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ANOPLOPHORA GLABRIPENNIS WITHIN-TREE DISTRIBUTION, SEASONAL DEVELOPMENT, AND HOST SUITABILITY IN CHINA AND CHICAGO

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ABSTRACT

Established populations of the Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), were first reported in the United States in New York in 1996, Illinois in 1998, and New Jersey in 2002. A federal quarantine and an eradication program were implemented in 1997, involving tree surveys and removal of infested trees. We recorded the number of *A. glabripennis* life stages found at several locations along the main trunk and major branches of naturally infested trees in China (species of *Populus*, *Salix*, and *Ulmus*) and Chicago, Illinois (species of *Acer*, *Fraxinus*, and *Ulmus*) during 1999 to 2002. Typically, *A. glabripennis* initiated attack near the crown base along both the trunk and main branches. The one exception to this pattern was on *Populus* trees in China that had branches along the entire trunk, in which case *A. glabripennis* initiated attack along the lower trunk. Larvae were the dominant overwintering stage in both countries. A host suitability index for *A. glabripennis* was calculated for each tree with the formula: (number of living life stages + number of exit holes) / number of oviposition pits. The mean host suitability index was higher on *Populus* and *Salix* than *Ulmus* in China, and generally higher on *Acer* and *Ulmus* than *Fraxinus* in Chicago. Eleven genera of trees (N = 1465 trees) were infested by *A. glabripennis* in Chicago; in decreasing order of tree frequency they included *Acer*, *Ulmus*, *Fraxinus*, *Aesculus*, *Betula*, *Salix*, *Celtis*, *Malus*, *Pyrus*, *Sorbus*, and *Tilia*. When the proportion of each genus of infested street trees (N = 958 trees in 7 genera) was compared to its proportion of all Chicago street trees based on a 2003 inventory (N = 539,613 trees in 45 genera), *A. glabripennis* showed a significant preference to infest the genera *Acer* and *Ulmus*. Based on our results, inspectors should focus their efforts on upper trunks and lower branches of *Acer* and *Ulmus* trees.

The Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), is one of the most damaging exotic forest insects to become established in the United States in recent years (Haack et al. 1997, Cavey et al. 1998). Established populations were first discovered in the United States in New York in 1996, Illinois in 1998, and New Jersey in 2002 (Poland et al. 1998, Haack 2003a). In addition, breeding populations and associated tree mortality were first reported in Austria in 2001, Japan in 2002, Canada in 2003, France in 2003, Germany in 2004, and Italy in 2007 (Hérard et al. 2005, Takahashi and Ito 2005, Haack 2006, Schroder et al. 2006, Maspero et al. 2007). Solid wood packaging material, such as crating and pallets, used in

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international trade was likely the principal pathway by which *A. glabripennis* was moved among all these countries (Haack 2006).

Anoplophora glabripennis is native to China and the Korean Peninsula where it infests many genera of living hardwood trees (Lingafelter and Hoebeke 2002, Williams et al. 2004). The principal hosts in Asia are species of *Acer* (maple), *Populus* (poplar), *Salix* (willow), and *Ulmus* (elm) (Yan and Qin 1992). To date, the principal hosts in the United States are *Acer*, *Aesculus* (horsechestnut), and *Ulmus* (Haack et al. 1997, Nowak et al. 2001). *Anoplophora glabripennis* is typically univoltine. Adults emerge throughout the summer months by chewing circular exit holes through the bark. Adults feed primarily on the outer bark of twigs and can live for several weeks, during which time they feed, mate, and oviposit. Ovipositing adult females chew a pit in the outer bark into which they deposit a single egg under the bark. Larvae first feed in the inner bark (phloem) and then tunnel deeper into the wood (xylem). Larvae generally keep their galleries clean by regularly expelling frass outside the tree at the point where oviposition occurred. Larvae feed throughout summer and fall, and if not fully developed, they continue to feed the following year. Most *A. glabripennis* pass the winter in the larval stage, with pupation occurring the following spring or summer. Pupation occurs at the distal end of the larval gallery in the wood. After transformation, new *A. glabripennis* adults chew out of the tree and thereby renew the cycle (Yan and Qin 1992, Haack et al. 1997).

