

Review of the emerald ash borer (Coleoptera: Buprestidae), life history, mating behaviours, host plant selection, and host resistance

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Abstract—As of summer 2014, the invasive emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), has become established in 24 states in the United States of America and has killed tens of millions of ash trees since its introduction into Michigan in the 1990s. Considerable research has been conducted on many aspects of EAB life history, natural history, ecology, and management strategies in an attempt to contain this devastating pest. In this article, we review the life history, mating behaviours, and host plant selection by EAB in North America as well as host resistance to EAB attack.

Introduction

The emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) is an Asian (*i.e.*, China, Japan, Korea, Mongolia, Eastern Russian) flat-headed borer that is primarily a pest of ash, *Fraxinus* Linnaeus (Oleaceae), species. It was discovered near Detroit, Michigan, United States of America and Windsor, Ontario, Canada in 2002 (Haack *et al.* 2002) and is infesting and killing native North American ash at unprecedented levels.

Based on dendrochronological evidence, EAB was likely introduced to North America in the 1990s (Siegert *et al.* 2014) and has been spreading rapidly through natural dispersal and human-assisted movement of infested logs, firewood, and nursery material. As of summer 2014, it has become established in 24 states in the United States of America (<http://www.emeraldashborer.info>). It has the potential to spread and kill ash trees throughout North America. Ash mortality in some infested forested areas could reach up to

99% within a number of years of EAB infestation (Knight *et al.* 2013). Forest inventories report almost 8 billion ash trees on United States of America timberlands valued at US\$282.25 billion (United States Department of Agriculture, Forest Service 2008). Ash is also one of the most prevalent trees in agricultural lands, shelterbelts, and urban areas. The projected costs to communities and landowners for treatment, removal, and replacement of urban ash trees within a 25-state area from 2009 to 2019 was estimated at US\$10.7 billion (Kovacs *et al.* 2010). In response to the threat posed by EAB, federal, state and provincial agencies imposed quarantines to restrict movement of ash from known infested areas, implemented large-scale surveys to detect new infestations, and have supported extensive research to understand EAB natural history, behaviour, and host interactions in order to develop effective management strategies.

In this paper, we review the life history, mating behaviours, and host plant selection by EAB.

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Other aspects of natural history, ecology, and management strategies have been reviewed elsewhere (Crook and Mastro 2010; Herms and McCullough 2014).

Life history

Emerald ash borer generally has a one-year life cycle, but may require two years to complete development in cooler climates, when attack densities are low, hosts are vigorous, or when oviposition occurs in late summer (Cappaert *et al.* 2005; Wei *et al.* 2007; Tluczek *et al.* 2011). In southern Michigan, EAB adults generally begin emerging from “D”-shaped exit holes in mid-May at about 250 growing degree days base 10 °C (DD₁₀) (450 growing degree days base 50 °F (DD₅₀)) (Brown-Rytlewski and Wilson 2004) and emergence continues throughout the summer. Peak adult activity generally occurs in late June or early July at 514–556 DD₁₀ (925–1000 DD₅₀) (McCullough *et al.* 2009a; Poland *et al.* 2011) and drops off sharply by the end of July at about 833 DD₁₀ (1500 DD₅₀) as the initial beetles to emerge die off and new emergence declines (Brown-Rytlewski and Wilson 2004; Poland *et al.* 2011).

Adults feed on the margins of ash leaves for 10–14 days before becoming sexually mature and mating (Rodriguez-Saona *et al.* 2007). They continue to feed and mate throughout their lifetime, which generally lasts three to six weeks (Bauer *et al.* 2004; Lyons *et al.* 2004). They are most active on sunny days with air temperatures above 25 °C (Wang *et al.* 2010) and often rest on leaves or in bark crevices on cool days and during rainy weather (Rodriguez-Saona *et al.* 2007). Emerald ash borer females deposit 60–80 eggs in nature and up to 258 eggs in the laboratory during their life span (Lyons *et al.* 2004). Eggs are deposited individually or in clusters in bark cracks or crevices (Bauer *et al.* 2004).

