Emerald Ash Borer Invasion of North America: History, Biology, Ecology, Impacts, and Management

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Abstract

Since its accidental introduction from Asia, emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), has killed millions of ash trees in North America. As it continues to spread, it could functionally extirpate ash with devastating economic and ecological impacts. Little was known about EAB when it was first discovered in North America in 2002, but substantial advances in understanding of EAB biology, ecology, and management have occurred since. Ash species indigenous to China are generally resistant to EAB and may eventually provide resistance genes for introgression into North American species. EAB is characterized by stratified dispersal resulting from natural and human-assisted spread, and substantial effort has been devoted to the development of survey methods. Early eradication efforts were abandoned largely because of the difficulty of detecting and delineating infestations. Current management is focused on biological control, insecticide protection of high-value trees, and integrated efforts to slow ash mortality.

INTRODUCTION

Emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), was first detected in North America in 2002 (14). Since its accidental introduction from Asia, this invasive pest has killed untold millions of ash trees (*Fraxinus* spp.) in forest, riparian, and urban settings (83). In some forests near the epicenter of the invasion in southeast Michigan, more than 99% of the ash trees with stems greater than 2.5 cm in diameter have been killed (44). All North American species of ash that EAB has encountered to date are susceptible to varying degrees, including green ash (*Fraxinus pennsylvanica* Marsh.), white ash (*F. americana* L.), and black ash (*F. nigra* Marsh.) (97), which are the most widely distributed and abundant ash species in North America. It appears increasingly likely that EAB could functionally extirpate one of North America's most widely distributed tree genera, with devastating economic and ecological impacts.

When EAB was discovered in North America, information on its biology, even in its native range in Asia, was scarce. For example, two pages that described some life-history traits were translated from a Chinese textbook (116) and a few taxonomic reports had been published in scientific journals (43). Over the past decade, a substantial amount of research in North America has addressed a wide range of topics related to EAB biology, ecology, impacts and management. Research review meetings were held annually in the United States from 2003 to 2007 and in 2009 and 2011. Published proceedings from these meetings (**http://www.fs.fed.us/foresthealth/technology/pub_titles.shtml**) provide a chronology of the research and regulatory response to the EAB invasion, effectively documenting the most costly biological invasion by an exotic forest insect to date. Here, we review advances in our understanding of EAB biology, ecology, and management that have occurred in the ten years since the initial detection of this pest in North America.

HISTORY AND ORIGIN OF THE EAB INVASION

Extensive ash decline and increasing mortality were noted in the greater Detroit, Michigan, metropolitan area as early as the summer of 2001, when they were initially misattributed by a local extension specialist to ash yellows (36), a disease caused by a phytoplasma. In June 2002, beetles reared from ash logs were submitted to the Michigan State University Department of Entomology, where they were identified as a member of the genus *Agrilus* and promptly shipped to taxonomic specialists in North America and Europe. On July 9, 2002, the specimens were identified by Dr. Eduardo Jendek of Bratislava, Slovakia, as *Agrilus planipennis*, and shortly thereafter, on August 7, 2002, specimens recovered from declining ash in nearby Windsor, Ontario, were confirmed as EAB (14).

Buprestid beetles typically colonize stressed trees (76). In southeast Michigan, however, EAB was observed killing healthy ash that had been regularly irrigated and fertilized, as well as naturally regenerated ash in forests where other tree species appeared healthy. By 2003, at least 5–7 million ash trees were dead or dying in a six-county area of southeastern Michigan, and it was becoming apparent that EAB had the potential to devastate ash on a continental scale (14, 41, 78).

In response, the Michigan Department of Agriculture imposed a state quarantine on July 16, 2002, to regulate movement of ash nursery trees, logs, and related products from infested counties (14). The state regulations were incorporated into a federal quarantine published by USDA APHIS (Animal and Plant Health Inspection Service) on October 14, 2003 (29). The same month, USDA APHIS convened a Science Advisory Panel to formulate recommendations for a program to contain and eradicate EAB (14). Eradication activities began in 2003 but were eventually terminated as it became apparent that economic and technological constraints had rendered the objective nonviable (34). As of September 2013, EAB infestations have been detected in 21 US states and two Canadian provinces. EAB was also identified in Moscow, Russia, in 2007 as the cause of mortality of green ash originally imported from North America and planted in landscapes (7).

