

Host tree resistance against the polyphagous wood-boring beetle *Anoplophora glabripennis*

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Abstract

Anoplophora glabripennis (Motschulsky) (Coleoptera: Cerambycidae: Lamiini) is an invasive wood-boring beetle with an unusually broad host range and a proven ability to increase its host range as it colonizes new areas and encounters new tree species. The beetle is native to eastern Asia and has become an invasive pest in North America and Europe, stimulating interest in delineating host and non-host tree species more clearly. When offered a choice among four species of living trees in a greenhouse, adult *A. glabripennis* fed more on golden-rain tree (*Koelreuteria paniculata* Laxmann) and river birch (*Betula nigra* L.) than on London planetree (*Platanus × acerifolia* (Aiton) Willdenow) or callery pear (*Pyrus calleryana* Decaisne). Oviposition rate was highest in golden-rain tree, but larval mortality was also high and larval growth was slowest in this tree species. Oviposition rate was lowest in callery pear, and larvae failed to survive in this tree species, whether they eclosed from eggs laid in the trees or were manually inserted into the trees. Adult beetles feeding on callery pear had a reduced longevity and females feeding only on callery pear failed to develop any eggs. The resistance of golden-rain tree against the larvae appears to operate primarily through the physical mechanism of abundant sap flow. The resistance of callery pear against both larvae and adults appears to operate through the chemical composition of the tree, which may include compounds that are toxic or which otherwise interfere with normal growth and development of the beetle. Unlike river birch or London planetree, both golden-rain tree and callery pear are present in the native range of *A. glabripennis* and may therefore have developed resistance to the beetle by virtue of exposure to attack during their evolutionary history.

Introduction

Plants have evolved a variety of strategies for defending themselves against herbivores, including escape in time or space, tolerance or accommodation by replacing or repairing damaged parts, confrontation or active defense using physical or chemical barriers, and specialized biological associations (Harris & Frederiksen, 1984). Painter (1958) proposed three general mechanisms of plant resistance to insects, which have become widely accepted by entomologists: non-preference or, more properly, antixenosis (Kogan & Ortman, 1978), tolerance, and antibiosis. Antixenosis may be considered a form of escape wherein the plant lacks certain qualities necessary for recognition by the insect as a potential host. Antibiosis

encompasses more direct physical and chemical defenses, which may be categorized as either constitutive, in which structures and compounds that confer resistance are routinely incorporated into a plant's tissues as it grows, or induced, in which structures or compounds are produced in response to attack (Berryman, 1988). Because trees are very long-lived plants that must survive for a considerable period of time before they begin to reproduce, they might be expected to accumulate constitutive defenses for general protection, and also to develop additional inducible defenses against pests that are life-threatening.

Anoplophora glabripennis (Motschulsky) (Coleoptera: Cerambycidae: Lamiini) is a wood-boring beetle that is native to eastern China and Korea (Lingafelter & Hoebeke, 2002) and has become an invasive pest in other parts of the world. It has been found infesting urban shade trees in North America in New York, Chicago, and Jersey City, USA (Haack, 2003), and in Europe in Braunau, Austria

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(Tomiczek, 2003). Adults undergo a 1 to 2-week period of maturation feeding on foliage and the tender bark of twigs of host trees before beginning to reproduce (Keena, 2002; Smith et al., 2002). Females then chew slits or holes through the bark of host trees and lay their eggs under the bark. Only a single egg is laid in each oviposition site (Lingafelter & Hoebeke, 2002), and females often chew many potential oviposition sites that they do not ultimately use for oviposition (Keena, 2002). Larvae feed in the cambium during their first few stadia and then bore into the wood, where they continue to feed, eventually forming a pupal chamber. Larval boring produces structural weakness and disrupts the flow of water and nutrients within host trees, leading to the death of branches and ultimately whole trees.

Anoplophora glabripennis is unusually polyphagous for a wood-boring insect that attacks living hosts; most such insects are specialized in dealing with the defenses of a relatively narrow range of host species (Haack & Slansky, 1987). Known hosts in China include species of *Acer*, *Alnus*, *Betula*, *Elaeagnus*, *Fraxinus*, *Malus*, *Platanus*, *Populus*, *Pyrus*, *Robinia*, *Salix*, *Sophora*, *Tilia*, and *Ulmus* (Nowak et al., 2001). In the USA, *A. glabripennis* has completed development on species in the genera *Acer*, *Betula*, *Fraxinus*, *Pyrus*, *Robinia*, *Salix*, and *Ulmus*, but also in species of *Aesculus*, *Albizia*, *Hibiscus*, and *Prunus* (Nowak et al., 2001), indicating that this beetle is expanding its host range as it invades new areas and encounters new potential host species. Furthermore, *A. glabripennis* can successfully attack apparently healthy host trees (Haack et al., 1997 and pers. obs.), unlike many wood-boring cerambycids that rely on the compromised defenses of stressed hosts to allow for larval establishment (Hanks, 1999).

