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# History and development of an isolated outbreak of Asian longhorn beetle *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in southern England

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- **Abstract** 1 Asian longhorn beetle *Anoplophora glabripennis* is a major international quarantine pest that is capable of killing a wide range of broadleaved trees. In 2012, an outbreak of *A. glabripennis* was discovered at Paddock Wood in southern England, which prompted an eradication programme and research to determine when the population had established, as well as how quickly it was spreading.
  - 2 Tree ring analysis of infested stems and branches showed that the first *A. glabripennis* adult emerged in 2003 and that the beetle had been present for approximately 10 years before it was discovered. However, the population had increased relatively slowly and, even though it could be shown that some beetles travelled 96–203 m to lay eggs in new trees, the population as a whole had not spread further than 234 m.
  - 3 Survival rates of larvae were similar to rates observed in other *A. glabripennis* populations, although failure at the egg-laying stage and adult mortality at or before emergence were higher than recorded elsewhere.
  - 4 A combination of factors appears to have allowed *A. glabripennis* to establish at Paddock Wood: the presence of a highly susceptible host (sycamore), multiple introductions of adult beetles over several years, and a run of warmer than average summers at the time of the initial colonization.

**Keywords** *Anoplophora glabripennis*, dispersal, invasive species, outbreak history, tree ring analysis.

# Introduction

Asian longhorn beetle *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae) is an invasive pest that is highly damaging to deciduous broadleaved trees, particularly to species of *Acer, Aesculus, Betula, Ulmus, Populus* and *Salix* (Hu *et al.*, 2009; Haack *et al.*, 2010; Meng *et al.*, 2015). It is native to China and Korea, but has been transported around the world in untreated wood packaging material and introductions have led to the establishment of populations in North America and Europe (Hérard *et al.*, 2006; Haack *et al.*, 2010). In 2012, a small population of *A. glabripennis* was found established at Paddock Wood in Kent in southern England, adjacent to a small commercial premises where a company had previously imported stone and slate from China. This was the first recorded outbreak of *A. glabripennis* in the U.K. (Straw *et al.*, 2015a, 2015b).

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Anoplophora glabripennis is particularly destructive because it attacks living, healthy trees, as well as stressed and dying trees (Lingafelter & Hoebeke, 2002; Hu et al., 2009; Haack et al., 2010). The adult females lay eggs under the bark and the larvae bore into the wood, creating galleries and tunnels that disrupt the vascular tissues and weaken the stems and branches, making them prone to breakage and collapse. The physical damage caused by the larvae also allows secondary organisms to invade, which further degrade the woody tissues. Complete development takes 1-3 years and successive generations of the beetle in the same tree lead to a progressive deterioration in conditions, eventually resulting in the death of the tree (Haack et al., 1997; Lingafelter & Hoebeke, 2002). In urban areas, severely infested trees soon become a hazard and the most visible impact of infestation is seen in the costs of removing and replacing highly valued ornamental trees along streets and in parks and gardens (Haack et al., 1997; Nowack et al., 2001; Faccoli & Gatto, 2016). In the wider environment, in woodlands and commercial forestry plantations, A. glabripennis has the potential to cause major

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economic losses through tree mortality and the degradation of timber and wood quality (Gao *et al.*, 1993; MacLeod *et al.*, 2002; Hu *et al.*, 2009).

In Europe, A. glabripennis is listed in the A1 Annex of the EU Plant Health Directive as a quarantine pest that requires regulation (EPPO, 2013a). The Directive requires Member States to survey and monitor for the pest and eradicate any outbreaks that are discovered. Consequently, immediately after A. glabripennis was discovered at Paddock Wood, a series of delimiting surveys was undertaken to determine the scale of the outbreak, and an eradication programme was put in place to remove and destroy all of the infested trees (Straw et al., 2015a). In total, 66 trees were found to be infested with A. glabripennis and these, as well as a further 2163 trees that potentially could have harboured the beetle, were felled and destroyed before the next generation of adults had an opportunity to emerge (Straw et al., 2015b).

When the trees were felled, they were searched thoroughly for signs of infestation: first to assist the management programme by identifying infested trees and the outer extent of the outbreak and, second, so that material containing A. glabripennis life stages could be recovered and analyzed to provide information on the biology of the pest and how long it had been present. In the present study, life-stage numbers and mortality are combined with the results from a tree ring analysis and the distribution of infested and non-infested trees, with the aim of indicating how quickly the population was increasing and how fast it was spreading. This information, combined with previous analyses of host selection and the life cycle and phenology of A. glabripennis at Paddock Wood (Straw et al., 2015a, 2015b), provides a case study on the performance of an isolated population of A. glabripennis in a relatively cool climate, and this can be used as a guide for future survey and monitoring work and the management of other outbreaks.

# Materials and methods

#### Study site, surveys and mapping

The outbreak of *A. glabripennis* in Kent was located 1.5 km north of Paddock Wood (latitude: 51°11'N; longitude: 0°24'E) in a rural area consisting of a mixture of agricultural fields, sheep grazed pastures and small woodlands, with a scattering of houses and gardens and light industrial units, all surrounded and connected by hedgerows and lines of trees. A busy main road ran through the middle of the outbreak area from north-to-south. This area is generally low-lying and flat at approximately 14 m a.s.l. and, for the U.K., it has a relatively warm and dry climate. Mean January and July temperatures at East Malling Research Station, 12 km north of Paddock Wood, during the period 2000–2012 were 5.2 and 17.6 °C, respectively, and mean annual rainfall was 660 mm (University of East Anglia CRU, 2014) (Fig. 1).

Surveys carried out to determine the extent of the *A. glabripennis* outbreak involved inspecting trees visually from the ground and any trees with signs of infestation were tagged and given an individual reference number. The surveys were started within the known area of infestation and progressed outwards and, eventually, they included all deciduous broadleaved trees out to a distance of 800 m and selected groups of preferred hosts (*Acer* spp.) out to 2.5 km. The location of each infested tree,



**Figure 1** Mean June–August temperatures (a) and total annual rainfall (b) at East Malling Research Station, 12 km north-east of Paddock Wood, from 2000 to 2012. The dashed lines indicate the mean June to August temperature during this period (17.0 °C) and the mean total annual rainfall (660 mm).

or suspected infested tree, was recorded using GPS and the position of the tree relative to permanent features (e.g. roads and buildings) and other infested trees was measured on the ground and plotted to within 1 m on large scale maps of the outbreak area.

