

Biology and Control of Emerald Ash Borer



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CHAPTER 10: RISK TO ASH FROM EMERALD ASH BORER: CAN BIOLOGICAL CONTROL PREVENT THE LOSS OF ASH STANDS?

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INTRODUCTION

Ash trees (*Fraxinus* spp.) are an important components of both natural forests and urban plantings in the United States and Canada (Federal Register, 2003; Nowak et al., 2003). There are approximately 16 species of *Fraxinus* native to North America (Harlow et al., 1996; USGS, 2014), each adapted to different ecological niches across a range of climate zones, soil types, and moisture gradients (Eyre, 1980). This abundant and diverse ash resource provides economic benefits, with ash timber alone valued at \$282 billion (Nowak et al., 2003). For instance, green ash (*F. pennsylvanica* Marsh.), the most widely distributed ash in North America, is a fast growing, moderately shade tolerant tree that grows in mixed hardwood stands along river bottoms and wetlands, in small lowland groves, or in upland mesic sites. It was planted extensively throughout North America as an ornamental landscape and street tree due to its rapid growth and hardiness, and as agricultural shelterbelts for livestock shelter and soil conservation (MacFarlane and Meyer, 2005; D'Orangeville et al., 2008). Ash trees are also a valuable ecological component of the deciduous forests of eastern North America, and provide food, cover, nesting sites, and habitat for mammals, birds, insects, and other organisms (Poland and McCullough, 2006; Gandhi and Herms, 2010; Koenig et al., 2013).

Clearly, the ecological and economic value of ash in North America justifies appropriate measures for its protection against the invasive emerald ash

borer (EAB, *Agrilus planipennis* Fairmaire), which threatens the persistence of ash in mixed hardwood stands. In this chapter, we will first review various ecological factors that may affect the potential for ash mortality due to EAB. We will then examine the population dynamics of EAB in its newly invaded region (North America) vs. its native range (northeast Asia), and attempt to identify critical or key biotic factors that may be employed or manipulated to suppress EAB population growth. Finally, we will review the current EAB biological control program that involves introduction and establishment of hymenopteran parasitoids from northeast Asia. In particular, we will examine whether natural enemies (parasitoids) can maintain EAB populations at an equilibrium density low enough to allow ash to regenerate and recover.

FACTORS AFFECTING ASH RISK FROM EAB INVASION

Ash trees were once relatively free of serious, major diseases (except for ash yellows in some limited areas) and insect pests in North America until the arrival of EAB (Barnes and Wagner, 2003; Pugh et al., 2011). EAB was first detected in North America in Michigan in 2002, and as of February 2014, it had been detected in 22 U.S. states and two Canadian provinces, killing millions of ash trees (see reviews in Herms and McCullough, 2014;) (Fig. 1) (see reviews in Herms and McCullough, 2014). All ash species native to North America that have been encountered by EAB to date are susceptible to EAB, including the most

common species: green, white (*F. americana* L.), and black (*F. nigra* Marsh.) as well as the less common blue (*F. quadrangulata* Michx.) and pumpkin ash (*F. profunda* [Bush] Bush). Although there is increasing evidence that EAB will attack all species of *Fraxinus*, innate susceptibility of ash trees varies with a variety of ecological factors such as physiological condition, habitat type, and species. Below are some ecological factors that may affect the likelihood of ash risk from EAB invasions in North America.



Figure 1. Mortality of overstory green ash trees caused by emerald ash borer in 2003, Kensington Metro Park, Brighton, Michigan. (Photo credit: Leah Bauer)

Ecological Habitats: Natural Forest vs. Urban Plantings

After its accidental introduction into North America, EAB established on ash trees in urban areas and subsequently spread into nearby natural forests (Haack et al., 2002; Michigan State University, 2014; Canadian Food Inspection Agency, 2014). Although EAB is a strong flier, long-range dispersal occurs primarily through human activities, often along roadways lined with ash trees. EAB spread has appeared to follow a wave pattern across the landscape through short-distance natural dispersal and as well as long-range dispersal assisted by human activities (Taylor et al., 2010; Prasad et al., 2010; Kashian and Witter, 2011). In Russia (Duan et al., 2012a; Straw et al., 2013) and northeastern China (Liu et al., 2007; Wei et al., 2004, 2007; Wang et al., 2010), EAB outbreaks have been noted primarily on North American ash trees planted in plantations or as street

trees. EAB populations have the potential to disperse quickly in urban areas due to widespread planting of susceptible ash species and human-assisted movement and storage of EAB-infested materials (see review in Herms and McCullough, 2014).