Aggressive eradication programs were initiated in North America, Europe, and Japan (Hérard et al. 2005, 2006; Takahashi and Ito 2005; Haack 2006). In each case, eradication efforts entailed surveying individual trees for signs and symptoms of infestation followed by insecticide treatment or cutting and destroying of all infested trees. When conducting surveys, inspectors look for *A. glabripennis* oviposition pits on the bark surface, extruded frass from larval feeding, and exit holes on the bark surface. Knowing where initial *A. glabripennis* oviposition is likely to occur on trees is important when developing surveys, especially when *A. glabripennis* population levels are low. There have been numerous studies on the within-tree distribution of various bark- and wood-infesting beetles (Coleoptera) with the objective of developing survey and sampling techniques (Haack and Benjamin 1982, Wilkinson and Haack 1987, Prenzel et al. 1999, Chung et al. 2003, Fierke et al. 2005, Timms et al. 2006).

While conducting *A. glabripennis* studies in China and the United States (Haack 2003b, Poland et al. 2006), we gathered within-tree and life-stage distribution data from several naturally infested trees. The principal objectives of our studies were to (1) record *A. glabripennis* within-tree distribution by tree species, (2) record the *A. glabripennis* developmental stages recovered by month of sampling, (3) estimate the suitability of each tree species sampled for *A. glabripennis* development, and (4) compare the genera of trees infested by *A. glabripennis* in Chicago to the general composition of all street trees in Chicago.

MATERIALS AND METHODS

We sampled 49 trees infested with *A. glabripennis* near Baiyin, Gansu Province (36.6°N, 104.2°E), and Wuji, Hebei Province (38.2°N, 115.0°E), China, in October 2000, June 2001, and April 2002. These trees consisted of 21 *Populus nigra* var. *thevestina* (Dode) Bean, 11 *Salix matsudana* Koidz, and 17 *Ulmus pumila* L. trees. Most of these trees were relatively small in diameter at breast height (DBH) (Table 1), and had been planted as windbreaks along roads and agricultural fields. We examined the entire trunk of each tree in 1-m-long increments, usually continuing along a major branch. We felled all trees with a chainsaw and then debarked and split them by hand with an ax and a knife. For each tree section, we recorded length and diameter, the number of oviposition pits, and number of exit holes. We also recorded the number of all living life stages encountered. This research was part of a larger study to evaluate the effects of systemic insecticides on *A. glabripennis* (Poland et al. 2006). The data presented here are from the control trees, which received no insecticide treatments.

In Chicago (41.8°N, 87.7°W), we sampled 38 infested trees in 1999, including 3 *Acer negundo* L. (boxelder), 20 *A. platanoides* L. (Norway maple), 13 *A. saccharinum* L. (silver maple), and 2 *Fraxinus pennsylvanica* Marsh. (green ash) trees. Most trees were felled during February to April 1999, with a few more felled in July and September 1999. These trees were relatively large street trees (Table 1) that were felled as part of the eradication program and thus the species sampled represented the trees removed on the days when we were present. For each tree, we cut trunk and branch sections approximately 1-m-long from the base, middle, and upper main trunk; along the trunk near mid-crown; and from the base of one major branch. For each log sampled, we recorded length, diameter, and the number of oviposition pits and exit holes present. We then debarked and split all logs with a log splitter and ax. We recorded the number of all living *A. glabripennis* life stages found.

In Chicago in June 2001, we sampled nine small-diameter infested trees [seven *A. negundo* and two *U. americana* L. (American elm) trees] that were growing along a fence row (Table 1). Because these trees were relatively short compared to the trees cut in Chicago in 1999, we cut trunk sections (ca. 1 to 2 m long) from the lower trunk, upper trunk, and crown positions. These sections were dissected and sampled as described above.

For all trees, the progression of attack was approximated by the distribution and relative proportion of different signs and developmental life stages of *A. glabripennis*. For example, sections with exit holes were assumed to have been infested earlier than sections with only larvae, and sections with late instar larvae were assumed to have been infested earlier than sections with only oviposition pits and eggs.

A host suitability index for *A. glabripennis* was estimated for each tree species. The suitability index value assigned to each tree was calculated on a per-tree basis as follows: number of living *A. glabripennis* life stages plus the number of exit holes divided by the number of oviposition pits. We recognize that an egg is not always laid in each oviposition pit (Zhao et al. 1993, Keena 2002, Smith et al. 2002), but used this approach to approximate initial oviposition.

