WHITE ASH SURVIVAL IN THE CORE OF THE EMERALD ASH BORER INVASION AREA

By

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ABSTRACT

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The invasive emerald ash borer (EAB); (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae), a secondary pest of stressed or declining ash (*Fraxinus*) trees in its native Asia, is the most destructive forest insect to ever invade North America. Since its arrival in the Detroit metropolitan area in the early 1990's, EAB has established in 31 states and three Canadian provinces. To date, hundreds of millions of ash trees have been killed and nearly 8 billion trees are threatened in U.S. forests.

While all North American ash species are susceptible to EAB, white ash (*Fraxinus americana* L.) appears to be an intermediate host that is not highly preferred, but still becomes infested and succumbs. Catastrophic levels of ash mortality, ranging from 80% to 99% of stems, were recorded in forested sites located in southeast Michigan and Ohio. Despite these reports, we have observed an unexpectedly high proportion of overstory white ash trees alive in southeast and south central Michigan with the longest history of EAB infestation. To quantify this survival, I intensively surveyed 28 sites in this region. I recorded 821 white ash trees ≥ 10 cm (DBH) in fixed radius plots (18 m) in a 1 ha site. Most (75%) white ash stems are alive and in good condition. More than half (68%) of the live white ash trees had external bark cracks left from previous EAB larval feeding, however, 91% of these trees recovered. In contrast, 95% of the 373 green ash (*F. pennsylvanica* Marsh.) trees recorded in the 28 sites are dead. This supports findings from previous plantation and urban ash tree studies reporting the preference of green ash trees over white ash trees where they co-occur.

Stand-level variables that could predict the percentage of white ash stems and basal area alive were evaluated. White ash stem density and distance from sites to the EAB origin were positively related to white ash survival, while total basal area of all overstory species and white ash were negatively related to white ash survival. Density of white ash stems and distance from sites to the EAB origin were positively related to the proportion of white ash basal area alive. White ash basal area averaged 1.5 ± 0.2 $m^2 \cdot ha^{-1}$, and ranged from 0.3 to 3.5 $m^2 \cdot ha^{-1}$ within sites, totaling 42.7 $m^2 \cdot ha^{-1}$ across sites. I also tallied regeneration and found white ash accounted for 64%, 79%, and 74% of the total recruits, saplings, and seedlings recorded across the 28 sites.

Given the impact and ongoing spread of this highly destructive pest, effective monitoring techniques are critical. I established two double decker (DD) trap types in 30 post-invasion sites located in the EAB origin in 2014, 2015, and 2016; one DD comprised of a dark green upper prism and a light purple lower prism (PG) baited with *cis*-3-hexanol, and one DD comprised of a dark purple prism on top and bottom (PP) baited with *cis*-3-hexanol and Manuka oil. A total of 580, 585, and 932 EAB adults were captured in 2014, 2015, and 2016, respectively. The PG trap captured significantly more EAB adults than the PP trap. Despite ample live white ash phloem available for EAB development, EAB density has not reached levels high enough to kill trees.

In additional to stand-level variables, site variables could also have an influence on white ash survival rates. I delineated a 1.5 km radial buffer from the center point of the 28 white ash sites. Using a combination of downloaded geographic data and data collected during surveys, I fit models at five linear distances (0 to 400 m, 400 to 800 m, 800 to 1200 m, 1200 to 1500 m, and cross-scale). Green ash presence, specifically those growing along roads, had negative effects on white ash survival. The proportion of woody wetlands and the presence of white ash trees, specifically those growing along roads, were also important predictors across multiple distances.

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INTRODUCTION

Since its arrival in the metropolitan area of southeast Detroit in the early 1990's (Siegert et al. 2014), emerald ash borer (EAB); (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) has become the most destructive and costly forest insect to invade North America (Aukema et al. 2011, Herms and McCullough 2014). To date, populations of this Asian-native beetle are known to occur in 31 states and three Canadian provinces (EAB.info 2017). Hundreds of millions of ash (*Fraxinus* spp.) trees in forests and landscapes have been killed by EAB, and more than 8 billion trees are threatened in U.S. forests (Poland and McCullough 2006, Pugh et al. 2011, Herms and McCullough 2014, Morin et al. 2016).

