POPULATION ECOLOGY

Oviposition Preference and Larval Performance of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in Four Eastern North American Hardwood Tree Species

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ABSTRACT *Anoplophora glabripennis* (Motschulsky) is an invasive wood-boring cerambycid beetle that kills hardwood trees. The host range of this species is unusually broad but is not well defined in the available literature and may include tree species that have not been reported as hosts because they have not previously been exposed to the beetle. We evaluated oviposition by *A. glabripennis* offered a choice of four common eastern North American forest and landscape hardwood tree species, and performance of the resulting larvae, under greenhouse conditions. Significantly greater numbers of oviposition sites were found on sugar maple, *Acer saccharum* Marshall, than on red maple, *Acer rubrum* L., green ash, *Fraxinus pennsylvanica* Marshall, or red oak, *Quercus rubra* L., with no significant differences among the other three tree species. Similarly, significantly greater numbers of living larvae were found in sugar maple than in the other tree species; however, more were found in red oak and fewer in green ash than expected, considering relative numbers of oviposition sites. After 90 d, mean mass of living larvae did not differ significantly among tree species. These results suggest that all four tree species may be suitable hosts for *A. glabripennis*. Most importantly, although larval establishment was poor in green ash and larval growth may have been retarded in red oak, larvae did survive and grow in both species. We recommend that these tree species be considered potential hosts when surveys are conducted to detect infested trees or when replanting infested areas.

KEY WORDS Cerambycidae, *Anoplophora glabripennis*, invasive species, oviposition preference, host suitability

ANOPLOPHORA GLABRIPENNIS (MOTSCHULSKY) is a wood-boring cerambycid beetle that is native to eastern China and Korea (Lingafelter and Hoebeke 2002) and was introduced into the United States in solid wood packing material (Haack et al. 1997). It was first discovered in North America infesting urban shade trees in New York in 1996 (Haack et al. 1997), then in Chicago in 1998 (Smith 2000), and in Jersey City in 2002 (NYT 2002). Larvae of this species feed under the bark and in the wood of a wide variety of hardwood tree species, killing branches and, eventually, whole trees. Losses of up to 1.2 billion urban shade trees, with a compensatory value of $669 billion, have been estimated if *A. glabripennis* becomes established and spreads across the United States (Nowak et al. 2001). This does not include associated losses such as degraded esthetics and lowered property values, nor does it include the even greater threat to the extensive American hardwood forests that support large lumber, maple sugar, and fall foliage tourism industries.

In most respects, oviposition biology and larval feeding behavior of *A. glabripennis* are consistent with what is known about other members of the cerambycid subfamily Lamiinae (Linsley 1961, Hanks 1999). After emerging, adults undergo a period of maturation feeding on foliage and the tender bark of twigs of host trees before beginning to reproduce; in *A. glabripennis*, this preovipositional period is typically 1–2 wk (Keena 2002, Smith et al. 2002). Members of the Lamiinae are distinctively hypognathous, which facilitates their unique oviposition behavior of chewing slits or holes through the bark of host trees to lay eggs under the bark (Hanks 1999). Only a single egg is laid in each oviposition site by *A. glabripennis* (Lingafelter and Hoebeke 2002), and females often chew many potential oviposition sites that they do not ultimately use for oviposition (Keena 2002). The upper trunk and major branches, where the bark is relatively thin and smooth, are reportedly favored by *A. glabripennis* for oviposition, but females will oviposit all along the trunk and even into exposed roots as the crown dies back because of girdling by boring larvae (Haack et al. 1997, Lingafelter and Hoebeke 2002). Larvae feed in the cambium during their first few stadia and then bore into the wood, where they continue to feed and eventually form a pupal chamber. Young and old trees are

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attacked indiscriminately (Haack et al. 1997, Lingafelter and Hoebeke 2002) and the beetles may complete their development in host material as small as 2 cm in diameter (this study and other unpublished data).

A. glabripennis is unusually polyphagous for a wood-boring insect that attacks living hosts. In general, polyphagy in herbivorous insects is not common (Bernays and Chapman 1994) and, because their intimate contact with the host makes them especially vulnerable to host defenses, insects that bore into living hosts tend to specialize on a narrow range of host species (Haack and Slansky 1987). Known hosts for *A. glabripennis* in China include species in the genera *Acer, Alnus, Betula, Elaeagnus, Fraxinus, Malus, Platanus, Populus, Pyrus, Robinia, Salix, Sophora, Tilia,* and *Ulmus;* in the United States, *A. glabripennis* has been found to complete development on species in the genera *Acer, Aesculus, Albizia, Betula, Fraxinus, Hibiscus, Prunus, Pyrus, Robinia, Salix,* and *Ulmus* (Nowak et al. 2001). Published reports listing particular host species within these genera are not widely available, however, and additional species and genera that have not been previously exposed to *A. glabripennis* may prove to be suitable hosts as the beetle invades new areas.

