PROGRESS and FUTURE DIRECTIONS in Research on the Emerald Ash Borer

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When the emerald ash borer (EAB) was discovered near Detroit, Michigan in July 2002, very little was known about it other than the fact that it was killing large numbers of ash trees throughout a widespread area in southeast Michigan (Poland and McCullough 2006). Ash mortality in the area had been noted for a few years, but was attributed to ash decline until damage and symptoms including galleries and exit holes became so prevalent that it was clear the beetle damage was not secondary but was in fact the causative agent of mortality. The beetle was identified by Eduard Jendek as *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), an exotic wood boring beetle native to Asia (Haack et al. 2002). Some basic aspects of its biology and general descriptions were available and translated from Chinese textbooks (Chinese Academy of Science 1986, Yu 1992), but nothing was known about how to detect or control it. Hence, research scientists quickly initiated projects to learn about this invasive species and develop tools to manage it.

Emerald ash borer adult feeding on ash leaf (photographer, Deborah Miller, USDA Forest Service)

BIOLOGY

Research on the biology of EAB in North America demonstrates that it is generally quite similar to the life cycle described for EAB in China (Chinese Academy of Science 1986, Yu 1992). The life cycle is typically completed in one year, but two years may be required, especially in vigorous hosts with light infestations, in cooler climates, or when eggs are deposited late in the season (Cappaert et al. 2005, Wei et al. 2007, Wang et al. 2010, Tluczek et al. 2011). Two years may also be required to complete development in cut logs or firewood, particularly when the wood has dried (Petrice and Haack 2007).

Adult beetles chew their way out of trees leaving D-shaped emergence holes. In the Great Lakes region of North America and at similar latitudes in Asia, adults begin emergence in May or June, activity peaks in late June to early July, and the flight period usually ends by September (Cappaert et al., 2005; Wei et al., 2007; Wang et al., 2010). Adults are most active on sunny days when air temperatures exceed 25°C [77°F] (Wang et al., 2010) and often rest in bark crevices and on leaves during rainy or cool weather (Rodriguez-Saona et al., 2007). EAB adults feed on ash leaves

(Fig. 1) throughout their life which can last for several weeks (Bauer et al. 2004, Lyons et al. 2004, Wang et al. 2010). Adults begin mating after 5-7 days of maturation feeding and females feed for an additional 5-7 days before beginning to deposit eggs in bark cracks or crevices.

Eggs hatch within two weeks and the larvae feed in the phloem and cambium through autumn creating serpentine-shaped galleries that are packed with frass. Larvae pass through four developmental instars (Cappaert et al. 2005) and most complete feeding in October or November. Pre-pupae overwinter in cells about 1.27 cm deep in the sapwood of thin-barked trees or in the outer bark of thick-barked trees. Pupation begins in mid-April and continues into May, followed by adult emergence approximately 3 weeks later. 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). EAB prepupae are intolerant of freezing and survive winter by accumulating high concentrations of glycerol and other antifreeze compounds to achieve supercooling points of about -30°C [-22°F] (Crosthwaite et al. 2011).

On-going research is exploring many other aspects of EAB biology and ecology such as overwinter survival, temperature influences on larval development, nutritional requirements for development of artificial diet and rearing methods, and factors that influence mating and reproduction.

HOST RELATIONS

Ash is the only larval host reported for EAB in China (Yu 1992; Liu et al., 2003; Zhao et al., 2005). EAB was synonymized [equated with] with two other Asian *Agrilus* species and one subspecies: *Agrilus feretrius* Obenberger (type Taiwan), *Agrilus marcopoli* Obenberger (type Mongolia), and *Agrilus marcopoli ulmi* Kurosawa (type Japan) (Jendek and Grebennikov, 2011). Other tree genera (*Juglans, Pterocarya,* and *Ulmus*) have been reported as larval hosts in Korea and Japan for *A. marcopoli* and *A. marcopoli ulmi* (Ko, 1969, Akiyama and Ohmomo, 1997). There are 27 species and one sub-species of ash, *Fraxinus,* native to Asia (Wei 1992) of which emerald ash borer mainly infests Manchurian ash (*F. manchurica*), Korean ash (*F. rhynchophylla*), and Chinese ash (*F. chinensis*) (Yu 1992), generally attacking only stressed trees. It also attacks the North American species, green ash (*F. pennsylvanica*), white ash (*F. americana*), and velvet ash (*F. velutina*), which are commonly planted in China (Liu et al. 2003, Zhao et al. 2005). North American ash species are attacked at higher levels than native Asian ash species in China; at one site 95% of North American green ash trees were moderately infested while no infestation was found in Korean ash trees of similar size planted side by side (Liu et al. 2007). In its introduced range in North America, emerald ash borer is able to attack every species of ash it has so-far encountered including black (*F. nigra*), blue (*F. quadrangulata*), green, pumpkin (*F. profunda*), and white ash and even healthy trees are attacked and killed (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 that are congeners [belonging to the same genus] of hosts reported for the synonomized *Agrilus* species in Korea and Japan. Non-hosts included American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), black walnut (*Juglans nigra*), shagbark hickory (*Carya ovatae*), and Japanese tree lilac (*Syringa reticulatae*). Adults landed and oviposited less frequently on non-ash logs compared to ash logs and no larvae were able to survive, grow, or develop in non-ash logs. Although all species of North American ash appear susceptible to emerald ash borer, preference and susceptibility vary among ash species. For example, Anulewicz et al. (2007)