In North America, EAB preferentially colonize stressed ash trees, but will attack healthy trees (Cappaert et al. 2005, Poland and McCullough 2006, McCullough et al. 2009*b*, Siegert et al. 2010, Flower et al. 2013*b*, Herms and McCullough 2014). Feeding and development of EAB can likely occur on all ash species in the U.S., including the four prominent species occurring in Michigan (Anulewicz et al. 2007, Tanis and McCullough 2012, 2015). Though all ash species are susceptible to EAB, there are interspecific differences in ash tree resistance or EAB host preference among species (Cappaert et al. 2005, Anulewicz et al. 2007, 2008, Rebek et al. 2008, Pureswaran and Poland 2009, Chen and Poland 2010, Tanis and McCullough 2012, 2015). Green ash (*Fraxinus pennsylvanica* Marsh.) and black ash (*F. nigra* Marsh.) are consistently highly preferred and vulnerable hosts of EAB (Cappaert et al 2005, Anulewicz et al. 2007, 2008, Rebek et al. 2008, Chen and Poland 2010), while blue ash (*F. quadrangulata* Michx.) is relatively resistant to EAB (Anulewicz et al. 2007, Tanis and McCullough, 2012).

White ash (*F. americana* L.) is considered an intermediate host for EAB (Anulewicz et al. 2007, Tanis and McCullough 2012, 2015). Previous studies showed green ash trees were preferentially colonized in multi-species plantations and in landscapes where green ash and white ash trees co-occurred (Anulewicz et al. 2007, Limback 2010, Tanis and McCullough 2015). While substantial white ash mortality has occurred in many areas in southeast Michigan (Gandhi and Herms 2010, Knight et al. 2013, 2014, Klooster et al. 2014, Smith et al. 2015), evidence suggests interactions between white ash trees and EAB may be relatively complex. We have observed an unexpectedly high proportion of overstory white ash trees alive in forested sites in southeastern and south central Michigan (McCullough, unpublished data), known as the EAB "core" of the invasion (Burr and McCullough 2014). In chapter one, I intensively surveyed 28 sites to quantify the abundance and condition of white ash trees and white ash regeneration, and evaluated stand-level variables that could influence white ash survival rates.

Given the impact and ongoing spread of EAB, effective monitoring techniques to detect newly infested areas are a critical aspect of managing this highly destructive pest. Previous studies have shown EAB adults do not produce long-range sex or aggregation pheromones (Lelito et al. 2007, Rodriguez-Saona et al. 2007, Crook and Mastro 2010, Ryall 2015). Beetles rely on olfactory and visual cues, including volatiles produced by stressed ash trees (Poland et al 2004, 2005), and visual attractants such as color (Francese et al. 2005*c*) to locate potential host trees and encounter mates. Live phloem must be available for larval development to sustain EAB populations. In chapter two, I compared EAB adult captures on two baited double decker trap types in 30 post-invasion white ash sites in southeastern and south central Michigan in 2014, 2015, and 2016. I also tallied white ash trees by diameter class in each site in 2014 and 2016. I related EAB captures to phloem area (m^2) of live white ash to determine whether phloem available for larval development limits EAB populations.

Characteristics of trees and sites can play a role in tree mortality caused by native or exotic pests. In a previous study, Knight et al. (2013) reported site-level variables (hydrology) and tree-level variables (ash density, crown class) were related to ash tree mortality once a stand was infested with EAB. In contrast, Smith et al. (2015) reported no relationship between site and stand variables and mortality rates in white, green, or black ash sites. A study by Jenkins et al. (2016) quantified ash mortality risks using “detection tree” data collected in Ohio from 2005 to 2007, while also incorporating distance to existing ash stands, campgrounds, roads, and railways that presumably provide corridors to facilitate EAB dispersal. They reported ash along riparian corridors are at high relative risk of EAB-induced mortality. In heterogeneous sites with urban, residential, and wooded areas, EAB preferentially colonized open-grown ash trees rather than those shaded in woodlots, which supports previous studies (McCullough et al. 2009*b,* 2009*c*). In chapter three, I evaluated an array of site-level variables in the 28 sites where I surveyed white ash survival. I fit models to five linear distances to identify if any variables were associated with rates of white ash survival.