EAB is indigenous to northeastern China, the Korean peninsula, and eastern Russia, where it functions as a secondary colonizer of ash trees native to Asia that are stressed, declining, or dying (7, 55, 113). A Chinese horticultural report published in 1966 documented extensive mortality of North American "garden" ashes (white ash) caused by unidentified species of *Agrilus*, foretelling the impact this insect would eventually have in North America (56). Although this or a closely related species also has been reported to be indigenous to Mongolia, Taiwan, and Japan, the presence of EAB in these areas has not been definitively confirmed.

Dendrochronological reconstruction showed EAB was established in southeast Michigan by at least the early 1990s and had begun to kill ash trees in the greater Detroit metropolitan area by 1998 (92). Although the origin of the North American infestation remains unknown, molecular evidence suggests China was likely the source (11). In addition, plantations of North American white and green ash were established as part of major reforestation efforts in China in the 1980s and 1990s, enabling EAB populations to build to high densities there (55, 113). Although the pathway and vector responsible for introducing EAB into North America remain unknown, EAB was probably imported into North America via crating, pallets, or dunnage made from infested ash (14).

EAB LIFE HISTORY

In North America, EAB completes its life cycle in one or two years (14, 106). In Ohio and Michigan, adult emergence generally begins between early May (southern Ohio) and mid-June (central Michigan), peaks from mid-June to early July, and is largely complete by early August (22, 79). Emerging adults leave distinct D-shaped exit holes (2–3 mm in diameter) in the trunk and branches. Despite substantial research, no long-distance pheromones from EAB have been reported. Rather, mating is facilitated by host selection in which males seek and locate females using visual (52) and olfactory cues (52, 82) and contact pheromones (51, 94).

Adults, which can live 3–6 weeks, require approximately one week of maturation feeding on the margins of ash leaves before mating begins (82, 112) but cause negligible defoliation. Females produce on average between 40 and 70 eggs (90, 113), with long-lived females capable of producing more than 200 eggs (113). Eggs are laid individually within bark cracks and crevices or beneath bark flakes and hatch within approximately two weeks (112). Upper portions of the canopy of large trees are typically colonized before the main trunk (14, 27, 106), making it difficult to detect early infestations.

Neonate larvae bore through the outer bark and begin feeding in galleries in the phloem and cambium, which typically also score the outer sapwood (14). Serpentine galleries disrupt the ability of trees to transport nutrients and water, eventually girdling branches and the trunk. As larval density builds within a tree, canopy thinning and branch dieback become evident. Once canopy decline becomes apparent, trees typically die within 2–4 years (39). Larvae feed from mid-summer into fall and complete four instars (14, 15). Most larvae complete their feeding and overwinter as prepupal fourth instars in small chambers in the outer bark or within the outer 1–2 centimeters of sapwood (14, 99). Pupation occurs in middle to late spring and adults emerge soon thereafter (14).

Availability of phloem determines the number of EAB that can develop and emerge from trees as adults. Data acquired by felling and debarking 148 ash trees killed by EAB showed that on average (± standard error) approximately 105 ± 5.7 EAB adults per square meter of phloem can emerge from green ash and white ash trees ≥13 cm in diameter, and 69 ± 5.9 beetles per square meter can develop on small ash (61). Larval densities can be two to three times higher in heavily infested trees, but intraspecific competition for phloem limits survival (106). Canopy dieback on green and white ash trees became apparent once emergence density of adults reached 25–35 adults per square meter (2).

In ash trees stressed by girdling, high larval densities, or other injuries, nearly all EAB develop within one year. However, a biennial life cycle has been documented and is most commonly observed in relatively healthy trees with low EAB densities (93, 106). In these trees, larvae overwinter as early instars, feed during a second summer, and then emerge the following spring. The two-year life cycle likely slows the intrinsic rate of EAB population growth in newly established, low-density populations where most host plants remain healthy (73). Although all instars can overwinter, pupation does not occur until spring, after prepupae have overwintered (14, 112). Prepupal larvae of the closely related bronze birch borer (*Agrilus anxius* Gory) must experience freezing temperatures before pupation can occur (8). If this is also true of EAB, it would synchronize the timing of adult emergence among insects with one- and two-year life cycles.