With the possible exception of antibiosis, most host plant defensive strategies are unlikely to be effective against *A. glabripennis*. Escape in time or space is only effective when close synchronization of host and herbivore phenology is crucial, or for annual plants that can grow in different locations each year. Tolerance is not a viable option because the extensive disruption of water and nutrient transport by phloem/xylem feeders such as *A. glabripennis* usually results in the death of the host tree. Therefore, if a tree cannot escape attack through antixenosis, which would seem to be limited by the unusually broad host range of *A. glabripennis*, it must have effective constitutive and/or inducible defenses (antibiosis). Moreover, the intimate association of phloem/xylem feeders with their hosts, and their complete inability to disperse except as adults, provides the host tree with greater opportunities to mount an effective defense (Mattson et al., 1988).

We evaluated the oviposition preferences of adult *A. glabripennis* offered a choice of four different tree species, and the performance of the resulting larvae, using

living trees in a greenhouse. The tree species selected for this study, river birch (*Betula nigra* L.), golden-rain tree (*Koelreuteria paniculata* Laxmann), London planetree (*Platanus × acerifolia* (Aiton) Willdenow), and callery pear (*Pyrus calleryana* Decaisne), are all common landscape trees that are commercially available for planting throughout North America; London planetree is also widely planted in Europe. These four tree species originated from different natural ranges, two within and two outside the native range of *A. glabripennis*. River birch is native to eastern North America and London planetree originated in London as a hybrid between the American planetree (*P. occidentalis* L.) and the Oriental planetree (*P. orientalis* L.); golden-rain tree and callery pear are both native to China and Korea (Dirr, 1990). None of these tree species have been reported as hosts for *A. glabripennis*, although three of the four species belong to genera that include known host species (golden-rain tree does not). Tree species from outside the native range of *A. glabripennis* may not be known as hosts simply because they have not yet been exposed to the beetle; species from within the native range of *A. glabripennis* which are not known as hosts may in fact be resistant to the beetle. We present evidence for antibiosis in golden-rain tree against larvae only, and in callery pear against both larvae and adults of *A. glabripennis*.

Materials and methods

Production of beetles and trees

Adults and larvae of *A. glabripennis* were obtained from a research colony of mixed ancestry maintained under quarantine conditions at The Pennsylvania State University (PSU). The colony was established with larvae from the United States Department of Agriculture (USDA) quarantine colony maintained at Cornell University, which was originally established with stock from China, and later augmented with stock from the infestations in New York and Chicago. The PSU colony has since been augmented with larvae from the USDA Forest Service quarantine colony maintained in Ansonia, Connecticut, which also contains stock originating from China, as well as from the infestations in the USA. Larvae were reared on a cellulose-based artificial diet, and the colony was maintained according to procedures described by Dubois et al. (2002) using Norway maple (*Acer platanoides* L.) for adult feeding and oviposition.

Nursery liners of each tree species used in experiments were obtained from J. Frank Schmidt and Sons (Boring, OR, USA) and Carlton Plants LLC (Dayton, OR, USA), planted in 76-l (#20) nursery containers filled with Fafard 52 pine bark medium (Fafard Inc., Agawam, MA, USA), and grown in an outdoor pot-in-pot nursery. Trees were moved

into a greenhouse as necessary to allow for acclimation to greenhouse conditions (several months in winter, a few weeks in summer) prior to the initiation of experiments. The trees were 4–5 years old at the time of the experiments.

