

REVIEW ARTICLE

Ecology and management of exotic and endemic Asian longhorned beetle *Anoplophora glabripennis*

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- Abstract**
- 1 The Asian longhorned beetle is native to China and Korea, and was found for the first time outside its native habitat in the U.S.A. in 1996, with subsequent detections being made in Canada and several European countries.
 - 2 We review the taxonomy, distribution, basic biology, behaviour, ecology and management of endemic and exotic *Anoplophora glabripennis*, including information that is available in the extensive Chinese literature.
 - 3 This species has caused massive mortality of *Populus* species in China and models have demonstrated that it could become established in many locations worldwide.
 - 4 *Anoplophora glabripennis* is polyphagous but prefers *Acer*, *Salix* and *Populus*, section *Aigeiros*.
 - 5 Although *A. glabripennis* adults do not disperse far when surrounded by host trees, they have the potential to fly more than 2000 m in a season.
 - 6 Volatile organic compounds from preferred host trees are attractive to *A. glabripennis* and this attraction is heightened by drought stress. Males and females orientate to a volatile released by female *A. glabripennis* and males attempt to copulate after contacting a sex pheromone on the female cuticle.
 - 7 At present, *A. glabripennis* is being (or has been) eradicated from areas where it has been introduced. After detection, extensive surveys are conducted and, if breeding populations are detected, at the very least, infested trees are removed and destroyed. Close attention is paid to imported solid wood packaging material to prevent new introductions.
 - 8 Standard practice to control *A. glabripennis* in China is to spray insecticides in tree canopies. In North America, largely as a preventative measure, systemic insecticides are injected into trees. Entomopathogenic fungi have been developed for the control of *A. glabripennis*, and entomopathogenic nematodes, coleopteran and hymenopteran parasitoids and predatory woodpeckers have been investigated as biocontrol agents.
 - 9 Ecological control of *A. glabripennis* in China involves planting mixtures of preferred and nonpreferred tree species, and this practice can successfully prevent outbreaks.

Keywords *Anoplophora glabripennis*, *Anoplophora nobilis*, Asian longhorned beetle, biocontrol, Cerambycidae, Coleoptera, eradication measures, invasive insects, IPM, longicorn beetle, poplar longhorned beetle, quarantine pest.

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Introduction

The Asian longhorned beetle *Anoplophora glabripennis* (Motschulsky) has been inadvertently exported from Asia into the U.S.A. and Europe principally via solid wood packing material (SWPM) used in international cargo. It poses an enormous threat to urban, suburban and rural forests in areas where it is introduced (Haugen, 2000; Nowak *et al.*, 2001). This beetle is native to Asia and occurs naturally in China and Korea (Cavey *et al.*, 1998). Although records of *A. glabripennis* in China are known from the Qing Dynasty (1644–1912), this beetle has only caused extensive damage subsequent to the 1980s (Yang, 2005). In China alone, *A. glabripennis* causes an estimated annual loss of more than 10 billion Chinese Yuan (approximately \$1.5 billion), which is equal to approximately 12% of the total economic losses caused by forest pests and diseases (H.J. Su, personal communication). Based on information concerning the current distribution, biology, and economic impact of *A. glabripennis* in Asia and North America, together with recent European interceptions, there is a significant risk that *A. glabripennis* could become established and cause damage to important forest and fruit tree species all over the world (MacLeod *et al.*, 2002). Based on this information, *A. glabripennis* is now considered a dangerous quarantine pest in North America and the European Community (USDA-APHIS, 1998; EPPO, 2004).

Anoplophora glabripennis has an enormous destructive potential because it attacks healthy trees and spends most of its life as a larva, boring inside tree trunks and large branches. This compromises the tree's vascular system, causes severe damage to the wood's structural properties, and eventually leads to the death of the attacked trees (Cavey *et al.*, 1998). In Chicago and New York City, efforts to control or eradicate the exotic *A. glabripennis* populations have led to the removal and destruction of all trees having signs of *A. glabripennis* attack (Haack *et al.*, 1997). These eradication efforts already cost many millions of dollars annually. The estimated maximum potential national urban impact of *A. glabripennis* in the U.S.A is a value loss of \$669 billion, with tree mortality of approximately 30%, and a reduction of total canopy cover of approximately 35% (Nowak *et al.*, 2001).

Many studies of *A. glabripennis* have been conducted in China, although the relevant literature is poorly reported outside of China because much of it is published in Chinese in journals that are not readily available. The present review covers selected literature, including Chinese studies, appearing from 1985 to the present, concerning the biological, taxonomic and ecological aspects of this pest as well, as measures that have been developed for the eradication and control of *A. glabripennis*.

Taxonomy

Anoplophora glabripennis belongs to the tribe Lamiini, subfamily Lamiinae, family Cerambycidae and order Coleoptera. The tribe Lamiini comprises eight additional genera: *Goes*, *Hebestola*, *Lamia*, *Monochamus*, *Microgoes*, *Neoptychodes*, *Plagiohammus* and *Plectrodera*. All species in these genera are xylophagous, attacking coniferous and deciduous trees.

The genus *Anoplophora* is composed of 36 species that occur throughout Asia, with the highest diversity in tropical and subtropical regions (Lingafelter & Hoebeke, 2002). Elytral characters are important morphological characters used for distinguishing *A. glabripennis* from other widely-distributed sympatric cerambycid species, such as *Anoplophora chinensis* (Förster).

The similarities among all the *Anoplophora* species have often resulted in taxonomic confusion (Fukaya, 2003). It has been suggested that *A. glabripennis* from Northern China and from Southern China are actually two separate species (Chen, 1989), although this is not generally accepted. In recent years, the relationship between the two most closely-related species within *Anoplophora*, *A. glabripennis* and *Anoplophora nobilis* (Ganglbauer) has been investigated (Gao *et al.*, 2000; Tang *et al.*, 2004). A study of external morphology showed that they have the same microreticulations at the elytral base, although there is variation in colour of the elytral spots (i.e. white in *A. glabripennis* and yellow in *A. nobilis*) (Luo *et al.*, 2000). *Anoplophora glabripennis* and *A. nobilis* are generally found in the same areas and they utilize similar host tree species (An *et al.*, 2004). The peroxidase and esterase isoenzymes of these two species were compared and no significant differences were found (Zhou *et al.*, 1995; Tang & Zheng, 2002). Results obtained from studies using random amplified polymorphic DNA also suggested that they belong to the same species (An *et al.*, 2004). A contrasting result was obtained by Kethidi *et al.* (2003), where two pairs of sequence-characterized-amplified-region primers were found to differentiate *A. glabripennis* from several other closely-related cerambycids, including *A. nobilis*. To solve this uncertainty, cross-mating experiments were conducted between *A. glabripennis* and *A. nobilis*. The results obtained showed that the F1 generation could produce a viable F2 generation (Gao *et al.*, 2000). Therefore, *A. nobilis* and *A. glabripennis* are now regarded as two forms of *A. glabripennis*, in agreement with Lingafelter & Hoebeke (2002).

Additionally, *A. glabripennis* has been reported as being a sister species of *Anoplophora chinensis* (Thomson). There is potential confusion between these two species; however, a clear difference between them is the smooth elytral base in *A. glabripennis* and tuberculate elytral base in *A. chinensis*. *Anoplophora chinensis* has two morphological forms: *A. chinensis* and the former *Anoplophora malasiaca* (Lingafelter & Hoebeke, 2002). *Anoplophora chinensis* occurs in China, and its major hosts belong to the genus *Citrus*, although it has a wide host range, and appears to be more similar to *A. glabripennis*. The *malasiaca* form only occurs in Korea and Japan and preferentially attacks willows and horticultural crops (apple and pear trees), as reported by Makihara (2000). A genetic study using marker genes (e.g. cytochrome *c* oxidase or mitochondrial DNA) should be performed to better clarify the phylogeographical relationship among the different species/forms in the *Anoplophora* group.

