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A review of *Agrilus biguttatus* in UK forests and its relationship with acute oak decline

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Agrilus biguttatus Fab. (Coleoptera: Buprestidae) is a European bark-boring beetle whose larvae feed in the vascular tissue of oak trees. Until recently, it was considered rare in Britain, but sightings have become more frequent and it is often found on weakened trees suffering from Acute Oak Decline (AOD). This rapidly acting syndrome is characterized by patches of dark sticky fluid exuding from cracks on the trunk, with areas of necrotic tissue beneath, probably caused by a pathogenic bacterial component. However, the frequent association of AOD with the larval galleries and distinctive adult exit holes of *A. biguttatus* has raised concerns that the beetle may be contributing to the AOD syndrome or hastening the mortality of affected trees. This review evaluates the potential role of *A. biguttatus* in the AOD complex. Information on the beetle's life cycle and ecology is assessed along with the apparent increase in its abundance and distribution in the UK, and likely mechanisms of host selection. Oak tree defences against the beetle are discussed, as well as risk factors influencing susceptibility. Research on related *Agrilus* species is reviewed so that insights into the relationship between the beetle, the bacteria and the host tree can be made through comparisons with more extensively studied species. Possible management options in an AOD context are considered, and priority areas for future research are identified.

Introduction

Tree decline diseases are characterized by a gradual and progressive reduction in health and vigour, caused by the actions of multiple biotic and abiotic agents (Manion, 1991). They are typically complex and difficult to define. Oak decline has been reported in many European countries and occurs in different forms (Petrescu, 1966; Delatour, 1983; Thomas *et al*., 2002; Thomas, 2008). In England, a distinctive novel form of oak decline is increasingly reported on native British oak species, *Quercus petraea* (Matt.) Leibl. and *Q. robur* L., often leading to mortality within just a few years of the appearance of the first symptoms (Denman and Webber, 2009; Denman *et al*., 2014). Termed Acute Oak Decline (AOD), it appears to involve a complex of interacting factors including a key bacterial component (Denman *et al*., 2014). Characteristic symptoms include sticky dark fluid exuding from bark cracks on the trunk, which develop over patches of necrotic cambial tissue beneath. In addition, oaks with decline symptoms in the UK are often seen to exhibit the distinctive D-shaped exit holes created by emerging adults of the two-spotted oak buprestid, *Agrilus biguttatus* (Fab.) (Coleoptera: Buprestidae), raising concerns that this native beetle is contributing to the AOD syndrome and/or mortality of the trees (Denman *et al*., 2010). Until quite recently, *A. biguttatus* (syn. *A. pannonicus*) was considered to be a vulnerable endemic species in the UK, developing on dying or even recently dead hosts (Shirt, 1987). However, distributional records over the last 25 years suggest an increase in both its abundance and geographical distribution in England (Allen, 1988; Hackett, 1995; Alexander, 2003; Figure 1), and its putative association with oak decline sites has led *A. biguttatus* to be considered by some authors as a pest in the UK (Gibbs and Greig, 1997) and across its European range (Moraal and Hilszczanski, 2000; Evans *et al*., 2004; Vansteenkiste *et al*., 2004). In fact, *A. biguttatus* has been long recognized as attacking weakened oak and as a key factor affecting tree mortality during periods of oak decline in Europe (e.g. Falck, 1918; Starchenko, 1931; Hartmann and Blank, 1992). This has led the United States Department of Agriculture to consider it a potentially invasive pest that could have a high economic and environmental impact (Davis *et al*., 2005; Yemshanov *et al*., 2013).

Recent investigations of 21 trees in the UK exhibiting symptoms of AOD show that 19 of them (90 per cent) have *A. biguttatus* galleries in the vascular tissue (Denman *et al*., 2014). These initial figures are consistent with ongoing research that shows the relationship (co-occurrence) is evident in many more cases (S. Denman, personal communication), prompting the need for a better understanding of the possible role of the beetle in the decline. Despite the recent emphasis on it as a pest insect, it has been relatively little studied. This review presents the life cycle and ecology of *A. biguttatus*, examines its changing distribution in the UK and considers the possible role that the species might play in the AOD complex. Research upon related and better-studied *Agrilus* species is included to review the mechanisms through which host trees become attractive and susceptible to colonisation. The paper concludes by identifying important gaps in our understanding of *A. biguttatus*, and suggesting future avenues for research.

Agrilus species worldwide and oak species as host trees

The buprestid genus *Agrilus* is extraordinarily species-rich, and >3000 species have been described globally (Bellamy, 2008). Larvae tend to develop within the vascular tissues of trees or woody plants and are often host-specific, a trait that likely contributed to their diversity through adaptive radiation (Farrell, 1998; Bernhard *et al*., 2005). Only a few species are considered pests, typically these are exotic introductions. The most damaging buprestid to date is the emerald ash borer (EAB), *A. planipennis* Fairmaire, an Asian species introduced to North America via infested wood packing material (Haack *et al*., 2002; Haack, 2005). Sharing no evolutionary history with the beetle, most American ash (*Fraxinus*) species exhibit little resistance and healthy trees are rapidly killed by the action of intensive larval feeding, making EAB an aggressive primary pest (Rebek *et al*., 2005, 2008). Extensive control measures have proved unsuccessful, and EAB continues to expand its range, having killed tens of millions of trees to date (Kovacs *et al*., 2010). Of great concern is the recent introduction of EAB to European Russia (Baranchikov *et al*., 2008), where its damage potential is now being realized (Straw *et al*., 2013). The native North American species *A. anxius* Gory (bronze birch borer) is considered to pose a similarly severe threat to European birch species that would probably have little resistance if it were introduced into Europe (Nielsen *et al*., 2011), prompting recent measures to try and prevent such an occurrence (EPPO, 2011).