During the period 1998-2003, 1465 infested trees, representing 11 genera, were removed in Chicago as part of an operational eradication program; 958 trees were classified as street trees and 507 were classified as being on private properties or in parks. No infested trees were found in Chicago from November 2003 to present (December 2007; Christine Markham, USDA Animal and Plant Health Inspection Service, personal communication). We calculated the proportion of all 1465 trees that each genus represented. We also calculated the percentage of all street trees in Chicago by genus based on the 2003 City of Chicago street tree inventory that included 539,613 trees, representing 45 genera (6 conifer and 39 hardwood genera).

The percent of *A. glabripennis* oviposition pits, living life stages, and exit holes within each tree section sampled were calculated on a per-tree basis by dividing the number of each insect parameter in a given section by the total number found for the tree. Similarly, the suitability index was expressed as a percentage value for each tree. Percentage values were transformed (arcsine square-root) to improve normality and analyzed using analysis of variance (ANOVA) (PROC GLM, SAS Institute, 2001). If the ANOVA was significant at the 0.05 level, then a Tukey multiple range test was used to separate the means. For each genus of trees, the proportion of all infested Chicago street trees was compared to the corresponding proportion of all Chicago street trees using the z-test ($\alpha = 0.05$).

Table 1. Number of *Anoplophora glabripennis* (ALB) oviposition pits, living life stages, and exit holes found on sampled trees in China and Chicago by tree species, and the mean (± SE) DBH and suitability index of each tree species that was estimated by dividing the total number of living life stages found plus exit holes by the number of oviposition pits.

Location	Mean	No. ALB signs or live life stages counted						
Tree species* (No. cut)	tree DBH (cm)	Oviposition pits	Eggs	Larvae	Pupae	Callow adults	Exit holes	Mean host suitability index (%)
China (2000, 2001 and 2002)								
Elm (17)	10.0 ± 0.8	1217	62	181	17	1	18	26.5 ± 4.8 b*
Poplar (21)	8.4 ± 0.6	1247	14	413	34	46	147	59.8 ± 6.5 a
Willow (11)	9.2 ± 1.2	584	21	197	15	23	55	51.9 ± 8.5 a
P =	0.27							0.0014
F =; d.f.	1.32; 2,46							7.73; 2,46
Chicago (1999)								
Boxelder (3)	20.0 ± 2.0	32	0	16	0	0	5	76.1 ± 12.1 a
Green ash (2)	22.0 ± 0.0	16	0	1	0	0	0	5.6 ± 5.6 b
Norway maple (20)	31.0 ± 2.6	1339	8	390	0	0	42	31.6 ± 3.5 ab
Silver maple (13)	40.3 ± 6.9	611	20	152	0	0	30	43.8 ± 10.2ab
P =	0.246							0.0126
F =; d.f.	1.46; 3,31							4.20; 3,34
Chicago (2001)								
American elm (2)	10.8 ± 2.3	48	0	25	0	0	0	52.1 ± 10.4
Boxelder (7)	11.0 ± 1.1	252	0	73	14	1	30	44.5 ± 13.0
P =	0.91							0.77
F =; d.f.	0.01; 1,7							0.09; 1,7

* Tree species were: American elm = *Ulmus americana*, boxelder = *Acer negundo*, elm = *Ulmus pumila*, green ash = *Fraxinus pennsylvanica*, Norway maple = *Acer platanoides*, poplar = *Populus nigra* var. *thevestina*, silver maple = *Acer saccharinum*, and willow = *Salix matsudana*.
** Means followed by the same letter within columns, for each of the three location-year sections individually, were not significantly different at the 0.05 level, Tukey multiple range test.

RESULTS AND DISCUSSION

Within-tree distribution in China. The trees sampled in China were relatively small in diameter with a mean (± SE) DBH of 9.1 ± 0.5 cm. Mean DBH did not differ significantly among the three species (Table 1). Initial *A. glabripennis* infestation occurred primarily along the main trunk near the first crown branches (2 to 4 m above groundline) in *Salix* and *Ulmus* trees; however, initial infestation in the *Populus* trees tended to start along the lower trunk, based largely on exit hole data (Table 2). These differences in the initial attack pattern were likely influenced by the differences in branching patterns of the three tree species. For example, initial branching in *Salix* and *Ulmus* trees started at 2 to 3 m above groundline, whereas branching in *Populus* trees occurred along the entire trunk beginning at groundline. Given that *A. glabripennis* adults feed on twigs throughout their lifespan and generally walk along branches to reach the trunk to oviposit (Keena 2002, Smith et al. 2002, Morewood et al. 2004, Smith 2006), the presence of branches along the entire trunk of the *Populus* trees would allow adult females to easily feed and oviposit near groundline. On several occasions we found *A. glabripennis* adults feeding and ovipositing at the base of the *Populus* trees that had numerous basal sprouts. In addition, Zhao et al. (1997) stated that *A. glabripennis* prefers to oviposit on the lower trunks of *Populus* trees where tree DBH is less than 15 cm. All *Populus* trees in our study were less than 15 cm DBH.