CHAPTER ONE

White ash (*Fraxinus americana*) survival in the core of the emerald ash borer (*Agrilus planipennis*) invasion

ABSTRACT

Previous studies have reported catastrophic levels of white ash (*Fraxinus americana* L.), green ash (*F. pennsylvanica* Marsh.) and black ash (*F. nigra* Marsh.) mortality caused by emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) in several forested areas in southeast Michigan and Ohio. We observed, however, a relatively high proportion of white ash trees remain alive in some southeast Michigan forests, despite the long history of EAB invasion across the region. To assess white ash survival, I inventoried overstory trees in fixed radius plots in 28 forested sites in southeast and south central Michigan in 2015. Overall, 75% of the 821 white ash stems (≥ 10 cm DBH) I recorded were alive. Most were in good condition; 95% of the live trees had ≤ 30% canopy dieback. Similarly, 66% of the white ash basal area was alive, averaging 1.0 ± 0.2 $m^2 \cdot ha^{-1}$ across sites. Most live white ash trees were previously colonized by EAB. Bark cracks over old larval galleries were observed on 68% of the live white ash, but callus tissue (i.e., wound periderm) had formed over or around 91% of those cracks. White ash regeneration was abundant, accounting for 64%, 79%, and 74% of the recruits, saplings, and seedlings recorded. Distance to locations where Asian parasitoids of EAB were released or recovered did not influence white ash survival rates. Although the long term survival of these trees is unknown, the persistence of white ash to date in some forested areas is encouraging.

INTRODUCTION

Since its discovery in 2002, emerald ash borer (EAB); (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) has become the most destructive and costly forest insect to invade North America (Aukema et al. 2011, Herms and McCullough 2014). To date, EAB populations are known to occur in 31 states and three Canadian provinces (EAB.info 2017). Although EAB preferentially colonizes stressed ash (*Fraxinus* spp.) trees, it can also colonize and kill healthy ash trees in North America (Cappaert et al. 2005, Poland and McCullough 2006, McCullough et al. 2009*a*, 2009*b*, Flower et al. 2013*b*). An extensive dendrochronological study showed the North American EAB invasion likely originated in the Detroit suburbs of Westland and Canton, in southeast Michigan by the early 1990's (Siegert et al. 2014). Since then, this beetle, which is native to Asia, has killed hundreds of millions of ash trees in forests and landscapes, and threatens more than 8 billion trees in U.S. forests (Poland and McCullough 2006, Pugh et al. 2011, Herms and McCullough 2014, Morin et al. 2016). Recent projections suggested an estimated 10.7 billion USD will be spent by 2019 for removal or treatment of roughly half of the municipal ash landscape trees likely to be affected (Kovacs et al. 2010). Impacts associated with the EAB invasion are not only economic but also ecological. Widespread ash mortality will likely have cascading effects in many forested ecosystems, altering species composition, understory light, temperature and moisture availability, increasing coarse woody debris and affecting carbon and nitrogen cycling (Gandhi and Herms 2010, Flower et al. 2013*a*, Burr and McCullough 2014, Wagner and Todd 2016).

Catastrophic levels of ash mortality, ranging from 80% to 99% of stems, have been recorded in forested sites dominated by white ash (*Fraxinus americana* L.), green ash (*F. pennsylvanica* Marsh.), and black ash (*F. nigra* Marsh.) in southeast Michigan and Ohio (Gandhi and Herms 2010, Flower et al. 2013*b*, Knight et al. 2013, Burr and McCullough 2014, Klooster et al. 2014, Smith et al. 2015). Smith et al. (2015) evaluated an array of site and stand-level variables from 2004-2007 and found distance from the individual sites in southeast Michigan to the core of the EAB invasion in the greater Detroit area was the only variable significantly related to the rate of ash mortality. In sites where either green, black, or white ash trees were abundant, Klooster et al. (2014) reported ash mortality rates from 2005 to 2009 ranged from 40 to 99.7 %. Knight et al. (2013) reported ash trees died more rapidly when ash densities were low compared to stands where ash trees were more abundant, but overall, 25% of the ash trees were killed three years after the infestation became apparent and 99% of ash were killed after six years.

Given the extent of ash mortality in forests, three EAB parasitoids native to China have been imported into the U.S. for classical biological control of EAB. Releases began in sites in southeast Michigan in 2007 (Federal Register 2007, Bauer et al. 2008, 2014, 2015) and are ongoing. Only a small proportion of parasitoid release sites were subsequently monitored to assess establishment (Duan et al. 2011, 2012*b*, 2013*b*, U.S. Department of Agriculture 2013, Abell et al. 2014, Bauer et al. 2014). Two species, the larval parasitoid *Tetrastichus planipennisi* Yang (Eulophidae) and the egg parasitoid *Oobius agrili* Zhang and Huang (Encyrtidae) (Yang et al. 2005), have become established in some release sites in Michigan (Duan et al. 2013*a*, Bauer et al. 2015), while establishment of the larval parasitoid *Spathius agrili* Yang (Braconidae) (Yang et al. 2006) in Michigan has not been verified (Bauer et al. 2008, Slager, *in press*). To date, however, there is no evidence that introduced parasitoids have slowed ash mortality rates (Bauer et al. 2008, 2015, Abell et al. 2012, Duan et al. 2015).

