Chapter 11: Future Directions in EAB-Affected Forests

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The ability of natural enemies to slow emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), population growth in a given area will play a major role in determining whether many native ash species can persist as functional components of forest ecosystems. Population growth of EAB, like that of any other organism, is determined by reproduction, development rate, and survival at each stage of development. Fecundity of female EAB is relatively high when compared to other phloem-feeding *Agrilus* species. For example, *A. difficilis* Gory can produce 36 eggs per female (Akers et al., 1986), *A. anxius* Gory, 55 eggs (Rutledge and Keena, 2012), *A. auriventris* Saunders, 140 eggs (Huangfu et al., 2007), while a female *A. auroguttatus* Schaeffer may produce 575 eggs (Lopez and Hoddle, 2014). In laboratory settings, EAB females can lay more than 275 eggs over the course of their life span. Although egg viability tends to diminish over time, even in the wild, on average, EAB can probably produce at least 40-60 offspring per female.

Most EAB larvae develop in a single year, but in newly infested ash that are relatively healthy a high proportion of larvae require two years to develop (Siegert et al., 2010; Tluczek et al., 2011), initially slowing the new population's growth rate (Mercader et al., 2011). Populations of EAB in northern latitudes where summers are short may also be more likely to require two years for development, a pattern previously observed with *A. anxius* (Barter, 1957). In stressed ash, including trees injured by increasing densities of EAB larvae, however, all or nearly all EAB develop in a single year (Tluczek et al,. 2011). Like other phloem-feeding insects, the survival of larvae of EAB is primarily limited by the availability of phloem of its host tree. Using data from several field studies, Mercader et al. (2011) estimated that an EAB larva requires approximately 10 cm^2 of ash phloem to complete development. Similarly, McCullough and Siegert (2007) reported an average of approximately 89-105 adult EAB could develop per m^2 of phloem in white ash (*Fraxinus americana* L.) or green ash (*Fraxinus pennsylvanica* Marshall). Canopy decline generally becomes apparent at a density of 25-35 EAB per m^2 (Anulewicz et al., 2007). Ash phloem available for larval feeding increases rapidly with the diameter at breast height (dbh) of the tree. For example, using methods of McCullough and Siegert (2007), a tree with a dbh of 30 cm can produce approximately 1335 adult EAB, while a 60 cm tree can produce 6285 beetles. Of course, not every m^2 of phloem will produce 90-100 adult EAB beetles. At the peak of the invasion, individual trees can harbor 200-300 early stage larvae per m^2 (Tluczek et al., 2011, Tanis and McCullough 2015), but intraspecific competition for phloem results in high mortality, typically of third instars. Nevertheless, when ash, particularly large ash, are abundant, EAB density in a given area will be very high during the peak of the invasion wave.

Given that few options are available for reducing female fecundity or slowing development of EAB, effective control tactics must limit survival of eggs, larvae, or adult beetles. Systemic insecticides protect landscape ash trees by substantially reducing survival of EAB adults and larvae, but these products are obviously not likely to be used in forests. Mortality of EAB attributable to parasitism and predation varies considerably among sites and among trees within sites. Relatively high rates of egg parasitism (ca 20%) (Abell et al., 2014), larval parasitism (10-70%) (Cappaert and McCullough, 2009; Duan et al., 2013; Tanis and McCullough, in press 2015), and

woodpecker predation (22-85%) (Lindell et al., 2008; Jennings et al., 2013; Duan et al., 2013; Flower at al., 2014; Tanis and McCullough, 2015) have been recorded at some sites in Michigan and Ohio. Duan et al. (2014) reported that in some Michigan sites, population growth rates for experimental (artificially established) EAB cohorts dropped from an R_0 value of 16.0 to 4.7 and from 19.4 to 4.6 for wild EAB cohorts. This drop, however, also reflects the progression of ash mortality at these sites. Mortality rates for overstory green ash, white ash and black ash (*Fraxinus nigra* Marshall) trees in much of southeast Michigan exceed 90% and few trees >10 cm dbh remain alive (Burr and McCullough, 2014; Flower et al., 2013; Knight et al., 2013; Klooster et al., 2014). Decreased EAB population growth rates, therefore, reflect the diminished availability of ash phloem for larval development together with increased mortality from natural enemies (Duan et al., 2014).