EAB prepupae are intolerant of freezing and survive winter by achieving low supercooling points of about −30°C by accumulating high concentrations of glycerol and other antifreeze compounds (20). Sobek-Swant et al. (99) found that winter acclimation can be reversed when temperatures reach 10°C–15°C, which could threaten overwintering survival in regions with winters characterized by intermittent warm spells. However, they concluded that ultimate distribution of EAB in North America is more likely to be limited by host availability than by climatic factors.

HOST INTERACTIONS

To date, all North American ash species encountered by EAB are susceptible to varying degrees (2, 3, 87). Black, green, and white ash are highly vulnerable (44), although white ash is somewhat less preferred (3, 97). EAB adults are preferentially attracted to, and larval density and growth rate are higher on, trees stressed by factors such as girdling (16, 63, 65, 106), but healthy trees are colonized as well (14). For all three species, mortality of trees ≥2.5 cm in diameter exceeded 99% by 2010 in sites near the infestation epicenter in southeast Michigan (44), and the signature of this widespread mortality is already apparent in large-scale forest inventory data (81).

Blue ash (*F. quadrangulata* Michx.) appears to be the most resistant North American ash species encountered by EAB to date (2, 103). More than 60% of blue ash in wooded areas in southeastern Michigan appeared healthy in 2011, whereas all white ash >10 cm in diameter in the same sites have been killed (103). Nearly complete mortality in forests that differ widely in ash density, edaphic factors, stand health, and community composition (44) suggests there is little opportunity for silvicultural practices to prevent ash mortality (45, 97). As EAB continues to spread, its ecological and economic impacts in North America are expected to rival or exceed those of chestnut blight and Dutch elm disease, invasive pathogens that devastated natural and urban forests in the twentieth century (31, 44).

There is strong evidence that ash species are the only hosts of EAB in North America. In a choice experiment, EAB adults landed on green ash almost exclusively (57), and field and laboratory studies that included confamilial relatives of ash found that larvae were unable to successfully develop on species other than ash (2, 4). There have been no observations, even in heavily infested sites, of EAB colonizing non-ash species.

EAB is only an occasional pest of ash species indigenous to China, and infestations are consistently associated with stressed and dying trees (7, 54, 113). Thus, EAB behaves in Asia much as Nearctic *Agrilus* spp. do in North America, where species such as the bronze birch borer (*A. anxius* Gory) and the twolined chestnut borer (*A. bilineatus* Weber) preferentially colonize stressed birch (*Betula* spp.) and oak (*Quercus* spp.), respectively (76). Conversely, in China EAB has caused extensive mortality of North American ash species even at sites where EAB had little impact on Asian ash species (55, 113).

The high relative resistance of Asian species has been attributed to targeted defenses selected via coevolution with EAB (55, 87). Common garden studies confirmed that Manchurian ash (*F. mandshurica* Rupr.), which is native to China, is more resistant to EAB than North American white, green, and black ash are (87, 115). Comparative studies to elucidate the mechanistic basis of resistance of Manchurian ash to EAB have focused on induced and constitutive phloem chemistry, specifically phenolic compounds and defensive proteins (17, 28, 114, 115). Behavioral and physiological responses of EAB adults to foliar characteristics of North American and Asian ash species have also been compared (16, 82).

Because of their inherent resistance to EAB, Asian ash species may be a source of resistance genes that could be introgressed into North American species (115), and efforts to breed EAB-resistant ash are ongoing (47). Extensive surveys of ash stands in Michigan and Ohio where EAB-induced ash mortality exceeds 99% have revealed a very small proportion of ash that remain healthy and thus may provide a potential source of resistance genes in native ash populations (46). Genomic sequencing of Asian and North American ash species has also been conducted to provide a molecular foundation for targeted breeding (6, 88), and transcriptomic studies of EAB have focused on mechanisms by which larvae detoxify host defenses (75, 83, 84).

ECOLOGICAL IMPACTS OF EAB

Most EAB-induced ash mortality within an invaded stand occurs over just a few years (44), resulting in relatively synchronous, widespread gap formation with potentially cascading direct and indirect effects on forest community composition and ecosystem processes (31). These effects include altered understory environment, nutrient cycles, and successional trajectories; facilitation of the spread of light-limited invasive plants; and increased coarse woody debris. Furthermore, at least 282 arthropod species feed on ash, including at least 43 monophagous species native to North America that may be at risk of coextirpation as ash is eliminated from the ecosystem (32). Given that *Fraxinus* is one of the most widely distributed tree genera in North America (58), the ecological impacts of the EAB invasion are likely to be experienced on a continental scale.