While EAB can likely develop on all North American ash species (Herms and McCullough 2014), consistent interspecific differences in EAB host preference or host resistance have been observed (Cappaert et al. 2005, Anulewicz et al. 2007, 2008, Rebek et al. 2008, Pureswaran and Poland 2009, Chen and Poland 2010, Tanis and McCullough 2012, 2015). Green ash and black ash are consistently highly preferred and vulnerable hosts of EAB (Cappaert et al 2005, Anulewicz et al. 2007, 2008, Rebek et al. 2008, Chen and Poland 2010), while healthy blue ash trees (*F. quadrangulata* Michx.) are less preferred hosts of EAB (Anulewicz et al. 2007, Tanis and McCullough 2012, 2015).

While there is clearly substantial white ash mortality in many areas in this region (Gandhi and Herms 2010, Knight et al. 2013, 2014, Klooster et al. 2014, Smith et al. 2015), interactions between white ash trees and EAB may be less consistent or perhaps more complex compared with green ash or black ash. For example, in a plantation study where five ash species were arranged in randomized blocks, larval densities averaged (± SE) 41 ± 12 larvae per m^2 of phloem area on white ash trees compared to 220 ± 40 and 236 ± 36 larvae per m^2 on green ash and black ash trees, respectively (Tanis and McCullough 2015). Larval mortality on the green ash and black ash trees was very high, however, because of intraspecific competition for phloem. In another plantation with alternating green ash and white ash trees, green ash trees had nearly twice as many larval galleries as similarly-sized white ash trees (Limback 2010). Similarly, Anulewicz et al. (2007) reported green ash landscape trees were preferentially colonized over white ash trees in four residential areas where these species co-occurred in southeast Michigan.

We observed over the years that white ash trees in at least a few forested areas in the “core” of the EAB invasion in southeast and south central Michigan continued to survive, despite the presence of EAB in the sites for at least 10-12 years (McCullough, unpublished data). It was not clear, however, whether high rates of white ash survival were fairly common in areas with a long EAB history or were limited to a few sites that we simply happened to notice. I hypothesized that abundance of green ash, a preferred and highly vulnerable host of EAB, within or in close proximity to white ash-dominated sites could affect white ash survival, either negatively or positively. For example, high numbers of beetles emerging from heavily infested green ash trees could subsequently colonize and kill white ash trees. Conversely, green ash trees could function as sinks by attracting most of the ovipositing EAB females, perhaps reducing pressure on less preferred white ash trees, particularly if interspecific competition resulted in high mortality of larvae on the green ash. Distance to parasitoid release and recovery sites or distance to the epicenter of the EAB invasion in the greater Detroit metropolitan area could also influence white ash survival.

To address these questions, I identified and surveyed white ash growing in forested sites across much of the core region of the EAB invasion in southeastern and south central Michigan. My goals included documenting white ash survival rates, evaluating whether green ash or the presence of other overstory species were related to white ash survival, and determining whether other stand-related factors were consistently related to white ash survival.

I also quantified regeneration in these sites to assess potential long-term species composition and to evaluate whether species composition of regeneration reflected overstory composition. Previous studies showed that in sites where nearly 100% of the overstory ash trees were killed by EAB, ash seed banks were rapidly depleted, and ash regeneration sharply declined (Burr and McCullough 2014, Klooster et al. 2014, Smith et al. 2015). Orphan cohorts, consisting of previously established seedlings and saplings too small to be colonized by EAB remained, but competition with co-occurring species could limit the chances that young ash reach the overstory (Burr and McCullough 2014, Herms and McCullough 2014).