Forest Service technicians checking a double decker trap for emerald ash borers (photographer, Therese Poland, USDA Forest Service)

found significantly higher canopy dieback and emerald ash borer attack density in green ash than in white ash trees at the same sites, and in white ash compared to blue ash trees at the same sites. Similarly, Tanis et al. (2012) found greater persistence of blue ash compared to white ash and suggested it was more resistant to emerald ash borer. Black ash experienced greater EAB-induced mortality than white or green ash in 31 permanent vegetation plots in forest stands in Upper Huron River Watershed, although all three species were severely impacted (Gandhi et al. 2008). Differences in susceptibility to emerald ash borer among ash species have been found to be related to differences in host volatiles, nutrition, and defense compounds. Pureswaran and Poland (2009a) found that emerald ash borer adults preferred to feed on green, white and black compared to European (F. excelsior), blue, or Manchurian ash and the relative amounts of antennally-active volatiles varied among ash species. Emerald ash borer also prefers to feed on mature leaves compared to newly flushed leaves, on leaves grown in sun compared to leaves grown in shade, and on leaves from trees that had been stressed by girdling compared to leaves from

Injecting ash tree with systemic insecticides (photographer, Therese Poland, USDA Forest Service)

healthy trees (Chen and Poland 2009). Preferences were related to lower defense compounds (trypsin and chymotrypsin inhibitors) and greater nutritional value with higher levels of amino acids and protein to carbohydrate ratios.

In a common garden study near the initial infestation area in Michigan, emerald ash borer attack densities and tree mortality were significantly higher in white and green ash cultivars than in a Manchurian ash cultivar (Rebek et al. 2008). It is hypothesized that the greater susceptibility of North American ash species compared to 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 close evolutionary history with emerald ash borer that is lacking with North American species.

Eyles et al. (2007) analyzed phloem chemistry of different ash species and found differences in the array of phenolic compounds among ash species and that hydroxycoumarins and calceolariosides A and B were unique to Manchurian ash. More recently, Whitehill et al. (2011) also found differences in qualitative phenolic profiles among ash species with Manchurian ash being most different from the green ash variety 'Patmore', and white ash variety 'Autumn Purple' cultivars. However, they found the hydroxycoumarins and calceolariosides were present in highly susceptible black ash and European ash, refuting their role in resistance to emerald ash borer. Similarly, Cipollini et al. (2011) found differences in phenolic profiles among ash species, with 9 phenolics unique to Manchurian ash. Different species of ash also respond differently to emerald ash borer adult and larval feeding. In response to 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 were increased in black ash (Chen et al. 2011a). Larval feeding also induced volatile emission of (E)-ß-ocimine and (Z,E)-a-farnesene in black ash, increased levels of carbohydrates and phenolics, and decreased levels of proteins and amino acids (Chen et al. 2011b). Emerald ash borer larvae utilized green ash amino acids more efficiently than those of white or black ash and was were able to eliminate phenolics through excretion and enzymatic conversion (Chen et al. 2012).

Asian ash species are being explored as a potential source of genetic resistance and efforts to breed EAB resistant ash are ongoing (Koch et al. 2012). A small proportion of ash have survived and remain healthy in ash stands throughout Michigan and Ohio where over 99% of the ash trees have been killed by EAB. These lingering ash trees are being evaluated as a potential source of resistance genes in native ash populations (Knight et al. 2013). Genomic sequencing of Asian and North American ash species has also been conducted to provide a molecular foundation for targeting resistance breeding (Bai et al. 2011), and transcriptomic studies of EAB are exploring mechanisms by which larvae detoxify host defenses (Mittapalli et al. 2010, Rajarapu et al. 2011,).