Once the initial distribution of infested trees had been determined, a boundary at 100 m was established to delimit an official area of infestation. Thereafter, from April through to August 2012, all infested trees and all trees in genera known to be a host of *A. glabripennis* that were growing within the infestation area were cut at ground level and, except for samples retained for analysis, were destroyed by burning (Straw *et al.*, 2015a). As the trees were felled, they were cut into smaller manageable pieces and each piece was searched carefully for signs of *A. glabripennis* infestation. This inspection process led to the discovery of further infested trees that had not been identified by the visual surveys. As these new trees were located, the 100-m boundary of the infestation area was extended and any new trees that were brought within the boundary were also felled and inspected and destroyed. This process was continued until no more infested trees were found (Straw *et al.*, 2015a).

## Sample collection and processing

Stems and branches that contained *A. glabripennis* life stages, or which showed signs of infestation or damage, were cut into smaller pieces 20-40 cm in length. These samples were packaged securely and transported under licence (FERA Scientific Licence 6647/198760/0) to Forest Research at Alice Holt, where they were stored at 15 °C in a secure quarantine facility. Each sample was labelled with the tree number, species, diameter of the main stem at 1.3 m above the ground (diameter at breast height; DBH) and felling date. Trees were searched as thoroughly as possible for signs of infestation, and they were deliberately over-sampled in an attempt to ensure that no infested material was missed. The final dataset is therefore considered to represent as complete a picture as possible of the *A. glabripennis* population and the distribution of infested trees.

## Life stages of A. glabripennis

Sample processing started as soon as the first material was brought in from the field and was completed by mid-September. The length and diameter of each stem and branch section were measured and a record was made of whether the wood was alive or dead at the time of collection. The external surface of the sample was then examined and the number of oviposition pits and adult exit holes were recorded. When an adult female *A. glabripennis* lays an egg, it chews an oviposition pit in the bark through which it inserts an egg into the tissues between the cambium and sapwood. These oviposition pits are distinctive and can be counted on the surface of the bark (Ric *et al.*, 2007).

After the young larva has hatched, it excavates a small, irregular gallery on the surface of the sapwood under the bark. Later, during the late third-instar or early fourth-instar stage, the larva tunnels into the wood and generally bores upwards, eventually producing a tunnel some 10-30 cm in length. Fully grown larvae pupate in an enlarged chamber at the end of the feeding tunnel. The adult beetle emerges within this pupal chamber and then chews its way to the outside, through a circular exit hole that is typically 10 mm in diameter (Sánchez & Keena, 2013).

All of these features were visible in the samples from Paddock Wood. After the numbers of oviposition pits and exit holes had been recorded, the bark was removed from each sample and the numbers of egg-laying sites and small galleries under the bark were counted. Sites where eggs had been laid were recognized by the presence of an oval patch of dark brown necrotic tissue, which develops around the egg after it has been deposited (Ric *et al.*, 2007; Meng *et al.*, 2015). The samples were then split using hand tools to reveal larval feeding tunnels in the wood and to recover *A. glabripennis* life stages, which were preserved in 70% industrial methylated spirits. Larvae were classified as alive, dead, missing or taken by a bird. Later, the body length and head capsule width of each larva were measured and recorded.

#### Tree ring analysis

Samples that contained adult exit holes, both current exit holes and old exit holes formed in previous years, were dried at room temperature and, once dry, they were cut transversely with a band saw through the middle of each exit hole. The resulting cross-sections were polished using a series of fine sand papers to reveal the individual growth rings formed before and after the adult *A. glabripennis* had emerged. The number of growth rings formed after the adult emerged was used to determine the year in which emergence had taken place. At Paddock Wood, adults of *A. glabripennis* emerged late in the season and the outer edge of the exit holes almost always occurred in line with the outer edge of the current growth ring, which made dating the year in which the adults emerged relatively straightforward (Straw *et al.*, 2015b).

In samples consisting of live stems and branches, the last complete growth ring was formed in 2011, the year before the trees were felled, whereas, in dead stems and branches, the last growth ring, although it may have been formed in 2011, could also have been formed in an earlier year if the stem or branch had been dead for some time. For simplicity of analysis, the last growth ring in dead material was assumed to have been formed in 2011, and where this may have influenced how the data were interpreted is highlighted in the Results section and is considered further in the Discussion.

The year when the adult A. glabripennis emerged was determined for all exit holes found in the samples, and this information was used to estimate how many adult A. glabripennis emerged each year over the whole period that the beetle was present at Paddock Wood. The year in which the adult emerged was also used to estimate when the egg that produced the adult was laid, assuming that the full life cycle from egg to adult took either 2 or 3 years. The majority of A. glabripennis at Paddock Wood appear to have required 3 years to complete their development, although a proportion may have been able to complete their life cycle in 2 years (Straw et al., 2015b). Oviposition at Paddock Wood occurred relatively late in the year and the majority of eggs over-wintered before hatching. As a result, a life cycle completed in 2 years (24 months) actually spanned three calendar years, and a life cycle completed in 3 years (36 months) spanned a period of four calendar years. For example, under a 2-year life cycle, adults emerging in 2011 would have started as eggs that were laid in late summer or autumn 2009. Under a 3-year life cycle, the eggs would have been laid in 2008 (Straw et al., 2015b).

Two cohorts of established *A. glabripennis* larvae were present in the samples from Paddock Wood, represented by larvae 10-35 mm in length that had over-wintered once and larvae >35 mm in length that had over-wintered twice (Straw *et al.*, 2015b). The presence of these larvae, and a small number of newly-hatched first and second-instar larvae in the samples, was also used to estimate when eggs were laid.

#### Rate of spread and colonization of new trees

Once it had been determined from which trees adults had emerged in each year and where eggs had been laid, it was possible to reconstruct how the *A. glabripennis* outbreak had developed over time. The information from the tree ring analysis was combined with the location of the infested trees to determine which trees were colonized in each year and how the beetle had spread. Distances from trees from which adults emerged to trees on which eggs were laid in the same season were calculated for all trees that could be shown to have received eggs in the same year. The shortest distance from a tree from which an adult emerged to a tree that received eggs was identified as the minimum egg-laying distance (MED). The MED had a value of zero if adults emerged from the same tree on which eggs were being deposited, or it could be many metres if the tree on which eggs were deposited was a long way from the nearest tree from which an adult emerged. MED values were estimated for all trees that received eggs in each year, and median and maximum MED values were compared between years and when the date of egg-laying was based on either a 2- or 3-year life cycle.