Within-tree distribution in Chicago. The 38 trees sampled in 1999 were relatively large street trees with a mean DBH of 33.3 ± 2.9 cm; mean DBH did not differ significantly among the four species sampled in 1999 (Table 1). The nine trees sampled in 2001 were relatively small with a mean DBH of 10.9 ± 0.9 cm; mean DBH did not differ significantly between the two tree species sampled in 2001 (Table 1). For all species combined, the trees sampled in Chicago in 1999 were significantly larger than the trees sampled in Chicago in 2001 or in China ($F = 49.2$; df = 2,90; $P < 0.0001$). Overall, for the 1465 infested trees removed in Chicago during the *A. glabripennis* eradication program from 1998 to 2003, mean DBH was 37.2 ± 0.6 cm (Fig. 1).

The *A. glabripennis* colonization patterns were broadly similar among the four tree species sampled in Chicago in 1999 (Table 3). These trees were mostly in their first to third year of infestation based on the presence of various life stages and exit holes. For example, of the 35 trees sampled in Chicago in 1999 that were included in Table 3, we found oviposition pits on all 35 trees, living life stages in 33 trees, but exit holes in only 13 of the trees. We did not try to determine the age of the exit holes, i.e., current year vs. prior year. Typically, infestation occurred first in the upper trunk and major crown branches of these *Acer* and *Fraxinus* trees. The two *Fraxinus* trees sampled in this study were lightly infested, with all living life stages found in the mid-crown trunk section. Similarly, in the lightly infested *A. negundo* trees sampled in our study, *A. glabripennis* exit holes were first found in the mid-crown trunk section, suggesting that this was the first region infested. However, in the *A. platanoides* and *A. saccharinum* trees, initial *A. glabripennis* attack appeared to occur over a larger portion of the upper trunk and crown (Table 3).

Based on the observations in China and Chicago described above, we suggest inspectors focus their surveys on the upper trunk and lower portion of major branches of the principal host trees present in any particular area. Targeting the upper trunk and lower portion of major branches would be recommended for all sizes of trees that have a clear trunk. However, for trees with branching along the entire trunk or with several basal suckers, inspectors should examine the entire trunk, starting from groundline.

Table 2. Mean percent of trunk samples that contained *Anoplophora glabripennis* oviposition pits, living life stages (eggs, larvae, pupae, and callow adults), and exit holes by within-tree location (meters above groundline) and tree species (elm, *Ulmus pumila*; poplar, *Populus nigra* var. *thevestina*; and willow, *Salix matsudana*) for trees sampled in China during October 2000, June 2001, and April 2002.