METHODS

Site selection

To avoid biasing my site selection, I used a county atlas to identify 70 areas of public forestland (state, county, or municipal property). These areas were distributed across 11 counties in southeast and south central Michigan that were invaded by EAB at least 10-12 years earlier (Pugh et al. 2011, Siegert et al. 2014). I queried managers of each area about the presence and distribution of white ash and excluded 30 areas where white ash was scarce or absent. In spring 2014, I scouted the remaining areas and selected 28 sites where white ash trees, live or dead, were relatively abundant (Fig 1.1). Most areas were comprised of second growth forests that had regenerated on abandoned agricultural land, near floodplains, or following other disturbances.

I recorded coordinates of a center point established in the midst of the white ash trees in each site, then delineated a rectangular 1 ha area around each center point. Four non-overlapping macroplots, each with a radius of 18 m, were established in each cardinal direction from the center point within the 1 ha area using ArcMap 10.3.1. At the center of each macroplot, I established a subplot (radius 7 m) to quantify recruits and saplings by species and a microplot (radius 1.7 m) to survey seedling species (Fig 1.2).

Macroplots

Between late May and mid-August 2015, I recorded DBH of all live and dead trees ≥ 10 cm DBH by species within each macroplot. Canopy dieback of live trees was visually assessed in increments of 10% in early to mid-summer after trees were fully flushed, where 10% indicated a nearly full, healthy canopy and 90% indicated a nearly dead canopy (Zarnoch et al. 2004). Although standing dead ash were encountered in nearly all sites, fallen ash trees and other forms of coarse woody debris were scarce or non-existent within and beyond my plots. Counts of live and dead white ash trees overall and by DBH class were summed for the four macroplots in each site and standardized per ha. Total (live and dead) and live basal area ($m^2 \cdot ha^{-1}$) were calculated for all overstory species, for all white ash trees, and for all green ash trees, when present. Relative importance values (RIV) for the five most abundant overstory species across sites and within each site were calculated following methods of Kent and Coker (1992).

Evidence of EAB colonization, including D-shaped exit holes left by emerging adults and larger holes left by woodpeckers preying on EAB larvae, were recorded as absent, scarce (≤ 4 holes visible), medium (5-8 holes visible), or abundant (≥ 9 holes visible) on white ash and green ash trees. Number of bark cracks above larval feeding galleries on the trunk were also tallied. If callus tissue (i.e., wound periderm) and bark were growing along the perimeter or over the surface of old larval galleries, I categorized the galleries as "healed".

Asian parasitoid release and recovery data were obtained from the MapBioControl database, a geospatial framework used to monitor parasitoid release, recovery, and spread (MapBioControl 2016). A total of 565 release sites and 107 recovery sites were identified in Lower Michigan, where 103 release and 77 recovery sites were located in southeast and south central Michigan. The type and quality of data reported in MapBioControl varied considerably. Frequently, no information on parasitoid recovery was available for release sites and conversely, recovery sites were not necessarily locations where parasitoids were released. Despite these limitations, I identified the parasitoid release and/or recovery sites closest each of the 28 sites I surveyed.

Regeneration

Number and species of recruits (stems ≥ 3.0-9.9 cm DBH) and saplings (DBH < 3.0 cm; height ≥ 45.0 cm) were tallied from May to August 2015 in subplots and number of seedlings (<

45.0 cm height) were recorded by species in microplots (Fig 1.2). Ash and elm seedlings were recorded only to genus due to difficulty in distinguishing species. Recruit, sapling, and seedling counts from subplots and microplots were summed by species (or genus) and standardized per ha for each site.

Statistical analysis

Severely declining overstory trees with ≥ 80% canopy dieback appeared unlikely to recover (Fig 1.3), and were classified as "dead" for analyses. To evaluate survival rates among size classes, white ash trees were grouped into three DBH classes: pole-sized (10.0-20.0 cm), medium (20.1-30.0 cm), and large (> 30.1 cm) trees. Variables were tested using the Shapiro-Wilk test. If variables were not normal and could not be normalized by transformations, the nonparametric Kruskal-Wallis test was used to compare ranks of percent white ash survival among DBH classes. Pairwise multiple comparisons with Tukey's adjustment were used to identify differences among DBH classes when the Kruskal-Wallis test was significant. Tests were conducted using R statistical software (R Core Development Team, http://www.R-project.org) at α of $P < 0.05$.