Age of Ash: Mature Trees vs Saplings

Although the diameter at breast height (DBH) of ash trees does not significantly influence the probability of EAB oviposition or infestation (Marshall et al., 2011; Klooster et al., 2014; Jennings et al., 2014), EAB infestations in North America have first killed mature (canopy) ash trees rather than smaller understory saplings (Capeart et al., 2005). Recent studies have further shown that ash saplings with DBH <2.5 cm are rarely attacked by EAB (Marshall et al., 2011, 2013). It is conceivable that young ash saplings have both physical (e.g., smooth-bark surface) and chemical (secondary compound) characteristics that are less attractive to EAB oviposition than canopy ash trees (e.g., Marshall et al., 2013). It is also possible that saplings with stem diameters smaller than <2.5 cm are too small to be colonized and killed. Klooster et al. (2014) found that mortality of green, white, and black ash trees in mixed stands with stems equal to or greater than 2.5 cm exceeded 99% in southeastern Michigan forests by 2009, suggesting that there is little resistance or tolerance in these ash populations, and that EAB does not discriminate based on chemical or physical attributes when populations are high.

Species and Variety

Liu et al. (2003), studying EAB in China, reported higher EAB densities in North American species (green ash and velvet ash, *F. velutina* Torr.) than in Asian species (*F. chinensis* Roxb.; *F. chinensis* var. *rhynchophylla*). In a common garden trial in Michigan, Rebek et al. (2008) confirmed the presence of interspecific variation in responses to EAB infestations between the Asian (*F. mandschurica* Rupr.) and North American species (*F. pennsylvanica* and *F. americana*). Exposed to similar EAB infestation pressure, the Asian species, Manchurian ash, suffered far less mortality and yielded far fewer



Figure 2. Inter-species variation in ash resistance to emerald ash borer infestation in its native range (Vladivostok, Russia). North American green ash trees (*F. pennsylvanica*) planted in the 1970s on the left side of the tramline show late stages of EAB infestation symptoms (canopy declines, exit holes, bark splits etc.). Oriental ash (*F. rhynchophylla* or *F. manschurica*) were planted in the 1980s on the opposite side of the tramline show little signs of EAB infestation. (Photo credit: Jian Duan)

adult beetles than several cultivars of North American green and white ash. Duan et al. (2012a) also observed similar interspecific variation in resistance to EAB infestations between the Asian species *Fraxinus rhynchophylla* Hance and North American green ash (*F. pennsylvanica*) in the Russian Far East, the possible native range of EAB (Fig. 2). The higher resistance of Asian ash may have resulted from a long co-evolutionary history with EAB (Liu et al., 2003; Rebek et al., 2008), thereby restraining EAB densities within its native range.

Seed Banks and Regeneration

Kashian and Witter (2011) examined the potential for ash canopy tree recovery in EAB-affected stands from 2007 to 2009, measuring regeneration at 45 sites in southeastern Michigan (USA) following stand decline from EAB infestation. White, green, or black ash regeneration was abundant at all sites, particularly of the smallest ash height classes, but new seedling density dropped significantly between 2007 and

2009. This dramatic decrease in new seedlings was interpreted to be the result of a depleted seed bank, because few or no nearby mature ash trees existed to provide seed. Recent sampling in small pure stands of green ash suggest that seed production during ash mast years (on both surviving mature ash and sprouts from killed trees) may be sufficient to maintain a significant – though greatly reduced – pool of ash regeneration that may allow ash to persist at low levels (D. M. Kashian, unpub.). It remains to be seen if ash regeneration will be high enough to repopulate sites with mature trees in Michigan where pre-EAB ash density was lower, especially because the future dynamics of EAB populations in the region are still uncertain.