Height above groundline (m)	**Elm (N = 17)**	**Poplar (N = 21)**		**Willow (N = 11)**		**All (N = 49)**	
Oviposition pits							
6 m	11.6 ± 3.3	1.2 ± 0.7	d	0.0 ± 0.0	d	4.9 ± 1.5	c
5 m	12.3 ± 2.9	4.5 ± 2.0	cd	0.4 ± 0.3	d	6.6 ± 1.5	c
4 m	22.4 ± 4.4	12.0 ± 3.0	bc	13.1 ± 3.8	c	15.9 ± 2.2	b
3 m	20.4 ± 3.2	21.1 ± 3.8	ab	20.7 ± 3.8	bc	20.8 ± 2.1	ab
2 m	16.1 ± 2.9	23.9 ± 3.9	ab	38.6 ± 5.5	a	24.5 ± 2.5	ab
1 m	17.8 ± 5.4	37.7 ± 6.4	a	27.2 ± 3.7	ab	28.4 ± 3.6	a
N (trees) =	17	21		11		49	
P =	0.1351	0.0001		0.0001		0.0001	
F =; d.f.	1.73; 5,95	16.6; 5,117		25.4; 5,55		21.6; 5,279	
Life stages							
6 m	12.9 ± 5.1	0.5 ± 0.3	d	0.0 ± 0.0	c	4.8 ± 2.0	c
5 m	11.8 ± 4.7	3.8 ± 1.6	cd	0.0 ± 0.0	c	5.9 ± 1.9	c
4 m	21.8 ± 4.6	10.4 ± 2.3	bc	11.0 ± 3.2	bc	14.3 ± 2.1	b
3 m	28.7 ± 6.2	23.9 ± 3.7	ab	31.0 ± 5.4	ab	27.1 ± 2.9	a
2 m	11.5 ± 3.3	28.0 ± 4.3	a	36.7 ± 7.8	a	24.5 ± 3.1	ab
1 m	14.1 ± 6.5	33.6 ± 5.0	a	21.3 ± 4.8	ab	24.3 ± 3.5	ab
N (trees) =	16	21		11		48	
P =	0.0651	0.0001		0.0001		0.0001	
F =; d.f.	2.16; 5,89	21.02; 5,117		15.21; 5,55		18.2; 5,273	
Exit holes							
6 m	16.7± 16.7	1.5± 1.5	b	0.0 ± 0.0	b	4.4 ± 3.6	c
5 m	0.0± 0.0	11.4 ± 6.6	ab	0.0 ± 0.0	b	6.3 ± 3.8	bc
4 m	27.0± 15.3	17.4 ± 6.7	ab	8.3 ± 6.2	b	17.8 ± 5.3	abc
3 m	39.7± 18.9	18.4 ± 5.3	ab	40.3 ± 10.4	a	27.7 ± 5.8	a

Table 2. Continued.

Height above groundline (m)	**Elm (N = 17)**	**Poplar (N = 21)**		**Willow (N = 11)**		**All (N = 49)**	
2 m	14.3± 14.3	21.0 ± 8.0	ab	43.7 ± 10.5	a	24.0 ± 6.1	ab
1 m	4.8± 4.8	31.0 ± 9.2	a	7.6 ± 4.1	b	20.2 ± 5.8	abc
N (trees) =	7	17		6		30	
P =	0.3493	0.0490		0.0001		0.0029	
F =; d.f.	1.16; 5,35	2.32; 5,94		10.78; 5,30		3.76; 5,171	

* Means followed by the same letter within columns for each parameter were not significantly different at the 0.05 level, Tukey multiple range test.

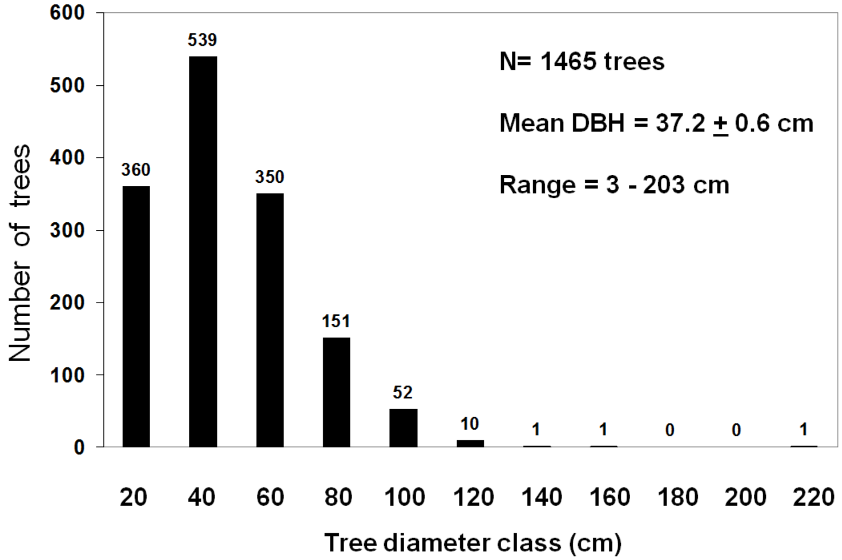

Figure 1. Frequency diagram depicting the number of trees by 20-cm diameter-at-breast-height increments that were apparently infested with *Anoplophora glabripennis* and removed in Chicago during the 1999-2003 eradication program.