Worldwide, a number of *Agrilus* species utilize oak species as host trees, and several have been reported to contribute to their decline or mortality. The gold-spotted oak borer *A. auroguttatus* Schaeffer (GSOB) has been brought for the first time into contact with 'naïve' host species of oak in South California, through anthropogenic introduction, where it has become a primary mortality agent of healthy trees (Coleman and Seybold, 2008, 2011). More often, where host and pest species have co-evolved, healthy trees are generally able to resist attack, so trees tend to be physiologically stressed or altered in biochemical status before they become susceptible. In North America, the native two-lined chestnut borer *A. bilineatus* Weber is a key factor contributing to the death of weakened oak (Haack and Benjamin, 1982), whereas in Europe *A. sulcicollis* Lacordaire, *A. angustulus* Illiger and *A. biguttatus* have all been similarly implicated (Moraal and Hilszczanski, 2000). In total, four of the eight known British *Agrilus* species have been recorded colonizing oak (Levey, 1977; James, 1994; Hodge, 2010; Sage, 2010). Of these, *A. biguttatus* is the largest species, its larvae developing within the bark of the main stem, whereas those of the other species tend to develop in branch bark, or in trees of small stem diameters (Bily, 1982; Moraal and Hilszczanski, 2000). Trapping trials at AOD sites in England caught all four species associated with oak (Brown, 2013), although *A. biguttatus* was the only species consistently present. *Agrilus sulcicollis*, first recorded in England in 1992 (James, 1994) and recently introduced to North America (Haack *et al*., 2009; Jendek and Grebennikov, 2009), was recorded at all the southern and eastern sites. This species typically prefers to be higher in the crown or on smaller hosts (Moraal and Hilszczanski, 2000) but has been observed on main stems at AOD sites, where small exit holes suggest that it may also breed.

Life cycle and ecology of *A. biguttatus*

Adult *A. biguttatus* beetles are metallic green/blue in colour, with a narrow, elongate form; the front of the head is flattened, with prominent oval eyes. They can be readily distinguished from the other native British *Agrilus* species by the single pair of white spots located on the last third of the elytra, adjacent to the suture (Figure 1). At 10–13 mm in length, adults are generally larger than the other UK *Agrilus* species, but there is some size overlap. Distinguishing larvae of the different species is more difficult, but they may be differentiated from other wood-boring Coleoptera, being apodous, dorso-ventrally flattened, with a characteristic wide first thoracic segment (prothorax), which largely envelops the head, and narrowed second and third (meso- and meta-) thoracic segments. Posteriorly are two sclerotized spines on the anal segment (Figure 2) (Bily, 1982; Chamorro *et al*., 2012).

A large part of the life cycle of *A. biguttatus* takes place within the vascular tissue of mature oak (Moraal and Hilszczanski, 2000; Evans *et al*., 2004; Vansteenkiste *et al*., 2004). Adult beetles generally emerge from May to July (Habermann and Preller, 2003), with peak emergence periods likely to vary according to local and seasonal climate. Newly emerged adult beetles feed in tree crowns, primarily upon oak foliage, but also sycamore and beech (Wachtendorf, 1955; Habermann and Preller, 2003). Mate choice is made visually by males in flight, detecting females feeding on foliage below (Domingue *et al*., 2011). Mated females deposit eggs within cracks and crevices in the bark of suitable host trees, typically between bark plates where larvae have a minimal thickness of outer bark to tunnel through to reach the vascular tissue. Egg-laying has been observed under artificial conditions with initially soft-shelled eggs deposited in variable-sized clusters of up to 30 eggs (Katy Reed, personal communication; Wachtendorf, 1955). The preference for oviposition and subsequent initial larval development on the warmer south-facing side of host trees has been widely noted (Starchenko, 1931; Wachtendorf, 1955; Hartmann and Blank, 1992; Habermann and Preller, 2003). Egg development rate is temperature dependent and has been observed in laboratory conditions to take from 2 to 6 weeks accordingly (Katy Reed, personal communication) Newly hatched larvae burrow into the inner bark and develop by feeding in both the outer sapwood and phloem, creating sinuous galleries of up to 1.5 m long, which become steadily wider as the larvae grow, from <1 up to 3–4 mm diameter (Vansteenkiste *et al*., 2004). Larvae are reported to progress through five instars and, when fully grown, are between 25 and 43 mm in length (Moraal and Hilszczanski, 2000). Generation time is thought to take 1–2 years, varying geographically, suggesting a flexible life cycle responsive to local conditions, of which temperature and host vigour are probably the dominant factors. Larvae excavate pupal cells in the bark plates

Figure 1 Adult *Agrilus biguttatus*.

Figure 2 *Agrilus biguttatus* larva.

near to the surface, where they overwinter in a folded position (Figure 3). Pupation occurs in the spring, taking ~14 days (Habermann and Preller, 2003), after which the adult beetle emerges through a characteristic D-shaped exit hole, typically 2.5–4 mm wide (Figure 4).

