Anoplophora glabripennis (Motschulsky) (Coleoptera: Cerambycidae) is distributed widely across East Asia; its range encompasses much of the eastern half of China and the Korean peninsula (Wu and Jiang 1998, Lingafelter and Hoebeke 2002). Its population dynamics vary considerably across the range. The Asian longhorned beetle, as it is known in North America, is native to China (Haack et al. 1997, Lingafelter and Hoebeke 2002). Its population dynamics vary considerably across the range. The Asian longhorned beetle, as it is known popularly in the United States, undergoes outbreaks throughout much of China. Since 1949, reforestation and afforestation projects by the Chinese government have led to the planting of millions of hectares of forest monocultures (Hsiao 1982). Populus species primarily were planted in the northern part of the country, and the cultivars used were poorly adapted to the climatic conditions, resulting in tree water stress and enhanced vulnerability to insect borers (Luo et al. 2003). Outbreaks of A. glabripennis started in the late 1970s and have resulted in the destruction of millions of trees in the northern plantations (Lingafelter and Hoebeke 2002, Luo et al. 2003). Salix, Acer, and Ulmus, along with Populus, comprise the major host genera of A. glabripennis in China (Haack et al. 1997, Wu and Jiang 1999). Populus and Salix species have also been planted extensively as agricultural windbreaks, street trees, and highway greenbelts, producing a network of hosts throughout the cities and countryside and facilitating the spread of outbreaks.

In contrast with the situation in China, A. glabripennis does not undergo outbreaks in South Korea. It is not a common insect there, and its presence has been known primarily through a handful of specimens in museum collections (Lingafelter and Hoebeke 2002). The earliest specimens were collected in 1909, indicating that presence of the species did not result from the recent outbreaks in China and suggesting that it is endemic to South Korea. The discovery of A. glabripennis in the United States in the 1990s (Haack et al. 1997, Poland et al. 1998) has stimulated interest in the causes of the low density of the Korean populations. To date, outbreaks in the United States have been confined to urban forests in the New York and Chicago metropolitan areas. However, the likely behavior of A. glabripennis, if it should move into the surrounding diverse natural forests, is a matter of speculation (Peterson and Vieglais 2001). This question was the primary motivation for the work reported here.

After our discovery of a small population of A. glabripennis in Mt. Sorak National Park in 1999, we became interested in trying to locate more populations and to understand the causes of its apparent rarity in South Korea. In this paper, we report on our extensive and intensive surveys during the summers of 2000 and 2001 to investigate the distribution and abundance of Korean populations of A. glabripennis.
Materials and Methods

Our fieldwork in the summer of 2000 identified two native hosts of *A. glabripennis* in South Korea: the maple species *Acer mono* Maximowicz and *A. truncatum* Bunge. Our initial objective in summer 2001 was to locate natural forest stands with high densities of those tree species to search for beetles. We were often aided in our search by the commercial use of both tree species. *Koroseo* trees, as these species are known commonly in Korea, are tapped in early spring for their sap, which is sold in raw form as a health drink. Using binoculars, we scanned individual trees for adult beetles and signs of damage, which included oviposition pits chewed in the bark, adult emergence holes, and extrusions of larval frass. Eight sites were located in northern and central South Korea, while the ninth was located in the south of the country (Fig. 1).

We selected two sites for intensive survey: the Oknyo Tang rest stop in Mt. Sorak National Park and the Young Dae recreational forest, which is 13 km northeast of the Oknyo Tang site. The sites were selected because *A. glabripennis* populations had been observed in them since 2000. Evidence of beetle populations in and around the national park was gained by investigating plantings of *Acer saccharinum* L., a North American maple that is grown as an ornamental along roads and is particularly vulnerable to *A. glabripennis*. Several such plantings exhibited beetle damage, suggesting that *A. glabripennis* was present throughout the general area of the park albeit at low density.