To date, the primary strategy for control of *A. glabripennis* has been identification and removal of infested trees, with the U.S. federal government, New York, and Illinois spending $2.4 billion on this effort (Stewart 2002). Treated areas have been replanted with tree species not known to be hosts for *A. glabripennis* (Haack et al. 1997). To better understand the potential for *A. glabripennis* to colonize North America, as well as to help maximize the efficiency of the eradication effort, broader and more precise information is required about host preferences and suitability. Different species within known host genera must be evaluated, as well as species not reported as hosts. Efforts to evaluate tree species as hosts for *A. glabripennis* have been extremely limited to date because any studies conducted in North America require strict quarantine conditions. Oviposition preferences have so far been evaluated only on cut logs in no-choice experiments (Ludwig et al. 2002, Smith et al. 2002).

The objective for this study was to evaluate oviposition preferences of *A. glabripennis* offered a choice of four tree species, and performance of any resulting larvae, using living trees. The tree species evaluated are all common landscape and forest trees in eastern North America and include one species known to be a preferred host (sugar maple, *Acer saccharum* Marshall) (Haack et al. 1997); one species known to be an acceptable host (red maple, *Acer rubrum* L.) (Smith et al. 2002); one species known to be attacked but apparently less suitable for larval development (green ash, *Fraxinus pennsylvanica* Marshall) (Ludwig et al. 2002); and one species from a genus not known to include any hosts for *A. glabripennis* in North America or in China (red oak, *Quercus rubra* L.) (Haack et al. 1997, Nowak et al. 2001).

Materials and Methods

Adult beetles 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 New York and Chicago infestations. The PSU colony has since been augmented with larvae from the USDA Forest Service quarantine colony maintained in Ansonia, CT, which also contains stock originating from China as well as from the U.S. infestations. Voucher specimens of adult males and females have been placed in the Frost Entomological Museum at PSU.

Larvae were reared on a cellulose-based artificial diet and the colony was maintained according to procedures described by Dubois et al. (2002). Two- to three-day-old adult beetles were placed individually into 1.14-liter (1-quart) glass jars with perforated metal lids for 1–2 wk of maturation feeding before being used in the experiment. For maturation feeding, each beetle was provided with twigs from all four of the tree species included in the experiment.

Nursery liners of each tree species were planted in #20 plastic pots filled with Fafard 52 pine bark medium (Fafard Inc., Agawam, MA) and grown in an outdoor pot-in-pot nursery. Trees were moved into a greenhouse six months before the initiation of the experiment to allow for acclimation to greenhouse conditions. The oviposition preference experiment was conducted in a quarantine greenhouse using four large ($\approx$3 m high × 3 m long × 2 m wide) walk-in insect cages. Two trees of each species were placed in each cage and arranged in an alternating pattern (Fig. 1). Three male-female pairs of beetles were released in the center of each cage as adults became available, with each cage receiving one pair of beetles before any cage received a second pair and each cage receiving a second pair before any cage received a third. Each beetle in a cage was marked with a different color of fingernail polish on the elytra or pronotum for individual identification, and each pair of beetles was removed 30 d after being released into the cage. Throughout the experiment beetles were observed three or four times over the course of each day and the location of each beetle recorded at each observation.

After removal of all beetles, trunk diameter of each tree at a standard height of 15 cm above soil level was recorded and each tree was examined for feeding damage and potential oviposition sites (described and illustrated under Results). Because of the beetles' habit of chewing through leaf petioles and girdling small branches, leading to desiccation and losses of foliage and twigs, feeding damage was not quantified but was ranked based on visual inspections. For each oviposition site, height above soil level and diameter of the tree trunk at that point were recorded. The trees were held in the greenhouse for 90 d after the adult beetles had been removed to allow for egg hatch and