## Distribution of host and non-host trees

The influence of host availability on the development of the *A. glabripennis* outbreak was investigated by comparing egg-laying distances and the direction of spread with the distribution of host and non-host trees. The distribution of broadleaved trees was recorded when the eradication programme was being carried out. The infestation area was divided into smaller sectors and, before the trees were felled, all broadleaved trees with a stem diameter of  $\geq 2 \text{ cm}$  at 1 m above the ground that were growing in each sector were identified to species and counted. Trees along two field boundaries up to 100 m further west of the infestation area were also identified and recorded (Straw *et al.*, 2015a).

Trees recorded in the infestation area were divided into three host categories: (i) tree species that were attacked by *A. glabripennis* at Paddock Wood; (ii) tree species known elsewhere to be a host of *A. glabripennis* but which were not attacked at Paddock Wood; and (iii) tree species that were not attacked at Paddock Wood and which are extremely rare hosts of *A. glabripennis*, or are questionable hosts or are known not to be a host (non-hosts). Host status was determined using published information on *A. glabripennis* host plants (van der Gaag & Loomans, 2014).

## Results

Two-thirds of the trees attacked by *A. glabripennis* at Paddock Wood were sycamore *Acer pseudoplatanus* (Table 1), and this tree species contained 70% of all *A. glabripennis* larvae that were accounted for in the samples and 98% of adult exit holes (Table 2). A large proportion of the *A. glabripennis* larvae and exit holes in sycamore were recovered from one large tree located near the centre of the outbreak (tree 21). This tree had a DBH of 60 cm and contained 213 *A. glabripennis* larvae, pupae and teneral adults, as well as 498 exit holes. Only five other sycamore trees contained more than 10 *A. glabripennis* larvae (maximum = 35) and only one other tree contained more than 10 exit holes.

Amongst the other tree species that were attacked, only willow *Salix fragilis* contained more than 100 *A. glabripennis* larvae, and the majority of these larvae were less than 10 mm in length and were not definitely established (Table 2). Despite

 Table 1
 Tree species attacked by Anoplophora glabripennis at Paddock

 Wood

Tree species	Number of infested trees
Sycamore, Acer pseudoplatanus L.	43
Field maple, Acer campestre L.	9
Willow, Salix fragilis L.	4
Birch, <i>Betula pendula</i> Roth.	3
Poplar, <i>Populus x canadensis</i> Moench	2
Grey sallow, <i>Salix cinerea</i> L.	2
Box elder, <i>Acer negundo</i> L.	1
Horse-chestnut, Aesculus hippocastanum L.	1
Goat willow, Salix caprea L.	1
Total	66

the relatively high numbers of larvae in *S. fragilis*, only two *A. glabripennis* adults had emerged from this tree species (Table 2).

The current cohorts of *A. glabripennis* developing in the trees at the time the trees were felled were represented by oviposition sites where the egg, if present, had not developed further, small galleries under the bark where the larva had died and disappeared, and older, established larvae and pupae and adults (columns 2–8 in Table 2). In other circumstances, the egg sites (column 2) and small galleries under the bark (column 3) would have been expected to have produced or contain a live larva but, for some unknown reason, the egg was missing or had not hatched or the larva had disappeared (or, in a few cases, the larva had been taken by a bird). Oviposition sites and larval galleries from previous years that were partly or completely calloused over were also found in the samples but, because these belonged to older cohorts that would have produced adults in 2011 or earlier, they are not included in Table 2.

# Mortality during the egg and early larval stages

A large number of oviposition pits were counted on the surface of the samples (Table 2) and, although the majority of these were probably made in 2011, an unknown proportion may have been formed in previous years. Consequently, the total numbers of oviposition pits are not directly comparable with the numbers of egg-laying sites or larvae. Comparing the total number of oviposition pits observed (column 1 in Table 2), or which must have been present originally but were destroyed by subsequent feeding damage (columns 5–8 in Table 2), with the number of oviposition pits where an egg appeared to have been laid (columns 2–8 in Table 2) suggests, however, that approximately 25% of oviposition pits were made without an egg being deposited.

An oval patch of necrotic tissue was found under approximately half of the oviposition pits, although an egg or larva was not always found in these situations. Where an egg was found, it was not always clear whether the egg was viable but had not hatched, or was infertile and had died. Therefore, although the numbers of egg-laying sites that did not develop further provided an indication of failure at this stage, it was not possible to estimate the actual number of eggs laid or the actual percentage of eggs that hatched or would have hatched.

Table 2	Total n	umbers	of oviposition	, pits,	failed galleries,	living life	e stages	and adult	exit holes	of Anoploph	ora glabripe	<i>ennis</i> in	n different	tree sp	oecies at
Paddock	Wood	in 2012													

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]
Trees species	Oviposition pits	Egg-laying site, no further development	Small feeding gallery, no larva <sup>a</sup>	Recently hatched (≤10 mm)	Established larvae (10–65 mm)	Larva/pupa taken by bird	Dead/missing larvae	Live pupae/ adult	Adult exit holes <sup>b</sup>
Acer campestre	9	7	15	0	4	3	0	0	3
Acer negundo	0	1	1	2	0	0	0	0	0
Acer pseudoplatanus	1664	773	315	9	252	22	54	36	555
Aesculus hippocastanum	13	9	2	0	1	3	1	0	0
Betula pendula	2	2	7	0	2	6	2	0	0
Populus x canadensis	0	0	0	1	0	0	0	0	1
Salix caprea	17	8	0	0	0	0	1	0	0
Salix cinerea	16	20	3	0	10	0	2	0	3
Salix fragilis	520	282	29	77	8	10	30	0	2
Total:	2241	1102	372	89	277	44 <sup>c</sup>	90	36 <sup>d</sup>	564

<sup>a</sup>Small galleries beneath the bark formed in 2011 or 2012 that should otherwise have contained a larva. The larvae apparently died at an early stage before creating a tunnel into the wood. Not included in the numbers of established larvae that were dead or missing [7].