Life stages recovered. The proportion of *A. glabripennis* individuals recovered as eggs, larvae, pupae, and callow adults followed similar trends in China and Chicago (Table 4); only trees with living *A. glabripennis* life stages were included in Table 4. During winter and spring, in both China (April) and Chicago (February-April), we recovered mostly larvae and a few apparently viable eggs, indicating that larvae were the principal overwintering stage (Table 4). Although we recovered no pupae or callow adults in our samples from February through April, we did observe one *A. glabripennis* pupa in a Chicago tree that was felled during the eradication program in February 1999 but not included in our study. In June, in both China and Chicago, larvae were still the dominant within-tree life stage. Both pupae and callow adults were also found, but no eggs (Table 4). Apparently, by June, larvae had emerged from all overwintering eggs and no new adult oviposition had yet begun. The two trees sampled in Chicago in July 1999 had only current-year oviposition pits on the bark surface, and only eggs were found in the samples. In fall (October) in China, we found mostly larvae and eggs, but also a few pupae and callow adults (Table 4). This pattern of seasonal development is consistent with earlier reports (Yan and Qin 1992, Haack et al. 1997). The fact that *A. glabripennis* can overwinter in multiple life stages helps explain why adult emergence is staggered over time, which results in adults feeding and ovipositing throughout summer and fall. During the eradication program in Chicago, for example, live *A. glabripennis* adults were observed on trees primarily during July to October, but in one warm year an adult was found ovipositing in early December.

Table 3. Mean percent of trunk samples that contained *Anoplophora glabripennis* oviposition pits, living life stages (eggs, larvae, pupae, and callow adults), and exit holes by within-tree location and tree species (boxelder, *Acer negundo*; Norway maple, *Acer platanoides*; silver maple *Acer saccharinum*; and green ash, *Fraxinus pennsylvanica*) for trees sampled in Chicago in 1999.

Location above groundline*	Boxelder (N = 2)	Norway maple (N = 18)	Silver maple (N = 13)	Green ash (N = 2)	All (N = 35)
Oviposition pits					
Section 5	33.3 ± 0.0	23.0 ± 5.1 b**	22.5 ± 4.8 ab	5.6 ± 5.6 b	22.4 ± 3.2 b
Section 4	50.0 ± 16.7	45.6 ± 6.5 a	34.3 ± 7.7 a	80.2 ± 8.7 a	43.6 ± 4.8 a
Section 3	16.7 ± 16.7	30.1 ± 7.6 ab	31.2 ± 7.4 a	14.3 ± 14.3 ab	28.8 ± 4.9 ab
Section 2	0.0 ± 0.0	0.2 ± 0.2 c	2.7 ± 2.2 b	0.0 ± 0.0 b	1.1 ± 0.8 c
Section 1	0.0 ± 0.0	1.1 ± 1.1 c	7.7 ± 7.7 b	0.0 ± 0.0 b	3.4 ± 2.9 c
N (trees) =	2	18	13	2	35
P =	0.0513	0.0001	0.0003	0.0168	0.0001
F =; d.f.	5.12; 4,5	18.6; 4,85	6.19; 4,60	8.96; 4,5	29.5; 4,170
Life stages					
Section 5	66.7 ± 33.3	19.6 ± 4.8 b	30.4 ± 8.1 a	0.0 ± 0.0	26.1 ± 4.7 a
Section 4	16.7 ± 16.7	52.6 ± 7.1 a	31.2 ± 8.2 a	100.0 ± 100.0	43.7 ± 5.5 a
Section 3	16.7 ± 16.7	27.8 ± 7.3 b	27.7 ± 9.3 a	0.0 ± 0.0	26.2 ± 5.3 a
Section 2	0.0 ± 0.0	0.0 ± 0.0 c	7.7 ± 7.7 ab	0.0 ± 0.0	3.0 ± 3.0 b
Section 1	0.0 ± 0.0	0.0 ± 0.0 c	0.0 ± 0.0 b	0.0 ± 0.0	0 ± 0 b
N (trees) =	2	17	13	1	33
P =	0.1819	0.0001	0.0014	n.a.	0.0001
F =; d.f.	2.40; 4,5	22.5; 4,80	5.08; 4,60	n.a.	22.2; 4,160
Exit holes					
Section 5	0.0 ± 0.0	7.1 ± 7.1	23.6 ± 19.4		12.9 ± 8.3
Section 4	100.0 ± 100.0	44.6 ± 16.8	27.3 ± 19.5		42.2 ± 12.4
Section 3	0.0 ± 0.0	33.9 ± 17.4	29.1 ± 19.8		29.5 ± 11.8
Section 2	0.0 ± 0.0	0.0 ± 0.0	20.0 ± 20.0		7.7 ± 7.7
Section 1	0.0 ± 0.0	14.3 ± 14.3	0.0 ± 0.0		7.7 ± 7.7

Table 3. Continued.