Distribution and abundance

Agrilus biguttatus is widespread across central Europe, extending east to the Ukraine and south to North Africa (Bily, 1982; Davis *et al*., 2005). Most of this range is characterized climatically as mild to warm, or having warm continental summers. The British population is at the northerly limit of this range and until the 1970s was regarded as exhibiting a relictual distribution, occurring in just a few ancient woodland sites such as the New forest and Sherwood (Fowler, 1888; Allen, 1973; Alexander, 2003). Increasingly frequent observations since the mid-1980s suggest an expanding geographical range in Britain (Foster, 1987; Allen, 1988; Hackett, 1995). Recent records expand the known distribution of the beetle as far west as Wiltshire and Gloucestershire, and as far north as Manchester (Keith Alexander, personal communication; Figure 5). Of particular note is that the distribution of AOD in the UK covers a similar range to that of *A. biguttatus*. Contrasting with the apparent expansion in range and abundance of *A. biguttatus* is the likelihood that under-recording of the buprestid is likely to have been a factor in the past, due to lower awareness of the beetle, limited survey effort and a lack of recognition of the characteristic exit holes (Hackett, 1995). However, recent range expansion has been reported elsewhere along its northerly limit, into Denmark (Pedersen and Jørum, 2009), and increasing abundance was described in the Netherlands in the mid-1990s (Moraal and Akkerhuis, 2011).

Figure 3 Pre-pupal larva of *Agrilus biguttatus*, exposed within its pupal cell excavated in the outer bark of host oak tree.

Figure 4 D-shaped exit hole created in the outer bark by an emerging adult *Agrilus biguttatus*.