In another study, Klooster et al. (2014) conducted extensive soil sampling in southeastern Michigan forests located within 45 km of the epicenter of the infestation and found no seeds after 2007, suggesting depletion of the seed bank. Once mortality of ash with stem diameters greater than 2.5 cm exceeded 99% in 2009, they observed no newly germinated seedlings (with cotyledons) either inside or outside their plots, which is also consistent with a depleted seed bank. They did observe that ash mortality decreased slightly in 2010 to about 97% as smaller saplings grew large enough to reach the 2.5 cm size class. However, EAB trapping revealed that a low-density EAB population continued to persist on this cohort of saplings. Based on these patterns, Klooster et al. (2014) concluded that the long-term fate of ash in these sites will depend on the establishment of a dynamic equilibrium between current ash regeneration, EAB, and its natural enemies.

Natural Enemies

Several species of larval and egg parasitoids have been discovered in the native range of EAB. Field studies in Asia show that these natural enemies cause up to ~70% parasitism of EAB larvae or eggs in EAB's native range (Liu et al., 2003, 2007; Duan et al., 2012a). It is very likely that these Asiatic natural enemies exert important top-down effects on EAB population dynamics and may potentially limit outbreaks of EAB in Asia to levels that do not

cause significant mortality to ash. However, natural enemies do not appear to have prevented EAB outbreaks on highly susceptible North American ash species that were planted in China (Liu, 1966; Wei et al., 2004). In contrast, parasitism by North American parasitoid species was minimal (<5%) when EAB was first detected in Michigan and is often low in other newly infested areas (e.g., Bauer et al., 2005; Duan et al., 2009, 2012b, 2013a). This lack of effective natural enemies in North America was the justification for introduction of Asian parasitoids into the United States for classical biocontrol of EAB. Whether or not the newly introduced EAB parasitoids will provide sufficient reduction of EAB populations to allow recovery or regeneration of ash needs continued study as part of the EAB biological control program.

EAB POPULATION DYNAMICS IN NEWLY INVADED AND NATIVE RANGES

The invasion wave of EAB in ash-dominated forests of a newly invaded region has been described as having three main stages: the cusp, crest, and core (Burr, 2012; Burr and McCullough, 2012). The cusp phase occurs at newly infested sites in the first few years as EAB populations slowly build, before their numbers rapidly increase and cause tree mortality in the crest phase. The core phase then occurs around 10 years after the initial infestation, by which time most ash trees have died and EAB populations have crashed. Burr (2012) characterized EAB population density and conditions of green ash overstory and regeneration from 2010 to 2011 in 24 forests sites in Michigan, which were at the three different stages of the EAB invasion wave. Recent studies suggest that host tree mortality (or depletion of host tree resources) is the major factor driving the invasive population of EAB to emigrate or disperse into new areas or forests (Mercader et al., 2009; Burr, 2012; Burr and McCullough, 2012). However, long-term studies of EAB population dynamics and its underlying regulation factors at different invasion stages are currently lacking in North America. Evidence gathered thus far in the native range of EAB has shown that EAB outbreaks in northeastern Asia are rare events in natural forests, and outbreaks occur

primarily in isolated plantations or urban plantings of mostly North American ash (*F. pennsylvanica*, *F. americana* or *F. velutina*) (Wei et al., 2004). While infestations within the native range of EAB can occasionally cause significant ash mortality in urban plantings or plantations, no important outbreaks (comparable to those in North American forests) have been recorded in canopy ash in native Asian forests (Liu et al., 2007; Williams et al., 2010; Duan et al., 2012a). Recent ecological studies of EAB population dynamics in in the Russian Far East and northeastern China suggest that natural enemies (larval and egg parasitoids) and host tree resistance are the two key factors that regulate EAB population dynamics in its native range (Liu et al., 2003, 2007; Duan et al. 2012a), and thus the lack of these two key mortality factors in North America may explain the severity of EAB damage there. Understanding the ecological mechanisms or key factors that regulate EAB population dynamics in both its native range and newly invaded areas will be critical for developing sustainable strategies for managing this invasive pest in North America.