The Oknyo Tang site consisted of a large parking lot surrounded by horticultural plantings. The plantings included 34 *A. saccharinum* trees, ranging in diameter at breast height (dbh) from 3.8 to 25.4 cm. The trees hosted a small population of *A. glabripennis*, which was counted for census purposes each year and ranged from 20 to 50 adult beetles in total at the site over the 2 yr of the study. Trees larger than 10 cm generally exhibited signs of damage. Natural forest stands with *A. mono* and *A. truncatum* lay northwest and southeast of the rest stop, with a highway and a stream separating them. The Young Dae recreational forest contained campgrounds. The study site was ~100 m from the forest entrance. Most of the infested *Acer* trees grew in a flat area between a stream and the gravel access road, and the stand continued up a steep slope south of the road.

Because *A. saccharinum* trees <10 cm in diameter were not observed to be attacked, we arbitrarily decided to investigate only *A. mono* and *A. truncatum* trees that were larger than 7 cm and flagged them at both sites in a preliminary triage before taking final measurements. All of the *A. mono* and *A. truncatum* trees larger than 7 cm were identified with metal tags and georeferenced with a Garmin GPS II Plus global positioning system. Finally, trees were measured precisely and examined for beetles and damage.

Results

From our observations, the host range of *A. glabripennis* seems to be limited to *Acer* species in South Korea. Before our initial discovery of a beetle population on *A. saccharinum* at Oknyo Tang in 1999, we inspected other tree genera generally cited as hosts in China and the United States, including *Populus, Salix, and Betula* (Haack et al. 1997, Wu and Jiang 1998), but did not find *A. glabripennis* on any of them after inspecting hundreds trees in each genus. After discovering the population on *A. saccharinum*, we conducted a brief survey in August 1999 of >200 trees of that species in street plantings in a northern neighborhood of Seoul without finding *A. glabripennis*. In subsequent years, we have examined numerous *A. saccharinum* trees planted as ornamentals throughout the South Korean countryside and found many that were infested. Several other *Acer* species grow in South Korea as well (Bang 1993, van Gelderen et al. 1994), and we have been able to survey most of them in our travels (Table 1). Of the 10 *Acer* species examined, we have observed beetles or their damage on 6, including 4 Asian and 2 North American species.

*Acer mono* is distributed widely throughout China and East Asia, whereas *A. truncatum* has a more limited distribution, primarily in Northern China and Northeast Asia (van Gelderen et al. 1994). Both species occur in South Korea, and *A. mono* is distributed widely throughout the country (Bang 1993). *A. mono* has been reported to grow over an elevational range of 100–1,400 m (Yim and Baik 1985). Our *A. mono* sites...
covered a subset of that range, from 200 to 800 m, with specific elevations as follows: Chuk Ryong San (500–600 m), Mt. Sori (200 m), Young Dae (400 m), Oknyo Tang (400–500 m), Ssanggok Valley (300–400 m), Popchusa Temple (400 m), Yongchun-Myon (300–400 m), Hilaungsa Temple (700–800 m), and Pia Valley (400–500 m). We found both tree species in two mesic montane habitats: rocky ravines, often with flowing water, and riparian habitats, with trees growing from the stream edge up the slopes on either side for considerable distances. *A. mono* was relatively plentiful at our study sites, averaging 45 stems and 0.76 m² basal area/ha at Young Dae and 76 stems and 1.28 m² basal area/ha at Oknyo Tang (Table 2). The trees were generally small: mean stem dbh was 13.6 cm at Young Dae and 11.5 and 16.1 cm in the stands north and south of the stream at Oknyo Tang, respectively. The height of trees in the northern stand at Oknyo Tang averaged 13 m (based on a sample of six co-dominant trees).

We discovered trees with *A. glabripennis* adults and evidence of damage or damage alone in six of our eight study sites in the northern one-half of South Korea (Fig. 1). We did not generally find evidence of *A. glabripennis* in mostly closed forest canopies. An example is the Chuk Ryong San site, where we spent 6 d and examined over 500 trees, primarily in dense closed canopy situations, without finding any beetles. In the end, we found one tree with beetle damage, which was growing in the open next to an access road in the park. The trees on which we typically found *A. glabripennis* grew singly in open sunny habitats along or near streams (or sometimes roads). As a caveat, one might argue that beetles were simply easier to find in open sunny habitats than in dark closed canopies of tall forest trees. Nevertheless, we expended considerable effort searching in the latter habitats. One notable example of an *A. glabripennis* host tree grew in the open on the bank above the stream at Oknyo Tang. This *A. mono* tree was interesting because it showed evidence of *A. glabripennis* infestation for several years, and its growth habit, which was bush-like with four to five large stems, seemed to have resulted from beetle activity. The main stems appeared to have been weakened by larval tunneling in the past and subsequently to have broken off, greatly reducing the tree’s stature.