<sup>b</sup>Total exit holes (i.e. current and older exit holes combined).

 $^{c}$ Includes 10 small larvae  $\leq$ 10 mm in length that were taken by birds from small galleries under the bark and 34 established larvae >10 mm in length taken from feeding tunnels in the wood.

<sup>d</sup>Thirty-three pupae and three adult beetles.

By contrast, larva that had hatched and started to feed could be counted accurately. Mortality during this early phase was high. Out of the total number of *A. glabripennis* larvae accounted for in the samples, 41% died and disappeared without trace in small galleries under the bark before making a tunnel into the wood, and 1% were taken from a small gallery under the bark by a bird. The remaining 58% of larvae developed further and tunnelled into the wood.

The percentage of *A. glabripennis* larvae dying in small galleries under the bark varied between sycamore trees. In tree 21, which was heavily infested, 24% of larvae died in small galleries under the bark before creating a tunnel into the wood, whereas, in the other sycamore trees, which were less heavily infested, 61% of larvae died before tunnelling into the wood. The difference in the percentage of larvae dying was significant ( $\chi^2 = 86.0, d.f. = 1, P < 0.001$ ).

## Mortality amongst older established larvae

Once larvae tunnelled into the wood, their chances of survival appeared to improve. Out of 437 larvae that had formed tunnels in the wood (including those found as pupae and adults), 72% were alive, 8% were taken by birds and 20% had died *in situ* (i.e. were either dead or missing) (Table 2). Survival in sycamore was significantly higher than in the other tree species. In sycamore, 81% of larvae in the wood were found alive, 4% were taken by birds and 15% died *in situ* (n = 356), whereas, in the other tree species, 31% were found alive, 25% were taken by birds and 44% had died *in situ* (n = 81) ( $\chi^2$  = 87.1, d.f. = 2, P < 0.001).

Mortality of older larvae also varied between sycamore trees. A lower percentage of larvae in the wood were found alive and more were taken by birds or died *in situ* in tree 21, the heavily infested tree (74%, 5% and 21% of larvae, respectively; n = 204),

compared with larvae in the other sycamore trees (90% alive, 2% taken by birds and 8% dead *in situ*, respectively; n = 152) ( $\chi^2 = 14.6$ , d.f. = 2, P < 0.001).

## Mortality at adult emergence

Three adult *A. glabripennis* that would have emerged in 2012 were found in the samples. The remains of a further 44 adult beetles were also recovered. Thirty-two of these had died and failed to emerge in 2011, whereas the others had died either in 2010 or in an earlier year. There was no obvious reason why these adults had died. Some were found dead inside their pupal chamber, but others had died when attempting to chew their way to the outside.

Twenty-seven of the adults that died in 2011 had not produced an exit hole. If these adults are added to the 259 adults that emerged successfully in 2011, or which managed to produce an exit hole before they died, then a total of 286 adult *A. glabripennis* were present in 2011. The death of 32 of these adults indicates an overall mortality rate before or at emergence of 11%. However, given that some of the exit holes found in dead wood may not have been dated accurately and the adults may have emerged in a previous year, this is probably an underestimate of adult mortality at this stage. By contrast, the numbers of adults found alive or dead in living stems and branches, where the exit holes were dated accurately, provides a maximum value for adult mortality. Ninety-six adults were present in live stems and branches in 2011 and, of these, 22 (or 23%) had died at or just before emergence.

#### Population establishment and increase

The year of emergence was determined or estimated for 555 exit holes out of a total of 564 exit holes that were found in the



Figure 2 The total numbers of adult *Anoplophora glabripennis* emerging each year at Paddock Wood, as indicated by the numbers of exit holes produced in each year. The numbers of exit holes that were found in live or dead stems and branches are indicated.

samples (Table 2). Nine exit holes were damaged either when the trees were felled or when the samples were processed and could not be dated. The earliest date for the emergence of an adult beetle was provided by a single exit hole formed in 2003 (Fig. 2). No exit holes were dated to 2004, but 11 exit holes were produced in 2005. All of the exit holes formed in 2003 and 2005 were found in live stems and branches and therefore the dating of adult emergence was accurate. The oldest exit hole found in dead wood had five growth rings to the edge of the cross-section, indicating that the adult emerged no later than 2006.

The total number of adult exit holes produced each year increased exponentially from 2005 to 2011 (Fig. 2), although this is probably an over-estimate of the actual rate of population increase. The combined number of exit holes found in live wood and dead wood and allocated to a particular year indicates the maximum number of adults that might have emerged in that year but, because some of the exit holes in dead wood may have been formed 1 or 2 years earlier, the number of adults that actually emerged in the year may have been lower. By contrast, exit holes found in live stems and branches were dated accurately and indicate the minimum number of adults that must have emerged in each year. The actual numbers of A. glabripennis emerging at Paddock Wood in each year will have been somewhere between these upper and lower estimates, and the increase in the numbers of adults emerging over time was therefore probably closer to a linear rather than an exponential rate of increase (Fig. 2).

The numbers of trees that contained *A. glabripennis* larvae in each year and the number of trees from which adults emerged are shown in Fig. 3. The numbers of infested trees in Fig. 3 are based on a 2-year life cycle and, on this basis, the first *A. glabripennis* eggs would have been laid in late summer or autumn 2001 and the first larvae, hatching from these eggs, would have occurred in 2002. If the presence of larvae had been based on a 3-year life cycle, then the first eggs would have been laid in 2001. From this time onwards, the number of infested trees increased steadily. In any one year, approximately half of the trees had new exit holes (Fig. 3).



Figure 3 The numbers of trees at Paddock Wood that contained established larvae of *Anoplophora glabripennis* (grey columns) or in which new exit holes were produced (black columns), in each year from 2001 to 2011. The numbers of trees with larvae are based on a 2-year life cycle.

## Adult emergence in 2012

In 2012, there were 134 mature A. glabripennis larvae  $\geq$ 35 mm in length in the infested trees and 36 pupae and adults, which would otherwise have emerged, or which did emerge into the sample bag, later in the season. Therefore, approximately 170 A. glabripennis adults might have been expected to emerge at Paddock Wood in 2012. This compares with 79–259 adults that emerged successfully in 2011, 63–124 adults that emerged in 2010 and 51–86 adults that emerged in 2009 (Fig. 2 and Table 3). (The upper and lower limits of the numbers of adults emerging are given by the number of exit holes in live wood and in live and dead wood combined, respectively.) It would appear, therefore, that the numbers of A. glabripennis adults emerging in 2012 would have been similar to or less than the numbers emerging in 2011, and that the population would not have continued to increase at the same rate as was seen in previous years (Fig. 2).