Geographical distribution

Anoplophora glabripennis was originally restricted to Asia, being present in four climatic zones of China and Korea (Cavey



Figure 1 *Anoplophora glabripennis* geographical distribution as of 2008. The green areas represent the native range and the blue circles represent infestation records outside the native area. The numbers represents the order in which the infestations were first reported: 1, New York City, New York, U.S.A., 1996; 2, Chicago, Illinois, U.S.A., 1998; 3, Braunau am Inn, Upper Austria, Austria, 2001; 4, Jersey City, New Jersey, U.S.A., 2002; 5, Yokohama, Kanagawa, Japan, 2002; 6, Toronto, Ontario, Canada, 2003; 7, Gien, Centre, France, 2003; 8, Neukirchen am Inn, Bavaria, Germany, 2004; 9, Corbetta, Lombardy, Italy, 2007; 10, Worcester, Massachusetts, U.S.A., 2008; according to Takahashi & Ito (2005), Hérard *et al.* (2006), Haack (2006), Maspero *et al.* (2007), APHIS and EPPO reports.

et al., 1998; Lingafelter & Hoebeke, 2002; Williams *et al.*, 2004a) (Fig. 1). In China, this beetle was first detected in the eastern regions, extending from Liaoning to Jiangsu and to Shanxi, Henan, and Hubei (Yan, 1985). After exotic tree species (e.g. *Populus*) that were suitable breeding sites for *A. glabripennis* had been planted over large areas, especially in the north, and had matured (Zhao *et al.*, 2007), this beetle was recorded throughout most of the whole country, with the exception of the central Asian provinces of Qinghai, Xinjiang and Tibet (Li & Wu, 1993). However, in recent years, *A. glabripennis* was also found in Tibet (Wang *et al.*, 2003) and Xinjiang Province (Y.Q. Luo, unpublished data).

Studies in natural forests in South Korea, where *A. glabripennis* is native but not common, suggest that these beetles are naturally adapted to riparian habitats and, thus, edges of habitats; this hypothesized specialization for edges of habitats helps to account for the ready adaptability of *A. glabripennis* to fragmented and disturbed habitats (Williams *et al.*, 2004a).

An unresolved question is whether *A. glabripennis* is also indigenous to Japan. On the basis of a collection record from 100 years ago (Cavey *et al.*, 1998), Japan has been included in the indigenous area of *A. glabripennis* (Yan & Qin, 1992; Zhang *et al.*, 2002). However, according to Makihara (2002), *A. glabripennis* is not present in Japan at the present time, lending support to suggestions that it is not native to Japan.

Anoplophora glabripennis was detected outside Asia for the first time in 1996 in New York City, although it had probably already arrived in that area at least by 1990, if not before (E. R. Hoebeke, personal communication). It is likely that it was transported from China to New York City within SWPM. After 1996, this species was found in an increasing number of places in North America (Chicago, 1998; New Jersey, 2002; Toronto, Ontario, Canada, 2003; Massachusetts, 2008) (Fig. 1). In August 2008, a new infestation site was discovered in Worcester, Massachusetts, as the first occurrence in New England (EPPO, 2008b). Outside North America, the first discovery was made in 2001 in Braunau am Inn, Austria (Tomiczek *et al.*, 2002) followed by a discovery in 2002 at Yokohama in Japan (where it was considered as an invasive species) (Takahashi & Ito, 2005). In France, the first infestation was discovered

in 2003, at Gien, and a second infestation in 2004, at Sainte-Anne-sur-Brivet (Hérard *et al.*, 2006). In Germany, the first infestation was discovered in 2004, at Neukirchen am Inn, and a second infestation in 2005, at Bornheim (EPPO, 2008a). In Italy, a small infestation was discovered in 2007, at Corbetta (Maspero *et al.*, 2007). In May 2008, *A. glabripennis* was officially declared as present and under eradication in France and in Germany (EPPO, 2008a). Indeed, *A. glabripennis* has been intercepted in many more locations but, in these cases, beetles were detected before they dispersed into the landscape; such locations include detections inside warehouses after emerging from SWPM (USDA-APHIS, 2008b) and after emergence from imported bonsai (Poland; Białoński, 2003).

Several models have been developed to predict the potential survival of *A. glabripennis* worldwide. The climate-matching model CLIMEX has been employed to match the climate where the beetle is native with potential introduction areas (MacLeod *et al.*, 2002). The potential occurrence of *A. glabripennis* in Asia, North America and Europe is shown in Fig. 2. In another study, ecological niches and potential geographic distributions in North America were modelled using the Genetic Algorithm for Rule-set Prediction (Townsend Peterson *et al.*, 2004). Combining the suitability of habitat with outbreak simulation, this model showed that *A. glabripennis* has the potential to invade much of eastern North America but only limited areas of western North America. Both models clearly showed that *A. glabripennis* is able to invade many areas. Based on temperature tolerances, *A. glabripennis* may cause severe forest damage in regions with latitudes in the range 21–43°N (Keena, 2006). However, global warming has not yet been considered when modelling the potential distribution of *A. glabripennis*, although climate change would certainly alter the distribution and impact of this species.

Biology and larval development

In China, *A. glabripennis* requires 1–2 years to develop from egg to adult and generally overwinters as a larva, although it has been found on rare occasions to overwinter as an egg

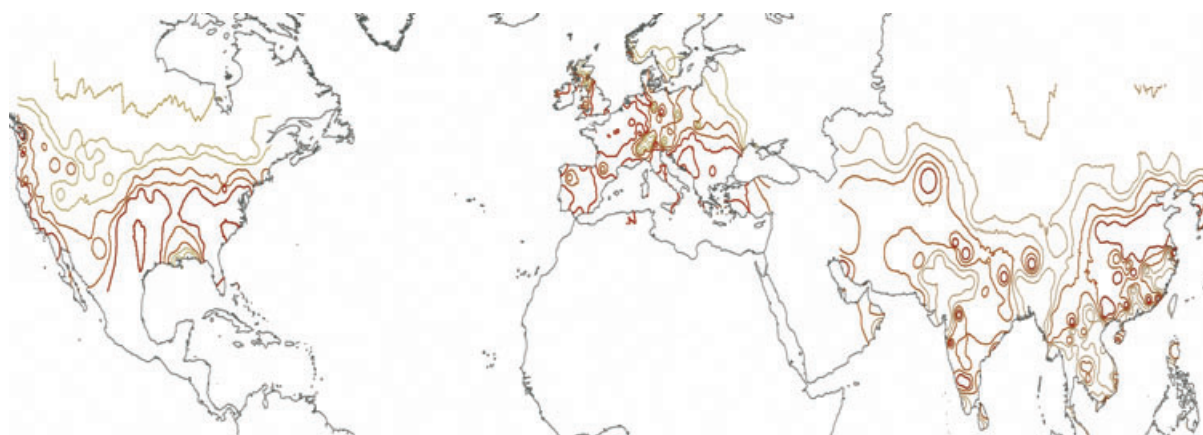


Figure 2 Potential distribution of *Anoplophora glabripennis* according to the predictive model of pest risk assessment developed by MacLeod *et al.* (2002). The original data points for North America, Europe and Asia were taken from MacLeod *et al.* (2002). These points were georeferenced on a virtual map and the original values of pest risk assessment were attributed to each point. Later raster analysis was performed using tools in ESRI® ArcMap™ 9.2 (ESRI, Redlands, California). Red, orange, and yellow lines indicate areas with pest risk indices of 75, 50, and 25, respectively.

or pupa (Li & Wu, 1993; Haack *et al.*, 2006). Voltinism may vary as a function of local climatic conditions, and a significant correlation has been established with latitude. For example, in Inner Mongolia (northern China), a single generation takes 2 years to develop, whereas, in Taiwan, one generation per year has been documented (Li & Wu, 1993). In Shandong Province (central-eastern China), approximately 90% of individuals complete one generation in 1 year. It has been estimated that overall in China about 80% of individuals can complete their development within 1 year and <20% require 2 years. However, the time to complete one generation may vary among populations in a single area, depending on the type of host in which the larvae develop. Under field conditions, it has been calculated that, to complete metamorphosis, *A. glabripennis* needs 1264.2 accumulated degree-days (DD) at a developmental threshold of 13.4°C (Yang *et al.*, 2000). Under laboratory conditions, however, the accumulated DD and the lower development temperature threshold for egg, first and second instar larvae were estimated as 250 DD at 10.2°C, 160 DD at 11.7°C and 232 DD at 11.4°C, respectively (Zhang *et al.*, 1995).