Closer observations of beetle abundance at Oknyo Tang and Young Dae reinforced our initial impression that *A. glabripennis* is a relatively rare species in South Korea. Infested trees were just 5.4, 6.5, and 9.5% of all the trees surveyed in the northern and southern stands at Oknyo Tang and in Young Dae, respectively (Table 2), and few *A. glabripennis* adults were observed at any of the sites over the 2–3 d of the surveys. We attempted to estimate the extent of beetle populations, as evidenced by oviposition pits, only in the northern stand at Oknyo Tang. Numbers of pits were quite variable among the six infested trees: 7, 14,

Table 1. Common *Acer* species in South Korea from the survey of Bang (1993), with the addition of *A. truncatum*

<table>
<thead>
<tr>
<th>Species</th>
<th>Section of genus</th>
<th>Native distribution*</th>
<th>Observed or A. glabripennis adults or damage observed?</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. ginnala</em> Maximowicz</td>
<td>Ginnala</td>
<td>Korea, Manchuria, Japan</td>
<td>Yes</td>
</tr>
<tr>
<td><em>A. tegmentosum</em> Maximowicz</td>
<td>Macrantha</td>
<td>Korea, Manchuria, Russia (Amur and Ussuri Rivers)</td>
<td>Yes</td>
</tr>
<tr>
<td><em>A. negundo</em> L.</td>
<td>Negundo</td>
<td>North America</td>
<td>Yes</td>
</tr>
<tr>
<td><em>A. palmatum</em> Thunberg</td>
<td>Palma</td>
<td>Korea, Japan, Taiwan, Eastern China</td>
<td>Yes</td>
</tr>
<tr>
<td><em>A. pseudopelikanum</em> (Paxton) Komarov</td>
<td>Palma</td>
<td>Korea, Manchuria, China</td>
<td>Yes</td>
</tr>
<tr>
<td>(Paxton) Komarov</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>A. incongruum</em> Mikael</td>
<td>Penaphylla</td>
<td>Eastern China</td>
<td>Yes</td>
</tr>
<tr>
<td><em>A. mono</em> Maximowicz</td>
<td>Platamodea</td>
<td>Northeast Asia</td>
<td>Yes</td>
</tr>
<tr>
<td><em>A. plataniolus</em> L.</td>
<td>Platamodea</td>
<td>Northern Europe</td>
<td>No</td>
</tr>
<tr>
<td><em>A. tibetana</em> Cheng</td>
<td>Korea, Manchuria, Northern China, Japan</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><em>A. saccharinum</em> L.</td>
<td>Rubra</td>
<td>Eastern North America</td>
<td>Yes</td>
</tr>
<tr>
<td><em>A. mono</em> Maximowicz</td>
<td>Trifoliate</td>
<td>Korea, Manchuria</td>
<td>No</td>
</tr>
<tr>
<td><em>A. fruticosum</em> Komarov</td>
<td>Trifoliate</td>
<td>Korea, Manchuria, Northern China</td>
<td>Yes</td>
</tr>
</tbody>
</table>

*From van Gelderen et al. (1994).