SURVEY AND DETECTION

Initial delimitation of the infested area in Michigan was based on visual surveys using external symptoms. Visual surveys along with tracebacks of nursery stock movement out of Detroit were used to detect new infestations of EAB through 2003. It became apparent that visual surveys were not effective for detecting low density infestations of EAB. Research demonstrated that adult beetles are attracted to volatiles emitted by stressed ash (Rodriguez-Sanoa et al. 2006) and preferentially oviposit on girdled trees (McCullough et al. 2009a, 2009b). As a result, the Michigan Department of Agriculture implemented a statewide grid of girdled trap trees in their EAB survey in 2004. Girdled trap trees were visually inspected during the summer to collect any captured EAB adults from sticky bands. Trees were felled during the fall/winter and bark was peeled from sections of the upper trunk and canopy to locate any EAB larvae and galleries (Hunt 2007, Rauscher 2006). Trap trees were used for detection surveys in Michigan and several surrounding states through 2008. While girdled trees are the most effective tool for EAB detection (McCullough et al. 2011, Mercader et al. 2013), debarking trees to locate larval galleries can be labor intensive and costly. Moreover, suitable trees may not always be available or accessible, especially in urban areas or when multi-year surveys are needed.

Considerable research has, therefore, been invested in efforts to develop effective artificial traps and lures to attract and capture EAB adults. Artificial traps were developed incorporating attractive olfactory and visual cues and first implemented for detection surveys in 2008 (Crook and Mastro 2010). Volatiles from ash trees leaves and bark elicit antennal responses and are attractive to EAB (Rodriguez-Saona et al. 2006; deGroot et al. 2008; Crook et al. 2008; Grant et al. 2010, 2011; Poland et al. 2011). Many of the volatiles present in ash bark are also present in Manuka oil (Crook et al. 2008).

The beetles are also attracted to specific wavelengths of violet and green light (Crook et al. 2012), and females are also sensitive to red ranges of the spectrum. EAB adults are attracted to traps colored different shades of green or purple hung in the open or in the canopy of ash trees (Francese et al. 2005, Crook et al. 2009, Francese et al. 2010). Males, that tend to hover near the canopy of ash trees, are captured in higher proportions in green traps hung in the canopy of ash trees; whereas, females, that oviposit on the trunks of ash trees are captured in higher proportions in purple traps hung below the canopy (Crook and Mastro 2011). In addition, there is recent evidence of close range or contact pheromones involved in mate recognition and mating behavior (Lelito et al. 2009; Pureswaran and Poland 2009b) and a female-produced volatile pheromone, cis-lactone, that increases attraction of males to green canopy traps baited with host volatiles (Silk et al. 2009, 2011; Ryall et al. 2012).


Tetrastichus planipennisi, larval parasitoid of emerald ash borer (photographer, David Cappaert, Department of Entomology, Michigan State University)

Traps used for detection surveys have evolved over the years to incorporate the latest research findings. Currently, national detection surveys conducted by USDA Animal Plant Health Inspection Service (APHIS) employ sticky purple prism traps hung in the canopy of ash trees and baited with the ash leaf volatile, cis-3-hexenol, and Manuka oil (APHIS 2014). Other promising traps under evaluation in pilot surveys include green multiple funnel traps baited with cis-3-hexenol, green sticky prism traps hung in the canopy of ash trees baited with cis-3-hexenol and the EAB pheromone cis-lactone, and purple and green double decker traps (Fig. 2) composed of a 10 foot PVC pole to which two sticky prisms are attached near the top and baited with cis-3-hexenol. Continued research on close range pheromones and improvements to trap designs and lures will lead to more effective detection tools.

CHEMICAL CONTROL

Soon after EAB was discovered studies were initiated to evaluate different insecticides as a means of rapid control. Early studies tested canopy sprays with persistent insecticide formulations (e.g., bifenthrin, cyfluthrin). Sprays were not popular because of problems such as potential drift, environmental contamination, non-target impacts on pollinators and beneficial predatory insects, and possible applicator exposure. Systemic insecticides are applied by injecting products directly into the trunks of trees (Fig. 3) or by application to the soil or as a basal trunk spray, eliminating most problems associated with cover sprays (Herms et al. 2009, McCullough et al. 2011, Herms and McCullough 2014). However, once high densities of EAB larvae have injured the vascular system of an ash tree translocation and efficacy of systemic insecticides are impaired.