Anoplophora glabripennis adults emerge from trees and are present in the field from April/May to October, with an emergence peak in July in Yinchuan, Ningxia Province (northwestern China). The initiation of adult emergence is influenced by accumulated annual temperature (Zhao & Yoshida, 1999). Studies in China showed that male adults live for 3–50 days, and females live for 14–66 days (Li & Wu, 1993), whereas laboratory studies in the U.S.A. reported a longevity of approximately 80 and 100 days at 25°C in males and females, respectively (Keena, 2006). In New York City and Chicago, adult *A. glabripennis* have been recorded from July to December (Haack *et al.*, 1996).

The mortality rates of the different stages of *A. glabripennis* has been studied under a range of environmental conditions. The results obtained indicated that eggs and first-instar larvae were the two most critical stages during which higher mortality levels occurred. Bacterial or fungal infections played an

important role in reducing larval survival during these early developmental stages (Tang *et al.*, 1996). Chinese studies have reported that eggs need 8–12 days to mature (Li & Wu, 1993) and laboratory studies in the U.S.A. documented egg hatch in 15.0 ± 0.6 days at 25°C (Keena, 2006). After eggs are laid and before they hatch, the inner part of the bark surrounding the oviposition site becomes degraded. After egg hatch, the larvae begin to feed on the decayed phloem around the oviposition site. As they progressively move under the bark, away from the egg niche, the second-instar larvae feed primarily on the healthy phloem/cambium and feed little on the nearby xylem. The early larval stages eat approximately 4 cm² of phloem when tunnelling laterally under the tree bark, before starting to tunnel into the xylem in the late third or early fourth instar. The larval galleries are at first horizontal and slightly curved but galleries later turn upward (i.e. usually away from the roots). As the larvae tunnel, they expel frass from the initial oviposition site. At pupation, each larva creates a chamber near the outer bark. The prepupal stage (average 21.8 days) is followed by a pupal stage (average 19.6 days). After melanization, adults spend several days resting before chewing a 6–18 mm exit hole (Lingafelter & Hoebeke, 2002). Field studies have shown that one larva is capable of destroying approximately 1000 cm³ of timber before pupation (Yan & Qin, 1992). The larger larvae are always well protected inside the heartwood and are scarcely affected by the outside environment, which includes being protected from applications of chemical pesticides to tree surfaces.

Adult behaviour

Adults feed throughout their lives on leaves, twigs or the tender bark of the host trees, causing damage to living trees (Li & Wu, 1993). *Anoplophora glabripennis* adult females undergo a period of obligatory maturation feeding after emergence. On emergence, females can copulate, although their ovaries are immature and feeding is necessary for ovarian maturation; laboratory studies have estimated the female maturation period

lasts 9–15 days (Keena, 2002; Smith *et al.*, 2002). Adult males have mature spermatozoa before emergence, and feeding is necessary only to sustain their normal activity (Li & Liu, 1997).

Adults are least active early in the day and become more active late in the day (Morewood *et al.*, 2004a). However, Keena & Sanchez (2007) reported that the reproductive behaviour of *A. glabripennis* is typical of diurnally active species of the subfamily Lamiinae. Both sexes mate repeatedly and with different partners (Morewood *et al.*, 2004a).

Most females lay 25–40 white eggs under natural conditions in China; usually, one egg is deposited in each oviposition site (Li & Wu, 1993). Under laboratory conditions, the highest recorded average fecundity was 66.8 eggs per female at 25°C, and estimates from the U.S.A. suggest that, in nature, fecundity may vary in the range of 30–178 viable eggs per female (Keena, 2002, 2006). Fecundity is positively correlated with beetle body size and negatively correlated with beetle age. Fecundity is strongly affected by host tree, with eggs per female ranging from 45.9 for the black willow (*Salix nigra* Marshall) to 193.3 for Norway maple (*Acer platanoides* L.) (Smith *et al.*, 2002). Similarly, the oviposition rates differed based on female food, with averages ranging from 1.80 eggs/day for *A. platanoides* to 0.54 eggs/day on *S. nigra* (Smith *et al.*, 2002).

In nature, females select an oviposition site based on stem diameter and bark thickness of the host tree but bark thickness appears to play the more important role (Zhao *et al.*, 1997). On cut wood, oviposition has been found to be negatively correlated with bolt surface area, bolt diameter and bark thickness (Smith *et al.*, 2002). In addition, *A. glabripennis* prefers host tree species with rough bark and leaves without epidermal trichomes and glands (Yang *et al.*, 1997). Based on infested trees in China and Chicago, *A. glabripennis* usually begins attacking trees near the base of the crown, on both the upper trunk and lower parts of major branches (Haack *et al.*, 2006). However, on *Populus* trees in China where branches occur all along the trunk, *A. glabripennis* commence attacks on the lower trunk. Beetles can reattack the same tree, year after year, by laying eggs further down toward the roots in successive years; however, studies documenting and investigating female decisions to continue ovipositing in the same tree rather than move to a different tree have not been conducted.

To locate suitable host trees, adult beetles are capable of flying several hundred metres or more in a single flight. The average annual population dispersal distance measured by Wen *et al.* (1998) was 106.3 m, and this dispersal was positively correlated with wind velocity and temperature. However, a mean dispersal distance of 266 m has been recorded using the mark–release–recapture method (Smith *et al.*, 2001). Further mark–release–recapture studies demonstrated that, although 72% of beetles were recaptured within 300 m of release points, some beetles were recaptured up to 2600 m away (Smith *et al.*, 2004). In these studies, beetle dispersal from release trees was positively associated with the abundance of beetles at the release tree and smaller female beetles moved greater distances and were more attracted to taller trees (Bancroft & Smith, 2005). In a mark–recapture using harmonic radar tracking techniques, Williams *et al.* (2004b) found that individual adults have an average movement of

approximately 3 m per day, with a total average movement distance of approximately 14 m in 9–14 days. The differences among these experiments may be explained, at least in part, by use of different methods for the different studies, different ages of beetles used, and the varying natural conditions under which studies were conducted. For example, *A. glabripennis* tends to fly farther to find suitable host trees when no host trees are present in the surrounding area, whereas, when host trees are densely planted, little dispersal by adult *A. glabripennis* occurs (Huang, 1991). A study of *A. glabripennis* infestations in New Jersey suggests that a low density introduction of these beetles remains localized for many years and spread is slow until, at some point, the local resource becomes over-exploited, at which time dispersal from hundreds of metres to over 1 km occurs (Sawyer, 2007b).

Host species

The major economic damage due to *A. glabripennis* reported globally is to poplars (*Populus*), maples (*Acer*), willows (*Salix*) and elms (*Ulmus*) (Sawyer, 2003; Haack *et al.*, 2006). In China, *A. glabripennis* has caused the greatest damage to poplar species. *Populus* (Fam. Salicaceae) comprises a genus of 22–80 species, where hundreds of hybrids, varieties and cultivars exist. In the 1960s and 1970s, poplar trees were planted extensively in China along roadsides, in farmland as shelterbelts, and in cities as ornamental trees. Moreover, the Chinese government promoted the establishment of plantations of poplar for pulpwood production and to counteract desertification in the northwest of China, forming the so-called ‘Green Wall’ by the Three-North Shelterbelt Programme, launched in 1978 (Ma, 2004) with a goal of 23 million ha of plantations by 2050 (Sigaud, 1999). Afforestation programmes usually employed monocultures of fast-growing species with low water-use efficiency that became water-stressed and were therefore more susceptible to insect pests (Cao, 2008). In addition, most of the poplars planted during these campaigns were species that were susceptible to *A. glabripennis* (Zhao *et al.*, 2007). These especially included poplars from the section *Aigeiros* and hybrids with parents from the section *Aigeiros*: *Populus nigra* L. var. *italica*, *Populus nigra* var. *thevestina*, *Populus × euramericana* (Dode) Guineir [also called *Populus × canadensis* (Moench)], which is a hybrid of *Populus deltoides* (Marsh.) × *P. nigra*. In addition, the hybrid *Populus × dakuanensis* (Hsu) (also called *Populus × dakuanensis* or *P. dukuanensis*, section *Tacamahaca*), which has low genetic diversity and is also very vulnerable to *A. glabripennis* was widely planted. Subsequent to the late 1970s, as these susceptible trees matured throughout China, populations of *A. glabripennis* increased exponentially and this cerambycid became the most serious forest pest in China (J. Wu, personal communication). Li *et al.* (2005) reported that there are approximately 6.67 million ha of poplar plantations in China, accounting for 20% of the total timber plantations of the country.