ECONOMIC AND CULTURAL IMPACTS OF EAB

An analysis of the economic impacts of nonnative forest insects found that EAB is already the most destructive and costly forest insect to invade the United States (5). Impacts of widespread ash mortality, as well as the regulations associated with EAB quarantine, have affected a broad range of plant-related industries, property owners, municipalities, and state agencies (5, 34). For example, restrictions on the sale of ash nursery stock affected more than 9,500 nurseries in southeast Michigan, and regulations to limit transport of ash logs affected more than 2,000 Michigan sawmills and logging companies, as well as producers that used ash for railroad ties, pallets, and tool handles. Such impacts will continue to spread as more counties and states are found to be infested and subsequently quarantined.

Much of the economic impact of EAB is associated with treatment and/or removal and replacement of high-value trees in urban and residential areas (48). Ash has been one of the most commonly planted trees in urban and suburban landscapes across the continental United States

(78, 85), comprising more than 20% of the trees in many municipalities across the country (48). An early effort to estimate economic impacts projected that communities in Ohio would likely incur costs of $1.0–4.2 billion if all amenity ash trees on public land were removed and replaced (102). Projected costs for removal and replacement of ash trees growing in parks, private land, and along streets in communities in four Midwestern states were estimated at $26 billion (101). Kovacs et al. (48) modeled the spread and economic impact of EAB from 2009 to 2019 and projected the discounted costs of treating or removing roughly half the affected urban trees would be $10.7 billion, and twice that if ash in adjacent suburban communities were included. A subsequent projection of EAB expansion through 2020 showed costs, primarily associated with landscape trees, would likely exceed $12.5 billion (49).

Mature trees add thousands of dollars to property values (1), decrease cooling costs, play major roles in storm water capture, reduce levels of airborne pollutants, and provide other ecosystem services. A range of human health benefits, including reduced incidence of cardiovascular disease and asthma, faster recovery from surgery, improved air quality, and increased physical activity, are associated with urban trees (21, 24, 30, 50, 107, 108). A recent study showed ash mortality due to EAB was correlated with an increase of more than 6,100 and 15,000 deaths due to lower respiratory disease and cardiovascular disease, respectively, in residents in a 15-state area (23). Analyses have shown that systemic insecticides are a viable option for protecting high-value ash trees (40, 61, 64), and results of a cost-benefit analysis found that protecting mature trees was more economically favorable than preemptive tree removal or allowing trees to die (111).

Whereas economic costs associated with EAB can be estimated, cultural impacts are much more difficult to assess and quantify. For several Native American and First Nation tribes in eastern North America, black ash is particularly valued as a spiritual resource. Black ash basketry, an art passed from generation to generation, serves as a means to preserve cultural values as well as a source of income. Basket-making families carefully select and harvest a few black ash trees each year from traditional harvest grounds. Multiple generations come together to debark and pound the logs with sledgehammers until the growth rings separate, producing long strips of wood that can be woven into baskets. Baskets of all shapes and sizes are produced. Some are destined for practical everyday use, and others are striking works of art. Cooperative efforts to collect and preserve ash seeds, including seeds from black ash trees, have been undertaken by a number of tribes and scientists from federal and state agencies and universities.

DISPERSAL AND DETECTION

Like many invasive species, the spread of EAB is characterized by stratified dispersal (72–74, 92). Infestations expand over relatively short distances through natural dispersal, in this case, adult flight. Long-distance dispersal occurs when humans transport infested material such as nursery stock or firewood, resulting in the establishment of localized satellite populations that are geographically disjunct from the main invasion front (73, 91). Satellite populations grow and eventually coalesce with each other and the primary invasion front, increasing the overall rate of spread.

Accurate projections of spread rates could have practical implications for survey and management. One of the first efforts to estimate the rate of EAB spread was based on the expansion of the area regulated by federal, state, and provincial quarantines (77). The extent of the area regulated by EAB quarantines, however, was influenced primarily by enhanced detection efforts and abilities rather than the actual spread of the infestation. Regulatory efforts to trace back nursery stock originating in infested areas of southeast Michigan, ongoing detection surveys, and outreach efforts have led to increasing awareness of EAB and the discovery of new infestations.