CAN BIOLOGICAL CONTROL SIGNIFICANTLY DECREASE ASH MORTALITY?

The Current Status

Classical biological control was initiated shortly after EAB detection in the United States due to the failure of eradication efforts (see Chapter 4). This program has introduced and achieved establishment of three exotic parasitoids (two larval parasitoids and one egg parasitoid) sourced from part of the native range in northeastern China (see Chapter 5). Field surveys in Michigan, Maryland, and New York show that one of the released larval parasitoids, *Tetrastichus planipennis* Yang, became widely established on EAB populations at both release and nearby control sites 3-4 years after release (Bauer et al., 2008, 2009, 2010; Gould et al., 2011; Duan et al., 2012b, 2013b; Jennings et al., 2013). Duan et al. (2013b) showed that parasitism of EAB larvae by *T. planipennis* in central Michigan steadily increased from <1% in the first year (2008)

after field releases to ~21% (release plots) and 12% (control plots) four years later (by 2012). While the introduced egg parasitoid, *Oobius agrili* Zhang and Huang, appears to have also established primarily at release sites in central Michigan and Maryland following releases between 2008 – 2011, rates of EAB egg parasitism varied from <5% to as high as ~28% among different release sites and years after field releases (Duan et al., 2010, 2012b; L.S. Bauer, unpublished data) and appear to be increasing. In contrast, establishment of the braconid larval parasitoid *Spathius agrili* Yang is less certain, and observed levels of field parasitism by this species have been minimal (<0.1%).

Currently, levels of parasitism by these introduced parasitoids are still much lower than those observed in their native range (Liu et al., 2007; Duan et al., 2012a; Yang et al., 2010). This is most likely due to the limited number of the wasps released in the initial phases of the program (2008-2011) and the short period of time available for the released parasitoids' populations to increase. With release of larger numbers of these parasitoids in North America in the next few years, it is possible that these parasitoids will greatly increase in abundance and inflict levels of EAB larval and egg parasitism that are comparable to those observed in their native ranges. With the development of effective mass-rearing methods, it is also conceivable that these biological control agents, particularly the egg parasitoid *O. agrili*, could be released in large numbers as a means of effectively preventing EAB populations from reaching levels able to kill ash trees, at least on a local scale.

The Premise of EAB Biological Control

The premise of EAB biological control is that EAB outbreaks are rare in China and other parts of EAB's native range, in part because of the presence there of more effective natural enemies that suppress outbreaks before they occur. It is commonly noted that there are many isolated stands of healthy saplings of North American ash species (green and velvet, respectively) in urban areas of the Russian Far East and China. It is thus plausible that EAB parasitoids in this region might have protected these susceptible ash trees at two different phases. First, saplings of

susceptible ash species in Asia might be colonized initially at low levels of EAB because there are fewer beetles coming from resistant trees, which would not be the case in North America. Moreover, survivorship of F₁ immature EAB stages on these saplings might be reduced by a rapid increase of parasitoid populations due to shorter handling times for parasitoids to attack hosts on saplings. This could retard EAB buildup on susceptible ash trees in Asia. Second, the abundance of EAB parasitoids in the native range may in fact allow their populations to increase rapidly via numerical response to incipient infestations of EAB on susceptible ash species and thus directly protect the trees while beetles are at relatively low density.

Factors Affecting the Efficacy of EAB Biological Control

The question then arises whether these introduced parasitoids can successfully establish in North America and effectively reduce the invasive EAB population to a sufficiently low level to allow ash for regeneration and recovery of ash overstory trees in forests. See Figure 3, a hypothetical model of EAB population dynamics with successful EAB biological control.

The following ecological factors are most likely to influence the success of the current EAB biological control program in North America:

Climatic matching and adaptability of the introduced parasitoids in North America.