Stand-level variables and white ash survival

I used multiple linear regression to identify variables that could predict the percentage of the white ash stems and basal area alive in the sites in 2015. Potential predictor variables included basal area and stems per ha of white ash, green ash, and all species combined (live and dead), and the distance from each site to the EAB origin near Westland, Michigan. Pearson's correlation coefficients were calculated for potential predictors and only variables with a correlation coefficient < 0.7 were included in the initial models to avoid multicollinearity (Elith et al., 2006, Wisz and Guisan, 2009). Generalized Variance Inflation Factors (VIFs) were considered for the remaining predictor variables (Neter et al. 1996, Brunsdon et al. 2012) and competing variables with the highest VIF values were eliminated until all VIFs were < 3. Multicollinearity diagnoses were conducted using R statistical software (R Core Development Team, http://www.R-project.org) at α of $P < 0.05$.

To assess whether varying levels of white ash survival could be related to effects of Asian parasitoids, I used ArcMap 10.3.1 to measure the Euclidean distance between each of the 28 sites and the nearest parasitoid release or recovery site. Simple linear regression was used to determine if distance between my sites and parasitoid release or recovery locations predicted white ash survival rates.

Regeneration

I calculated stems per ha by species, and determined species richness within and across sites. I identified the five most frequently recorded species in each regeneration stratum (recruits, saplings, seedlings), then calculated total and mean (± SE) density and relative frequency of these species. Counts of recruit, sapling, and seedling species within sites were compared to overstory white ash survival rates and live white ash basal area using linear regression.

RESULTS

Macroplots

I recorded 3,587 live and dead trees (DBH ≥ 10 cm) representing 44 different species across the 28 forested sites, including 821 white ash, 373 green ash and 2,393 stems of other species. The most abundant species co-occurring with white ash included green ash, American elm (*Ulmus americana* L.), black cherry (*Prunus serotina* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and red oak (*Quercus rubra* L.) (Table 1.1). Green ash, which was tallied in 27 sites and sugar maple, tallied in 22 sites, each accounted for approximately 10% of the total stems recorded but had relative importance values (RIVs) of 88.7 and 58.4, respectively. Sugar maple was not frequent but abundant when it occurred in the sites, while green ash was both frequent and abundant in the sites. Black cherry, American elm, and red oak accounted for 9%, 8%, and 6% (333, 296, and 215 stems) of the total stems and were recorded in 26, 26 and 18 sites, respectively (Table 1.1). Trees that co-occurred with white ash averaged 20.7 ± 2.0 cm DBH and most (74%) were ≤ 25 cm in DBH.

Overall, dead trees co-occurring with white ash were minimal, representing 18% of the stems recorded. I tallied 344, 76, and 30 dead green ash, American elm, and black cherry trees, respectively. Green ash accounted for 68% of all dead trees (mean DBH 17.9 ± 0.46 cm) and were recorded in 27 sites (Table 1.1). Live green ash trees were recorded in ten sites, representing 8% of the total green ash recorded. American elm (mean DBH 19.0 ± 1.1 cm) and black cherry trees (mean DBH 16.5 ± 1.3 cm) were recorded in 18 and 9 sites, respectively, and accounted for 15% and 6% of the dead trees.

White ash survival rates varied substantially among sites, ranging from 0% to 100% of the stems recorded (Fig 1.4), but across all sites, 75% of the white ash trees were alive. In 14 sites, ≥ 80% of the total white ash stems were alive, and at least 50% of the white ash stems were alive in 22 sites (Fig 4.1). Most (83%) of the live white ash stems had ≤ 10% dieback and 95% had ≤ 30% canopy dieback (Fig 1.3). Only 27 trees, representing < 2% of the total white ash stems, were severely declining with canopy dieback estimates of ≥ 80% (Fig 1.3). These trees were heavily colonized by EAB, as evidenced by abundant adult beetle exits and bark cracks along the trunk.

White ash survival varied with DBH, which ranged from 10.0 to 44.0 cm across the 28 sites. I recorded 685, 107, and 29 white ash trees in the pole-sized, medium, and large diameter classes, respectively, which averaged (± SE) 13.1 ± 0.1 cm, 24.1 ± 0.2 cm, and 35.1 ± 0.6 cm DBH, respectively. Overall, 77% of pole-sized trees and 63% of medium trees were alive, but only 45% of large trees were alive, which was significantly lower than survival rates for trees in the smaller DBH classes ($F = 6.42$; DF= 3,98; $P < 0.001$) (Fig 1.5). Mean DBH of dead white ash trees averaged 17.2 ± 0.5 cm and was significantly greater than mean DBH of live white ash trees ($t=4.61$; DF=277.6; $P < 0.0001$). Within sites, mean DBH of the white ash trees was significantly and negatively related to the proportion of those trees alive in 2015 (Fig 1.6).