Although in China, *A. glabripennis* populations predominantly increased on the poplar plantings from the sections *Tacamahaca* and *Aigeiros*, it prefers poplar species and hybrids of the section *Aigeiros*. In the *Aigeiros* section,

P. nigra, which is native to Europe, southwest and central Asia and northwestern Africa, is considered the most vulnerable species. In particular, the poplars *P. nigra* var. *Italica* and var. *Thevestina* are very susceptible to *A. glabripennis*. *Populus deltoides* is less susceptible, followed by *P. × euramericana*. Poplar species belonging to the sections *Tacamahaca* (balsam poplars) and *Leucoides* are also attacked by *A. glabripennis*, although at lower levels (Li & Wu, 1993). Poplar species belonging to the sections *Turanga* (e.g. *Populus euphratica* Oliv. and *Populus pruinosa* Schrenk.) and *Populus* [e.g. *Populus alba* L., *Populus hopeiensis* Hu et Chou, *Populus tomentosa* (Carr.) and *Populus tremula* (L.)] are considered less susceptible or slightly resistant (Bao *et al.*, 1999). No records have been found regarding reactions of *A. glabripennis* to poplars from the section *Abaso*. Table 1 presents a list of poplar species ranked in order of host preference of *A. glabripennis*.

Although *A. glabripennis* has caused vast economic damage to specific types of poplars in China, this species is very polyphagous. An extensive investigation of the different tree species attacked by *A. glabripennis* was conducted in the north-western Chinese region of Yinchuan, Ningxia Province. *Anoplophora glabripennis* was found to damage 34 tree species (excluding economic fruit tree species such as *Malus* spp. and *Pyrus* spp.) belonging to 14 genera in ten different families, as *Acer*, *Betula*, *Elaeagnus*, *Fraxinus*, *Hedysarum*, *Hippophae*, *Koelreuteria*, *Platanus*, *Populus*, *Robinia*, *Salix*, *Sophora*, *Tilia* and *Ulmus* (Li *et al.*, 1999a). However, it was not reported whether *A. glabripennis* is able to complete its development on all of these species. To measure susceptibility or resistance of trees to *A. glabripennis*, a field trial was conducted using 138 tree species (Gao *et al.*, 1997b); *Acer* was the most attractive genus, followed by several *Populus* species, such as *P. × dakuanensis*, *Populus simonii* Carr., *Populus cathayana* Rehd. and *Populus pseudo-simonii* Kitag.

Specific amino acids, such as aspartic acid, arginine, glycine, glutamate, serine, threonine and valine, were correlated positively with increasing host plant resistance (Yan *et al.*, 1996).

In North America, *A. glabripennis* has been reported to attack 18 deciduous tree species belonging to 12 genera. The more attractive included *Acer negundo* (L.), *A. platanoides*, *Aesculus* spp., *Betula* spp., and *Fraxinus pennsylvanica* (Marsh.) (Haack *et al.*, 1997; Lingafelter & Hoebeke, 2002). *Acer saccharum* (Marsh.) was preferred for oviposition in one laboratory study (Morewood *et al.*, 2003) but *A. glabripennis* preferred the North American understory striped maple, *Acer pensylvanicum* L. over *A. saccharum* (Hajek & Kalb, 2007). In the U.S.A. and Canada, maples are of great concern because they are very common in northeastern forests and are widely planted along city streets and in parks.

A list of species ranked in order of host suitability for *A. glabripennis* is reported in Table 2 (Gao *et al.*, 1997b; Sawyer, 2003). This list classifies host trees within 23 genera, although, within one genus, huge variability in host preference is possible (e.g. *Populus* spp.). There is great discrepancy between host preferences of *A. glabripennis* (the most attractive genus is *Acer*) and the greatest recorded damage (mostly *Populus*); presumably this discrepancy is a result of the enormous availability of *Populus* in the native range of *A. glabripennis*. In the U.S.A., a host suitability index was

developed for several tree species by taking into account the number of living life stages, the number of exit holes, and the number of oviposition pits found for each tree species (Haack *et al.*, 2006). It was found that *A. glabripennis* has different host suitability when comparing Chinese and North American forests. The host suitability index was higher for *Populus* and *Salix* compared with *Ulmus* in China, and generally higher for *Acer* and *Ulmus* than *Fraxinus* in North America (data from Chicago). Therefore, *Acer* and *Ulmus* are considered to be the main host trees in the U.S.A., although, in decreasing order, *Fraxinus*, *Aesculus*, *Betula*, *Salix*, *Celtis*, *Malus*, *Pyrus*, *Sorbus* and *Tilia* were also attacked (Haack *et al.*, 2006). In Europe, the largest infestation was recorded in Braunau am Inn, Austria, where a total of 106 trees was found to be damaged by *A. glabripennis*, with the majority (95 trees) in the genus *Acer*, followed by *Betula* (four trees), *Aesculus hippocastanum* L. (two trees) and *Fagus sylvatica* L. 'Atropunicea' (two trees), (Tomiczek & Hoyer-Tomiczek, 2007). In the other European outbreaks, the situation is very similar, with the exception of the outbreak at Sainte-Anne-sur-Brivet in France, where 37 *Betula* sp., 23 *Acer* spp. and 18 *Populus* sp. were found to be damaged from a total of 88 infested trees (Tomiczek & Hoyer-Tomiczek, 2007). In Italy, three *Betula pendula* Roth and one *Acer pseudoplatanus* L. were found to be severely infested by *A. glabripennis* (Maspero *et al.*, 2007).

Host-plant finding

The ability to perceive and respond to volatile organic compounds (VOCs) released by host trees plays an important role in host selection and reproduction of cerambycid species (Allison *et al.*, 2004). Several research projects have focused on the effects of VOCs released from the trunks or leaves of host species on adults. For example, an attraction test was performed using the highly susceptible host *A. negundo* and adults of *A. glabripennis* (Wen *et al.*, 1999). More than 66% of the beetles within a radius of 100 m were attracted to feed on *A. negundo*. In the same study, the greatest distance from which *A. glabripennis* could be attracted was found to be 240 m. The VOCs released from *A. negundo* were characterized by gas chromatography-mass spectrometry (GC-MS). A total of 32 compounds were identified, including alcohols, ketones, aldehydes, esters, terpenoids and carboxylic acids (Li *et al.*, 1999b). Hexanol, *trans*-2-hexenol, *cis*-3-hexenol, butyl acetate, hexanal and *trans*-2-hexenal were tested by electroantennography (EAG), and they all elicited strong antennal responses. To determine when the highest quantity of VOCs is released by *A. negundo*, a study on the release of VOCs was performed at different times in the summer (Li *et al.*, 2003). The quantities of VOCs released during the day varied throughout the summer; in July, the highest peak was found at 14.00 h, whereas, in August, the peak was at 10.00 h (Li *et al.*, 2002).