Adult longevity and oviposition preferences on four different tree species

The oviposition preferences of *A. glabripennis* offered a choice of river birch, golden-rain tree, London planetree, and callery pear, and performance of the resulting larvae were evaluated using living trees. Two trees of each species were placed in each of four large (ca. 3 m high, 3 m long, 2 m wide) walk-in insect cages within a quarantine greenhouse. Trees were pruned to approximately 2 m in height so as to fit within the cages. Tree species were arranged in an alternating pattern that was rotated such that trees of a given species were in different positions in each cage. The trees were watered twice daily for 10 min via an automatic drip irrigation system. Two to three-day-old adult beetles were placed individually into 1.14 l glass jars with screened lids for 2–3 weeks of maturation feeding before being used in the experiment. For maturation feeding, each beetle was provided with twigs (without foliage) from all four of the tree species included in the experiment, collected from the trees that were to be used in the experiment. After maturation feeding, three male-female pairs of beetles were released in the center of each cage and each beetle in a given cage was marked with a different color of fingernail polish on the pronotum for individual identification. Beetles were observed three or four times daily throughout the experiment and the location of each beetle was recorded at each observation. Beetles that died were replaced, and all beetles were removed from the cages after 30 days (28 May 2002–27 June 2002).

After removal of the beetles, the trunk diameter of each tree was recorded at 15 cm above soil level, and each tree was examined for feeding damage and potential oviposition sites. Because the beetles feed on both bark and foliage, and often chew through leaf petioles and girdle small branches leading to desiccation and losses of foliage and twigs, feeding damage could not be quantified but was ranked based on visual inspection. The trees were held in the greenhouse for 90 days after the adult beetles had been removed to allow for egg hatch and larval establishment. Each tree was then dissected, and the numbers of living and dead larvae, and the mass of each living larva were recorded. Considering the long life cycle of these insects, and the constraints on time and space for our experiments, no attempt was made to rear larvae through to maturity in the trees.

For a provisional assessment of adult survival on each of the four tree species separately, two adult females that had been on twigs (without foliage) of Norway maple for

maturation feeding for 2–3 weeks were transferred onto twigs (without foliage) of each of the four different tree species in the oviposition preference experiment. Twigs were obtained from 'extra' trees maintained in the greenhouse (10 trees of each species had been moved into the greenhouse for acclimation, but only eight of each species were used for the oviposition experiment). This twig-feeding experiment was initiated on 20 June 2002. The beetles were weighed and the twigs replaced weekly, and survival was assessed daily until the last female had died (3 October 2002).

Larval survival on callery pear

Because there was very little oviposition on callery pear (see Results), an additional experiment was conducted to evaluate larval survival in living callery pear trees. First-instar larvae that had been established on artificial diet were inserted into trees using the methods described by Ludwig et al. (2002). Five larvae were inserted into each of four callery pear trees and four sugar maple trees in the quarantine greenhouse on 12 September 2002. The larvae were allowed 4 weeks to become established in the trees before the trees were dissected to determine whether each larva was dead or alive.

Adult longevity and fecundity on callery pear

Adult longevity and fecundity were assessed for female beetles using three of the walk-in cages within the quarantine greenhouse, one cage containing sugar maple trees and two cages containing callery pear trees. For maturation feeding, beetles were provided with either sugar maple twigs before being placed on either sugar maple or callery pear trees, or provided with callery pear twigs before being placed on callery pear trees. Initially, two male-female pairs of beetles were released into each cage. Females that died were replaced when additional females became available; males were replaced or moved to different cages as required, to ensure that all females had access to mates. The experiment was conducted from 27 September 2002 to 18 November 2002, being terminated when the trees in each cage had been exposed to 75 female beetle-days. Females that died, as well as those removed at the end of the experiment, were dissected to determine egg load. Shortly after removal of the adult beetles, the trees were assessed for numbers of potential oviposition sites and numbers of eggs laid.

Statistical analyses

Trunk diameter at 15 cm and the mean mass of living *A. glabripennis* larvae were each compared among the tree species by single-factor analysis of variance (ANOVA) followed by Tukey's multiple comparison test. Because

Table 1 Oviposition by *Anoplophora glabripennis* offered a choice of four tree species (n = 8 per species) under greenhouse conditions

Tree species	Trunk diameter (mm) at 15 cm above soil (mean $\pm$ SE)	Trees (%) with oviposition sites	Oviposition sites (total)	Oviposition sites per tree (range)
Golden-rain tree	40.9 $\pm$ 0.6 ab	100	366	17–95 a
River birch	35.2 $\pm$ 0.5 c	100	83	2–27 ab
London planetree	37.5 $\pm$ 1.1 bc	88	139	0–75 b
Callery pear	43.9 $\pm$ 0.6 a	88	29	0–10 b

Differences among tree species are not statistically significant for mean trunk diameter (Tukey test, $P > 0.05$) or numbers of oviposition sites per tree (Nemenyi test, $P > 0.05$) followed by the same letter.

the numbers of oviposition sites and living larvae per tree showed severe deviations from normality and homoscedasticity, Friedman's non-parametric analysis of variance by ranks, followed by the Nemenyi non-parametric multiple comparison test was used to evaluate differences between tree species for these parameters. A single-factor ANOVA was used to test for differences in longevity among females held on twigs of the four different tree species. Fisher's exact test was used to compare the proportion of larvae surviving in callery pear trees to that in sugar maple trees. All statistical analyses were conducted as described by Zar (1999).