Table 2. Numbers, sizes, and basal areas* of *Acer mono* and *A. truncatum* trees, and infested trees and *A. glabripennis* adult numbers at two study sites in and near Mt. Surak National Park

<table>
<thead>
<tr>
<th>Site</th>
<th>Dates of survey</th>
<th>Survey area (ha)</th>
<th>Number of trees (number of stems*)</th>
<th>Mean stem dbh (cm) (SD)</th>
<th>Basal area of <em>Acer</em> spp. (m²)</th>
<th>Currently infested trees</th>
<th>Total A. glabripennis adults observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young Dae</td>
<td>25–27 VII 2001</td>
<td>1.71</td>
<td>83 (79)</td>
<td>13.5 (5.40)</td>
<td>1.32</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Oknyo Tang (north)</td>
<td>15–17 VIII 2001</td>
<td>1.85</td>
<td>112 (183)</td>
<td>11.5 (4.98)</td>
<td>2.23</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Oknyo Tang (south)</td>
<td>31 VII–1 VIII 2002</td>
<td>1.60</td>
<td>46 (65)</td>
<td>16.1 (11.3)</td>
<td>1.90</td>
<td>3</td>
<td>5</td>
</tr>
</tbody>
</table>

* Total cross-sectional area of stems at breast height.

**Many *Acer* trees had multiple stems growing from their bases.**
21, 22, 25, and >100. The survey was conducted using binoculars, given that the height of A. glabripennis damage averaged 5.4 m for the six trees and ranged from 3.9 to 8 m. The infested trees were generally along or close to the stream and associated road at both sites—within 100 m at Oknyo Tang and within 50 m at Young Dae.

Discussion

So why are populations of A. glabripennis so sparse in South Korea in contrast with the outbreak populations in China? We propose four possible factors that may serve in combination to limit populations in the natural forests of Korea: (1) a natural resistance of individual trees to beetle attack, (2) high forest tree diversity, (3) more effective regulation by natural enemies, and (4) a host range that is highly restricted to Acer species.

Resistance of trees to attack by wood-boring beetles may involve at least two mechanisms: plant defenses, such as allelochemicals and physical properties of the bark and wood, and the general "health" of a tree that results from an adequate supply of water and nutrients (Haack and Slansky 1987). Plant defenses certainly may play a role in the resistance of the Asiatic Acer species, but no research is known on this topic. Research on the effects of water stress in triggering insect outbreaks has suggested that stressed host plants are more attractive to a female insect, or at least, that a female can detect stressed hosts (Mattson and Haack 1987a, h). The female presumably attacks stressed hosts preferentially because they provide a less resistant developmental environment for her offspring. In a preliminary attempt to test this idea, we carried out a small field experiment at Oknyo Tang in 2002 to investigate the effects of girdling A. mono trees on oviposition rates by A. glabripennis. Although the experiment found that most of the female subjects laid more eggs in stressed trees than in ungirdled controls, the results were not significant at the 0.05 level, the experiment has not been replicated, and thus, the results are not presented here.

The species diversity of natural forests containing Acer species in South Korea may confer resistance to outbreaks of A. glabripennis at the stand level. Ecologists have contended for many years that habitats with a high diversity of plant species are relatively resistant to outbreaks of herbivores (Pimentel 1961, Root 1973). We did not attempt to quantify species diversity at our two study sites, but two recent studies provided considerable information on diversity in Mt. Sorak National Park (Yim and Baik 1985, Cho and Lee 2001). Yim and Baik (1985) investigated vegetational diversity in 16 sites throughout the park. Among 112 tree species in their survey, A. truncatum was ranked 14th overall in abundance, and A. mono was ranked 22nd. One of our study sites, Jiang-Soo Dae, was located 2 km east of Oknyo Tang. That site had Quercus mongolica Fischer ranked first, followed in order by Pinus densiflora Siebold and Zuccarini, Kalopanax pictus (Thunberg) Nakai, Ulmus davidiana Planchon, and Acer pseudosieboldianum (Paxton) Komarov. A. mono was ranked 16th in abundance (Yim and Baik 1985).

Cho and Lee (2001) surveyed vegetation in 10 m by 10 m quadrats in the northern part of the Mt. Sorak National Park, ~5 km southeast of Young Dae. They found A. mono in 12 of 18 quadrants and A. truncatum in 2. Species were ranked using "importance values," which were based on plot basal areas. A. mono was a major component in two quadrants, with importance values of 42 and 38%. The other dominant species in those quadrants were A. truncatum, Fraxinus rhynchophylla Hance, Quercus serrata Thunberg, Q. mongolica, and Styra sibassia Siebold and Zuccarini. Clearly the forests at Mt. Sorak National Park are very diverse, and this may contribute to the rarity of A. glabripennis.