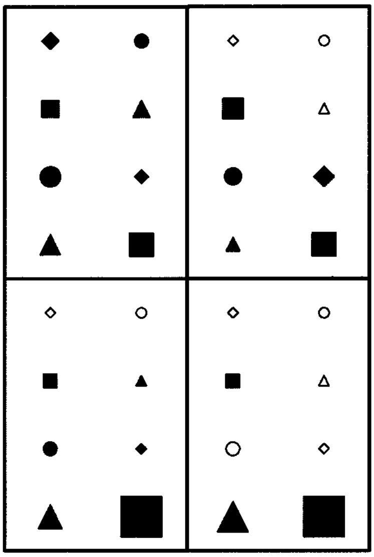

Fig. 1. Arrangement of trees within four walk-in cages in the quarantine greenhouse. Squares represent sugar maple, triangles represent red maple, diamonds represent green ash, and circles represent red oak. The size of the symbol for each tree is roughly proportional to the number of times *A. glabripennis* adults were observed on that particular tree. Open symbols indicate trees on which no oviposition sites were found. North is toward the upper right corner of the figure.

larval establishment. Then each tree was dissected and the number of living larvae and mass of each living larva were recorded.

Trunk diameter at 15 cm and mean mass of living *A. glabripennis* larvae were each compared among tree species by single-factor analysis of variance (ANOVA). Numbers of oviposition sites and living larvae per tree were each analyzed by two-factor ANOVA, the two factors being tree species and cage, to assess the consistency of the results for the different groups of beetles in the different cages. Chi-square contingency table analysis was used to compare numbers of living larvae among tree species with respect to the numbers of oviposition sites found in each tree species. All statistical analyses were conducted as described by Zar (1999).

Results

Adult *A. glabripennis* showed a distinct tendency to favor trees with maximum exposure to outside light, especially those trees on the southern ends of the cages (Fig. 1), but also showed clear preferences among tree species for feeding and oviposition. Adult feeding damage was most extensive on sugar maple, followed closely by red maple, with relatively little feeding damage on green ash or red oak, but more on red oak than on green ash. Overall, adult feeding preferences were ranked as sugar maple > red maple ≫ red oak > green ash. Numbers of oviposition sites per tree were significantly greater for sugar maple than for the other three tree species ($F = 5.89$; df = 3, 16; $0.005 < P < 0.01$), among which the differences were not statistically significant (Table 1). Differences among cages, representing different groups of beetles, were not statistically significant ($F = 0.29$; df = 3, 16; $P > 0.25$), nor was the interaction between tree species and cage ($F = 0.84$; df = 9, 16; $P > 0.25$). All trees were alive when the beetles were removed.

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

Tree species	Percentage of trees with oviposition sites	Total number of oviposition sites	Mean ± SE (range) oviposition sites per tree[a]
Sugar maple	100	321	40.1 ± 11.0 (16–101)a
Red maple	75	71	8.9 ± 3.8 (0–30)b
Green ash	50	83	10.4 ± 5.8 (0–46)b
Red oak	50	14	1.8 ± 0.8 (0–6)b

[a] Differences among means followed by the same letter are not statistically significant (Tukey test, $P > 0.05$).

Oviposition sites differed markedly in appearance from those usually illustrated for *A. glabripennis* [e.g., Fig. 2a in Lingafelter and Hoebeke (2002)]. Rather than the relatively large, round or oval pits these beetles chew in the thicker bark of older trees, oviposition sites in our young trees consistently took the form of narrow slits, 1–2 mm wide and 5–7 mm long, with their long axis perpendicular to the long axis of the tree trunk (Fig. 2). These slits were either straight or convex downward, always being created by the female in a head down position. Oviposition sites were not distributed evenly along the trunk of a tree but were clustered near the base and within the crown, often around branch points (Fig. 3). No direct relationship was found between trunk diameter and frequency of oviposition sites. Green ash had the largest trunk diameter (47.1 ± 0.6 mm), followed by red oak (37.2 ± 1.0 mm), sugar maple (32.2 ± 1.3 mm), and red maple (21.8 ± 0.7 mm), with each tree species being significantly different from the others ($F = 133.31$; df = 3, 28; $P < 0.0005$; Tukey test, $P < 0.05$).