Location above groundline*	**Boxelder (N = 2)**	**Norway maple (N = 18)**	**Silver maple (N = 13)**	**Green ash (N = 2)**	**All (N = 35)**
N (trees) =	1	7	5	0	13
P =	n.a.	0.1024	0.7565	n.a.	0.0576
F =; d.f.	n.a.	2.12; 4,30	0.47; 4,20	n.a.	2.43; 4,60

* Section 1 = base of trunk, Section 2 = mid-trunk, Section 3 = trunk section near base of crown, Section 4 = Trunk section near mid-crown, and Section 5 = base of a major branch.
** Means followed by the same letter within columns for each parameter were not significantly different at the 0.05 level, Tukey multiple range test.

Table 4. Percentage of living *Anoplophora glabripennis* life stages that were eggs, larvae, pupae, or callow adults at the time of tree dissection in China and Chicago during field studies from 1999 to 2002.

Location	**Percentage found by life stage (%)**				**No. of**	**No. of**
Month and year	**Eggs**	**Larvae**	**Pupae**	**Adults**	**life stages**	**trees**
China						
April 2002	15.5	84.5	0.0	0.0	197	11
June 2001	0	69.2	18.1	12.7	331	19
October 2000	20.7	78.3	0.1	0.9	496	17
Chicago						
February 1999	3.7	96.3	0.0	0.0	451	25
March 1999	0	100.0	0.0	0.0	56	1
April 1999	16.7	83.3	0.0	0.0	62	6
June 2001	0	95.1	4.7	0.2	113	8
July 1999	100	0	0	0	15	2
September 1999	0	100.0	0.0	0.0	5	1

Host suitability index. The mean host suitability index was significantly higher for *Populus* and *Salix* compared with *Ulmus* for the 49 trees sampled in China (Table 1). For the 38 mature trees sampled in Chicago in 1999, the mean host suitability index was highest for *A. negundo*, intermediate for *A. platanoides* and *A. saccharinum*, and lowest for *F. pennsylvanica* (Table 1). For the nine smaller trees sampled in Chicago in 2001, host suitability was similar between *A. negundo* and *U. americana* (Table 1).

The relatively high suitability of *Acer* species for *A. glabripennis* development may help explain the apparent preferential infestation of *Acer* trees by *A. glabripennis* in China (Sun et al. 1990, He and Huang 1993, Gao et al. 1993), Europe (Hérard et al. 2006), New York City (Haack et al. 1997), South Korea (Williams et al. 2004), and Toronto, Canada (Jean J. Turgeon, Canadian Forest Service, personal communication). Similarly, in laboratory tests, various species of *Acer* were generally found to be the most suitable for *A. glabripennis* larval survival and development, whereas *Fraxinus* species were among the least suitable of the tree species tested (Bancroft et al. 2002, Ludwig et al. 2002, Morewood et al. 2003). However, as Keena (2002) noted, adult females reared from lightly infested *Fraxinus* species were larger in average body size and more fecund than females reared from more heavily infested *Acer* species, indicating a trade off between initial egg density, host suitability, and subsequent vigor of the progeny adults.

Infested trees in Chicago. The six most commonly infested tree genera in Chicago, in decreasing order, were *Acer*, *Ulmus*, *Fraxinus*, *Aesculus*, *Betula* and *Salix* (Table 5). The other five infested genera (*Celtis*, *Malus*, *Pyrus*, *Sorbus*, and *Tilia*) were represented by only one or two trees each. It is not certain if *A. glabripennis* would have completed development in all of these latter five genera. At times trees were cut only because *A. glabripennis* oviposition pits were found (*Celtis*, *Malus*, *Pyrus*, and *Tilia*). The one *Sorbus* tree that was removed, however, had both oviposition pits and exit holes. In China, species of *Pyrus* and *Tilia* have been reported as occasional hosts, but not *Celtis* or *Sorbus* (Haack et. al. 1997, Lingafelter and Hoebeke 2002, Smith 2006, Sawyer 2007). Earlier reports of *A. glabripennis* infesting two *Prunus* trees and two *Robinia* trees in Chicago (Nowak et al. 2001) were not substantiated.