Dendrochronological evidence collected in several of the newly identified infestations showed EAB populations were established at least 3–8 years before they were discovered (92). Another modeling effort evaluated landscape effects on simulated spread of EAB across an Illinois county, but was limited at the time by lack of information on EAB biology (10). Prasad et al. (80) estimated EAB populations spread at a rate of 20 km per year and linked natural beetle dispersal with factors that could influence long-distance, human-assisted EAB spread, such as road networks, campgrounds, and human population density. Quarantines, public outreach, and increasing awareness of the impacts of EAB have presumably reduced the likelihood of human-assisted EAB dispersal, but much remains to be learned about natural dispersal.

Observations in laboratory and field settings have shown that EAB adults, particularly mated females, are relatively strong fliers. Females tethered to a flight mill flew an average of 1.7 km over 24 hours, and estimates suggest the maximum cumulative flight distance over the life span of a female could be as high as 9.8 km (105). Although flight mill studies are useful for comparisons between beetles of different ages or sexes, their results cannot be extrapolated to field situations, where beetles interact with hosts, conspecifics, potential predators, and weather (105). Given the pattern of spread and numerous unsuccessful eradication efforts, some proportion of mature females disperse and colonize trees more than 800 m from their emergence point. However, the proportion of females that engage in long-distance dispersal remain unknown (74).

Much of our current understanding of EAB dispersal has come from field studies that assessed realized EAB dispersal by systematically felling and debarking ash trees to locate larval progeny of a cohort of beetles that emerged from a known point of origin (71, 93). In two sites where ash trees were distributed linearly, along either a drainage ditch or a highway right-of-way, gallery distribution fit a negative exponential function. At least 70% of the larval galleries were on trees within 100 m of the emergence point of the parent beetles, although in one site, galleries were found 750 m from the origin (71). Two other large-scale studies using similar methods were conducted in heterogeneous sites with urban, residential, and wooded areas and found larvae up to 650 m from the origin (93). Beetles preferentially colonized a severely stressed ash in one site and appeared more likely to colonize open-grown trees, such as those in residential areas, than shaded trees in woodlots, a pattern noted in other field studies (63, 65). There was no relation between tree size and larval presence or density in any of the dispersal studies, nor was there any indication that prevailing winds affected dispersal, and beetles bypassed many presumably suitable ash trees surrounding the origin of these infestations. Within 200 m of the origin, beetles were most likely to colonize trees growing in areas with abundant ash, but beyond 200 m, ash abundance did not affect colonization (93).

Detection of EAB Infestations

The ability to detect, delineate, and monitor infestations is a key aspect of invasive pest management, and substantial resources have been invested into development of survey methods since EAB was first identified (19). EAB adults do not produce long-range pheromones (19) and regulatory programs initially relied on visual surveys to identify infested ash trees. However, it soon became clear that external signs and symptoms become apparent only after the local population density has increased (2), by which time multiple generations of beetles have dispersed (74, 93). Prevalence of a two-year life cycle in low-density infestations coupled with the propensity of beetles to initially colonize the upper canopy of trees (14, 27, 106) contributed to the inefficiency of visual surveys.

Ash trees that are girdled in spring to attract ovipositing females and then debarked in fall or winter to locate larvae have been used to detect or monitor EAB infestations, and numerous infestations were detected by regulatory officials using such "detection trees" (42, 86). Although girdled trees remain the most effective tool for EAB detection (69), locating and debarking trees can be labor intensive and suitable trees may be unavailable in urban areas or for multiyear surveys.

Considerable research continues to focus on development of artificial traps and effective lures to attract EAB adults (19). Beetles respond to visual cues, and electroretinogram assays have shown EAB are sensitive to specific wavelengths of red, violet, and green light (18). In the United States, operational detection surveys since 2008 have relied on sticky prism traps made from purple (or green) coroplast and suspended in the canopy of ash trees (19). Traps are baited with lures consisting of volatile host and similar compounds (35, 79). An alternative design, termed the double-decker trap, consists of two purple prism traps attached to a 3-m-tall PVC pipe (10 cm in diameter) that slides over a T-post and the prisms are baited with the same lures used in the canopy traps (62, 79).