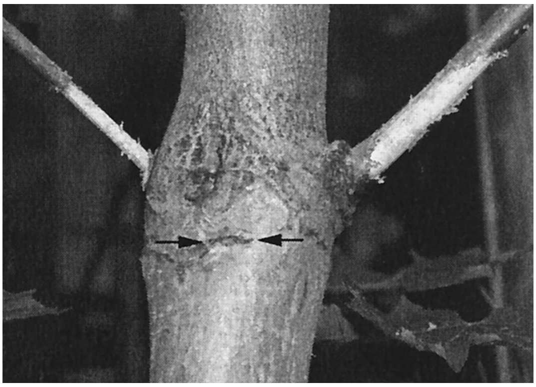

Fig. 2. *A. glabripennis* oviposition site (between arrows) on the trunk of a young sugar maple tree, with adult feeding damage (stripped bark) on adjacent branches.

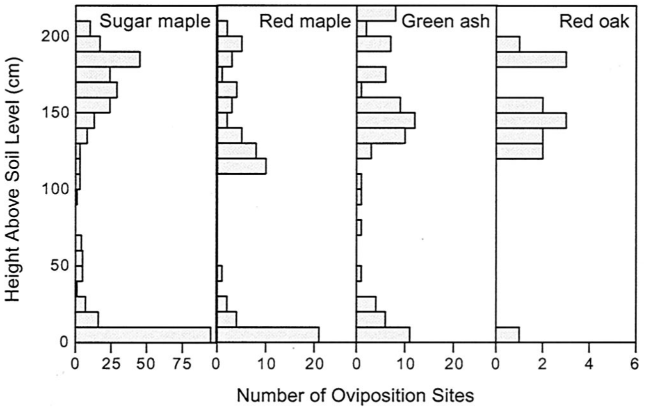

Fig. 3. Frequency distribution for vertical position of *A. glabripennis* oviposition sites in trunks of four different tree species exposed to adult beetles under greenhouse conditions. The main trunk of each tree was little >200 cm in height and there were no branches below 100 cm above the soil level.

Numbers of living larvae per tree were significantly greater for sugar maple than for the other three tree species ($F = 7.92$; df = 3, 16; $0.001 < P < 0.0025$), among which the differences were not statistically significant (Table 2). In addition, one sugar maple contained three individuals that had developed to the pupal stage; however, because pupae of *A. glabripennis* are very delicate (Dubois et al. 2002), they did not survive being extracted from the tree. Differences among cages, representing different groups of parent beetles, in numbers of living larvae per tree were not statistically significant ($F = 1.30$; df = 3, 16; $P > 0.25$), nor was the interaction between tree species and cage ($F = 0.38$; df = 9, 16; $P > 0.25$). The proportion of oviposition sites yielding living larvae varied significantly among tree species ($\chi^2 = 30.412$; df = 3; $P < 0.001$). Specifically, the ratio of living larvae to oviposition sites did not differ significantly between the two maple species ($\chi^2_c = 0.294$; df = 1; $0.50 < P < 0.75$) but did differ significantly for both green ash ($\chi^2_c = 10.476$; df = 1; $0.001 < P < 0.005$) and red oak ($\chi^2_c = 12.154$; df = 1; $P < 0.001$) compared with the maples (Table 2). Absolute survival rates were not determined directly because numbers of eggs laid or hatched cannot be determined without destructive sampling, which would have prevented evaluation of larval establishment and growth. Mean mass of living larvae was lowest for red oak, although the differences among tree species were not statistically significant (Table 2), even when green ash was excluded from the analysis because of the very small sample from that tree species ($F = 2.88$; df = 2, 71; $0.05 < P < 0.10$). By the time the trees were dissected for larval evaluation, one sugar maple tree had been killed by girdling but all other trees were still alive.

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

Tree species	Mean ± SE (range) living larvae per tree[a]	Oviposition sites (%) yielding living larvae[b]	Mean ± SE (n) larval mass in grams[c]
Sugar maple	6.9 ± 1.4 (1–14)a	16.2b	0.32 ± 0.02 (52)
Red maple	1.8 ± 0.9 (0–7)b	19.7b	0.34 ± 0.04 (14)
Green ash	0.2 ± 0.2 (0–2)b	2.4c	0.43 ± 0.05 (2)
Red oak	1.0 ± 0.9 (0–7)b	57.1a	0.16 ± 0.04 (8)

[a] Differences among means followed by the same letter are not statistically significant (Tukey test, $P > 0.05$).

[b] Difference between percentages of oviposition sites with the same letter is not statistically significant (see text for details of analysis).

[c] Differences in mean mass among tree species are not statistically significant ($F = 2.37$; df = 3, 72; $0.05 < P < 0.10$).

