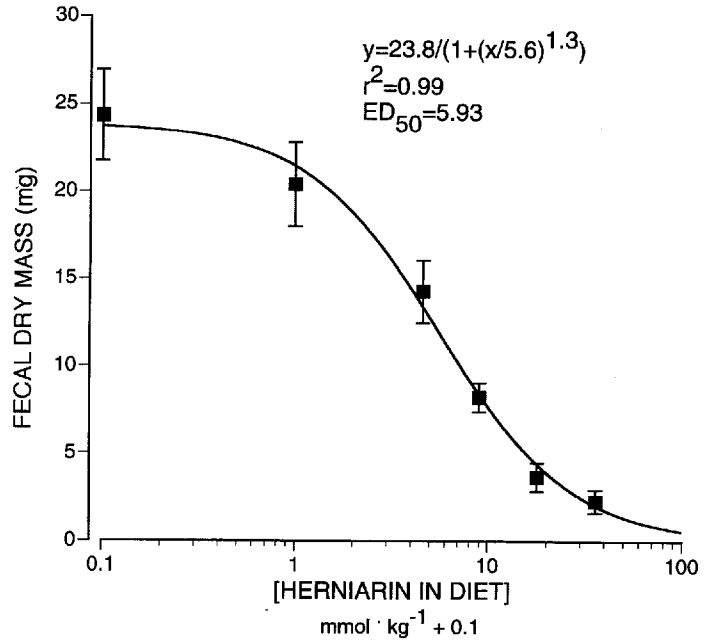

Fig. 3. Feeding intensity (fecal dry mass) as a function of herniarin content in an artificial diet. Each symbol represents a mean of 10 observations.

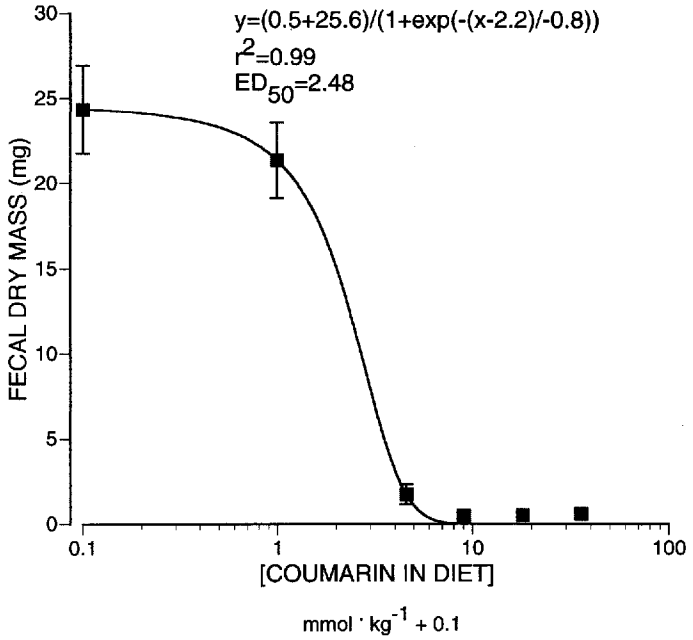

Fig. 4. Feeding intensity (fecal dry mass) as a function of coumarin content in an artificial diet. Each symbol represents a mean of 10 observations.

Data herein indicate that *P. ×yedoensis* and *P. mahaleb* would be good candidates for further study and possible inclusion in plant improvement programs directed at landscape and tree fruit production. *Prunus ×yedoensis* was unusual in that it was the only taxon in the subgenus *Cerasus* tested that had considerable cyanide potential. A hybrid of unknown origin, *P. ×yedoensis* is sexually compatible with most other flowering cherries. Additional study of this taxa and others in the subgenus *Cerasus* could lead to discovery of genotypes with greater cyanide potential that subsequently could be used in a breeding program to enhance host plant resistance. *Prunus mahaleb*, a common cherry rootstock, is also a member of the subgenus *Cerasus*, which includes many other flowering cherries, suggesting the potential for hybridization. Perry (1987) reported the existence of hybrids of *P. avium* x *P. mahaleb* for use as clonal rootstocks. Increased study of *P. mahaleb* hybrids to determine the inheritance of coumarins could lead to more naturally pest-resistant plants. Taxa in the subgenera *Padus* (*P. serotina, P. padus, P. virginiana*) and *Laurocerasus* (*P. laurocerasus*) were found to be resistant to beetle feeding and had high cyanide potential. Unfortunately, sexual incompatibility with *Prunus* in other subgenera may limit their use in conventional breeding and improvement programs (Layne and Sherman, 1986).

Our research demonstrated a wide range of host plant resistance to feeding by adult Japanese beetles and further indicated that prunasin, herniarin, and coumarin are important factors in host-plant resistance to this pest. Selection and development of taxa with enhanced concentrations of prunasin and/or coumarins may yield more pest resistant plants. Further work is warranted to screen additional taxa for cyanide potential and coumarin compounds to identify plants that could be used in selection and improvement programs. Alternatives to chemical control of insect pests are becoming increasingly desirable. Using landscape plants such as *P. padus, P. laurocerasus, P. virginiana, P. ×yedoensis, P. mahaleb*, and *P. besseyi* with natural resistance to Japanese beetle will lessen the need for chemical control measures.

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