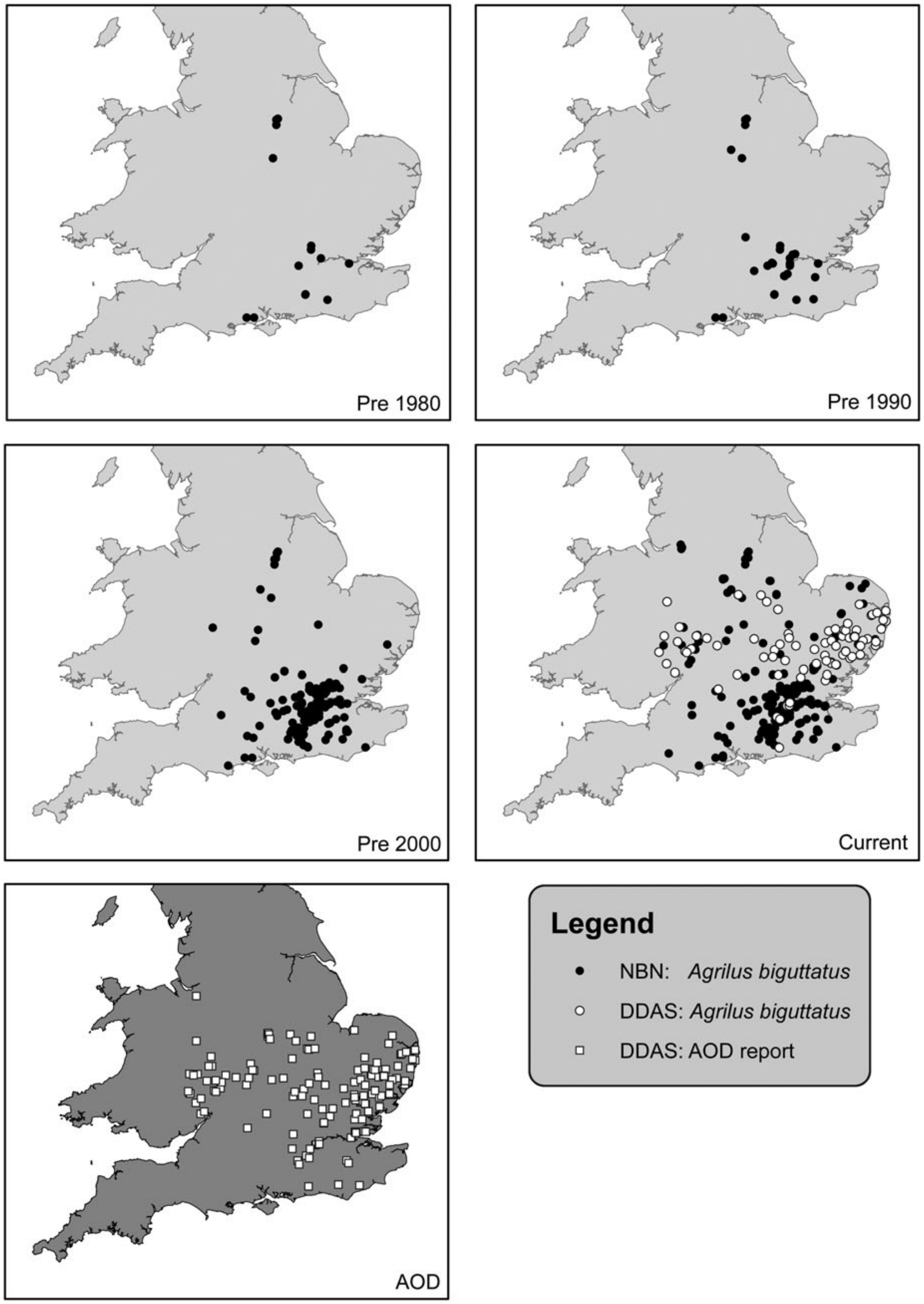

Figure 5 The historical distribution records of *Agrilus biguttatus* in the UK, pre-1980s to present time, and the reported distribution of AOD to date. Number of *A. biguttatus* sightings: 1800s–1979, $n = 23$; 1980–1989, $n = 36$; 1990–1999, $n = 159$; 2000 to present, $n = 200$. The information used here was sourced through the NBN Gateway website and included the following resources: Biological Records Centre, National Trust, Natural England, Countryside Council for Wales, Royal Horticultural Society, Leicestershire & Rutland Coleoptera, Suffolk Biological Records Centre, Kent & Medway Biological Records Centre, Norfolk Biodiversity Records Centre, Worcester Biological Records Centre, Herefordshire Biological Records Centre, Tullie House Museum and the personal records of Keith Alexander (Accessed November 2012). The NBN and its data contributors bear no responsibility for the further analysis or interpretation of this material, data and/or information. Copyright © Crown Copyright. All rights reserved NERC 100017897 2004. Additional points are included from Forest Research Disease Diagnosis and Advisory Service (DDAS). © Crown copyright. All rights reserved. Forestry Commission. 100025498. [2013].

A warming climate may be one cause of the apparent increase in the British *A. biguttatus* population (Alexander, 2003; Broadmeadow and Ray, 2005). In addition to its preference for oviposition on south-facing stems, this thermophilic species basks in full sunlight and is more active when it is warm (Allen, 1988; Habermann and Preller, 2003; Domingue *et al*., 2011). However, host availability may have also contributed a role. For example, in 1987, a severe storm across southern Britain caused windthrow to an estimated 15 million trees and damaged many others, temporarily increasing the abundance of susceptible hosts for attack (Hackett, 1995). Host availability would have been further influenced by the major droughts in 1990–92 and 1995–97, which were widespread and protracted (Marsh *et al*., 2007), causing tree stress and mortality. Drought stress impairs the ability of trees to resist attacks from secondary organisms, including wood-boring buprestids (Mattson and Haack, 1987; Wargo, 1996; McDowell *et al*., 2008; Jactel *et al*., 2012). The generalized decline of oak is believed to have been intensified across Europe by drought, in combination with other stress factors such as severe defoliation by caterpillars (Thomas, 2008).

Host selection

Agrilus biguttatus primarily lays eggs on *Quercus robur* and *Q. petraea*, although other occasional hosts have been reported, including *Q. pubescens* Willd., *Q. ilex* L., *Q. suber* L., *Q. pyrenaica* Willd. and *Q. cerris* L. together with *Fagus sylvatica* L., *Castanea sativa* Mill. and very rarely *Q. rubra* L. (Bily, 1982; Moraal and Hilszczanski, 2000; Davis *et al*., 2005). Female beetles are thought to select oviposition sites on host trees that are physiologically stressed by one or a combination of factors (Moraal and Hilszczanski, 2000; Vansteenkiste *et al*., 2004). In addition to drought, reported triggers of decline include severe defoliation by caterpillars (including gypsy moth *Lymantria dispar* L., and oak leaf roller moth *Tortrix viridana* L.), foliage colonisation by powdery mildew (*Erysiphe alphitoides* Griffon & Maubl.) or damage caused by winter frosts (Falck, 1918; Starchenko, 1931; Wachtendorf, 1955; Jacquiot, 1976; Hartmann and Blank, 1992; Gibbs and Greig, 1997). Root decay fungi such as *Armillaria* spp. (Fr.:Fr.) Staude., *Gymnopus* (syn. *Collybia*) *fusipes* (Bull.) Gray and *Phytophthora* spp. de Bary also play a key role in the early stages of oak decline (Marçais *et al*., 2011).

Agrilus biguttatus exhibits a preference for larger, mature hosts measuring at least 30–40 cm DBH (diameter at breast height, 1.3 m) (Moraal and Hilszczanski, 2000), and having an inner bark thickness of >10–13 mm (Vansteenkiste *et al*., 2004). Sufficient inner and outer bark thickness is likely to be important to protect developing larvae from predatory woodpeckers and parasitoid wasps, as well as allowing the construction of pupal cells. Beetle colonisation takes place on the main stem, from the buttress up to 16–20 m above ground, occasionally extending to larger branches (Wachtendorf, 1955; Vasanthakumar *et al*., 2008). Larger-scale attacks have been observed on more open oak stands (Starchenko, 1931; Habermann and Preller, 2003). The increased light and warmth facilitates faster development, which limits larval exposure time to predators and parasitoids, and to host defence mechanisms.