Total basal area of species co-occurring with white ash averaged 10.7 ± 1.3 $m^2 \cdot ha^{-1}$. White ash basal area (live and dead) averaged 1.5 ± 0.2 $m^2 \cdot ha^{-1}$, and ranged from 0.3 to 3.5 $m^2 \cdot ha^{-1}$ within sites. Live white ash basal area averaged 1.0 ± 0.2 $m^2 \cdot ha^{-1}$ and comprised 66% of the total white ash basal area (live and dead) summed across all sites (42.7 $m^2 \cdot ha^{-1}$). Green ash basal area (live and dead) averaged 1.0 ± 0.8 $m^2 \cdot ha^{-1}$ and ranged from 0 to 3.8 $m^2 \cdot ha^{-1}$ within sites. Dead green ash basal area averaged 0.9 ± 0.2 $m^2 \cdot ha^{-1}$ and comprised 95% of the total green ash basal area recorded across all sites (27.4 $m^2 \cdot ha^{-1}$), while live green ash basal area averaged 0.05 ± 0.02 $m^2 \cdot ha^{-1}$ across sites.

Evidence of EAB colonization was apparent on all dead overstory white ash trees. Woodpecker holes were observed on the trunk of 99% of the dead white ash trees, while exit holes left by EAB adults and bark cracks above larval galleries were observed on 90% and 68% of the dead white ash trees, respectively. The dead green ash (344 trees) were also clearly killed by EAB. I could see woodpecker holes and EAB adult exit holes on 96% and 88% of the dead green ash, respectively, and when bark was intact, cracks over old galleries on the trunk were apparent on 59% of these trees.

Evidence of EAB colonization was also common on nearly all live white ash trees. Exit holes and woodpecker holes could be seen on 37% and 53% of the live white ash trees, respectively. Bark cracks were observed on 68% of live white ash trees, but these trees had formed callus tissue (i.e., wound periderm) over or around the edge of 91% of these cracks, which I considered to be “healing”. Proportion of live white ash trees with woodpecker holes increased as DBH class increased. Overall, 52%, 58%, and 69% of the white ash trees in the pole-sized, medium, and large DBH classes had woodpecker holes, respectively (Table 1.2). The percentage of live white ash trees with bark cracks varied among DBH classes, where 69%, 64%, and 54% of the live stems in the pole, medium, and large DBH classes, respectively, had one or more bark cracks over old galleries. Overall, 54% of the live white ash trees in the large DBH class and 62% of trees in the pole-sized and medium DBH classes were forming wound periderm around and over old larval galleries.

I tallied only 29 live green ash trees across the 28 sites. Nearly all (93%) of those trees had at least five woodpecker holes visible. Bark cracks were present on 22 of the live green ash trees, but cracks on only two trees appeared to be healing (Table 1.2).

White ash stems

I considered 11 potential variables as predictors of survival rates for white ash stems. Four were dropped because of multicollinearity, including basal area of dead green ash, density of stems (live and dead) of all species, density of live stems of all species, and density of live green ash stems. Four variables were significant predictors of white ash survival rate. Total basal area of all overstory species and total basal area of white ash were significantly and negatively related to white ash survival, while white ash stem density and the distance from sites to the EAB origin near Detroit were positively related to survival (Table 1.3). Overall, the model with the four predictors explained 49% of the variability in the proportion of white ash stems alive in 2015 (Table 1.3).

White ash basal area

I considered 13 variables as potential predictors of the proportion of white ash basal area alive in our 2015 surveys. Six variables were dropped because of multicollinearity, including basal area of dead green ash, density of live green ash stems, density of total stems (live and dead), density of total live stems, density of live white ash stems, and total (live and dead) white ash basal area. Only two of the remaining variables were significant predictors; density of total white ash stems and distance from the sites to the EAB origin were positively related to the proportion of white ash basal area that was alive in 2015 (Table 1.4). Overall, the model with the two predictors explained 61% of the variability in the proportion of white ash basal area that was alive (Table 1.4).