The cumulative influence of mortality due to native and introduced natural enemies on EAB population trajectories is not yet clear, particularly in areas where the EAB invasion is relatively recent. Populations of EAB in southeast Michigan were established for more than a decade before the first introductions of Asian parasitoids (Gould, 2007) and the first observations of significant larval parasitism by native *Atanycolus* spp. (Liu et al., 2003; Cappaert and McCullough, 2009; Siegert et al., 2014). In states with more recent infestations, however, Asian parasitoids have been introduced within a few years of detection. Whether earlier introduction and establishment of Asian parasitoids will effectively slow the progression of ash mortality in these areas remains to be seen.

Many of the Michigan stands decimated by EAB are characterized by abundant ash regeneration, including seedlings and saplings. Although ash saplings down to 2.5 cm in diameter can be colonized by EAB (Cappaert et al., 2005), trees <10 cm in diameter often escape colonization even during the peak of the EAB invasion wave (Herms et al., 2010; Burr and McCullough, 2014; Klooster et al., 2014; Smith et al., in press 2015). The fate of these young trees will likely determine whether ash persists as a functionally viable component of forest ecosystems in North America. Ash trees must be at least 8-10 cm in diameter before they begin to produce seed (Kennedy, 1990), and frequency of seeding years varies among ash species. Seed crops can be heavy, but losses from unfilled seeds and seed predation (e.g., ash seed weevils [*Lignyodes* spp.]) can be substantial (Solomon et al., 1993), and seeds do not persist in the seed bank over time (Klooster et al., 2014). Ash seedlings are tolerant of shade and may persist in closed canopy stands for several years (Kennedy, 1990). As ash mature, they become increasingly intolerant of shade, and generally require full or nearly full exposure to sun to reach the overstory (Baker, 1949; Gucker, 2005). Canopy gaps resulting from mortality of overstory ash can facilitate recruitment of young ash if gaps are not filled by lateral in-growth of other overstory trees (Bartlett and Remphrey, 1998, Burr and McCullough 2014) or regeneration of competing species (Flower et al., 2013, Smith et al., 2015).

The ability of natural enemies, including native and introduced parasitoids, to prevent young ash from being killed by EAB may play a critical role in the long term survival and persistence of ash across much of North America. Density of EAB in a local area clearly declines as ash trees, particularly large ash trees, are killed. Effects of egg and larval parasitoids on EAB survival may become more pronounced in these areas after the EAB invasion wave goes through and the availability of ash phloem to support EAB has dropped substantially. Complete mortality of EAB life stages is not likely to be necessary; in general, most ash trees are remarkably resilient and tolerate a low level of larval feeding (McCullough et al., 2015). Thus, while ash may no longer function as a dominant overstory species, natural enemies may enable ash trees to persist at some level, providing food and habitat for populations of native insects and mites that are ash specialists (see Chapter 2). The consistent preference for small diameter trees demonstrated by *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae), one of the introduced larval parasitoids (Abell et al., 2012; Duan et al., 2013), may be particularly beneficial in this regard.

Given the current and potential impacts of EAB in North America, biological control research and evaluation efforts must continue. Possible effects

of interspecific differences among North American ash in resistance to EAB and the implications of these differences for biological control warrant consideration. Blue ash, *Fraxinus quadrangulata* Michx., growing on fertile sites, for example, appears to be relatively resistant to EAB, while black ash is highly vulnerable to EAB (Tanis and McCullough, 2012; Klooster et al., 2014; Herms and McCullough, 2014). Biological control agents may be more successful at a blue ash site because of its inherent higher resistance to EAB. Conversely, at sites dominated by black ash, introduced parasitoids may be overwhelmed and unable to demonstrate any numerical response to EAB before all or nearly all trees are killed. Evaluating factors associated with relative resistance and vulnerability of different ash species could have important implications for identifying sites where introduced parasitoids are likely to be most effective.