Because elevated damage by *A. glabripennis* has been reported to occur on water-stressed *A. negundo* trees, the VOCs released from water-stressed plants of this species were investigated (Jin *et al.*, 2004). The results obtained showed that, when the trees were subjected to drought stress, nine volatile

Table 1 Categorization of poplar species as hosts for *Anoplophora glabripennis*

Category	Species/hybrids	Section
Very good hosts	<i>Populus nigra</i> : 'Pyramidalis', 'Italica', 'Thevestina'	Aigeiros
	<i>Populus deltoides</i> 'Brangarsi'	Aigeiros
	<i>Populus</i> × <i>euramericana</i> : 'Luisa Avanzo', 'Bellini', 'Guardi'	Aigeiros
Good hosts	<i>Populus</i> × <i>xiaozhuannica</i> , <i>P.</i> × <i>xiaozhuannica</i> : 'Opera', 'Popularis'	Aigeiros × Tacamahaca
	<i>Populus nigra</i>	Aigeiros
	<i>Populus deltoides</i>	Aigeiros
	<i>Populus lasiocarpa</i>	Leucooides
	<i>Populus pseudoglauca</i>	Leucooides
	<i>Populus cathayana</i>	Tacamahaca
	<i>Populus gansuensis</i>	Tacamahaca
	<i>Populus pseudosimonii</i>	Tacamahaca
	<i>Populus simonii</i>	Tacamahaca
	<i>Populus ussuriensis</i>	Tacamahaca
	<i>Populus simonii</i> × <i>P. nigra</i> 'Pyramidalis': 'Baichensis', 'Taiqing', 'Italica'	Aigeiros × Tacamahaca
	<i>Populus nigra</i> × <i>P. simonii</i>	Aigeiros × Tacamahaca
	<i>Populus</i> × <i>beijingensis</i>	Aigeiros × Tacamahaca
	<i>Populus</i> × <i>berolinensis</i>	Aigeiros × Tacamahaca
	<i>Populus</i> × <i>dakuanensis</i>	Tacamahaca
	<i>Populus</i> × <i>russki</i>	Aigeiros
<i>Populus stalinetz</i>	Aigeiros	
Occasional hosts	<i>Populus</i> × <i>xiaohei</i> , <i>P.</i> × <i>xiaohei</i> 'Heilin-1'	Aigeiros × Tacamahaca
	<i>Populus deltoides</i> : 'Nankang', 'Qingji #1,2', 'Shanhaiguan', 'pyramidalis'	Aigeiros
	<i>Populus balsamifera</i>	Tacamahaca
	<i>Populus alba</i> 'Pyramidalis'	Populus
	<i>Populus alba</i> × <i>Populus bolleana</i>	Populus
	<i>Populus alba</i> × <i>Populus tomentosa</i>	Populus
	<i>Populus deltoides</i> × <i>P. simonii</i>	Aigeiros × Tacamahaca
	<i>Populus</i> × <i>euramericana</i> (= <i>P.</i> × <i>canadensis</i>)	Aigeiros
Rare hosts or resistant hosts	<i>Populus</i> × <i>euramericana</i> 'Veruirubens', 'Vegeherata 272', 'G-158', 'I-214', 'Triplo', 'Gattoni', 'Cima'	Aigeiros
	<i>Populus euphratica</i> , <i>P. euphratica</i> : 'Pyramidalis', 'PE-214'	Turanga
	<i>Populus pruinosa</i>	Turanga
	<i>Populus alba</i>	Populus
	<i>Populus davidiana</i>	Populus
	<i>Populus hopeiensis</i>	Populus
	<i>Populus tomentosa</i> , <i>P. tomentosa</i> 'Hopeinica', 'Honanica'	Populus
	<i>Populus tremula</i>	Populus
	<i>Populus tremuloides</i>	Populus

Populus classification with respect to section according to Weilun & Wen (2005), Wang (2004) and Gao *et al.* (1997b).

compounds (acetophenone, butyl alcohol, pentyl alcohol, *trans*-2-hexenol, *cis*-3-hexenol, pentanal, pentanoic acid, hexanol and hexanoic acid) increased, whereas the sesquiterpene longifolene decreased. After the trees were watered, the amount of acetophenone increased further, whereas all the others VOCs decreased. Using GC coupled with electroantennographic detection (GC-EAD), three compounds (butyl alcohol, pentyl alcohol and *cis*-3-hexenol) elicited the strongest antennal responses. These three compounds may play an important role in signalling to *A. glabripennis* the presence of water-stressed trees that are highly susceptible to insect attack. Moreover, these results are in agreement with the general observation from Chinese poplar forests indicating that *A. glabripennis* populations increase to outbreak levels after the trees have undergone several years of drought stress (Gao *et al.*, 1997a).

A study was conducted comparing the relationship between VOCs released by some poplar and willow species and the susceptibility of these trees to *A. glabripennis* attack (Li *et al.*, 2002). VOCs were collected from the leaves of four tree species: *Populus* × *xiaozhuannica* (Hsu and Liang) 'Opera' (a hybrid between *P. nigra* 'Italica' and *P. simonii*), *P. alba* 'Pyramidalis' (Bunge), *P. tomentosa*, and *Salix matsudana* (Koidz). The results showed that the more susceptible trees (e.g. *P.* × *xiaozhuannica* 'Opera') released more esters and terpenoids, whereas resistant trees (e.g. *P. tomentosa*) released more alcohols and aldehydes (Li *et al.*, 2002). Peroxidase was also found to have a close relationship with host resistance against *A. glabripennis*; resistant trees displayed a higher degree of peroxidase activity (Hou *et al.*, 2000). Recently, the VOCs of *Acer mono* Maxim., *Acer truncatum* Burge, *A. negundo*, and *A. platanoides* were identified and linked with

Table 2 Worldwide categorization of host trees species for *Anoplophora glabripennis*

Category	Genus	Common Name
Very good hosts	<i>Acer buergerianum</i> Miq	Trident maple
	<i>Acer mono</i> Maxim.	Painted maple
	<i>Acer negundo</i> L.	Boxelder
	<i>Acer saccharum</i> Marsh	Sugar maple
	<i>Acer truncatum</i> Bunge.	Purple blow maple
	<i>Aesculus hippocastanum</i> L.	Horsechestnut, buckeye
	<i>Populus</i> spp. ^a	Poplar
	<i>Salix babylonica</i> L.	Willow
	<i>Salix matsudana</i> Koidz.	
	<i>Ulmus pumila</i> L.	Elm
Good hosts	<i>Betula</i> spp.	Birch
	<i>Platanus</i> spp.	Plane tree, sycamore
Occasional hosts	<i>Celtis sinensis</i> Pers.	Hackberry
	<i>Elaeagnus angustifolia</i> L.	Silverberry, Russian Olive
	<i>Sorbus</i> spp.	Mountain ash
Rare hosts or resistant hosts	<i>Fraxinus americana</i> L.	White ash
	<i>Fraxinus mandshurica</i> Rupr.	Manchurian ash
	<i>Fraxinus sogdiana</i> Bunge	Ash (no common name)
	<i>Hibiscus</i> spp.	Rose-of-Sharon
	<i>Malus</i> spp.	Apple, crab apple
	<i>Morus</i> spp.	Mulberry
	<i>Prunus</i> spp.	Cherry, plum
	<i>Pyrus</i> spp.	Pear
	<i>Quercus</i> spp.	Oak
	<i>Robinia</i> spp.	Black locust
	<i>Tilia</i> spp.	Linden, basswood
	<i>Ailanthus altissima</i> (Mill.) Swingle	Tree of heaven
	<i>Alnus</i> spp.	Alder
	<i>Albizia julibrissin</i> Durazz.	Mimosa, silk tree
	<i>Broussonetia papyrifera</i> (L.) Vent.	Paper mulberry
	<i>Catalpa bungei</i> C. A. Mey.	Catalpa
	<i>Cercis chinensis</i> Bunge	Chinese redbud
	<i>Melia azedarach</i> L.	Chinaberry

The table is based on the host preference categorization proposed by Gao *et al.* (1997b), integrated with the categorization by Sawyer (2003).

^aA detailed categorization of the different species of the *Populus* genus is shown in Table 1.

feeding damage of *A. glabripennis*. The feeding preference was *A. negundo* > *A. mono* > *A. truncatum* > *A. platanoides*. Ketones, alcohols and aldehydes were proportionally lower and alkanes and esters were proportionally higher for the most suitable hosts (Zhang *et al.*, 2008).