Discussion

Our results reconfirm the unusually polyphagous nature of *A. glabripennis* and indicate that the known host range of this beetle may continue to expand as it invades new areas and encounters additional tree species. In particular, oaks are not known hosts for *A. glabripennis* and therefore have been used to replant infested areas in New York (Haack et al. 1997). However, our results show that red oak is acceptable to adults for feeding and oviposition, even in the presence of more preferred hosts, and larvae can become established and survive for at least 90 d. These results corroborate those of Ludwig et al. (2002), where *A. glabripennis* larvae artificially inserted into red oak trees showed survival and growth after 60 or 90 d comparable to those inserted into sugar maple trees. However, another invasive wood-boring cerambycid showed similar larval survival but greatly delayed adult emergence when artificially introduced into logs of novel host species compared with its native host species (Hanks et al. 1995). Because of constraints on time and space, we were unable to rear *A. glabripennis* through complete development in the trees used for this experiment, thus it remains to be determined whether larvae can complete development in red oak.

Insects that have a broadly polyphagous feeding habit may be at an advantage with respect to the availability of suitable food and the ability to find it with little search effort (Bernays and Chapman 1994). This may be particularly true for a temperate-zone insect feeding on hardwood trees that generally occur in mixed forests, the composition of which changes over time. In the case of *A. glabripennis,* a broad host range combined with its propensity to attack trees of almost all ages would place this beetle in a good position to maintain itself in a given area of hardwood forest over the long term, despite changes in age structure and species composition that occur with forest succession. Such characteristics also make this beetle especially dangerous as an invasive species.

Adult beetles showed clear and consistent differences among the different tree species in preference for feeding and oviposition, but these differences did not always reflect the suitability of the trees for development of the beetles' progeny. As expected, sugar maple was most preferred by adults for feeding and oviposition, and the resulting larvae were very successful. Less expected was the beetles' acceptance for oviposition of trees that proved to be suboptimal for larval establishment and growth. Despite relatively large numbers of oviposition sites in green ash, very few larvae became established, although those that did showed growth comparable to larvae in the maples. In contrast, red oak was least preferred for oviposition, but larvae were very successful in establishment and showed considerable growth, although they may not have grown as quickly as larvae in the other tree species.

The principles of natural selection suggest that adults should maximize their fitness by preferentially ovipositing on those hosts on which the performance of their progeny is optimal. However, a large minority (24%) of the published studies that address the relationship between oviposition preference and larval performance fail to support such a prediction (Mayhew 1997). A number of confounding factors have been proposed to account for such discrepancies (Thompson 1988), at least one of which clearly applies to *A. glabripennis* in this instance. Because the tree species tested are native to North America and not to China, there has been little opportunity for natural selection to act against adults ovipositing on unsuitable hosts or to improve the performance of larvae that find themselves in suboptimal hosts. Even in its native China, the broad host range of *A. glabripennis* might produce inconsistency in natural selection for any particular host and thus, prevent directional selection for a strong relationship between oviposition preference and larval performance (Thompson 1988). To our knowledge, only one previous study has examined the relationship between oviposition preference and larval performance in a wood-boring cerambycid beetle. In that case, ovipositing adults preferentially selected the host species that produced the highest larval survivorship under experimental conditions, but under field conditions this preference resulted in lower larval survivorship because of severe competition among high numbers of larvae (Hanks et al. 1993).

Oviposition preferences based on tree species clearly outweighed any affect of tree size, with both the most preferred and the least preferred species being intermediate in terms of trunk diameter. However, the relatively low rate of oviposition on red maple compared with sugar maple may be due in part to the very small size of the red maple trees. With a trunk diameter averaging little >2 cm near the base, the red maples might have been close to a threshold below which they would be simply too small to support complete development of these large beetles, and natural selection should favor those beetles that recognize and avoid such inadequate hosts for oviposition.

The distinctly bimodal distribution of oviposition sites within trees was unexpected, considering what is known about oviposition by other wood-boring lamiine cerambycids. Coniferophagous species such as *Monochamus scutellatus* (Say) prefer larger-diameter hosts, or the largest-diameter portion of a given host, for oviposition (Hughes and Hughes 1982, 1987), which would provide the most resources for developing progeny. In contrast, many lamiine species that attack hardwoods prefer smaller trees, no >20 cm in diameter and often much less (Brooks 1923; Solomon 1968, 1972, 1974; Nord et al. 1972a, b), which may help to minimize the energy they expend chewing oviposition sites through the thinner bark of younger trees. Both young and old trees are attacked by *A. glabripennis,* and this species is known to favor areas where the bark is relatively thin and smooth for oviposition on older trees (Haack et al. 1997, Lingafelter and Hoebeke 2002). However, the consistency of the bark was quite uniform, unlike the distribution of oviposition sites, in the young trees used for our study.