In urban, residential, and even rural areas, effects of combining two or more EAB management tactics should be studied. Systemic insecticides, including products with emamectin benzoate, azadiractin, dinotefuran, or imidacloprid, are translocated in xylem to the canopy branches and foliage (Mota-Sanchez et al., 2009; Tanis et al., 2012). In contrast to cover sprays of insecticides applied to the outer bark, when systemic materials are used, egg parasitoids, such as the introduced *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae), will not encounter the insecticide. Larval parasitoids, whether native or introduced, will not attack dead EAB larvae nor will woodpeckers attempt to prey on dead larvae. Using systemic insecticides may therefore offer two benefits: ash trees treated with an effective product are protected from EAB injury and insecticide-reductions in overall EAB density may cause parasitoids or predators to concentrate their efforts on infested but untreated trees. The combination of systemic insecticides and natural enemies could yield an additive effect or perhaps even a synergistic effect if natural enemy reproduction or host searching behavior is enhanced (Barclay and Li, 1991; Suckling et al., 2012). Understanding more about how to optimize the spatial distribution of trees treated with systemic insecticides in a given locality to enhance parasitism or predation rates could be productive. For example, field studies consistently show girdled ash trees are highly attractive to adult EAB, especially in recently infested sites (McCullough et al., 2009a,b; Mercader et al., 2013). Opportunities may exist to employ girdled or stressed ash to concentrate both EAB and parasitoid populations in selected areas.

Much remains to be learned about native parasitoids, including their host-seeking behavior, cues that elicit parasitism, and the ability of these species to learn and adapt to a new host. Most native parasitoids and insect predators of phloem-feeding beetles are opportunistic habitat specialists, rather than host specialists (Kennedy and McCullough, 2002) and, as such, may be capable of developing on many species, genera, and even families of insects (but see Taylor et al., 2012). Native parasitoids including *Atanycolus* spp., *Phasgonophora sulcata* Westwood (Hymen.: Chalcididae), and *Spathius floridanus* Ashmead (Hymen.: Braconidae), while not well studied, are frequently recovered from trees colonized by native wood- or phloem-borers and in some areas, parasitism of EAB larvae by one or more native species is increasing (Duan et al., 2012).

Many parasitoids are adept at learning combinations of olfactory and visual cues associated with potential host insects and modifying their responses accordingly (Turlings et al., 1993). As an invasive insect population spreads, opportunities for native parasitoids to encounter and adapt to the new invader increase (Vet and Groenewold 1990; Turlings et al., 1993; Grabenweger et al., 2010). Assemblages of native parasitoids may respond and adapt to an invader relatively quickly, but their ability to affect dynamics of an invasive species varies considerably. For example, native generalist parasitoids quickly adapted to light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) in California and high parasitism rates contributed to population suppression (Wang et al., 2012). In contrast, native parasitoids had little effect on citrus leafminer (*Phyllocnistis citrella* Stainton [Lepidoptera: Gracillariidae]) populations in Spain and responded in a negative density-dependent manner to high pest populations (Vercher et al., 2005). Research on the ability of native parasitoids to adapt and respond to

EAB invasion is needed and could lead to practical and effective tactics to augment parasitism rates by these species.

Considerable research has been conducted to identify semiochemical attractants or visual cues used by native and introduced EAB parasitoids including pheromones for *T. planipennisi*, and *S. agrili* and *S. floridanus* (Bauer et al., 2011, Cossé et al., 2012) and responses of *P. sulcata, S. agrili,* and *S. floridanus* to host kairomones associated with either EAB or ash trees (Roscoe et al., 2011, Johnson et al., 2014). Other research has addressed parasitoid response to visual stimuli including trap colors (Cooperband et al., 2013) and mechano-reception of vibrations by EAB larvae (Ulyshen et al., 2011). Further studies on olfactory, visual, and perhaps vibrational cues used by parasitoids to locate potential hosts may improve EAB biological control. Pre-release conditioning or oviposition manipulation with semiochemicals, for example, might increase parasitoid efficacy. Attractive lures or aerial application of volatile compounds could perhaps provide a means to attract or enhance parasitoid populations.

Given the ongoing expansion of EAB, the economic costs resulting from urban infestations and the still unknown ecological ramifications of this invader for forest ecosystems, it seems clear that an integrated approach is needed to deal with EAB. Understanding and enhancing the collective effects of native and introduced parasitoids and predators on EAB will be crucial if native ash species are to persist in North America.