Results

Adult *A. glabripennis* showed clear preferences for certain tree species, but they also tended to favor trees around the outside edges of the cages with maximum exposure to ambient light, resulting in high variability in the frequency of beetle observations on different trees of a given species. This positional effect was taken into account by the placement of trees of a given species in different positions in each cage, and by considering each group of four trees as a separate replicate for statistical analyses of numbers of oviposition sites and larvae per tree. Numbers of oviposition sites per tree were significantly greater for golden-rain tree than for London planetree or callery pear [$(\chi^2)_c = 16.350$, d.f. = 4,8, $P < 0.001$], with river birch intermediate (Table 1). Adult feeding damage was most extensive on golden-rain tree, followed closely by river birch, with relatively little feeding damage on London planetree or callery pear, although some feeding was evident on both of the latter two species. Overall, adult feeding preferences were ranked as golden-rain tree > river birch >> London planetree > callery pear.

During the oviposition preference experiment, more than half of the beetles of each sex died and had to be replaced, and even some of the replacement beetles died before the end of the 30-day period. The cause of this

mortality was not apparent. Autopsies showed no signs of pathogens, but did reveal evidence of malnourishment, including empty guts, very little fat body, and very few developing eggs compared to beetles feeding on twigs of Norway maple in the rearing colony. Except for beetles transferred to callery pear, the mass of females transferred from twigs of Norway maple to the twigs of one of the tree species from the oviposition experiment initially increased and then remained remarkably constant in most cases, before declining in the week or two before each beetle died (Figure 1). Beetles transferred to callery pear failed to increase in mass and also had the shortest longevity, although the differences in longevity were not statistically significant ($F_{3,4} = 5.06$, $0.05 < P < 0.10$) due to the small numbers of beetles available for that experiment.

Similar numbers of living larvae per tree were found in each tree species, with the notable exception of callery pear [$(\chi^2)_c = 18.774$, d.f. = 4,8, $P < 0.001$], in which no living larvae were found (Table 2). Absolute survival rates were not determined because the numbers of eggs laid or hatched could not be counted without destructive sampling, which would have prevented the evaluation of larval establishment and growth. Despite this limitation, considerable numbers of dead larvae were only found in golden-rain tree, and most of them had evidently drowned in sap, which was exuded abundantly at sites of injury, including sites of adult feeding damage, and became quite solid as it dried outside the bark. In addition, the mean mass of living larvae was lowest for golden-rain tree, with significant differences ($F_{2,94} = 96.71$, $P < 0.0005$) among all three tree species in which living larvae were found (Table 2).

Callery pear had adverse effects on both the survival and fecundity of adult female beetles, as well as on survival of larvae. Only 6% (n = 18) of the larvae inserted into callery pear trees were still alive after 4 weeks, compared to 78% (n = 18) of the larvae inserted into sugar maple trees, a highly significant difference (Fisher's exact test, $P = 0.00001$). The two adult females that were released on sugar maple trees after maturation feeding on sugar maple twigs were

Table 2 Larval performance of *Anoplophora glabripennis* in each of four tree species (n = 8 per species) under greenhouse conditions

Tree species	Living larvae per tree (range)	Larvae found dead (total)	Larval mass (g) [mean $\pm$ SE (n)]
Golden-rain tree	0–20 a	19	0.08 $\pm$ 0.01 (55) c
River birch	0–6 a	0	0.74 $\pm$ 0.09 (21) a
London planetree	0–10 ab	0	0.14 $\pm$ 0.02 (21) b
Callery pear	0–0 b	2	n/a

Differences among tree species are not statistically significant for numbers of living larvae (Nemenyi test, $P > 0.05$) or mean larval mass (Tukey test, $P > 0.05$) followed by the same letter.