Eggs hatch within two weeks at 25 °C and the larvae feed in the inner phloem, outer xylem, and cambium creating serpentine-shaped galleries that are packed with frass. Larvae have four developmental instars (Cappaert *et al.* 2005) and most larvae complete feeding in October or November in Michigan. Pre-pupae overwinter in cells about 1.25 cm deep in the sapwood of thin-barked trees or in the outer bark of thick-barked trees. In southern Michigan, pupation begins in mid-April

and continues into May, followed by adult emergence approximately three weeks later (Bauer *et al.* 2004). Some EAB overwinter as young larvae in their galleries and then require a second year of development before emerging as adults (Cappaert *et al.* 2005; Tluczek *et al.* 2011).

Mating behaviours

Emerald ash borer adults become sexually mature ~10–14 days after feeding on host plants (Lelito *et al.* 2007; Rodriguez-Saona *et al.* 2007). Mating behaviours are observed mostly between 10:00 and 17:00 hours during the day (Rodriguez-Saona *et al.* 2007) and typically take place on the host trees. Males hover around tree canopies and may locate potential mates using visual cues as they often drop out of the air and land directly on top of females (Lelito *et al.* 2007). The visual cues are not sex-specific, however, since EAB males approach both sexes of pinned dead EAB (Lelito *et al.* 2007; Rodriguez-Saona *et al.* 2007). Olfactory cue(s) from EAB females start playing a role after initial physical contact as evidenced by arrestment and longer copulation attempts with females (Lelito *et al.* 2007) or even at a distance of up to 5 cm from EAB females (Pureswaran and Poland 2009a). Mating is prolonged, lasting 50 minutes on average (Pureswaran and Poland 2009a). After mating, EAB pairs separate and there appears to be no mate guarding. In laboratory studies, EAB females mated repeatedly with multiple males throughout their lifetime (Lyons *et al.* 2004). Routledge and Keena (2012) found that mating with multiple males is likely the best strategy for EAB females to maximise fecundity.

Two contact pheromones, 3-methyltricosane (Lelito *et al.* 2009) and 9-methyl-pentacosane (Silk *et al.* 2009), have been isolated and identified from cuticles of EAB females. Application of 3-methyltricosane solution to dead and dichloromethane-washed EAB females increased time male EAB spent in contact with females as well as time spent attempting copulation. However, EAB males spent less time on washed females and females on which the compound was reapplied compared with unwashed EAB females; therefore, the effects of 3-methyltricosane might be synergised by other compounds such as 9-methyl-pentacosane (9-Me-C₂₅), which is only found in sexually mature females (Silk *et al.* 2009).

Application of 9-Me-C₂₅ to dead and *n*-hexane-washed EAB females elicited copulation attempts by males similar to those observed for dead and unwashed EAB females. Furthermore, the number of copulation attempts and the length of arrestment by EAB males were similar on dead and unwashed females and on dead washed females with 9-Me-C₂₅ reapplied (Silk *et al.* 2009).

One volatile pheromone, (3*Z*)-dodecen-12-olide [(3*Z*)-lactone], has been identified from sexually mature EAB adults (Bartelt *et al.* 2007; Silk *et al.* 2011). (3*Z*)-Lactone was detected from both sexes by Bartelt *et al.* (2007), but only in EAB females by Silk *et al.* (2011). (3*Z*)-Lactone elicits antennal responses in both sexes of EAB adults (Bartelt *et al.* 2007; Silk *et al.* 2011). Exposure to UV light converts (3*Z*)-lactone to (3*E*)-lactone, which also elicits antennal response in both sexes of EAB adults (Silk *et al.* 2011). Green sticky prism traps baited with (3*Z*)-lactone alone (released at ~22 µg/day at 25 °C) attracted significantly more EAB males than unbaited control traps at two sites in Ontario, Canada, but not in Michigan, United States of America (Silk *et al.* 2011). Green sticky prism traps baited with the green leaf volatile (3*Z*)-hexenol (released at ~17 mg/day at 20 °C) in combination with either of the isomers released at ca. 22 µg/day at 25 °C also attracted more EAB males than traps baited with the green leaf volatile alone. Ryall *et al.* (2012) further confirmed that a combination of (3*Z*)-hexenol and a low release of (3*Z*)-lactone was most effective in attracting EAB males to green sticky prism traps suspended high in the canopy.