Because of the extremely low population levels, we have not observed much parasitism or predation on A. glabripennis. Several parasitoids of the egg and larval stages of Anoplophora species (i.e., other than A. glabripennis) have been reported in China, and a colydidid beetle, Dastarcus longulus Sharp, is a common larval-pupal parasitoid of A. glabripennis there (Qin and Gao 1988, Wang et al. 1999). As predators, woodpeckers have been cited as important factors in the mortality of A. glabripennis in China. One study reported predation rates of 31-36% on larvae (Gao et al. 1994). The most obvious source of mortality that we have observed in South Korea has been woodpecker predation, which we have seen occasionally on A. mono trees at Oknyo Tang.

Our observations have suggested that the host range of South Korean A. glabripennis is limited to Acer species. Our searches in 1999 on genera cited as hosts in China and the United States, including Populus, Salix, Betula, and Ulmus (Haack et al. 1997, Wu and Jiang 1998), did not locate A. glabripennis. Of course, we cannot be certain that populations do not exist somewhere in South Korea on species of those genera, but we did not discover any after several weeks of intensive search. The failure to find beetles may be understandable in Seoul, where we did not even observe them on A. saccharinum, a very vulnerable host. This extensive urban environment simply may be too hostile to support beetle populations, or perhaps, may be too far from source populations in natural forests. However, A. glabripennis similarly was not found on Populus, Salix, Betula, and Ulmus in and around Mt. Sorak National Park in the neighborhood of infested A. saccharinum. We speculate that the apparent limitation of A. glabripennis to Acer species as hosts may also be a factor in its relative rarity. In contrast, Chinese beetle populations have a much broader host range that probably resulted from recent natural selection after exposure to large areas of stressed and potentially vulnerable tree species and cultivars, many of which are not native to China (Luo et al. 2003).

Finally, we offer a hypothesis about the basic ecology of A. glabripennis in natural habitats that may help to explain its variable population dynamics across its
A. glabripennis may be characterized as an "edge specialist," inhabiting the forest margin. Because stream banks are a small part of the area of a natural forest, specialization in this habitat, combined with the other limiting factors already discussed, may prevent beetle populations from growing large, as is the case in South Korea. However, as humans open up sylvan environments—through forest fragmentation, wide spacing in plantation monocultures, and planting rows of trees along streets and highways and between agricultural fields—they create many edges to be exploited by an edge specialist. Several published studies have noted the phenomenon of edge-dwelling species and observed the association of forest fragmentation and one of its consequences, the proliferation of edges, with increased risk of insect outbreaks (Bellinger et al. 1989). If our hypothesis is correct, A. glabripennis is preadapted by its basic ecology to thrive in forest habitats constructed or disturbed by humans. Given the availability of edge habitats in China, coupled with the availability of newly selected host species and their vulnerability as a result of climatic stress, it is little wonder that A. glabripennis has become an outbreak species in the past few decades.

The population dynamics of A. glabripennis in South Korea stand in sharp contrast to those in China. The species maintained sparse populations in our study plots in Mt. Sorak National Park, and nowhere in the country did they exhibit outbreak dynamics. Its rarity in South Korea probably results from the combined controlling effects of the resistance of the native host species and the diverse forest stands, the activities of natural enemies, and its relatively narrow host range. So how are A. glabripennis populations likely to behave should they ultimately establish in the United States (Peterson and Vieglais 2001)? Based on our hypothesis of the species as an edge specialist, it is tempting to speculate that A. glabripennis may continue to be a problem in urban forest habitats, but will simply "disappear into the woodwork" of the diverse natural forests of the northeastern United States. However, this speculation begs the question on two critical issues: the known vulnerability of our native Acer species (let alone species in other genera) (Keena 2002, Smith et al. 2002) and the unknown effectiveness of our indigenous natural enemies.

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