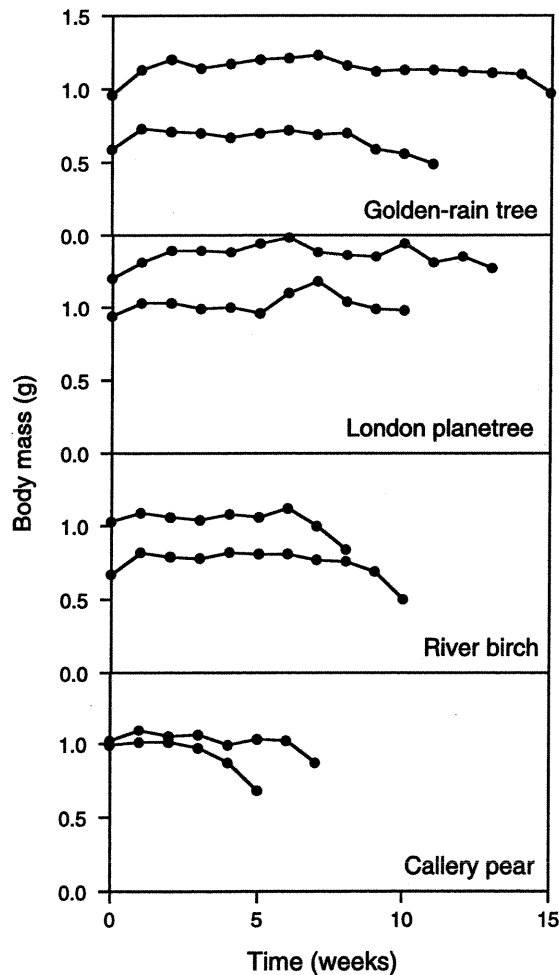


Figure 1 Mass of individual adult female *Anoplophora glabripennis* after transferral from twigs of Norway maple to twigs of one of four different tree species.

removed after 37 and 38 days, at which time they were 54 and 59 days old; these beetles were killed and found to contain 29 and 7 eggs, respectively. Of the females released on callery pear trees after maturation feeding on sugar maple twigs, two died when they were 32 and 46 days old

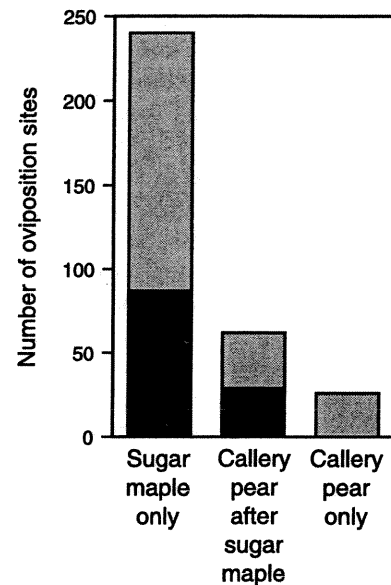


Figure 2 Total numbers of potential oviposition sites and eggs laid by female *Anoplophora glabripennis* on sugar maple or callery pear trees after maturation feeding on either sugar maple or callery pear twigs. The solid portion of each column represents the number of oviposition sites in which eggs were laid.

and were found to contain 8 and 0 eggs, respectively. The two females that replaced them were removed when they were 34 and 32 days old and were found to contain 1 and 13 eggs, respectively. Of the females released on callery pear trees after maturation feeding on callery pear twigs, four died at ages ranging from 25 to 39 days and the final two replacement beetles were removed when they were 13 and 25 days old. None of these six beetles were found to contain any eggs. Although these females chewed a few potential oviposition sites in the bark of the callery pear trees, none of the oviposition sites contained an egg. In contrast, females that were given sugar maple twigs for maturation feeding did lay eggs in callery pear trees, but in smaller numbers than females that were maintained on sugar maple (Figure 2).

Discussion

We have demonstrated clear differences in the preference of adult *A. glabripennis* for different tree species (Morewood et al., 2003; this study), and have found evidence of resistance to the beetle in two species of common landscape trees, namely golden-rain tree and callery pear. Both of these tree species are native to China and Korea (Dirr, 1990) where they may have been exposed to attack by *A. glabripennis* during their evolutionary history. Interestingly, the preferences shown by adult beetles do not necessarily reflect the relative suitability of the host trees for development of their progeny. In particular, adults showed the strongest preference for oviposition in golden-rain tree, but their progeny showed the highest mortality and lowest growth rates in this tree species. It remains to be determined whether *A. glabripennis* larvae can complete development in golden-rain tree, but currently available information suggests that the apparent preference of *A. glabripennis* adults for this tree species should have been selected against. On the other hand, we recognize that the confines of the cages may have influenced the results of our study, particularly with respect to the apparent preferences of adults offered a limited number of choices. However, even if confinement within a cage caused the beetles to attack trees that they would normally ignore in the field, such results would contribute to a conservative approach in surveying for signs of infestation and in selecting trees for future planting. Such information is critical to ongoing efforts to eradicate this invasive species, and we plan to confirm whether or not golden-rain trees can support the complete development of *A. glabripennis*.