Host plant selection

Ash trees are the only larval hosts reported for EAB in China (Yu 1992; Liu *et al.* 2003; Zhao *et al.* 2005), although other tree genera, *Juglans* Linnaeus (Juglandaceae), *Pterocarya* Kunth (Juglandaceae), and *Ulmus* Linnaeus (Ulmaceae), have been reported as larval hosts in Korea and Japan for *Agrilus marcopoli* Obenberger, and *Agrilus marcopoli ulmi* Kurosawa (Ko 1969; Akiyama and Ohmomo 1997), with which EAB was synonymised (Jendek and Grebennikov 2011). To date, all North American ash species encountered by EAB are susceptible (Anulewicz *et al.* 2008; European and Mediterranean Plant

Protection Organization 2013). Ash mortality within stands in North America can reach up to 99% regardless of ash basal area, its relative dominance, relative density, overall stand density, stand basal area, or any measure of species diversity (Smith *et al.* 2005; Knight *et al.* 2013). This suggests that EAB is very efficient at locating host trees even when they are rare within mixed species stands.

Visual orientation

EAB preferentially attacks open grown ash trees (McCullough *et al.* 2009a, 2009b) suggesting that visual tree silhouette may play a role in host location. Attack densities are also higher on stressed trees (McCullough *et al.* 2009a, 2009b). Ash stressed by girdling can be differentiated from non-girdled ash two months after the girdling event based on hyperspectral and high-resolution panchromatic imagery in conjunction with ground-based spectral data (Bartels *et al.* 2007). Male and female EAB are sensitive to light in the ultraviolet (UV), violet, and green (420–430, 460, and 530–560 nm, respectively) ranges of the visible spectrum, while mated females are also sensitive to light in the red (640–670 nm) range (Crook *et al.* 2009, 2012). The beetles are attracted to traps coloured different shades of green or purple hung in the open or in the canopy of ash trees (Crook *et al.* 2009; Francese *et al.* 2010). Males, that tend to hover near the canopy of ash trees (Rodriguez-Saona *et al.* 2007), are captured in higher proportions in green traps hung in the canopy of ash trees and baited with green leaf volatiles; whereas, females, that oviposit on the trunks of ash trees are captured in higher proportions in purple traps hung below the canopy and baited with bark sesquiterpenes (Crook and Mastro 2010; Grant *et al.* 2011).

Chemical orientation

Adult beetles were attracted to ash stressed by feeding damage or treatment with methyl jasmonate (Rodriguez-Saona *et al.* 2006). At least 16 volatile compounds from stressed ash elicited antennal responses by EAB including hexanal, (*E*)-2-hexenal, (*Z*)-3-hexen-1-ol, 3-methylbutylalldoxime, 2-methyl-butylalldoxime, (*Z*)-3-hexen-1-yl acetate, hexyl acetate, (*E*)-β-ocimene, linalool, 4,8-dimethyl-1,3,7-nonatriene, and *E,E*-α-farnesene. In field studies, traps baited with the

leaf alcohol (*Z*)-3-hexen-1-ol alone or combined with other green leaf volatiles (Rodríguez-Saona *et al.* 2006; de Groot *et al.* 2008; Grant *et al.* 2010; 2011; Poland *et al.* 2011) were attractive to EAB. Sesquiterpene levels were found to be elevated in the bark of girdled ash trees and six sesquiterpenes consistently elicited antennal responses by both male and female *A. planipennis* (Crook *et al.* 2008). Five of the compounds identified to be active by electro-antennographic detection (EAD) were α -cubebene, α -copaene, 7-*epi*-sesquithujene, trans- β -caryophyllene, and α -caryophyllene (humulene). The sixth EAD-active compound was later identified as eremophilene (Cossé *et al.* 2008). The essential oils, Manuka oil containing α -cubebene, α -copaene, trans- β -caryophyllene and α -humulene, and *Phoebe* oil that contains 7-*epi*-sesquithujene in addition to the other four compounds found in Manuka oil, were attractive to *A. planipennis* (Crook *et al.* 2008). Ash leaf volatiles and bark sesquiterpenes play an important role in host location for both males and females.

Host plant resistance

In its native range, EAB is considered a nuisance pest and generally only attacks dying or stressed Asian ash species (Liu *et al.* 2007), often growing under poor site conditions (Wei *et al.* 2004). Of the more than 20 species and subspecies of *Fraxinus* native to Asia (Wei 1992; Wallander 2008; Hinsinger *et al.* 2013), EAB mainly infests Manchurian ash (*F. mandshurica* Ruprecht), Korean ash or Chinese ash (*F. chinensis* Roxburgh) (Yu, 1992), generally attacking only stressed trees. On the other hand, North American ash trees, green ash (*F. pennsylvanica* Marshall), white ash (*F. americana* Linnaeus), and velvet ash (*F. velutina* Torrey), commonly planted in Asia (Zhao *et al.* 2005) suffer high EAB infestations and mortality (Wei *et al.* 2004; Duan *et al.* 2012): at one site in China 95% of green ash trees were moderately infested while no infestation was found in Korean ash trees of similar size planted beside them (Liu *et al.* 2007).