The precise method of host selection by *A. biguttatus* is unclear, but attraction to susceptible oak may be mediated via changing visual and biochemical cues. These cues signal the altered quality of tree defences due to natural senescence, defoliation, drought stress and damage from biotic and abiotic agents. Visual cues may be important to some degree, since EAB clearly demonstrates colour attraction, landing preferentially on purple- or light green-coloured traps (Francese *et al*., 2008; Crook *et al*., 2009). The reason for these preferences is unclear but may involve a response to the wavelengths of reflected light associated with good quality oviposition (stems) or feeding (foliage) sites. Notably, trapping studies in the UK have recently demonstrated that *A. biguttatus* exhibits similar colour preferences (Brown, 2013). The importance of host volatiles to some *Agrilus* species has been more clearly established. For example, elevated levels of bark sesquiterpenes and green-leaf volatiles, released by stressed or damaged ash trees, are attractive to EAB, generating large electrophysiological responses in their antennae (Rodriguez-Saona *et al*., 2006) and increasing trap catches when used as lures (Crook *et al*., 2008; Crook and Mastro, 2010). Consideration of host selection by the North American species *A. bilineatus* may be helpful as it shares a similar life cycle and host preference with *A. biguttatus* (Haack and Benjamin, 1982). Both species are native buprestids attacking oak hosts with which they have co-evolved. Oak bark volatiles have been demonstrated to be attractive to *A. bilineatus*, which can locate potential hosts within 24 h of a stress-inducing injury (phloem-girdling) (Dunn *et al*., 1986a). Non-girdled control trees and recently dead (xylem-girdled) trees were not attractive to *A. bilineatus*. Despite a 1 : 1 sex ratio, over 80 per cent of individuals attracted were female, presumably searching for suitable oviposition sites (Dunn *et al*., 1986a). *Quercus robur* also releases volatiles when under insect attack (Vrkocova *et al*., 2000), which could increase their attraction to *A. biguttatus*. Mass attack has been shown to overwhelm host tree defence mechanisms and result in increased larval survival rates in EAB (Duan *et al*., 2010). In some circumstances, this strategy may be utilized by *A. biguttatus*, for instance where >700 adults have been recorded emerging from a single tree (Moraal and Hilszczanski, 2000).

Moisture-content is an important factor in *Agrilus* larval development. EAB larvae have been shown to more often feed downwards on the host stem, where the phloem tissue has a higher water content than above the feeding area (Chen *et al*., 2011). This behaviour was shown experimentally to improve growth and decrease mortality of the larvae. This probably explains why both *A. bilineatus* (on oak) and EAB (on ash) have been shown to lay successive generations of eggs below earlier-laid ones on their host trees (Haack and Benjamin, 1982; Cappaert, *et al*., 2005). Investigation of experimentally killed oak trees found that *A. bilineatus* larvae within the phloem died, probably due to desiccation (Duan *et al*., 2010). The relationship of *Agrilus* with water stress in the host tree therefore appears to be finely balanced. Drought lowers the resistance of trees to attack, but the window of opportunity for the beetle is limited, as the death of the tree causes a reduction in water content, which will be lethal to inadequately developed larvae.

Host response and resistance

Deciduous trees employ a combination of physical and chemical defences against wood-boring insects, many of which are generalized responses induced by wounding. Their complex nature means that it can be difficult to determine the precise form of resistance against a specific pest. Reduced defensive capabilities are likely to increase the colonisation success of *A. biguttatus*, resulting in increased feeding damage. It is generally considered that girdling (i.e. severing the phloem and/or xylem tissues) causes the death of the tree (Moraal and Hilszczanski, 2000). However, it has been demonstrated that experimentally phloem-girdled oaks tend to recover in the absence of *Agrilus* (Dunn *et al*., 1986b), and it may be that a host defence mechanism, triggered by larval feeding, in fact hastens the death of the tree (Jacquiot, 1976). Oaks are known to produce tyloses in response to localized *Agrilus* damage to the sapwood (Vansteenkiste *et al*., 2004). These are outgrowths of specialized parenchyma cells projecting into the xylem vessels, which prevent fluid movement, and are part of the general compartmentalisation process to limit damage or prevent pathogen movement around a wound. Multiple and widespread larval galleries may cause extensive tyloses, leading to serious impairment of water transportation within the tree. This may be further exacerbated by drought conditions, and tree death may follow (Jacquiot, 1950a; Jacquiot, 1976).

One of the earliest symptoms of an *A. biguttatus* attack has been reported as the exuding of fluid from bark cracks located above areas of necrosis. This has been considered to be a host response to larval damage (e.g. Falck, 1918; Jacquiot, 1950a; Hartmann and Blank, 1992) and may be a defence mechanism against *Agrilus* attack, by drowning larvae (e.g. Hanks *et al*., 1991). However, these symptoms closely match those described for AOD and may be the result of bacterial infection rather than *Agrilus* attack, which can also occur without the production of these symptoms. Oaks do not have a preformed fluid defence like the resin production of many conifers, and the role of localized fluid exudation is uncertain. The sticky exudates characteristic of AOD and other maladies (also termed slime-flux or stem bleeding) tend to be produced when pathogens enter wounded oak bark. The reaction may be produced too slowly to be an adaptive defence against boring insects (Dunn *et al*., 1990), although mid-instar larvae have been seen to be apparently drowned in their galleries on an AOD symptomatic oak (Denman *et al*., 2014).