When compared to the overall population of street trees in Chicago, the genera *Acer* and *Ulmus* were infested at a rate significantly higher than their actual proportion of the tree population (Table 5). Similarly, *Aesculus*, *Celtis*, *Fraxinus*, *Pyrus*, and *Tilia* were significantly underrepresented among the infested street trees when compared to their overall percentage of the city street-tree population (Table 5). There were no trees identified as either *Malus* or *Salix* in the Chicago street tree inventory. Given the above infestation trends, we recommend that inspectors concentrate their survey efforts on the most common host tree genera in their locality, especially *Acer* and *Ulmus*.

There were 30 genera of hardwood trees (N = 137,601 trees) that were part of the Chicago street tree inventory that were not recorded as being hosts of *A. glabripennis* in Chicago. In decreasing order of tree frequency, the genera were: *Gleditsia, Quercus, Populus, Platanus, Catalpa, Ginkgo, Alianthus, Prunus, Crateagus, Gymnocladus, Morus, Nyssa, Robinia, Alnus, Magnolia, Zelkova, Juglans, Hibiscus, Cercis, Maclura, Crataegus, Amelanchier, Fagus, Carpinus, Liquidambar, Corylus, Phellodendron, Cornus, Liriodendron,* and *Ostrya.* Of these 30 genera, *Alnus, Carpinus, Fagus, Hibiscus, Morus, Platanus, Populus, Prunus, Quercus* and *Robinia* have been reported as ovipositional hosts on at least one occasion in China, Europe, and New York, although complete development has not been documented in all cases (He and Huang 1993, Haack et al. 1997, Nowak et al. 2001, Hérard et al. 2006). For example, in Europe, *A. glabripennis* exit holes were found on *Fagus*, but the infested *Carpinus*, *Platanus*,

Table 5. The number of trees in Chicago that were found to be infested with *Anoplophora glabripennis* during 1998-2003 and the evidence of infestation recorded; number of infested trees that were on private property or along streets; number of infested street trees expressed on a percentage basis; number and proportion of all street trees in Chicago based on the 2003 inventory; and a *z*-test comparison of the proportions of infested street trees to the overall street tree inventory by tree genus.

	Number of infested trees					All Street trees		Street tree z-test	
Genus	**All**	**Evidence***	**Private**	**Street**	**(%)**	**Number**	**%**	**z**	***P***
Acer	1102	EH, OP	312	790	(82.46)	230,012	42.63	24.9	< 0.001
Aesculus	17	EH, OP	15	2	(0.21)	4762	0.88	2.05	= 0.041
Betula	11	EH, OP	10	1	(0.10)	1469	0.27	0.70	= 0.483
Celtis	1	OP	0	1	(0.10)	8512	1.58	3.54	< 0.001
Fraxinus	64	EH, OP	7	57	(5.95)	91,532	16.96	9.03	< 0.001
Malus	1	OP	1	0		0	n.a.		
Pyrus	1	OP	1	0		8399	1.56	3.77	< 0.001
Salix	9	EH, OP	9	0		0	n.a.		
Sorbus	1	EH	1	0		616	0.11	0.54	= 0.590
Tilia	1	OP	0	1	(0.10)	23,315	4.32	6.34	< 0.001
Ulmus	252	EH, OP	146	106	(11.06)	22,824	4.23	10.4	< 0.001
Unknown	5	EH, OP	5	0		1027	0.19		
Total	1465		507	958		539,613			

* Evidence of *A. glabripennis* infestation was based on the presence of oviposition pits (OP), exit holes (EH), or both.

and *Prunus* trees were destroyed prior to any adult emergence (Franck Hérard, USDA Agricultural Research Service, personal communication.)

The results of our studies indicate that (1) *A. glabripennis* will oviposit throughout the trunk and major branches of host trees, but often starts along the upper trunk and lower portions of major branches; (2) initial infestation can occur along the lower trunk on trees with branches or basal suckers near groundline; (3) larvae are the primary overwintering stage; (4) *Acer* species are highly suitable hosts for *A. glabripennis* development; and (5) *Acer* and *Ulmus* species are preferentially infested in Chicago.

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