In its introduced range in North America, EAB attacks almost exclusively native, green ash, white ash, and black ash (*F. nigra* Marshall). Although blue ash (*F. quadrangulata* Michaux) is native to North America, a study by Tanis and McCullough (2012) indicates that in a natural stand it is not as

quickly or severely impacted by EAB infestation relative to white ash, even though it has been shown that EAB can carry out its full life cycle in both species (Anulewicz *et al.* 2008). This may be explained, in part, by blue ash being less preferred than white ash in an adult beetle choice feeding study (Pureswaran and Poland 2009b). In contrast to EAB attack on stressed trees in the native range, EAB in the introduced range kills healthy trees (Poland and McCullough 2006). Anulewicz *et al.* (2008) compared adult landing and oviposition on logs of several North American ash species and on non-ash species including American elm (*Ulmus americana* Linnaeus; Ulmaceae), hackberry (*Celtis occidentalis* Linnaeus; Ulmaceae), black walnut (*Juglans nigra* Linnaeus; Juglandaceae), shagbark hickory (*Carya ovata* (Miller) Koch; Juglandaceae), and Japanese tree lilac (*Syringa reticulata* (Blume) Hara; Oleaceae). Adults landed and oviposited more frequently on ash logs compared with non-ash logs and no larvae were able to survive, grow, or develop in non-ash logs. Recently, Cipollini (2015) found EAB infesting white fringe tree (*Chionanthus virginicus* Linnaeus (Oleaceae)) in Ohio, United States of America, which represents the first expansion of EAB onto a non-ash host in North America. Although all species of North American ash appear susceptible to EAB, preference and susceptibility vary among species. Canopy dieback and EAB attack density are significantly higher in green ash than in white ash trees at the same sites, and in white ash compared with blue ash trees at the same sites (Anulewicz *et al.* 2007; Tanis and McCullough 2012).

Emerald ash borer attack and tree mortality were significantly higher in white and green ash cultivars than in a Manchurian ash cultivar planted in a common garden trial near the initial infestation in southeast Michigan (Rebek *et al.* 2008). It is hypothesised that the greater susceptibility of North American ash species compared with Asian ash species, at field sites in both China and North America, may be due to resistance mechanisms that developed in Asian ash species through their evolutionary history with EAB that is lacking with North American species.

Differences in susceptibility to EAB among ash species may be related to differences in host volatiles, nutrition, and defense compounds (Eyles *et al.* 2007; Chen and Poland 2009, 2010;

Pureswaran and Poland 2009b; Cipollini *et al.* 2011; Chen *et al.* 2011a, 2011b, 2011c; Whitehill *et al.* 2011, 2012). Pureswaran and Poland (2009b) found that EAB adults preferred to feed on green, white, and black compared with European, blue, or Manchurian ash and the ash species differed significantly in the relative amounts of antennally active volatiles. Emerald ash borer also prefers to feed on mature leaves compared with newly flushed leaves, on leaves grown in sun compared with those in shade, and on leaves from trees that had been stressed by girdling compared with leaves from healthy trees (Chen and Poland 2009). The preference might be driven by greater concentrations of total proteins in foliage from sunny areas (Chen and Poland 2009). Insects are generally limited by nutrients such as nitrogen (White 1993). Greater concentrations of total phenolics in ash leaves in the sun (Chen and Poland 2009) do not appear to impede EAB's preference, probably due to EAB adults' ability to excrete or detoxify phenolics. Concentrations of total phenolics in EAB frass were significantly greater than the concentrations in ash leaves that EAB adults fed upon, irrespective of ash tree species (Chen and Poland 2010). Girdled ash trees attract more EAB than non-girdled trees (McCullough *et al.* 2009b). However, the attraction might be attributable to volatiles released by girdling rather than changes in nutritional and defensive chemistry triggered by girdling. Girdling in green ash seedlings elevated concentrations of total non-structural carbohydrate (TNC), which reduces the protein to TNC ratio (Chen and Poland 2009). Protein to TNC ratio is an indicator of nutrient balance (Lee *et al.* 2002). Besides water content, protein or amino acid contents might also contribute to selection of downward feeding behaviour by EAB larvae observed both in laboratory and field studies (Chen *et al.* 2011a). Emerald ash borer larvae fed upon artificial diets supplied with casein (source of proteins) or yeast (source of amino acids) generally had lower mortality and higher biomass than those fed upon diets with neither components.