Ludwig et al. (2002) found evidence that larval survival was inversely correlated with tree diameter and directly correlated with height in the tree, but could not determine which factor might be responsible because height and diameter are highly correlated with each other. In our study there was no evidence of any relationship between oviposition and trunk diameter except that produced by the bimodal distribution of oviposition sites with respect to height on the trunk. Some wood-boring Lamiinae, including the closely-related *Anoplophora chinensis* (Forster) [= *A. malasiaca* (Thomson); (Lingafelter and Hoebeke 2002)], attack almost exclusively near the base of the trunk (Ritchie 1920, Brooks 1923, Lieu 1945, Adachi and Korenaga 1989, Adachi 1990); other species prefer to attack higher on the trunk (Solomon 1972) and may distribute their attacks from ground level up to a height of several meters (Tapley 1961; Solomon 1972, 1974). In contrast, in our study *A. glabripennis* oviposited both near the base of the tree and higher on the trunk, but left a distinct gap between the base of the trunk and the bottom of the crown. Woodpeckers are often cited as the most important predators of wood-boring cerambycid larvae (Brooks 1923; Linsley 1961; Solomon 1968, 1972, 1974) and it may be that larvae near ground level and near branch points within the canopy are less vulnerable than those in a clearly-exposed small-diameter tree trunk. Similarly, adults on the exposed trunk may be more vulnerable to predation during oviposition, which may take up to half an hour or more (unpublished data).

In conclusion, our results indicate that living trees in a greenhouse provide a useful means of evaluating host preferences of adult *A. glabripennis* as well as suitability for larval development. Given a choice of tree species, adults showed clear preferences for feeding and oviposition. Eggs hatched and larvae became established in the trees and even developed as far as the pupal stage in the most preferred host, which was unexpected in such a short period of time. This experimental system has allowed us to demonstrate that red oak is an acceptable host for adult feeding and oviposition and a potentially suitable host for larval development. We have also shown that the beetles will oviposit extensively at the base of trees, at least in cases where the bark is thin and smooth. We recognize that the confines of the cages may have influenced the results of our study, but emphasize that experiments with living trees represent an important improvement over those with cut logs. Furthermore, even if confinement within a cage leads to beetles attacking trees that they would normally pass over 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 the ongoing efforts to eradicate this invasive species and we plan to confirm whether or not red oak trees can support complete development of *A. glabripennis.*

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References Cited

Adachi, I. 1990. Control methods for *Anoplophora malasiaca* (Thomson) (Coleoptera: Cerambycidae) in citrus groves II. Application of wire netting for preventing oviposition in a mature grove. Appl. Entomol. Zool. 25: 79–83.

Adachi, I., and R. Korenaga. 1989. Control methods for *Anoplophora malasiaca* Thomson (Coleoptera: Cerambycidae) in citrus groves. I. Comparison of effects in several methods for preventing oviposition. Appl. Entomol. Zool. 24: 315–318.

Bernays, E. A., and R. F. Chapman. 1994. Host-plant selection by phytophagous insects. Chapman & Hall, New York.

Brooks, F. E. 1923. Oak sapling borer, *Goes tesselatus* Haldeman. J. Agric. Res. 26: 313–318.

Dubois, T., A. E. Hajek, and S. Smith. 2002. Methods for rearing the Asian longhorned beetle (Coleoptera: Cerambycidae) on artificial diet. Ann. Entomol. Soc. Am. 95: 223–230.

Haack, R. A., and F. Slansky, Jr. 1987. Nutritional ecology of wood-feeding Coleoptera, Lepidoptera, and Hymenoptera, pp. 449–486. *In* F. Slansky, Jr. and J. G. Rodrigues [eds.], Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York.

Haack, R. A., K. R. Law, V. C. Mastro, H. S. Ossenbruggen, and B. J. Raimo. 1997. New York's battle with the Asian long-horned beetle. J. For. 95(12): 11–15.

Hanks, L. M. 1999. Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annu. Rev. Entomol. 44: 483–505.