Host selection by *A. glabripennis* may also be driven by some repellent volatiles that signal the presence of nonhost

trees. One compelling example is given by the high resistance of callery pear, *Pyrus calleryana* (Decne.), a native of China that is resistant to both larvae and adults of *A. glabripennis* (Morewood *et al.*, 2004b). *Anoplophora glabripennis* laid far fewer eggs on callery pear compared with golden-rain tree (*Koelreuteria paniculata* Laxmann), river birch (*Betula nigra* L.) and London plane [*Platanus × acerifolia* (Aiton) Willd.]. Moreover, the few larvae that hatched on callery pear failed to survive. Adult beetles feeding on callery pear had reduced longevity and females feeding only on callery pear failed to develop any eggs.

These negative effects may be caused by the chemical composition of the tree, including toxic compounds and/or secondary metabolites that interfere with normal beetle development (Morewood *et al.*, 2004b). Two other plants, *Ailanthus altissima* (Mill.) and the chinaberry tree *Melia azedarach* (L.), have strong negative effects on the larval growth of *A. glabripennis* (Zhao *et al.*, 1994). The monoterpenes β -pinene and β -caryophyllene (referred to as β -syringene in the original study) have been identified from *A. altissima* and *M. azedarach* and these VOCs effectively repel *A. glabripennis* adults (Tang *et al.*, 1999).

Pheromones

Studies have been conducted to characterize the pheromones of *A. glabripennis*. Preliminary experiments have shown that male orientation is influenced by volatiles released by females (Li *et al.*, 1999c), although these substances were not chemically identified. Further investigations revealed that two dialkyl ether volatiles, 4-(*n*-heptyloxy)-butanal and 4-(*n*-heptyloxy)-butan-1-ol, are potential male-produced pheromones in this species (Zhang *et al.*, 2002). They are secreted by males in a ratio of 1:1 and they elicit strong EAG responses in both males and females. Olfactometer experiments showed that they were significantly attractive to adults, although they do not seem to be involved in sex recognition (Zhang *et al.*, 2002).

GC-MS analysis of female cuticular extracts showed that five monounsaturated compounds were consistently more abundant in females than in males (Zhang *et al.*, 2003). These compounds were identified as the alkenes (*Z*)-9-tricosene, (*Z*)-7-pentacosene, (*Z*)-9-pentacosene, (*Z*)-7-heptacosene and (*Z*)-9-heptacosene, with a relative ratio of 1:2:2:1:8. Males attempted to mate when contacting a surface coated with a synthetic mixture of these compounds, indicating that the blend effectively elicits copulatory behaviour in males (Zhang *et al.*, 2003).

Recently, a contact sex pheromone of *A. chinensis* (previously *A. malasiaca*) was discovered from the ether extract of 200 females. Three male-active compounds have been newly characterized as a group of γ -lactones called gomadalactone A, B and C (Mori, 2007; Yasui *et al.*, 2007). It is not known whether chemicals similar to the gomadalactones might also occur in *A. glabripennis*. It is often very difficult to distinguish between sex, aggregation and defence pheromones in coleopteran species, and individual compounds can function in several ways (e.g., see Suzuki *et al.*, 1988; Verheggen *et al.*, 2007). Thus, it is possible that, for *A. glabripennis*, the

female-produced contact sex pheromone or the male-produced pheromone resulting in attraction may also have additional functions.

Artificial rearing

The nutritional and rearing requirements for *A. glabripennis* were first studied by Zhao *et al.* (1999). Five different artificial diet protocols were compared, where the major differences were the content of poplar bark powder. The average larval development period was similar among the five diets, ranging from a minimum of 32 days to a maximum of 267 days, and related to rearing temperature and whether a cold period was required for pupation or not. The highest pupation rate (approximately 72%) was observed when adopting a diet, where poplar bark powder was mixed with starch, sugar, cholesterol and vitamin C. The females reared on this diet laid an average of 160 eggs, with 62.0% eclosion. This diet was later modified and included in a comparative study with two other artificial diets previously developed for the cerambycids *Plagiohammus spinipennis* (Thomson) and *Monochamus carolinensis* (Olivier) (Dubois *et al.*, 2002). The results of these trials showed that females grew faster when cellulose was included instead of sawdust, although males grew faster on diets with sawdust. The cellulose-based diet was further modified by increasing the water content from 50% to 64.6% (w/w), allowing faster development to the adult stage. The use of an artificial diet based on cellulose instead of powdered phloem or bark drastically reduced the time needed for diet preparation and standardized the rearing procedure (Dubois *et al.*, 2002).

Recently, a modification of an artificial diet for rearing the red oak borer *Enaphalodes rufulus* (Haldeman) was developed to further reduce the cost of rearing by developing a 'pourable' diet (the Dubois diet solidifies before distribution into rearing containers) (Keena, 2005). For the pourable diet, when three antifungal compounds were added, larval survival and development rate improved (Keena, 2005).

Dubois *et al.* (2002) and Keena (2005) reported that not all larvae of *A. glabripennis* require a chill period before pupation. This chill can be required to induce pupation, otherwise larvae will often continue moulting with little weight gain. *Anoplophora glabripennis* larvae that stabilize in weight gain but do not pupate by 18–20 weeks on an artificial diet should be subjected to a chill period at $10 \pm 1^\circ\text{C}$ and $85 \pm 10\%$ relative humidity for 84 days (Keena, 2005). After 84 days of chill, mean time to pupation was 48–51 days. Because of the length of time required for development and the need to change the artificial diet occasionally and provide freshly cut wood for oviposition, it is very expensive to rear *A. glabripennis*. North American researchers have estimated that rearing *A. glabripennis* costs at least US\$ 21 per beetle, excluding overhead costs (Keena, 2005).

Pest management

Preventing introductions

The life cycle of *A. glabripennis* combines concealed immature stages, flying adults and a tendency to lay small numbers

of eggs in several trees, so it is very difficult to prevent spread of *A. glabripennis*. The USDA Animal and Plant Health Inspection Service (APHIS) has established domestic quarantine regulations that prohibit the local transport of potentially infested wood or wood products from areas where *A. glabripennis* infestations have been found. APHIS has also instituted stringent shipping regulations that require fumigation of all SWPM from China (USDA-APHIS, 1998). Similar regulations have also been established in other countries (Schroder *et al.*, 2005). Currently, the European Union, the U.S.A. and 32 additional countries enforce some level of compliance with the ISPM 15 regulations 'Guidelines for regulating wood packaging material in international trade'; for example, refusing entry to any wooden package that does not comply with the ISPM 15 regulations (Wilson, 2006).

Eradication measures

Intensive surveys for trees infested by *A. glabripennis* have been conducted in several countries to verify whether this pest insect had already established. Detection practices include a visual inspection of all potential host trees in the potentially infested areas, concentrating on adult emergence holes, oviposition scars, sap flow and larval frass. For large trees, inspection with binoculars from the ground is not very effective and inspection from a hydraulic lift improves detection. However, the most efficient (and costly) method for detection in the U.S.A is the use of trained tree climbers searching for signs of beetles within tree canopies.

In areas where *A. glabripennis* has been detected as a new invasive species, eradication programmes have been adopted (Haack *et al.*, 1997); these include felling, removal and chipping or incineration of infested trees (Smith *et al.*, 2001). In the U.S.A., trees are usually surveyed for beetles within an 800 m radius of each infestation point and trunk or soil injections with imidacloprid are applied to each potential host tree within this radius (USDA-APHIS, 2006). Between 2000 and 2005, over 600 000 trees were preventively treated with imidacloprid in the U.S.A. Such methods require time, are labour-intensive and are thus costly.