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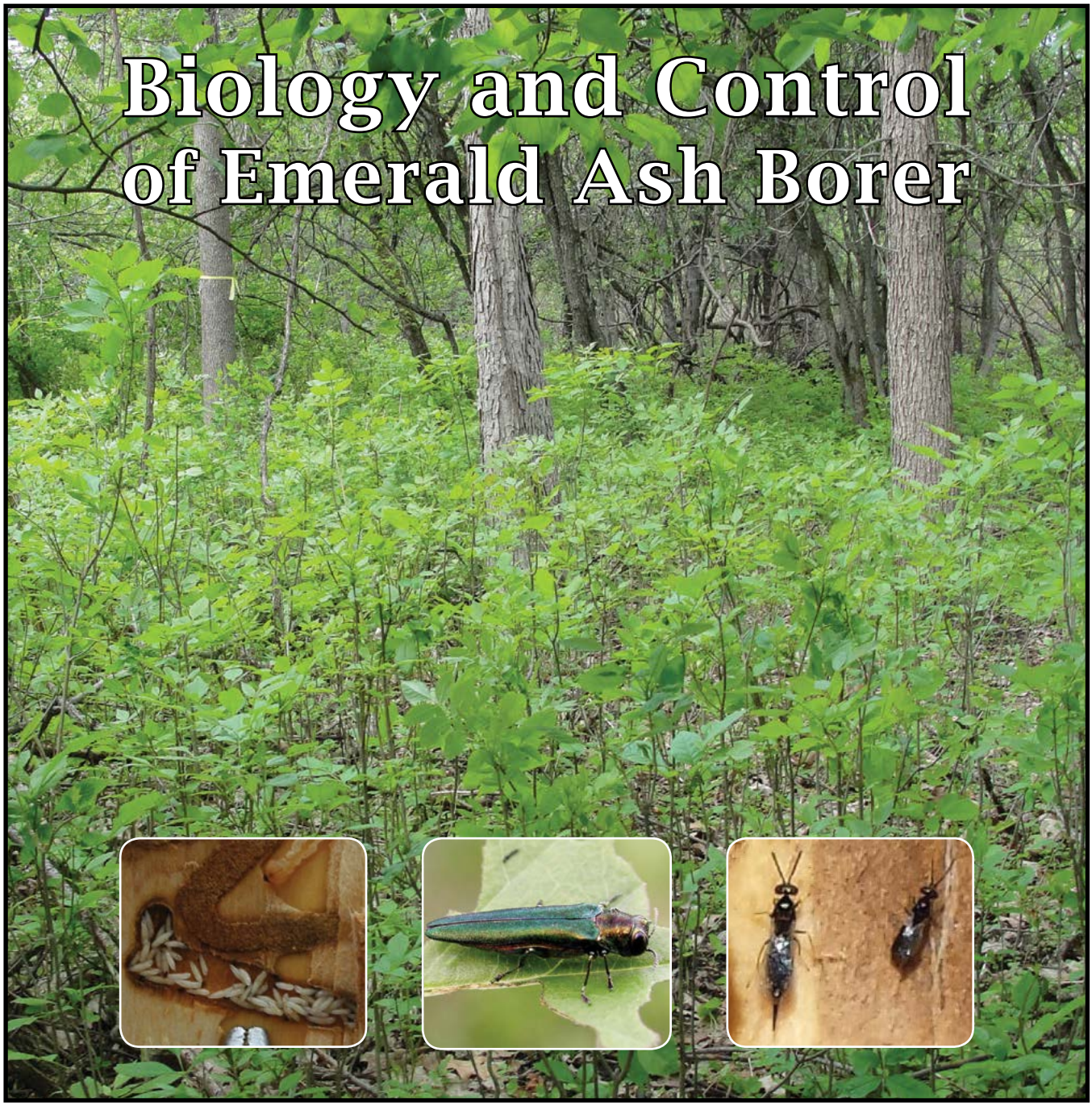

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On the cover: Cover design by Sheryl Romero and Denise Binion, Forest Health Technology Enterprise Team. Background image: Understory green ash seedlings (*Fraxinus pennsylvanica*, Oleaceae) released after large ash trees were killed by emerald ash borer in Okemos, Michigan in 2014, photo by Leah S. Bauer; (bottom row, left to right) Fully mature *Tetrastrichus planipennisi* larvae break free of emerald ash borer larval skin and pupate in the larval gallery under the tree bark. (Photo credit: Clifford Sadof); EAB adult and typical leaf feeding damage. (Photo credit: Deborah Miller, USDA Forest Service, Bugwood.org); Emerging *Tetrastrichus plannipennisi* adults. (Photo credit Leah S. Bauer).

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