Adult feeding and oviposition on all four of the tree species tested indicate that antixenosis does not occur in these trees with respect to attack by *A. glabripennis*; however, the occurrence of antibiosis soon became apparent through the extensive premature mortality of adult beetles. In contrast, in a previous experiment conducted under the same conditions, but with different tree species (Morewood et al., 2003), a few males died prematurely but all of the females survived the 30-day experimental period and most lived for several weeks after being removed from the trees and returned to the rearing colony. Although too few beetles were available for the adult twig-feeding experiment in this study to produce statistical significance, the results pointed to callery pear as the most likely cause of adult mortality. This was further supported by the observation that no larvae survived in callery pear, even though eggs laid in callery pear did hatch and the neonates began to feed and construct galleries.

Antibiosis against *A. glabripennis* is constitutive in both golden-rain tree and callery pear, but operates through

very different mechanisms with different effects. Although it does not become apparent until an attack is initiated, 'pitching out' a wood-boring insect with a strong flow of resinous sap is considered a constitutive defense because the sap and component resins must be produced prior to the initiation of attack so that they can be immediately mobilized (Christiansen et al., 1987). This is primarily a physical defense mechanism, either smothering the attacking insect or forcibly removing it from the tree, although the resins may also have toxic effects, at least in conifers. The reduced longevity of adults on cut twigs indicates that the antibiosis is a result of the constitutive chemical composition of callery pear bark and/or wood, rather than an induced response of living trees. Unlike golden-rain tree, callery pear affects the survival of both larvae and adults, and further prevents adult females from developing any eggs. Such effects may be caused by the presence of toxins, antinutritive compounds, or inhibitors of growth or reproduction, a lack or deficiency of a key nutrient, or an imbalance in essential nutrients (Painter, 1966).

To our knowledge, the only previous studies of host tree resistance to a wood-boring cerambycid beetle are those of Hanks et al. (1991, 1995, 1999) on the eucalyptus longhorned borer [*Phoracantha semipunctata* (Fabricius)] introduced into California. A key characteristic conferring resistance to that beetle in *Eucalyptus* trees was a high water content of the outer bark, which prevented establishment of first-instar larvae (Hanks et al., 1991, 1999). Different individuals and species of *Eucalyptus* varied in their level of resistance to the beetle according to their irrigation status and inherent drought tolerance, respectively (Hanks et al., 1995). Those results led to recommendations for planting resistant species of *Eucalyptus* and for minimizing the vulnerability of susceptible species through adequate irrigation (Paine et al., 1995).

Currently, the only viable option for control of *A. glabripennis* is the removal of infested trees. Direct control with chemical or microbial insecticides is problematic because the adults are mobile and long-lived, and the immature stages live entirely within their host trees and are thus protected from exposure to pesticides. Biological control agents are being sought and evaluated, but few have been found and none are yet available for use (Smith et al., 2003). Host tree resistance represents a promising strategy that offers the potential for reducing the impacts of current and future infestations of *A. glabripennis*. Resistant trees could be used to restock areas where infested trees have been removed, as well as to minimize the probability of establishment of *A. glabripennis* in areas with a high risk of infestation.

We plan to further investigate the antibiosis of both golden-rain tree and callery pear against *A. glabripennis*. If

golden-rain tree proves to be unsuitable for complete larval development, this species might be used as a 'trap tree' to attract adults and prevent their successful reproduction. Our studies of callery pear to date have only involved the 'Aristocrat' cultivar, which was selected because its growth form and branch angles make it much more resistant to storm damage than other cultivars (Hensley et al., 1991; Kuser et al., 2001). We hypothesize that other cultivars of callery pear may also show antibiosis against *A. glabripennis*, but other species of pear may not, considering that *Pyrus* (species not indicated, but possibly *P. communis* L.) has been reported as a host of *A. glabripennis* (Nowak et al., 2001; Lingafelter & Hoebeke, 2002). Once the biochemical basis for antibiosis of callery pear against *A. glabripennis* has been elucidated, the compounds involved might be manipulated to help protect more vulnerable trees from this invasive pest.

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