Callus formation is more evidently an important defence mechanism against *A. biguttatus* (and other bark-boring beetles), by overgrowing larval galleries (Jacquiot, 1976; Vansteenkiste *et al*., 2004). This is likely to be most effective against either the early larval instars which feed and move more slowly than the later instars, so can be overgrown by the callus tissue (Dunn *et al*., 1990; Duan *et al*., 2010), or against overwintering larvae (Fierke and Stephen, 2008). Jacquiot (1976) reported that *A. biguttatus* frass when added to fresh oak tissue induced a callusing response, but the chemical components involved were not identified, and the reaction may have been a generalized wound response against microbial action. A similar process follows wounding or pathogen infection, where callus forms to cover the damaged area with a thick protective layer, eventually allowing a normal growth ring structure to resume on its outer layers (Pearce, 1996). A strong callusing response is a good indicator of tree vigour (Dunn *et al*., 1990) and correlates with the tree's ability to repel an attack and successfully recover. In AOD, the callus tissue is lignified, giving the host tissue greater strength and resilience against further pathogen and insect attack (Denman *et al*., 2014). Following wounding, lignin and suberin deposition in the surrounding tissues limits desiccation and pathogen entry (Biggs, 1985) and may also play an antifeedant role. Other chemical defences deployed by angiosperms against phloem-feeding insects include diverse secondary metabolites such as phenolics which can act as feeding deterrents or enzyme inhibitors (Bennett and Wallsgrove, 1994) and defensive proteins which may be directly toxic or disrupt nutrient uptake (Zhu-Salzman *et al*., 2008). Manchurian ash, *Fraxinus mandshurica* Rupr. is the most resistant species to EAB and produces phenolic compounds with antifeedant and growth inhibiting effects (Whitehill *et al*., 2012).

Our present understanding of a host tree's ability to resist attack is that it is limited by its carbohydrate reserves. A study by Dunn *et al*. (1987) found that white oak (*Q. alba* L.) trees with low winter starch reserves were more susceptible to attack by *A. bilineatus* the following year. Those trees with the lowest starch reserves were the most heavily attacked and were killed. Reserve levels in the dormant season reflect the vigour of a tree, and its success in the production of the carbohydrates through photosynthesis. Starch reserves are important for the production of defensive compounds and callus tissue. Dunn *et al*. (1990) found that trees successfully colonized by *A. bilineatus* had a limited ability to produce callus tissue. Similarly, studies of callus formation by the oak *Q. rubra* against attack by the native cerambycid beetle *Enaphalodes rufulus* Haldeman found healthy oaks (as defined from increment cores) to exhibit better compartmentalisation and faster wound closure, with associated lower larval survival rates, than declining oaks (Fierke and Stephen, 2008; Haavik and Stephen, 2011). The health of the tree is critical in its ability to respond to attacking insects. Drought stress, defoliation or disease all deplete carbohydrate reserves and suppress the ability to respond to *Agrilus* attack.

A. biguttatus and AOD

AOD in the UK is typically identified on established oaks (>50 years old), which are also preferred by *A. biguttatus* for their thick bark, required for larval development and pupation. The spongy necrotic tissue typically found beneath the bark in AOD trees consistently yields a suite of bacterial species including *Gibbsiella quercinecans* gen. & sp. nov. and *Brenneria goodwinii* sp. nov. (Brady *et al*., 2010, 2012; Denman *et al*., 2012), but larval galleries of *A. biguttatus* are also frequently found in close proximity to the lesions. *Agrilus biguttatus* activity was apparent on 90 per cent of trees sampled for bacterial isolations (Denman *et al*., 2014; Denman personal communication), illustrating that the similar distribution of *A. biguttatus* and AOD sites in the UK (Figure 1) also occurs at the level of individual trees. Not all of the symptomatic trees displayed exit holes, perhaps hinting at a role for host resistance against developing larvae (Brown, 2013). A study in Belgium also found correlation between 'AOD-type' symptoms (bark cracks and fluid exudation) and the presence of *A. biguttatus* galleries, with exit holes only present on some of the trees (Vansteenkiste *et al*., 2004). This suggests a wider co-occurrence between the buprestid attack and necrosis, although both factors have been reported in isolation. Stem bleeding has also been reported in association with GSOB (Coleman and Seybold, 2008, 2011), but studies have focused on fungal associates (Lynch *et al*., 2014). Species of *Gibbsiella* and *Brenneria* bacteria have however been isolated from a black oak tree, *Q. kelloggii* Newb. in a GSOB-infested site (Denman, 2010), and from several coast live oak, *Q. agrifolia* Née (Lynch *et al*., 2014). *Gibbsiella* species have also been isolated from digestive tracts of larval insects including EAB (Rizzi *et al*. 2013).

At present, the interaction between *A. biguttatus* and the microbial component of AOD is unclear. In continental Europe, it has been reported that buprestid attack precedes the development of lesions, with wound sites facilitating infection by microorganisms (Jacquiot, 1950b; Hartmann and Blank, 1992; Vansteenkiste *et al.*, 2004). The situation in the UK may involve bacteria exploiting areas of damage created by larval feeding; this could be essential for microbial colonisation, and the insect frass might provide an initial substrate upon which bacteria could bloom prior to tissue degradation and lesion formation. Work is underway to investigate the relationship between beetle and bacteria, but at present, the cause and effect-order remains unclear. *Agrilus biguttatus* may be attracted to a bacterial component of AOD or may simply be selecting weakened hosts predisposed to decline. This latter scenario would imply that both beetle and pathogen are secondary pests and that host condition is the critical factor in determining which trees suffer from AOD.