The reduction in the rate of adult emergence was most marked in the large, heavily infested sycamore compared with the other sycamore trees (Table 3). Ninety-eight *A. glabripennis* were ready to emerge from tree 21 in 2012, which was toward the lower estimate of the number of adults emerging in 2011. By contrast, 66 adult *A. glabripennis* would have been expected to emerge in 2012 from the other sycamore trees, which was twice as many as had emerged in 2011, suggesting that the numbers of *A. glabripennis* in these trees were increasing (Table 3). Very few adults emerged from the other tree species at Paddock Wood and the six adults expected to emerge in 2012 was the same as the number that emerged in 2011 (Table 3).

#### Minimum egg-laying distances and the rate of spread

Distances between trees from which adults emerged to trees where eggs were laid were generally less than 20 m. Based on a 2-year life cycle, the median MED varied from 3 to 18.5 m between years (Table 4). Within each year, however, there were a small number of larger between-tree movements that resulted in eggs being laid at much greater distances. In the last 4 years

**Table 3** The total number of adult *Anoplophora glabripennis* estimated to have emerged at Paddock Wood in 2009, 2010 and 2011<sup>a</sup>, and the number that would have been expected to emerge in 2012<sup>b</sup>

	Sycamore	)	
Year	tree 21	trees 1-20/22-43	Other tree species
2012 (expected) <sup>b</sup>	98	66	6
2011	59-223	14-30	6
2010	51-106	9–15	3
2009	46-80	5-6	_

<sup>a</sup>Estimated from the number of adult exit holes dated to these years. The lower limit of the range in adult numbers is provided by the number of exit holes in live material, which were dated accurately; the upper limit is provided by the total number of exit holes in live and dead material, assuming that all of the exit holes in dead material were dated to the correct year (in reality, a proportion may have been formed in previous years). All of the exit holes in non-sycamore hosts were found in living stems and branches.

 $^{b}$ Equivalent to the total number of mature larvae ( $\geq$ 35 mm in length), pupae and adults recovered from the samples in 2012.

(2008–2011), the largest distances that must have been moved approached or exceeded 100 m (Table 4).

With a 3-year life cycle, eggs would have been laid 1 year earlier and this influenced the calculation of MED values in two ways. First, egg-laying movements occurred 1 year earlier and, second, because fewer trees were producing adult beetles at the time the eggs were estimated to have been laid, the median MED was higher than when the distances were calculated using a 2-year life cycle (Table 4). However, maximum egg-laying distances were the same whether or not they were estimated using a 2- or 3-year life cycle; with a 3-year life cycle, they just happened to occur 1 year earlier (Table 4).

Calculating MED values on the basis of either a 2- or 3-year life cycle, whichever gave the shortest distance (i.e. the most conservative estimate), did not greatly reduce the median MED and it did not affect the maximum distances that adult females must have moved to lay eggs (Table 4). The calculation of median and maximum MED values was generally robust to this variation in the length of the life cycle.

In 2012, the furthest distance from the first tree to have been infested (tree 21) to the outermost tree that contained an *A. glabripennis* larva was 234 m (Fig. 4). It had taken 8 years (2003–2011) for the *A. glabripennis* population to spread outwards to this distance, which is equivalent to a mean rate of spread of 29.3 m per year.

#### Pattern of spread and host availability

The spatial distribution of the infested trees is illustrated in Fig. 4, along with an indication of the main between-tree movements and the dates when these main movements took place (based on a 2-year life cycle). From 2001 to 2004, the initial infestation was confined to the large sycamore (tree 21) adjacent to the industrial unit from where the first beetles appear to have escaped. In 2006 and 2007, adults crossed the main road and eggs were laid in the hedgerow on the opposite side and, in 2008 and 2009, there was a general movement south when several new trees were colonized

at distances of up to 39–96 m. In 2009, at least one egg was laid in an *Acer campestre* located 82 m north of the main infestation (Fig. 4). A single adult *A. glabripennis* emerged from this tree in 2011.

In 2010, at least one egg was laid 203 m north of the main centre of infestation, although this did not result in permanent establishment because the larva was taken by a woodpecker. In 2011, three other trees were colonized at the north end of the infestation area, at distances of 87–129 m from the *A. campestre* in the hedgerow to the south that produced a single adult beetle in 2011, or at 146–191 m from trees further south that also produced adults in that year (Fig. 4). These three trees contained 10 very small *A. glabripennis* larvae that had hatched only recently in 2012 from eggs laid in 2011.

The star symbols in Fig. 4 indicate where an adult *A. glabripennis* was captured in 2009 and the suspected sighting of another adult in 2007 (Straw *et al.*, 2015a). These adult beetles were spotted at greater distances from the centre of the infestation than trees that received eggs and in which larvae eventually developed, which demonstrates that individual adult beetles dispersed further than the distribution of trees with eggs indicated. The beetle that was seen in 2007 was more than 300 m north of the main area of infestation, although this was not appreciated at the time.

The distribution of deciduous broadleaved trees at Paddock Wood is illustrated in Fig. 5. A total of 168 sycamore trees were recorded, of which 162 occurred in the gardens and field boundaries in the southern half of the infestation area. The *A. glabripennis* outbreak was confined almost entirely to this southern zone. Outside the infestation area, sycamore was generally very scarce. The small number of *A. glabripennis* larvae found at the northern end of the infestation area occurred in other tree species. The largest MED values occurred in this northerly direction, along the main road, across areas where there were no sycamore trees. The adult beetles making these movements appear to have passed over a large number of other apparently suitable host species, such as *A. campestre, Populus* spp. and *Salix* spp., without stopping to lay eggs.