Eyles *et al.* (2007) analysed phloem phenolics of the Manchurian ash cultivar "Mancana", the green ash cultivar "Patmore", and the white ash cultivar "Autumn Purple" (Cipollini *et al.* 2011), and found that hydroxycoumarins and two

phenylthanoids (*i.e.*, calceolariosides A and B) were unique to "Mancana". In addition to the three ash species analysed by Eyles *et al.* (2007), Whitehill *et al.* (2012) further compared phloem phenolics of a black ash cultivar "Fall Gold", blue ash seedlings, and European ash seedlings and discovered that hydroxycoumarins and the two phenylthanoids were also detected in black ash and European ash, which are both susceptible to EAB infestation, indicating they are not unique to Manchurian ash and likely do not play a role in EAB-resistance. Whitehill *et al.* (2012) found differences in qualitative phenolic profiles among ash species that coincided with their phylogenetic relatedness. The phenolic profile of Manchurian ash, was most different from the green ash variety "Patmore", green ash seedlings, and the white ash variety "Autumn Purple" and most similar to the more closely related black ash cultivar "Fall Gold", and European ash seedlings. Cipollini *et al.* (2011) also found differences in phenolic profiles among ash species, identifying nine phenolics unique to the Manchurian ash cultivar "Mancana". Most of these compounds were also subsequently identified in other species that are susceptible to EAB by Whitehill *et al.* (2012), leading the authors to conclude that much of the phytochemical variation detected in these studies was most likely due to evolutionary divergence and not related to differences in EAB-resistance. However, results reported by both Cipollini *et al.* (2011) and Whitehill *et al.* (2012) indicated that lignans and lignan derivatives might contribute to resistance to EAB. Chakraborty *et al.* (2014) further examined the role of phenolics, including lignans and their derivatives, by comparing responses of the black ash cultivar "Fall Gold" and the Manchurian ash cultivar "Mancana" to EAB larval feeding: they failed to detect pinoresinol dihexoside, which was reported to be unique to "Mancana" by both Cipollini *et al.* (2011) and Whitehill *et al.* (2012), but identified eight compounds that were significantly affected by larval feeding, including two pinoresinol derivatives. In both "Fall Gold" and "Mancana", seven of these compounds decreased or remained the same and only pinoresinol A, increased significantly in response to larval feeding. No qualitative differences in the metabolic profiles of "Mancana" and "Fall Gold" were reported, but quantitative differences were detected between

the two cultivars after being fed upon by EAB larvae. Further study of inter- and intra-specific variation of phenolics using a more genetically diverse sampling strategy is necessary to better understand their roles in resistance of ash to EAB.

Understanding the mechanisms that EAB larvae use to cope with different kinds of phenolics can also help elucidate the roles that phenolics play in ash tree defense responses. EAB larvae of all instars are able to eliminate phenolics from susceptible black ash, green ash, and white ash through excretion and enzymatic conversion (Chen *et al.* 2012). Genes coding various detoxification enzymes such as superoxide dismutase, catalase, and glutathione peroxidase have been detected in EAB larvae, prepupae, and adults (Rajarapu *et al.* 2011).

In addition to constitutive defenses that are present at all times, herbivory can induce production of defensive compounds and responses may differ among ash species. In black ash, EAB larval feeding induced volatile emission of (*E*)- β -ocimene and (*Z,E*)- α -farnesene, increased levels of carbohydrates and phenolics, and decreased levels of proteins and amino acids (Chen *et al.* 2011c). In response to EAB adult feeding, green and white ash had higher levels of induced volatile emission than black ash, levels of total phenolics decreased in white ash, and chymotrypsin inhibitors increased in black ash (Chen *et al.* 2011b). Differences in induced defensive responses among ash species may partially explain differences in EAB preference and host susceptibility.