In contrast to canopy traps, double-decker traps are designed to be placed in full sun near the edge of wooded areas with ash or near open-grown ash trees to provide beetles with a highly apparent point source of volatiles and to take advantage of the beetles' preference for sunny conditions (69, 79). Field studies evaluating trap design, color and placement, and lure composition have yielded inconsistent results (79), perhaps reflecting local variation in site conditions. Where EAB densities are low, baited double-decker traps have been most effective, and at higher densities double-decker and canopy traps have been equally effective (60, 69, 79). Contact or close-range pheromones that appear to mediate close-range attraction of EAB to mates have also been identified and, when integrated with a better understanding of EAB dispersal and host selection behavior, may eventually lead to more effective detection tools (51, 82, 89, 94, 95).

MANAGEMENT OF EAB

Early Eradication Efforts

Beginning in 2003, USDA APHIS, in cooperation with other federal and state agencies, developed a plan that called for containing the known EAB infestations in southeast Michigan and Windsor, Ontario, while eradicating localized, satellite populations, termed outliers (14, 38, 41). There was no practical way to reduce EAB populations on a large scale with insecticides, particularly given the size of the infestations. It was theorized that if the rate of EAB expansion could be significantly slowed, the high ash mortality in the core would reduce EAB carrying capacity, collapsing the EAB population and potentially providing opportunities to drive population densities below the Allee threshold and thus to extinction (100). Quarantines to limit the risk of new EAB introductions were imposed to regulate transport of ash trees, logs, firewood, and related items out of infested areas (38, 41).

Establishment of a 5- to 10-km-wide ash-free firebreak perimeter of the generally infested area in southeast Michigan, which would prevent natural EAB spread, was proposed as part of the containment effort (14, 41). An ash-free zone was never initiated in the United States, largely because of the difficulty of delineating the primary infestation, which continued to expand as more infested trees were discovered. In 2004, an ash-free zone was implemented just east of the Windsor, Ontario, area that connected Lake Erie with Lake St. Clair. However, it proved unsuccessful as EAB populations were subsequently found to have been established beyond the ash-free barrier even before it was created.

Officials in the United States continued efforts to locate outlier populations with visual surveys of ash trees, trace backs of ash nursery stock shipped from southeast Michigan, and public outreach activities. Most outlier sites that were identified had resulted from inadvertent, long-distance transport of infested ash nursery stock, sawlogs, or firewood, often well before EAB was identified and quarantines established in 2002. One or more outlier populations were targets of eradication in Michigan, Ohio, Indiana, Maryland, and Virginia annually between 2003 and 2009. Because EAB was known to be capable of dispersing at least 750 m per year (71), eradication protocols called for removal and destruction of all ash trees within an 800-m radius of trees known to be infested to eliminate asymptomatic but potentially infested trees (14, 39, 41, 66, 93). The goal of eradicating EAB was eventually abandoned as additional outlier infestations were discovered in more states and funding became limited (34).

North American Natural Enemies

Soon after EAB was discovered in North America, a search began for evidence of mortality attributable to native parasitoids, predators, and pathogens. Native parasitoids were occasionally observed, but parasitism rates were extremely low as was mortality due to predatory insects and pathogenic fungi (9, 14, 55). Woodpeckers, which typically prey on late instar and prepupal EAB larvae in winter or early spring, represented the single greatest mortality factor affecting EAB populations in North America (14, 27), and all woodpecker species native to Michigan were observed to feed on EAB larvae (53). Larval mortality attributable to woodpecker predation in individual ash trees ranged from 0 to 90% and was highly variable among sites (14, 53). However, the effects of woodpecker predation on EAB population dynamics remain unclear.

In 2007, a researcher noted a high proportion of parasitized EAB larvae in a debarked tree in a heavily infested site in southeast Michigan. The parasitoid, originally identified as *Atanycolus hicoriea* (Hymenoptera: Braconidae), was later determined to be a previously undescribed solitary ectoparasitoid, which was subsequently named *Atanycolus cappaerti* (12, 59). Since then, parasitism of EAB larvae by native *Atanycolus* spp., primarily *A. cappaerti*, has been frequently observed and appears to be increasingly common, at least in Michigan (13). Relatively high parasitism rates have been recorded most often in areas where EAB is well established, likely reflecting a numerical response of *Atanycolus* sp. to high EAB densities (25). Although other native parasitoids continue to be recovered from EAB, the overall parasitism rates of these species are generally low (25, 26).