Declining oaks are likely to be attractive to *A. biguttatus*, but the lesions themselves may be attractive to ovipositing adults. Bleeding cankers on native black oak in North America (e.g. *Q. kelloggii* and *Q. agrifolia*) infected by *Phytophthora ramorum* Werres (Sudden Oak Death) have been shown to be highly attractive to bark and ambrosia beetle species that usually colonize recently dead or severely weakened trees (McPherson *et al.*, 2008). The close relationship of *A. biguttatus* with AOD also raises the question of whether the buprestid might also be acting as a vector for the pathogens, either between individual trees or within trees via larval galleries. The sticky exudates could cause the beetles to pick up bacteria and act as an incidental vector. This type of transmission need not be limited to *A. biguttatus* and raises the possibility of many insect species acting as non-specific vectors, as is the case with Fire Blight, *Erwinia amylovora* (Burrill) Winslow (Hildebrand *et al.*, 2000), and oak wilt *Ceratocystis fagacearum* (Bretz) Hunt (Juzwik and French, 1983).

If AOD bacteria are vectored by *A. biguttatus*, the most likely opportunities for transmission would be during feeding or egg-laying. Feeding wounds on oak leaves are a possible route for infection, although they are located far from the observed symptoms. Similar transmission was recorded in the case of Dutch elm disease. The causal fungus, *Ophiostoma novo-ulmi* Brasier, is vectored by *Scolytus* bark beetles feeding on the bark of twigs in the canopy (Webber and Brasier, 1984). *Agrilus biguttatus* egg-laying takes place near the stem symptoms, but with no maternal gallery produced, any potential mode of bacterial transmission is unclear and likely requires a more complex association than is apparent. To date, no *Agrilus* species has been demonstrated to actively vector a plant pathogen. A small percentage of adult *A. bilineatus* emerging from oak trees infected with *Ceratocystis fagacearum* were found to be carrying spores of the fungus, but no experimental transmission was shown (Rexrode, 1968). Similarly inconclusive studies upon *A. biguttatus* have investigated associations with fungi including *Ceratocystis kubanicum* Potl., of which spores have been isolated from adults (Kryukova, 1976), and *Fusarium eumartii* Carp. (Tiberi and Ragazzi, 1998). *Fusarium solani* (Mart.) Sacc. has been isolated from larval *A. angustulus* on oak (Bohàr, 1992), and the bacterium *Pseudomonas pseudoalcaligenes* Monias has been isolated from the mouthparts of *Agrilus nubeculosus* Fairmaire attracted to *Acacia senegal* (L.) Willd. (El Atta *et al.*, 2011), but in common with all other studies, vectoring was not demonstrated. Studies of the gut microbiota of *A. planipennis* have, however, shown that some bacterial types are present throughout the different life stages (larvae, pre-pupa, pupa and adult) indicating potential for longer-term associations (Vasanthakumar *et al.*, 2008).

Management considerations for AOD-affected areas

Any proposed management programme should consider that *A. biguttatus* is a native British beetle and, until recently, considered rare. At this time, whether it has a causal role in AOD is unclear, and to date, there is no evidence to contradict its status as a secondary stem-boring beetle attacking weakened oak. In woodland managed for conservation, a low level of tree death partly mediated by *Agrilus* would be acceptable as a natural process that helped to maintain levels of deadwood. However, if there is concern over *Agrilus*-associated tree death, factors that may have lowered the resistance of the tree against attack should be considered. This would include drought stress, root decay and defoliation. Such primary stress factors may be reversible, and the trees may recover. Good silvicultural management and care for underlying tree health may be sufficient to reduce the impact of this insect.

Nevertheless, *A. biguttatus* populations are thought to have increased considerably in parts of the UK, and unacceptable levels of colonisation of trees with high commercial or amenity value may be considered for control, for example in high-value plantations. The direct damage of larval feeding on the timber of infested oak is limited, since only the outer sapwood is affected. However, in the longer term, trees that have recovered from attacks will exhibit signs of callusing and wound-recovery, which will remain in subsequently formed wood, creating aesthetic and possibly mechanical deficiencies (Vansteenkiste *et al.*, 2004). Prompt removal of severely declined or recently dead trees should limit damage to the timber caused by secondary wood-boring insects, including longhorn beetles (Cerambycidae) and oak pinhole borer (*Platypus cylindrus* Fab.). In a notable parallel, *P. cylindrus* also appears to have recently increased in abundance and is now being considered a pest species of hardwood timber (Tilbury, 2010).

Agrilus biguttatus population levels are likely to be influenced by a number of natural processes, including predators and parasitoids. Harsh winters may have less influence, as overwintering stages may be cold tolerant; EAB pupae accumulate high concentrations of glycerol and antifreeze chemicals allowing them to survive cold winters (Crosthwaite *et al.*, 2011). A study investigating the biotic causes of mortality in EAB found host tree defences to be the most important mortality factor, followed by woodpecker activity (Duan *et al.*, 2010). However, predation rates by woodpeckers has been shown to vary greatly between individual trees (0–100 per cent of pupae and large larvae) (Lindell *et al.*, 2008). Predation of *A. biguttatus* by woodpeckers may be locally important in the UK (D. Inward, personal observation), and maintaining environments attractive to woodpeckers may help to regulate populations of the buprestid. Larvae of *A. biguttatus* are known to be parasitized by wasps including the ichneumonid *Deuteroxorides elevator* Panzer (Kenis and Hilszczanski, 2004) and the braconid *Spathius curvicaudis* Ratzeburg (Moraal and van Achterberg, 2001). The latter is a native species that locates larvae within the bark before laying multiple eggs on or close to it (Shaw, 1988). With a multivoltine life cycle, the wasp has the potential to respond rapidly to an increasing prey population, yet its importance in this role has yet to be evaluated. The related species *Spathius agrili* has been shown to have significant impacts on *A. planipennis* populations in China, where the wasp and buprestid are native. Parasitism rates of up to 90 per cent have been demonstrated in some ash tree stands (Yang *et al.*, 2010), and the wasp is currently being investigated as a potential biocontrol agent in the USA (Gould *et al.*, 2011).