The adaptability of the introduced Asiatic parasitoids to the climatic and other ecological conditions (e.g., host's phenology) in North America would have profound impacts on their successful establishment and efficacy in controlling EAB populations. Climatic matching analysis showed that the climatic conditions in northeast China, where *T. planipennisi* and *O. agrili* originated, generally matches that of the midwestern and northeastern United States, where EAB has firmly established (Federal Register, 2007). Thus, it is not surprising that both species appear to have become well established in Michigan and other midwestern states shortly after their field releases. However, the establishment of the other Chinese larval parasitoid, *S. agrili*, has been less certain in Michigan and other northern states in the United States. This is most

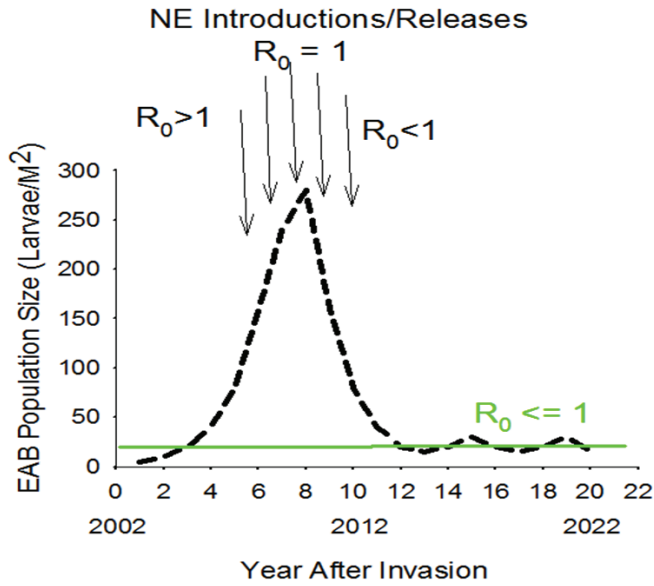


Figure 3. A schematic illustration of emerald ash borer population dynamics with successful biological control: Released parasitoids should reduce the EAB population to a low “equilibrium” density that allows ash regeneration and recovery to canopy trees.

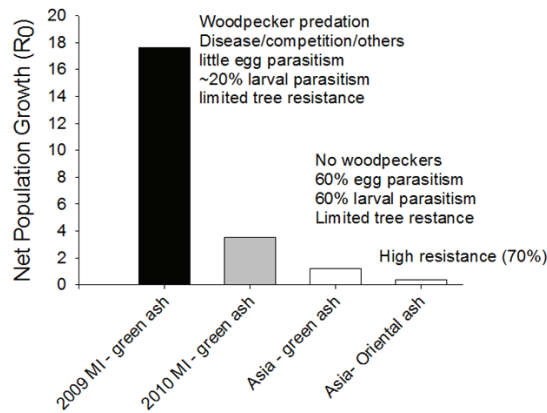


Figure 4. Comparison of net reproductive rate (R_0) of an emerald ash borer population in North America vs. Asia when different levels of dominant mortality factors are present or absent from life tables constructed in two study periods (2008–2009 and 2009–2010) in central Michigan, the epicenter of the North American invasion. $R_0 > 1$ results in population increase; $R_0 = 1$ results in a stable population; $R_0 < 1$ results in successful suppression of EAB population growth.

likely because the source of *S. agrili* was further south in Tianjin, China (southeast of Beijing on the coast) where temperatures are moderated by the China Sea. In contrast to *S. agrili*, the congener *Spathius galinae* Belokobylskij & Strazanac was collected from the Russian Far East and is thus likely to be more cold tolerant than *S. agrili* (Duan et al., 2012a; Belokobylskij et al., 2012; Khun et al., 2013). Climate matching analysis indicates that the climate in the central region of the United States is potentially more suitable for *S. agrili* than the more northern areas where most releases have been made to date. Climate matching analysis further indicates that the portion of the US suitable for *S. galinae* is considerably further north than for *S. agrili* (Gould and Duan, 2013).

The size or age of ash trees to be protected.