## Discussion

## Population increase and spread

The single exit hole dated to 2003, formed by an adult that would have started out as an egg in either 2000 or 2001, indicates that A. glabripennis had been present at Paddock Wood for approximately 10 years before it was discovered. Other outbreaks of A. glabripennis have also shown a delay of 5-10 years between establishment and the time when the infestation was first reported (Hérard et al., 2006; Sawyer et al., 2007, 2010; Dodds & Orwig, 2011; Favaro et al., 2013; Loomans et al., 2013; Turgeon et al., 2015) and this appears to be a common feature of outbreaks of wood-boring pests. The cryptic nature of the wood-boring life style means that infestations usually remain undetected for several years and it is not until a substantial amount of damage has accumulated, and dieback and tree mortality have become noticeable, that the outbreak attracts attention and action is taken (Fielding et al., 1991; Izhevskii & Mozolevskaya, 2010; Siegert et al., 2014).

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	2-Year life cycle	)		3-Year life cycle	•	2- or 3-Year life cycle			
Year	Median distance (m)	Maximum distance (m) <i>n</i>		Median distance (m)	Maximum distance (m) <i>n</i>		Median distance (m)	Maximum distance (m)	
2003	0	0	1	0	0	1	0	0	1
2004	_	_	1	_	_	3	_	_	1
2005	3.0	4	3	18.5	33	4	3.0	4	3
2006	18.5	33	4	34.5	36	4	3.5	33	4
2007	14.0	32	4	30.0	88	10	14.0	32	4
2008	4.0	88	10	13.0	96	14	3.0	88	13
2009	13.0	96	17	17.5	203	26	14.0	96	13
2010	13.5	203	26	11.0	33	28	10.5	203	34
2011	4.0	129	35	4.5	129	9	2.5	129	27

Table 4 Median and maximum distances (m) between trees from which adult Anoplophora glabripennis emerged and on which eggs were laid in the same year (minimum egg-laying distances)

Distances are calculated assuming either a 2- or 3-year life cycle, or a combination of two and three life cycles, whichever gave the shorter distance between trees. *n*, total number of between-tree egg-laying movements (i.e. the number of trees on which eggs were laid).

The small population of *A. glabripennis* at Paddock Wood was not increasing or spreading quickly, especially compared with *A. glabripennis* outbreaks in other countries. Sawyer *et al.* (2007) describe the development of an outbreak of *A. glabripennis* at Carteret in New Jersey, U.S.A., which started in 1996. Within 8 years, 54 trees had produced adult beetles and possessed exit holes and trees up to 2.5 km from the initial site of infestation were being attacked. At Paddock Wood, only 19 trees contained adult exit holes 8 years after the first beetle emerged and the population had spread outward by only 234 m. At Carteret, 1979 adults emerged.

Anoplophora glabripennis outbreaks in Jersey City and Linden in the U.S.A., and at Cornuda in Italy, also showed faster rates of increase and spread than at Paddock Wood. In Jersey City, 446 *A.* glabripennis adults emerged from 113 host trees within 5 years of the first adult emerging and the population had spread 250 m (Sawyer *et al.*, 2004). At Linden in New Jersey, *A. glabripennis* adults had emerged from more than 500 host trees after 5-6 years and trees at distances of 2.4-3.2 km were being attacked (Sawyer *et al.*, 2010). At Cornuda in north-east Italy, *A. glabripennis* was present for approximately 5 years before it was discovered, by which time it had infested at least 576 trees and the area of infestation covered  $2 \times 2$  km (Favaro *et al.*, 2013).

The faster rate of increase of the A. glabripennis populations in New Jersey and Italy was probably related to the warmer climates at these locations. Although increases in population numbers and rate of spread are influenced by host species, the density and distribution of host trees, and the nature of the landscape across which the beetles have to disperse (Hu et al., 2009; Sawyer et al., 2010), climatic conditions, especially summer temperatures, appear to be the main factor determining individual and population performance in A. glabripennis. In New Jersey and Italy, climatic conditions are optimal for A. glabripennis and the majority of individuals complete their life cycle in 1 year (Haack et al., 2006, 2010; Keena & Moore, 2010; Faccoli et al., 2015; Favaro et al., 2015). The relatively rapid rate of development and shorter generation time enables populations in these regions to build up quickly. In southern England, in contrast, the climate is cooler and A. glabripennis

requires 2-3 years to complete its life cycle (Straw *et al.*, 2015b). Under these conditions, population increase and spread appear to be much slower.

#### Mortality of eggs, larvae and pre-emergent adults

The extended life cycle of *A. glabripennis* in southern England arises primarily because adults emerge late in the season and lay their eggs during the autumn. Eggs laid at this time of the year generally do not hatch but overwinter and hatch during the next summer. This adds an extra 10-12 months to the life cycle. The majority of larvae at Paddock Wood then required a further 2 years to complete their development, resulting in a life cycle that lasted a total of 3 years (Straw *et al.*, 2015b). After they had hatched, however, the survival rates of larvae at Paddock Wood were similar to the survival rates of larvae in other outbreaks.

At Paddock Wood, 42% of larvae in small galleries under the bark died before they tunnelled into the wood and, of these, 41% died *in situ* for no apparent reason and 1% were taken by birds. In China, Zhao *et al.* (1993) and Tang *et al.* (1996) recorded 38-47% mortality amongst early stage larvae in galleries under the bark and, in New Jersey, Sawyer *et al.* (2004) indicated that approximately 15% of larvae died at this stage. At Corbetta in Italy, however, Hérard *et al.* (2009a, 2009b) found that 79% of larvae disappeared during this initial phase, primarily because of predation by birds. This high rate of predation by birds appears to be atypical and it may have been a particular feature of the outbreak at Corbetta, which was concentrated in four adjacent heavily infested trees.

Survival rates were higher once larvae tunnelled into the wood. At Paddock Wood, 72% of *A. glabripennis* larvae that were found in tunnels in the wood were alive, which is comparable with the 72–85% of larvae that survived to the adult stage in China after they had established and were feeding in the wood (Zhao *et al.*, 1993; Tang *et al.*, 1996) and with the 60% of established larvae in the wood that survived to the pupal and adult stage at Carteret in the U.S.A. (Sawyer *et al.*, 2004). In Italy, in the heavily infested trees at Corbetta, only 36% of the larvae that were not taken by birds from small galleries under the bark were found alive. The other 64% had died *in situ* (Hérard *et al.*, 2009a).