Management of *A. biguttatus* has not been studied in Britain but has been considered in a range of forests in continental Europe (Wachtendorf, 1955; Hartmann and Kontzog, 1994; Oosterbaan *et al.*, 2001; Evans *et al.*, 2004). Management of trees with stem bleeds should follow advice to minimize the spread of bacteria (see below). Specific management should focus on those that exhibit a sudden and rapid decline, including significant foliage and twig loss, and signs of *Agrilus* presence (exit holes and galleries beneath the bark). Removal of heavily colonized trees may reduce population growth, but caution is urged to avoid the creation of open habitat where sun-warmed stems offer attractive new oviposition sites to female beetles. This can be countered by underplanting with shade-bearing woody species (Wachtendorf, 1955) or mixed species edge planting, especially along the southern side of woodland. Removal of colonized trees should be completed prior to the spring emergence of new adults, and the bark may be removed from stems and destroyed to prevent later emergence of beetles that have completed larval development. Movement of wood, particularly as firewood, has been identified as an important pathway in the dispersal of many xylophagous insects (Haack *et al.*, 2010), and the destination of any infested material should be considered. Smaller branch material is not utilized by *A. biguttatus* and can remain *in situ*, and trees standing dead for more than a year will be unlikely to yield any further individuals. If replanted, young oak will not provide a resource for *Agrilus*, until the trees mature (>50 years old) and bear a suitably thick bark layer.

Direct chemical control of the beetle would prove difficult due to its cryptic life cycle, spent primarily beneath the bark. Pyrethroid insecticides, applied externally to the stem, have been used experimentally with some effect (Habermann and Preller, 2003), where the application of the insecticide prior to adult emergence gave good control of beetles in their pupal chambers within the outer bark, but did not penetrate to affect the feeding larvae in the phloem or sapwood. Systemic insecticides have been successfully trialled in North American ash trees against EAB via soil drenches, trunk injections and spraying of the lower stem. If the trees had not declined too far, control was often effective using these treatments, although success on larger trees was more inconsistent (Herms *et al.*, 2009). Drawbacks include the need for regular repeat applications, and the associated expense, although this might be justified for important amenity trees. However, systemic insecticides used on a keystone species such as oak would cause the mortality of many other non-target invertebrates. In the EU, several neonicotinoid pesticides are currently subject to a two-year ban owing to their negative effects on non-target insect species such as bees.

Acute oak decline is not a quarantine disease in the UK, so there are no statutory requirements regarding disease management. Management decisions should therefore be guided by prevention of spread and protection of areas not yet affected. Once a better understanding of the significance of *Agrilus* in AOD is obtained, specific evidence-based management research can get underway. Until then however, recommendations are based on the precautionary approach as set out by Denman *et al.* (2010). Considering that *Agrilus* and bacteria appear to be the two key factors in AOD, managing destruction of the bark layers that they occupy may be the most important aspect to reducing spread. Removing and burning these layers within a very short time after felling should reduce the risk of spread, and sanitation of footwear and felling equipment must be carried out thoroughly as a precautionary measure.

Conclusions and suggested research

The beetle–bacterial interaction within the AOD complex forms a key element of the syndrome but is the least understood and hence the most in need of further research. Better understanding of the abiotic stress factors predisposing an otherwise healthy oak tree to attack is essential. The point at which an oak tree becomes attractive to an ovipositing *A. biguttatus* should be identified through a comparative study of healthy and symptomatic trees, focusing upon the chemical basis of attraction and the role of host (and perhaps bacterial) volatile chemicals. Similarly, investigation of the status of host defences across the range of severity of AOD would identify the stage at which a tree becomes susceptible to successful attack. This may assist in the management of AOD by identifying 'at risk' trees, as well as those so heavily infested that they have little chance of recovery.

The southerly distribution of *A. biguttatus* in the UK is determined by specific but poorly understood environmental parameters, such as the thermal requirements of the different developmental stages. Determining the influence of temperature on development is essential to understanding how life cycle duration and seasonal timing of emergence vary across the geographical range of the beetle. It will inform management and enable predictions to be made about the impact of climate change.

There is an absence of data on population levels of *A. biguttatus* in the UK, and even less is known about the status of its natural predators. Quantitative survey data on the distribution and abundance of both the buprestid and its natural predators would set a baseline from which future changes in population levels and range can be monitored and inform management decisions. Of equal importance is the need to characterize the microbial component of the AOD syndrome and the pathogenic capability of individual species. Although no evidence exists to suggest that *A. biguttatus* is acting as a vector, the relationship between beetle and pathogens could be to be mutually beneficial, and the order of their colonisation would yield essential information regarding the pathogenic process. Only addressing these numerous and challenging knowledge gaps would provide an insight into the longer-term impacts of AOD upon our native oak species.

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