Ash trees are fast growing, an expected lifespan of 200 to 300 years, and normally produce seeds after 30 – 40 years (Garden Guide, 2014). Although the size or age of ash trees (often measured as DBH) does not appear to significantly influence the probability of EAB infestation or tree mortality (see previous section), bark thickness as a function of tree age or size can have significant effects on the efficacy of EAB larval parasitoids in finding and attacking host larvae. For example, Abell et al. (2012) showed that EAB larvae infesting ash trunks with a DBH > 11.2 cm are rarely parasitized by the larval parasitoid *T. planipennisi* because this species has an ovipositor ranging in length from 2.0-2.5 mm and thus cannot oviposit through bark that is thicker than 3.2 mm. Based on these findings, Abell et al. (2012) recommend releasing *T. planipennisi* only in early-successional stands with small ash trees, but not in mature forests where ash was mostly larger. For protection of large ash trees (DBH > 12 cm), parasitoids such as *S. galinae*, with much longer ovipositors (4.5 – 5.5 mm) should be considered for use in EAB biocontrol programs. Based on regression analysis of bark thickness and DBH (Abell et al., 2012), it is estimated that *S. galinae* could successfully oviposit through bark in trees up to 29 mm DBH, greatly enhancing its usefulness as a biological control agent.

Level of ash tree resistance to EAB.

Host tree resistance is a dominant factor that can have a “bottom-up” effect on EAB population growth in

its native range (see previous section). Levels of host tree resistance will also have effects on the success of natural enemies, particularly larval parasitoids, in controlling EAB populations that have already infested ash trees. For example, there is strong evidence that EAB larvae develop more slowly and more often express semi-voltinism in healthy ash trees compared to artificially girdled, or previously-infested ash trees (McCullough et al., 2009; Duan et al., 2010). The slower larval development and a semi-voltine life cycle may provide a much wider window for foraging parasitoids to attack host larvae, and thus result in higher control efficacy. A population dynamics model parameterized with observed larval and egg parasitism rates (~60%) in Asia, showed that natural enemies in Asia can quickly reduce the rate of EAB population growth when accompanied by moderate to high levels of host plant resistance (Fig. 4) (JJD unpub; see also Chapter 9).

CONCLUSIONS

Ash trees were once relatively free of serious, major diseases and insect pests in North America until the arrival of EAB, which was first detected in North America in Michigan in 2002. As of February 2014, EAB had been detected in 22 U.S. states and two Canadian provinces, killing millions of ash trees. The ecological and economic value of ash justify appropriate measures to manage this invasive pest, and the current EAB biological control program was initiated shortly after its detection in the United States due to the failure of eradication efforts. The premise underlying the classical EAB biological control program is that EAB outbreaks are rare in China and other parts of its native range, in part because effective natural enemies prevent or quickly suppress EAB outbreaks.

The EAB biological control program has resulted in the introduction and successful establishment in North America of three exotic parasitoids (two larval parasitoids, *T. planipennisi* and *S. agrili*, and one egg parasitoid, *O. agrili*) sourced from the native range of EAB in northeastern China. An additional species of EAB parasitoid, *S. galinae*, is also currently under review for potential release against EAB in the

northeast United States. The key question is whether these introduced parasitoids, once established, can effectively regulate the EAB population at sufficiently low densities such that an equilibrium can be maintained between EAB and its natural enemies that permits survival and regeneration of ash in North American forests.

To answer this question, we examined various factors that may potentially affect the risk to ash from EAB invasion, including population dynamics of EAB in both the newly invaded region and its native range (northeast Asia), and dominant biotic factors that regulate EAB populations in its native range. We suggest that ash tree resistance and natural enemies (parasitoids) are the two dominant biotic factors that have the potential to regulate EAB population dynamics. A population dynamics model parameterized with the egg and larval parasitism rates (~ 60%) observed in EAB's native range suggests that natural enemies coupled with moderate to high levels of host plant resistance has the potential to reduce the growth rate of EAB populations below replacement, and thus maintain EAB populations at low-density, equilibrium levels, which should permit survival and regeneration of ash in the aftermath of EAB invasion in North America forests.

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