Figure 4 The location of the trees attacked by Anoplophora glabripennis at Paddock Wood and the main egg-laying movements between trees. The year(s) in which the most significant between-tree movements took place are indicated. Tree species are indicated by different symbols:  $\bullet, \bullet, Acer$  pseudoplatanus;  $\blacksquare, Acer$  campestre;  $\blacktriangle, \bigstar, Salix$  spp.;  $\diamond, Betula pendula; \lor, \lor Populus x canadensis; \blacktriangleright, Acer negundo; \blacktriangleleft, Aesculus hippocastanum (red symbols, trees with no adult exit holes; black symbols, trees with holes). Black star, location where an adult$ *A. glabripennis*was caught in 2009; white star, approximate location where an adult*A. glabripennis*was reported in 2007. The red line marks the boundary of the outbreak area at 100 m from the infested trees. (The location of the large*A. pseudoplatanus*with 498 exit holes has been shifted 14 m to the east to avoid obscuring other trees.)

In contrast to larval survival, oviposition and egg development at Paddock Wood appear to have been less successful compared with *A. glabripennis* populations elsewhere. Approximately 25% of the oviposition pits at Paddock Wood do not appear to have received an egg, which is similar to the 30% of pits that did not contain an egg at Corbetta in Italy (Hérard *et al.*, 2009a), but whereas only 13% of the eggs that were laid at Corbetta failed to hatch, 55% of egg-laying sites at Paddock Wood failed to develop further. Egg-laying sites were identified in the Paddock Wood material by the presence of an oval patch of necrotic tissue beneath an oviposition pit and, although the numbers of sites not developing further may have been an overestimate of egg failure, because some sites may not actually have had an egg and some of the eggs that were found may have hatched eventually, the apparent rate of failure was considerably higher than that observed in Italy. In poplar plantations and on *Ulmus pumila* in



**Figure 5** The distribution of tree species at Paddock Wood within and to the west of the *Anoplophora glabripennis* outbreak area. The circular charts indicate the percentage of the total number of deciduous broadleaved trees occurring in each sector or field boundary that belonged to species attacked by *A. glabripennis* at Paddock Wood, or were potential host species but were not attacked, or which are extremely rare, questionable or unsuitable hosts (non-hosts). The total number of trees in each sector or field boundary is indicated next to the chart. Tree species that contributed more than 14% of the total trees in a sector or field boundary are abbreviated: Ac, *Acer campestre*; A, other *Acer* spp.; Al, *Alnus* spp.; Ca, *Carpinus betulus*; Co, *Corylus avellana*; Cr, *Crateagus monogyna*; Po, *Populus* spp.; Pr, *Prunus* spp. (other than *P. spinosa*); Psp, *Prunus spinosa*; S, *Salix* spp. The red line marks the boundary of the outbreak area within which all host and potential host trees were felled.

China (Zhao *et al.*, 1993; Tang *et al.*, 1996) and at Carteret in the U.S.A. (Sawyer *et al.*, 2004), 3–9% of oviposition pits did not contain an egg and 10%, 25% and 15% of eggs, respectively, failed to hatch.

A higher rate of failure at the egg stage at Paddock Wood may be related to the majority of eggs being laid in the autumn, when conditions were relatively cool, and the eggs then having to spend a prolonged period under the bark before they hatched in the subsequent year. Sub-optimal conditions at the time when adults of *A. glabripennis* were emerging at Paddock Wood may also explain why 11-23% of the adults died before or at emergence. In China, Zhao *et al.* (1993) and Tang *et al.* (1996) found that only 5-6% of adults died at this stage.

#### Dispersal and colonization of new trees

A notable feature of the *A. glabripennis* outbreak at Paddock Wood was that the infestation was concentrated in one large, heavily infested tree close to the original site of introduction. A similar pattern of infestation, with most of the population contained within a single large tree or close group of trees, has been observed during the early phases of other outbreaks (Sawyer *et al.*, 2004, 2007; Hérard *et al.*, 2009a, 2009b; Turgeon *et al.*, 2015) and it reflects the strong tendency for adult *A. glabripennis* not to disperse far but, instead, to remain on and re-infest their natal tree (Lingafelter & Hoebeke, 2002; Haack *et al.*, 2010). Significant dispersal may only occur when this natal tree starts to deteriorate and becomes a less suitable host (Sawyer *et al.*, 2007).

The initial tree attacked at Paddock Wood was in decline and this may explain some of the variation in larval mortality. The mortality rate of early stage larvae under the bark was significantly lower in tree 21 than in the other sycamore trees (24% versus 61%), whereas the mortality of older established larvae in the wood was significantly higher (26% versus 10%). The lower rate of mortality amongst early stage larvae is consistent with better establishment in this large tree because it was less able perhaps to produce a wound response where eggs had been laid and small larvae were starting to feed, whereas the higher rate of mortality amongst older larvae suggests increased intraspecific competition in a declining resource. The majority of older larvae that died were found dead in situ or were missing in heavily infested stems and branches. Sawyer et al. (2004) and Hérard et al. (2009a) also recorded high rates of mortality amongst older larvae in heavily infested trees, apparently as a result of competition. In the other sycamore trees at Paddock Wood, which had been colonized recently or were being attacked for the first time, it appears that early stage A. glabripennis larvae found it harder to establish but, once they had tunnelled into the wood, their survival was better.

Adult *A. glabripennis* generally disperse by walking, which is why most adults remain on or near their natal tree but, when conditions are suitable, males and females also disperse by flying. Flight is the main means of long-distance movement. The majority of individuals do not appear to fly further than 100–500 m, although small numbers have been recorded to travel as far as 2.4–2.6 km (Zhou *et al.*, 1984; Wen *et al.*, 1998; Smith *et al.*, 2004). The propensity for adult *A. glabripennis* to

fly and the distances flown are related to ambient temperatures (Zhou *et al.*, 1984; Bancroft & Smith, 2005). On hot summer days in China and the U.S.A., adult *A. glabripennis* fly readily but, in a cooler climate, conditions may not be as suitable for flight and this may be one of the reasons why the population at Paddock Wood was not spreading quickly.

Relatively large insects such as *A. glabripennis* need to warm up before they can fly and flight generally does not occur unless temperatures rise above a minimum threshold temperature. We have not be able to find any published information, however, on the minimum temperature required for flight in *A. glabripennis*, or in closely-related species such as *A. chinensis* (Forster). In the laboratory, adult *A. glabripennis* show normal levels of activity between 16 and 28 °C (Zhou *et al.*, 1984), and maximum female fecundity occurs at 23–24 °C (Keena, 2006). In the field, adults become active once temperatures rise above 20 °C (Lingafelter & Hoebeke, 2002; Bancroft & Smith, 2005). Therefore, the majority of adult *A. glabripennis* probably fly only when temperatures exceed 20 °C, and the numbers flying are likely to increase as temperatures rise from 20 to 28 °C.