Unlike mobile adult beetles, EAB larvae must survive or die in the tree on which the eggs are deposited. Therefore, host plant defense mechanisms that kill or negatively impact larval performance are likely to play critical roles in ash defense against EAB. Recent studies report host defense responses are found in both Manchurian and green ash and are responsible for at least a portion of larval mortality in both species; however, a higher proportion of host-killed larvae were reported in the EAB-resistant Manchurian ash (Duan *et al.* 2010, 2012, 2013). Egg bioassays performed by affixing eggs directly to potted grafts or seedlings in the greenhouse, demonstrated that the Asian species *F. chinensis*, *F. floribunda* Wallich, *F. lanuginosa* Koidzumi, *F. mandshurica*, *F. paxiana* Lingelsheim, and *F. spaethiana* Lingelsheim were all resistant to EAB compared with green ash based on levels of larval development

and mortality. In the resistant species, most if not all larvae are killed by host defenses and the small number of surviving larvae exhibit stunted or slower development while in the susceptible species only a small number of larvae are killed by host defenses and the majority develop successfully (J.K., personal observation). Research on ash plant resistance has been conducted at the molecular level. Four proteins (PR-10 protein, an aspartic protease, a phenylcoumaran benzylic ether reductase, and a thylakoid-bound ascorbate peroxidase) identified in a resistant Manchurian ash cultivar, "Mancana" and have been proposed to contribute to the resistance of this cultivar based on the two-fold greater expression levels relative to the susceptible black ash cultivar "Fall Gold" (Whitehill *et al.* 2011). However, a separate transcriptomic analysis and subsequent RT-qPCR validation across three separate genotypes of Manchurian, black and green ash demonstrated that expression of a major allergen like PR-10 was lower in Manchurian ash than in black ash and did not differ between Manchurian and green ash (Rivera Vega 2011). This may be because the two studies compared different members of the same gene family, but it highlights the importance of validation of genes and/or proteins across genetically diverse samples. mRNA levels of several genes involved in plant defense response signalling, including two classes of transcription factors (WRKYs, MYBs), calcium-dependent protein kinases, ethylene response factor and lipoxygenase 3, were higher in Manchurian ash than in black and green ash (Bai *et al.* 2011). Lipoxygenases have long been known to be involved in plant resistance to biotic and abiotic stressors (Shukle and Murdock 1983; Siedow 1991) and they are generally induced in resistant plants at higher levels than susceptible ones (Chen *et al.* 2009).

Knowledge of ash resistance to EAB has been applied to ash breeding programmes using both traditional and hybrid breeding approaches (Koch *et al.* 2012). In traditional breeding, genetic materials from rare surviving ash trees in areas heavily infested by EAB are preserved by grafting for use as parents. In hybrid breeding, susceptible native ash species were crossed with resistant Asian species and backcrosses are performed if necessary. Grafts from surviving ash trees and hybrid ashes are being evaluated for susceptibility to EAB in feeding and

oviposition preference studies and studies to evaluate development and survival of larvae from eggs affixed to the trees (J.K. and T.M.P., personal observation). Transgenic techniques are also being used to develop resistant ash species/varieties (Pijut *et al.* 2010). The identification of the genes encoding defensive compounds confirmed to have a role in EAB-resistance will greatly facilitate the development of EAB-resistant ash through both breeding and transgenic approaches.

Final comments

A greater understanding of EAB natural history and host interactions will help contribute to the development of survey and management tools including traps and lures, landscape level management programmes, and resistance breeding programmes. Survey and management tools developed by research are now being implemented in an integrated strategy and tested in a multi-agency pilot slow ash mortality (SLAM) study. The approach incorporates (1) surveys of EAB infestation and distribution using artificial traps; (2) ash host survey to determine area at risk and plan location of detection traps and treatments; (3) population suppression through insecticide treatment of landscape trees and trees in a buffer zone around positive detections, girdling trap trees that are subsequently felled and debarked to detect and destroy beetles, removal of infested trees and ash use, and release of natural enemies for biological control; (4) regulatory control to prevent artificial movement; and (5) public outreach (Poland and McCullough 2010; McCullough and Mercader 2012). The SLAM approach is most likely to be successful when implemented in areas with new infestations where the populations of EAB are relatively low and isolated. Landscape-level management strategies including SLAM and biological control, insecticide treatments in urban areas, collection and preservation of ash seed, and development of more resistant ash, offer hope for the protection of ash and persistence of the genus at some level in urban and natural forests.

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