Eradication measures have been quite successful in the Chicago area, where *A. glabripennis* was declared eradicated in 2008, after four seasons without finding adult beetles or signs of infestation (USDA-APHIS, 2008a). Between 1998 and 2006, approximately 1800 trees were removed as part of the Chicago eradication programme and 2006 was the last year when imidacloprid was applied to trees. However, on 1 August 2008, an adult Asian longhorned beetle was detected in the city of Deerfield, Illinois, approximately 20 km north of the northern boundary of the previously regulated area of Chicago (EPPO, 2008b). Eradication of *A. glabripennis* was also successful in Yokohama, Japan, where chemical treatments were applied in September 2002 and heavily damaged trees were removed and destroyed (Takahashi & Ito, 2005). No more beetles were captured or observed and, in 2005, the Yokohama eradication effort was reported as successful.

Other infestations have not yet been declared eradicated and efforts are ongoing. In the U.S.A., over 6000 trees had been

removed and destroyed in New York as well as over 600 in New Jersey by the end of 2005 (USDA-APHIS, 2006). In New York and Chicago, most trees that were removed were infested by *A. glabripennis* and relatively few high risk trees were also removed. In Canada, subsequent to 2003, an estimated 25 000 potential host trees have been removed in the Greater Toronto area, only 600 of which were infested by *A. glabripennis* (NAPPO, 2007). In Germany, a quarantine zone with a radius of 2 km was established around the *A. glabripennis* infestation in 2004, and a total of 16 infested trees were destroyed on site by felling and burning (Schröder *et al.*, 2005).

Physical control measures

Measures for physical control of *A. glabripennis* have been very important in China. Major approaches have included the removal of heavily damaged trees and the replacement of susceptible trees with resistant trees such as *A. altissima* (Mill.). In addition, local forestry organizations have promoted other physical control measures, such as catching adults, killing eggs and young larvae, and blocking frass holes (Gao & Li, 2001). As an example, in Yinchuan (Ningxia Province, northwestern China), a public campaign among the local students during the summer 2007 led to the collection of approximately 500 000 beetles (Forest Protection News of China, 2007). In Bengbu (Anhui Province, central-eastern China), in the summer of 2005, visible oviposition sites in willow and poplar trees were manually inspected and eggs were removed. One year later, a drastic decline in the *A. glabripennis* population was recorded (S. Liu, personal communication). These physical control measures can be effective in maintaining the *A. glabripennis* population below pest thresholds, especially in the case of young trees and in urban areas. However, measures for physical control are very laborious, expensive and time-consuming.

Chemical control measures

The most widely adopted method for controlling high populations of *A. glabripennis* in China consists of spraying the pyrethroid cypermethrin in the canopies of host trees to kill adults (Liu *et al.*, 1999). Another commonly used chemical control strategy utilizes bamboo or wooden sticks containing aluminium phosphide that are inserted into larval frass holes, generating phosphine to kill the *A. glabripennis* larvae (Zhao *et al.*, 1995a). As the sticks are deeply inserted into larval frass holes, this measure is generally safe to the public and is still widely used in China.

Injections of systemic insecticides into the trunks of infested trees and the application of trunk-coating insecticides comprise effective measures with a low environmental impact (Zhao *et al.*, 1995b). In particular, injecting tree trunks with the organophosphate insecticide methamidophos not only controls *A. glabripennis*, but also piercing-sucking insect pests (Zhang *et al.*, 1994). It has been demonstrated that approximately 90% of the first- to fourth-instar larvae and 65% of adults are killed by injecting methamidophos into the trunks of poplar trees (Zhu *et al.*, 1998). Moreover, 3 months after injection, the mortality

of adults feeding on these treated poplars remained at 70–80% (Xu *et al.*, 1999).

The toxicity of several systemic insecticides was studied under laboratory and field conditions, demonstrating that the neonicotinoid imidacloprid and azadirachtin can be very effective against *A. glabripennis* (Poland *et al.*, 2006a, 2006b). Imidacloprid was found to translocate rapidly inside trees after injection and to persist at lethal levels for several months. However, studies have differed regarding the extent to which imidacloprid is distributed uniformly within trees (Poland *et al.*, 2006a; Lewis & Molongoski, 2007). An antifeedant response of *A. glabripennis* to imidacloprid-treated poplars has been reported (Wang *et al.*, 2005; Poland *et al.*, 2006a); such an antifeedant response could increase dispersal. However, the results obtained from studies evaluating imidacloprid-treated trees in New York City showed that *A. glabripennis* escaped or survived treatment in only 11 of almost 250 000 at-risk, treated trees in New York, Illinois and New Jersey, resulting in the emergence of only nine adults from treated trees (Sawyer, 2007a). The treatment of trees with imidacloprid is considered a key component in the eradication of *A. glabripennis* in Chicago.

In China, a control method based on coating tree trunks with an insecticide (cypermethrin) has been developed, taking advantage of the tendency of *A. glabripennis* adults to walk along tree trunks after emergence (Xu *et al.*, 2003b), as well as when searching for mates or moving from feeding sites (twigs) to oviposition sites. Adult beetles become contaminated when passing along the trunk or the tree branches where an insecticide has been applied in a band around the tree. This method appears to be particularly effective when used on smaller 'trap trees'. Moreover, a new formulation has been developed in an effort to prolong the time of efficacy and reduce the negative environmental impact of pesticide treatments. This formulation consists of microcapsules that break easily to release the effective component cypermethrin after coming into contact with *A. glabripennis* adults. The microcapsules are sprayed on the trunks or leaves of infested trees and the results of several trials appear to be very promising (Zhang *et al.*, 1999b; Pan *et al.*, 2001; Sun *et al.*, 2003).

Biological control measures

Biological control of *A. glabripennis* has focused on the application of entomopathogenic fungi, nematodes, insect parasitoids and predators. Entomopathogenic fungi are promising natural enemies because of their potential to create epidemics. Several strains of *Beauveria* and *Metarhizium anisopliae* (Metsch.) Sorok. were found to be strongly virulent against larvae of *A. glabripennis* (Zhang *et al.*, 1999a; Dubois *et al.*, 2008). One virulent strain of *Beauveria brongniartii* (Sacc.) Petch isolated from *A. chinensis* was shown to be highly effective against adults of *A. glabripennis* (Shimazu *et al.*, 2002). In the U.S.A., although *B. brongniartii* was studied in early trials, it was unclear whether it is native to North America and, if not, whether this fungal species could be then used for control; therefore, studies have focused on use of a strain of *M. anisopliae* that is already registered for pest control (Dubois *et al.*, 2008).

A bio-pesticide formulation has been developed in Japan for infecting cerambycid adults and has also been adapted for *A. glabripennis*. Nonwoven fibre bands containing cultures of entomopathogenic fungi with surfaces covered with infective spores are applied around trunks or branches of trees (Higuchi *et al.*, 1997). In Japan, trees are treated in this way to control longhorned beetles in orchards, as well as to control the vector of pinewood nematode, *Monochamus alternatus* (Hope) (Shimazu *et al.*, 2002). Fungal bands can be stored in sealed polyethylene bags for over 400 days at 5°C (Higuchi *et al.*, 1997). Comparisons of the efficiency of different methods for releasing *B. brongniartii* in field sites demonstrated better results with *B. brongniartii*-impregnated nonwoven fabric bands compared with spray applications of spore solutions (Xu *et al.*, 2003a). Evaluations of the efficiency of *M. anisopliae* and *Beauveria* spp. applied in fibre bands have been carried out in confined areas and in open field conditions (Dubois *et al.*, 2004a, b; Hajek *et al.*, 2006). Bands impregnated with *M. anisopliae* and *B. bassiana* were shown to be effective against *A. glabripennis* in open field conditions, even 63 days after treatment (Hajek *et al.*, 2003). The longevity of *A. glabripennis* adults was reduced and the daily oviposition rate per female consistently decreased in fungal treatment areas compared with controls. Laboratory studies demonstrated that, in addition to decreased oviposition, some offspring also die as a result of infection, most likely because of external contamination from the mother (Hajek *et al.*, 2006). It has been demonstrated that *B. bassiana* (Bals.) Vuill. applied as fungal bands, could spread up to 50 m in natural forest conditions (Hu *et al.*, 2005). Spores of *M. anisopliae* applied on bands spread down tree trunks, especially in association with rain events (Shanley & Hajek, 2008). Fungal infections could also be spread by adult beetles contaminating their environments after exposure to fungal bands (Shanley & Hajek, 2008).