Classical Biological Control

Once efforts to eradicate EAB were terminated, classical biological control efforts came to the forefront. Exploration began in China to identify EAB parasitoids, and substantial efforts, first in China and later in quarantine facilities in the United States, were undertaken to conduct host range testing and develop protocols for mass rearing and release (110). Three species are currently being mass reared and released: an egg parasitoid (*Oobius agrili* Zhang and Huang) (Hymenoptera: Encyrtidae), a larval endoparasitoid (*Tetrastichus planipennisi* Yang) (Hymenoptera: Eulophidae), and a gregarious larval ectoparasitoid (*Spathius agrili* Yang) (Hymenoptera: Braconidae) (33, 109). Asian parasitoids were first released at sites in southeast Michigan in 2007 (109, 110). Production increased annually, and in 2012, more than 350,000 wasps were released in 14 states. Several releases appear to have resulted in successful establishment, although establishment of *S. agrili* in Michigan has been limited, possibly because of cold weather (25–27). Recent studies suggest that *T. planipennisi* may be most successful at sites with young ash trees whose thin bark is unlikely to impede oviposition (25). Exploration and evaluation of additional Asian parasitoid species for potential introduction are ongoing (25).

Although establishment is a critical first step in classical biocontrol, effects of the parasitoids on EAB population growth rates will likely require assessment over multiple years. Parasitism of phloem-feeding buprestids is not uncommon (104). However, evidence that parasitoids exert appreciable density-dependent effects on population growth of buprestids is limited, and stronger evidence suggests populations are generally regulated from the bottom-up by the availability of suitable hosts (76). The high level of mortality of North American ash trees planted in China (55, 113) also suggests there may be a low probability that introduced parasitoids will prevent EAB populations from building to high densities and causing widespread ash mortality. Successful biological control with introduced or native parasitoids may be most likely to occur at sites with blue ash or other relatively resistant ash species, or in areas where the EAB invasion wave has passed and EAB populations have collapsed to very low densities.

Insecticidal Control

Insecticide trials conducted in the first few years following the discovery of EAB in North America generated inconsistent results. In some cases, systemic insecticides adequately protected trees from EAB, but the same treatments failed or produced mixed results in other trials (40, 67). Some studies conducted over multiple years revealed that EAB damage continued to increase despite ongoing treatment (40). Research on systemic insecticides for protecting ash trees has advanced considerably in recent years, and new products and application methods have become available. Systemic insecticides to control EAB include products (*a*) applied as soil injections or drenches, (*b*) injected into the base of the trunk, or (*c*) sprayed on the basal 1.5 m of the trunk (40, 98). One product with the active ingredient emamectin benzoate has provided up to three years of nearly 100% EAB control in some trials (37, 61, 64, 98). These advances have dramatically increased the likelihood that ash trees can be protected successfully throughout the EAB invasion wave. Moreover, analyses have shown that costs of protecting trees are substantially lower than costs of removal, especially when the value of ecosystem services provided by trees, such as storm water capture, is considered (61, 96, 111).

Integrated Management to SLAM

An increased understanding of EAB biology and its impacts has motivated interest in managing populations to slow the onset and progression of ash mortality in outlier sites, municipalities, and residential areas. A pilot project, termed SLAM (SLow Ash Mortality), was initiated in 2008 to develop, implement, and evaluate an integrated strategy for EAB management (39). This effort focuses on slowing EAB population growth, which in turn slows the rate at which tree mortality advances. Management options include destroying EAB life stages before adults can disperse and reproduce, concentrating and then eliminating adult beetles and their progeny, and reducing the amount of food (ash phloem) available for the development of large numbers of EAB larvae.

Potential management tactics that can be integrated into a SLAM program include the use of emamectin benzoate insecticide applications, which can be effective for up to three years, and girdling ash trees in spring to attract ovipositing EAB females (63, 65), and then debarking or otherwise destroying the trap trees before the larvae can develop. Harvesting ash trees for timber or as a local source of firewood can provide economic benefits to landowners while reducing the phloem available for EAB development (68). Evaluation of these tactics in isolation found that treating trees with the systemic insecticide was most effective at slowing EAB population growth, use of girdled trap trees was intermediate, and phloem reduction was least effective (72, 73).