At Paddock Wood, there were not many days during the period when *A. glabripennis* adults were active when temperatures would have exceeded 24-25 °C. For example, from 2000 to 2012, there were only 7–8 days during August, on average, when maximum daily temperatures exceeded 24 °C (range 0–17 days). In September, there were only 3 days, on average, with temperatures greater than 24 °C (range: 0–8 days) and, in October, there were no days above 24 °C. Females also lay fewer eggs when temperatures are cooler (Keena, 2006; Meng *et al.*, 2015). Consequently, a reduction in adult activity and dispersal, along with a reduction in realized fecundity, were probably important contributory factors limiting the rate at which the Paddock Wood population was able to increase and spread.

In the last 2-3 years at Paddock Wood, some adult females of *A. glabripennis* moved at least 96–203 m to lay eggs in new trees, although their offspring appear to have struggled to establish, especially in non-sycamore hosts (Straw *et al.*, 2015a). The difficulty of establishing in new trees, combined with the decrease in numbers in tree 21, meant that fewer *A. glabripennis* adults would have emerged in 2012 and the previous increase in population numbers would not have been sustained.

To reach the trees where they eventually laid eggs, female beetles appear to have passed over or rejected a large number of apparently suitable hosts, such as A. campestre, Populus spp. and *Salix* spp., without laying eggs. Therefore, in the relatively cool climate at Paddock Wood, where conditions were generally sub-optimal for A. glabripennis, the beetle was concentrated in the most favourable host species (sycamore) and tree species that are utilized elsewhere, where the climate is warmer, were hardly attacked. Sycamore was scarce in the area surrounding the outbreak and, within the infestation area, sycamore was almost completely restricted to the southern part of the site close to the industrial unit and gardens where the beetle was introduced (Fig. 5). Given the apparent dependence of the A. glabripennis at Paddock Wood on sycamore, it is perhaps not surprising that the outbreak was almost completely restricted to this one small area where sycamore was present (Fig. 4), and the lack of sycamore elsewhere may have been another reason why the population had not spread further.

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#### Implications for management

The present study indicates that there were a particular set of circumstances that allowed *A. glabripennis* to become established at Paddock Wood. First, it was fortuitous that a highly favoured host species, sycamore, was growing close to the yard where pallets and crates imported from China were being stored. In particular, there was one large sycamore tree within 80–100 m that appeared to be especially suitable for colonization.

Second, adults of *A. glabripennis* were probably introduced over a period of several years. Adults of *A. glabripennis* must have been introduced in 2000 or 2001 to lay the egg that resulted in the single beetle that emerged in 2003. This adult beetle, however, would not have been able to continue the infestation on its own. It could have been a male or, if it was a female, it would have needed a mate. The emergence of *A. glabripennis* adults in 2005 and 2006, from eggs laid in 2002, 2003 and/or 2004 (depending on whether the life cycle was 2 or 3 years), when no adults emerged at Paddock Wood or when only one adult emerged, also suggests that further adult beetles were introduced in at least some of these years.

The third condition that may have favoured establishment is that the period when adult beetles appear to have been introduced, and when the first generation was emerging and laying eggs, coincided with a run of particularly warm years during 2003–2006, when summer temperatures were higher than average and rainfall was lower than average (Fig. 1). The higher temperatures would have favoured larval development, adult activity and oviposition, and the combination of hot summer weather and low rainfall, which are conditions less favourable for plant growth, may have decreased the ability of the host to resist attack.

Without this combination of factors, it would have been harder for A. glabripennis to have established at Paddock Wood, although it had established and was spreading, albeit slowly, and the trees attacked first were deteriorating and sooner or later would have died. The relatively slow rate of spread and the difficulty that the pest appeared to be having in colonizing new trees were probably important factors in the success of the eradication programme, which was based on felling and destroying all host trees within a radius of 100 m. No further signs of A. glabripennis have been seen at Paddock Wood since the trees were felled in 2012. It is clear, however, that some adult females of A. glabripennis travelled more than 100 m to lay eggs and, in the future, should another outbreak be discovered in the U.K., it might be prudent to fell trees out to 200-300 m. In other countries, where A. glabripennis has the potential to spread more rapidly or was found to be spreading more quickly than first anticipated, host trees have been felled outwards to distances of 400-800 m (Hérard et al., 2009b; Haack et al., 2010; EPPO, 2013b; Turgeon et al., 2015).

Although perhaps desirable, felling outwards to a greater distance has cost implications. At Paddock Wood, the 100 m boundary of the infestation area enclosed 11.5 ha, within which 2133 trees were felled and destroyed (Straw *et al.*, 2015a). The total cost of the control programme in 2012, when the trees were felled, was £0.65 mn (£0.15 mn for surveys; £0.5 mn for felling and burning trees, administration and public outreach). By contrast, if the boundary of the infestation area had been set at 200 m, the total area enclosed would have been 29.3 ha and

an estimated 5460 trees would have needed to have been felled. The total cost of this operation, assuming that survey costs would have remained the same, would have been  $\pounds 1.43$  mn, which is more than double cost of felling outward to 100 m.

From 2012 onward, annual surveys have been carried out in and around the original outbreak area at Paddock Wood in an attempt to locate any residual infestation. These surveys will continue until at least 2018, and those that have been completed have cost, on average, approximately £0.21 mn per year. The cost of these follow-up surveys would not have changed greatly had trees been felled outwards to 200 rather than 100 m. The main increase in costs occurs in the first year when the trees are felled. Therefore, over the whole course of the eradication programme, felling trees outward to 100 m will result eventually in a total cost of approximately £1.9 mn, whereas, if trees had been felled out to 200 m, the total cost would be £2.7 mn, an increase of 42%. Compared with the costs of A. glabripennis control programmes in North America, which have exceeded \$373 mn (Haack et al., 2010), the cost of eradicating A. glabripennis from Paddock Wood has been relatively small. In a local context, however, the time, effort and cost of dealing with what was a very small and isolated outbreak of A. glabripennis has not been inconsiderable.

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