The infectivity of four species of entomopathogenic nematodes belonging to the families Steinernematidae and Heterorhabditidae, to larvae of *A. glabripennis* has been evaluated (Solter *et al.*, 2001). All four species were able to infect the larval stages, although *Steinernema carpocapsae* (All) and *Heterorhabditis marelatus* (Liu & Berry) were the more effective species. In another comparison of seven different nematode species, it was shown that the two species *S. carpocapsae* and *Steinernema feltiae* (Filipjev) were most effective against *A. glabripennis* larvae (Fallon *et al.*, 2004). In laboratory bioassays, it was demonstrated that a concentration of 5000 nematodes of *S. carpocapsae* (Agriotas and Beijing strains) per beetle was effective in killing larvae and pupae of *A. glabripennis* (Wang *et al.*, 1996). In a field study, where similar protocols were adopted, 7500 nematodes per beetle were necessary to reduce the *A. glabripennis* population by approximately 85% (Liu *et al.*, 1998).

A detailed investigation of the insect natural enemies attacking *A. glabripennis* has been carried out in the region of Ningxia (northwest China). *Dastarcus helophoroides* Fairmaire (= *Dastarcus longulus* Sharp) (Coleoptera: Bothrideridae) was found to be the major natural enemy attacking *A. glabripennis* larvae and pupae (Wang *et al.*, 1999). This beetle is an external parasitoid of several cerambycid beetles and xylocopid hymenopterans. The newly-hatched predator larvae search for

the larvae or pupae of their hosts and paralyze them prior to feeding (Togashi & Itabashi, 2005). *Dastarcus helophoroides* has been reared on a large scale on an artificial diet, and has been employed in field experiments as a promising biocontrol agent (Ogura *et al.*, 1999). Another external parasitoid of larval *A. glabripennis* is the bethylid *Scleroderma guani* (Xiao et Wu) (Hymenoptera: Bethyridae) (Cheng *et al.*, 2003); the many experiments conducted investigating use of this parasitoid for control have often yielded promising results. A similar species, *Scleroderma sichuanensis* Xiao, was recently employed successfully as a biological control agent against larvae of *A. chinensis* in China (Kaishu, 2006). In Italy, a new species of a gregarious endoparasitoid was identified from the field-collected eggs of *A. chinensis* and taxonomically described for the first time as *Aprostocetus anoplophorae* Delvare (Hymenoptera: Eulophidae) (Delvare *et al.*, 2004). The probable origin of this egg parasitoid is Japan or China, most likely arriving in Europe on imported bonsais infested with eggs of *A. chinensis*. *Aprostocetus anoplophorae* may represent an important biological control for *A. glabripennis* because it is also able to parasitize this species (Hérard *et al.*, 2005).

Among predators, the Chinese woodpecker *Dendrocopos major* (Beicki) has been shown to play an important role in reducing both larval and adult populations of *A. glabripennis* (Li *et al.*, 2000). In the forests surrounding Wulate City (Inner Mongolia Province), there is an ongoing project on the ecological impact of *D. major* on *A. glabripennis* populations (J.F. Hu, unpublished data). In an effort to increase the natural woodpecker population, different types of artificial nests have been tested under field conditions and the occurrence of woodpecker offspring has been recorded. Woodpeckers strongly impact *A. glabripennis* populations in the winter and spring, when the birds preferentially feed on older larvae and pupae.

Forest management

In China, outbreak populations of *A. glabripennis* subsequent to the 1980s have been linked with forest composition; it was found that forests with diversified species could dramatically suppress outbreaks of longhorned beetles, whereas forests of only one susceptible tree species were at risk (Yan & Yan, 1999). Trees that are resistant are often slow-growing and of less commercial value, whereas, in comparison, trees preferred by *A. glabripennis* are often fast-growing with higher commercial value. To create the optimal economic and ecological benefits, trees of attractive species, such as *A. negundo*, can be planted together with repellent species, such as *P. calleryana*, *A. altissima* or *M. azedarach*, to create in the forest a 'push and pull' effect and thus avoid the creation of outbreak populations that can decimate forests (Luo *et al.*, 2003). To design and improve diverse stands, several research projects were carried out to select clones of *Populus* spp. to plant along with tree species that are resistant to *A. glabripennis*. A forest resistance index was designed as a measure of susceptibility of different forest types to *A. glabripennis* attack (Zhou & Yang, 1996). It has been hypothesized that rich forest communities would be less susceptible (i.e. when preferred tree species are grown together

with resistant tree species, they may keep the population of *A. glabripennis* below the economic threshold (Yan & Yan, 1999). In Ningxia Province, for example, populations of *A. glabripennis* decreased drastically after the pure poplar forest was changed to mixed forest by replacing susceptible tree species with resistant species (Luo *et al.*, 2003). On the basis of this strategy, new forest plantations with mixed species are presently being designed, although this approach is limited because it cannot be applied to areas that are already heavily infested by *A. glabripennis*.

Conclusions

Anoplophora glabripennis is native to China and Korea, although the information available on this species in these two countries is very different. Although *A. glabripennis* populations are generally low in Korea, in China, *A. glabripennis* has been a tree-boring pest of unprecedented proportions causing massive tree mortality subsequent to the 1980s. The extent of the problem in China is especially caused by extensive plantings of susceptible *Populus* spp., many of which are at least partially exotic. Although the massive mortality of plantations of susceptible poplars in northern China as a result of afforestation efforts beginning in 1978 is no longer seen, *A. glabripennis* remains a problem; species, hybrids and clones of poplar that are at least in part susceptible are still being planted to some extent because they often display desirable characteristics (e.g. especially fast growth). In addition, willow trees are traditionally planted and many willows are susceptible (Table 2). In China, control methods often include the removal of the most susceptible tree species and the use of chemical insecticides to kill adults.

With today's global economy, one might expect that with huge populations of *A. glabripennis* in China, this pest might be transported elsewhere. Beginning in 1996, *A. glabripennis* was found in New York City, although it was certainly introduced before then. Subsequent to 1996, *A. glabripennis* has also been found infesting trees in two other US states, in Toronto, in Canada, in four European countries (with detection in Italy as recently as 2007) and in the U.S.A. in 2008, as well as in Japan. At all locations where it has been found, eradication programmes have been undertaken, often at great expense. Eradication requires cutting and disposing of infested trees and often systemic insecticides have been applied to susceptible trees in surrounding areas. At present, two eradication programmes are considered successful, whereas others continue. The fact that *A. glabripennis* has usually been introduced into more urban areas and not in native forests makes eradication more feasible; in addition, because *A. glabripennis* often do not fly very far, this aids the possibility of eradication, although difficulties in detecting these beetles is a definite concern for eradication efforts.

Whether *A. glabripennis* will be found in more locations remains to be seen; however, because detection is difficult as a result of the beetle's habitat, this beetle is always found breeding in trees long after its introduction. It is highly likely that *A. glabripennis* would be able to establish itself in many more areas worldwide because of its strong

adaptability, broad host range and ability to spread through SWPM transport. It is therefore necessary to work toward preventing introductions and, at the same time, to develop early warning systems to detect this species as early as possible in newly-infested areas. An effective monitoring method could be achieved by concentrating on the use of attractive volatile compounds, such as pheromones and/or kairomones. Attractant traps may improve the detection and control of *A. glabripennis* considerably, although more information about the chemical ecology of this species is necessary and effective traps must be designed.

Although all introduced infestations of *A. glabripennis* have been (or are being) eradicated, it is still possible that *A. glabripennis* will become established in one of the areas it has invaded. Therefore, it is necessary also to consider control strategies. Methods for physical, chemical and biological control have been developed in China and are being investigated in the U.S.A. Presently, in areas where *A. glabripennis* has been introduced, eradication efforts utilize detection, the removal of host trees (either infested or not infested but within the infestation area) and chemical control. Work in China on ecological management (e.g. improving forest stand diversity) comprises an important approach for maintaining populations of *A. glabripennis* below the economic threshold density.

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