Ideally, EAB management options should be integrated into a site-specific strategy that considers the distribution, abundance, and condition of ash trees; EAB population density; and local constraints. A timber harvest, for example, could be a suitable tactic in a forested setting but would probably not be practical in a residential area. In contrast, insecticide treatments are more viable in residential or urban areas where trees are readily accessible. Simulation models of EAB dispersal and population dynamics developed from numerous field studies were used to evaluate effects of treating varying proportions of ash trees with emamectin benzoate in a residential neighborhood (61). Results showed that without any insecticide treatment, all ash trees would be dead within ten years of the initial EAB introduction, a pattern consistent with mortality rates observed in many communities in southern Michigan and northern Ohio. The simulation showed that if 20% of trees were treated annually, beginning four years after the introduction of EAB, 90% of the trees would remain after ten years because of an area-wide reduction in EAB population growth. Cumulative economic costs of treatment were at least fourfold lower than costs of removing and replacing trees as they declined. In another simulation, protecting landscape ash trees with emamectin benzoate yielded lower costs and greater benefits than did removal (either preemptive or removal as the trees died) and replacement with other tree species (111).

An integrated effort to slow ash mortality is not expected to eradicate an EAB infestation nor eliminate ash mortality. Slowing local EAB population growth, however, allows managers and property owners to be proactive and develop a long-term approach, rather than react to overwhelming numbers of dying, dead, and often hazardous trees. It also allows for continued research and technology development, which may yield more options for EAB management and increase the effectiveness of existing technologies.

CONCLUSION

In terms of invasive forest pests, EAB may well represent a worst-case scenario. Various watch lists developed by regulatory officials and scientists identify potentially invasive forest pests and are used to target high-risk imports and prioritize interception efforts and detection surveys (70). Because EAB was not considered a major pest and had not been well studied in its native range, it never appeared on any such list, which exemplifies the difficulty of predicting how a nonindigenous species will fare in a new habitat. The difficulty of detecting low-density EAB infestations undermined original eradication efforts and continues to present a management challenge. Much has been learned about EAB in the past decade, and management efforts are likely to evolve as more knowledge is acquired. However, despite the staggering and well-documented economic impact of the EAB invasion, federal funds allocated to EAB regulatory and research programs in the United States have decreased substantially. The ability to protect landscape trees with systemic insecticides has progressed considerably and is increasingly recognized as an efficacious and cost-effective option for high-value ash in urban and residential areas. Options for protecting ash in forested settings, however, are limited, and the effects of native or introduced natural enemies on EAB population growth and spread remain to be seen. The future of the ash resource in North America is precarious, and if the EAB invasion of Russia continues to expand, ash in Western Europe will also be threatened (7).

SUMMARY POINTS

1. EAB, a phloem-feeding buprestid native to Asia, was first detected in North America in southeast Michigan and nearby Windsor, Ontario, in 2002. As of September 2013, EAB had been detected in 22 US states and two Canadian provinces, and untold millions of ash trees have been killed. EAB has become the most destructive and economically costly forest insect to ever invade North America.

2. There is substantial interspecific variation in resistance of ash to EAB. Asian species that share a coevolutionary history with EAB are generally resistant unless stressed. In North America, native ash share no coevolutionary history with EAB, and green, black, and white ash are highly vulnerable, with nearly 100% mortality rates observed in some forests near the invasion epicenter, whereas blue ash is more resistant. Efforts to identify resistance mechanisms are under way and may eventually yield resistant hybrids or cultivars.
3. There is no evidence that EAB produces long-range pheromones. Visual surveys rarely detect infestations until populations have increased and multiple generations of EAB have dispersed. Continued development of effective survey methods and an improved understanding of EAB dispersal behavior are needed to effectively detect and manage EAB.
4. The ability to protect valuable landscape ash trees with systemic insecticides has progressed substantially in recent years. The trunk-injected insecticide emamectin benzoate controls EAB for up to three years, providing municipalities and property with an economically viable option for conserving mature ash trees.
5. Federal agencies in the United States have invested heavily in classical biological control. Three species of parasitoids native to China have been reared and released, with at least two establishing at several sites. Parasitism of EAB by native *Atanycolus* spp. is increasingly common, and relatively high parasitism rates have been recorded in areas with well-established EAB populations. However, the ability of native or introduced parasitoids to slow EAB population growth and ash mortality remains uncertain and will require long-term evaluation.
6. The EAB invasion of North America exemplifies the difficulty of assessing risk and predicting the impact of exotic insects in new habitats. In its native Asia, EAB is not a major pest and was never included on any watch list of potentially invasive or high-risk nonindigenous forest insects.

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