Hanks, L. M., T. D. Paine, and J. G. Millar. 1993. Host species preference and larval performance in the wood-boring beetle *Phoracantha semipunctata* F. Oecologia (Berl.) 95: 22–29.

Hanks, L. M., J. G. Millar, and T. D. Paine. 1995. Biological constraints on host-range expansion by the wood-boring beetle *Phoracantha semipunctata* (Coleoptera: Cerambycidae). Ann. Entomol. Soc. Am. 88: 183–188.

Hughes, A. L., and M. K. Hughes. 1982. Male size, mating success, and breeding habitat partitioning in the white-spotted sawyer *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae). Oecologia (Berl.) 55: 258–263.

Hughes, A. L., and M. K. Hughes. 1987. Asymmetric contests among sawyer beetles (Cerambycidae: *Monochamus notatus* and *Monochamus scutellatus*). Can. J. Zool. 65: 823–827.

Keena, M. A. 2002. *Anoplophora glabripennis* (Coleoptera: Cerambycidae) fecundity and longevity under laboratory conditions: comparison of populations from New York and Illinois on *Acer saccharum.* Environ. Entomol. 31: 490–498.

Lieu, K.O.V. 1945. The study of wood borers in China—I. Biology and control of the citrus-root-cerambycids, *Melanauster chinensis*, Forster (Coleoptera). Fla. Entomol. 27: 62–101.

Lingafelter, S. W., and E. R. Hoebeke. 2002. Revision of *Anoplophora* (Coleoptera: Cerambycidae). Entomological Society of Washington, Washington, DC.

Linsley, E. G. 1961. The Cerambycidae of North America. Part I. Introduction. University of California Publications in Entomology, Volume 18. University of California Press, Berkeley, CA.

Ludwig, S. W., L. Lazarus, D. G. McCullough, K. Hoover, S. Montero, and J. C. Sellmer. 2002. Methods to evaluate host tree suitability to the Asian longhorned beetle, *Anoplophora glabripennis.* J. Environ. Hortic. 20: 175–180.

Mayhew, P. J. 1997. Adaptive patterns of host-plant selection by phytophagous insects. Oikos 79: 417–428.

Nord, J. C., D. G. Grimble, and F. B. Knight. 1972a. Biology of *Oberea schaumii* (Coleoptera: Cerambycidae) in trembling aspen, *Populus tremuloides.* Ann. Entomol. Soc. Am. 65: 114–119.

Nord, J. C., D. G. Grimble, and F. B. Knight. 1972b. Biology of *Saperda inornata* (Coleoptera: Cerambycidae) in trembling aspen, *Populus tremuloides.* Ann. Entomol. Soc. Am. 65: 127–135.

Nowak, D. J., J. E. Pasek, R. A. Sequeira, D. E. Crane, and V. C. Mastro. 2001. Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. J. Econ. Entomol. 94: 116–122.

[NYT] New York Times. 2002. Tree-munching Asian beetles are discovered in Jersey City. New York Times, 11 October 2002, New York.

Ritchie, W. 1920. The structure, bionomics, and economic importance of *Saperda carcharias* Linn., "the large poplar longhorn." Ann. Appl. Biol. 7: 299–343.

Smith, M. T. 2000. Biocontrol and IPM for the Asian longhorned beetle. IPM Practitioner 22(7): 1–5.

Smith, M. T., J. Bancroft, and J. Tropp. 2002. Age-specific fecundity of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on three tree species infested in the United States. Environ. Entomol. 31: 76–83.

Solomon, J. D. 1968. Cerambycid borer in mulberry. J. Econ. Entomol. 61: 1023–1025.

Solomon, J. D. 1972. Biology and habits of the living beech borer in red oaks. J. Econ. Entomol. 65: 1307–1310.

Solomon, J. D. 1974. Biology and damage of the hickory borer, *Goes pulcher*, in hickory and pecan. Ann. Entomol. Soc. Am. 67: 257–260.

Stewart, B. 2002. A devastating invader behind closed doors. New York Times, 14 October 2002, New York.

Tapley, R. G. 1961. The white coffee borer, *Anthores leuconotus* Pasc., and its control. Bull. Entomol. Res. 51: 279–301.

Thompson, J. N. 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol. Exp. Appl. 47: 3–14.

Zar, J. H. 1999. Biostatistical analysis, 4th ed. Prentice-Hall, Upper Saddle River, NJ.

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