Initially only a few systemic insecticide products were available, mainly with imidacloprid as the active ingredient and efficacy trials yielded inconsistent results (Herms et al. 2009). New systemic insecticides are now available and application technology has improved. An emamectin benzoate-based insecticide was first registered in the US in 2010 and is currently the most effective product available (Herms and McCullough 2014), providing two to three years of nearly complete EAB control (Herms et al. 2010, Smitley et al. 2010, McCullough et al. 2011, 2012,). Many municipalities and private landowners are now protecting ash trees from EAB with emamectin benzoate.

Dinotefuran is a highly soluble new generation neonicotinoid product. It can be applied as a basal trunk spray and is effective if applied annually. It is popular among arborists when many small trees require treatment (McCullough et al. 2011, Herms and McCullough 2014). Imidacloprid-based insecticides must be applied annually and continue to be used for EAB control with variable efficacy. Azadirachtin is a natural insecticide derived from the neem tree (Azidirachta indica). Azadirachtin products are not toxic to EAB adults, but impair reproduction and control young larvae. They provide one to two years of tree protection, depending on local EAB density (McKenzie et al. 2010).

Economic analyses have shown that insecticide treatment is highly cost effective in urban settings compared to the costs of removing trees killed by EAB (Kovacs et al. 2010). Treating a portion of the trees in a given area may also slow the rate of EAB population growth (Mercader et al. 2011). However, broadscale applicaton of systemic insecticides is not practical for

EAB management in forests, woodlots, riparian zones or other natural areas due to high costs associated with individual tree treatment and environmental concerns that may limit use of insecticides in natural areas. Effective biological control of EAB, whether by native natural enemies or introduced parasitoids, may be critical to preventing the functional loss of many ash species in forest ecosystems across North America (Klooster et al. 2014, Knight et al. 2013). Biological control and systemic insecticides are not mutually exclusive and may result in additive or even synergistic negative effects on EAB populations (Barclay 1987, Berec et al. 2007, Suckling et al. 2012). Future research will focus on new and improved insecticide formulations and application methods along with integration of insecticide control with other tactics for area-wide management of EAB.

NATURAL ENEMIES AND BIOLOGICAL CONTROL

In 2003, surveys were initiated for natural enemies of EAB in Michigan and China. In southeast Michigan (2003-2004) and a more recent survey in Pennsylvania (2008), <4% of EAB larvae were found parasitized by native and naturalized non-native parasitic wasps (Bauer et al. 2012). Ectoparasitoids are the most common group attacking EAB larvae, and of those, *Atanycolus* spp. and *Spathius* spp. (Braconidae) are the most prevalent in Michigan. No EAB egg parasitoids have been found in North America. In northeast China three parasitoid species were found attacking EAB: *Oobius agrili* (Encyrtidae), an egg parasitoid; and *Tetrastichus planipennisi* (Eulophidae) and *Spathius agrili* (Braconidae) two larval parasitoids (Fig. 4). At one site in Jilin province, combined parasitism by *O. agrili* and *T. planipennisi* was estimated to reduce EAB densities by 74% in green ash trees (Liu et al. 2007). *S. agrili* was later found at that site but was rare. These three EAB parasitoid were studied extensively for non-target impacts in containment/quarantine laboratories, and approved by US Environmental Protection Agency for environmental release in late July 2007 (USDA APHIS 2014b)

The three species of Asian parasitoids were first released at sites in southeast Michigan in 2007 (USDA APHIS 2010). In 2009, the APHIS EAB Biocontrol Facility in Brighton, MI became operational, after transfer of improved rearing methods and parasitoid cultures from the Forest Service and Center for Plant Health Science and Technology (CPHST) laboratories. Production has increased annually, and in 2012, more than 350,000 wasps were released in 14 states. Several releases have resulted in successful establishment, although establishment of *S. agrili* in Michigan has been limited, possibly because of cold weather (Duan et al. 2009, 2010, 2012). Exploration and evaluation of additional Asian parasitoid species for potential introduction are ongoing (Duan et al. 2012), including another *Spathius* species, *S. galinae,* native to Russian Far East, that may be more adapted to cooler climates (Belokobylskij et al. 2012). Current research is evaluating effects of the parasitoids on EAB population growth rates and ash tree health and will require assessment over multiple years.

FUTURE OUTLOOK FOR ASH MANAGEMENT

Survey and management tools developed by research are now being implemented in an integrated strategy and tested in a multi-agency pilot SL.ow A.sh M.ortality (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, clusters of girdled trap trees that are felled and debarked to detect and destroy beetles, removal and utilization of infested trees, and release of natural enemies for biological control; 4) regulatory control to prevent artificial movement; and 5) public outreach. The SLAM approach is most likely to be successful when implemented in areas with new infestations that are relatively small 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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