I used simple linear regression to examine the relationship between white ash survival (percent of stems alive) and distance between the sites and the closest locations where Asian parasitoids of EAB were released and/or recovered. Distances between the white ash sites and the nearest parasitoid release or recovery site recorded in the MapBioControl database ranged from 0.09 to 47.7 km and 0.04 to 47.9 km, respectively. There was little influence of distance to parasitoid release sites ($R^2 = 0.002$) or recovery sites ($R^2 = 0.009$) on white ash survival rates (Fig 1.7).

Regeneration

Recruits

Not surprisingly, white ash dominated all three regeneration strata (Table 1.5). Overall, 1,601 recruits (DBH ≥ 3.0 and < 10.0 cm) representing 25 species were recorded across the 28 sites. White ash comprised 64% of the 1,028 recruits tallied and were present in all 28 sites. Number of white ash recruits recorded in individual sites ranged from 3 recruits in two sites to 171 recruits in one site. I recorded < 10 white ash recruits in five of the 28 sites and > 30 in 11 sites. Overall, density of white ash recruits averaged 596 ± 118.9 stems per ha. In 18 sites, white ash recruits comprised ≥ 50% of all recruits, while in one site, white ash comprised < 20% of the recruits. This site also had the fewest white ash overstory trees and the lowest white ash basal area (live or dead). The linear relationship between the percent of white ash trees (≥ 10 cm DBH) alive in our surveys and the density of white ash recruits was weak ($y = 0.0001x + 0.677$, $R^2 = 0.013$, $P = 0.56$), as was the linear relationship between total white ash basal area (live and dead) and the density of white ash recruits ($y = -0.0003x + 1.686$, $R^2 = 0.038$, $P = 0.32$).

Species composition of recruits was similar to composition of overstory trees recorded in macroplots, but American elm, hawthorn (*Crataegus* spp.), sugar maple, and black cherry, which were important overstory species, collectively accounted for ≤ 8% of the total recruits recorded. Green ash, an abundant, albeit mostly dead overstory species, was nearly absent in the recruit stratum (Table 1.5). A total of 23 live green ash recruits were recorded in nine of the 28 sites.

Seven sites had a single green ash recruit, while two other sites had 14 recruits. No dead green ash recruits were encountered. Other species of recruits recorded in our plots included box elder (*Acer negundo* L.), black walnut (*Juglans nigra* L.), white oak (*Q. alba* L.), and American beech (*Fagus grandifolia* Ehrh.), which collectively accounted for 12% of the recruits tallied. American elm recruits were recorded in 19 of the 28 sites, while none of the other species were recorded in more than 13 sites.

Saplings

A total of 2,849 saplings (DBH < 3.0 cm; height ≥ 45.0 cm) representing 25 species were recorded. White ash accounted for 79% (2,256) of all saplings and were present in all 28 sites, averaging 1,683 ± 168.6 stems per ha. In 24 sites, white ash accounted for ≥ 50% of all saplings, and in two sites, white ash accounted for 100% of the saplings. Percent survival of overstory white ash trees was not significantly related to the density of white ash saplings within sites ($y = 0.001x + 0.591$, $R^2 = 0.110$, $P = 0.08$), nor was the linear relationship between total white ash basal area (live and dead) and the density of white ash saplings significant ($y = 0.0002x + 1.236$, $R^2 = 0.07$, $P = 0.189$).

Other abundant sapling species included American elm, black cherry, sugar maple, and hawthorn (Table 1.5). As with recruits, green ash saplings were rare. A total of ten green ash saplings were alive in four sites; no dead green ash saplings were recorded. American elm was encountered in 18 sites and was again the most abundant species, representing 6% of saplings recorded. No other species accounted for more than 3% of the total saplings.

Seedlings

A total of 5,973 seedlings (height < 45.0 cm) representing 24 species were tallied in the 28 microplots. Ash and elm seedlings were recorded only by genus due to the difficulty in differentiating between species. Ash seedlings dominated all sites, accounting for 30% to 100% of seedlings within sites and 74% (4,397) of all seedlings. Percent survival of overstory white ash trees was not related to the density of white ash seedlings within sites ($y = 0.003 x + 0.717$, $R^2 = 0.001$, $P = 0.858$), but total basal area of white ash trees (live and dead) was positively related to the density of ash seedlings ($y = 0.004x + 0.963$, $R^2 = 0.296$, $P = 0.003$). Sugar maple, black cherry, and elm were relatively common and abundant (Table 1.5). Sugar maple represented 8% of the total seedlings, and was present in 17 of the 28 sites. Elm represented ~ 2% of the seedlings and was present in 16 sites while black cherry and sugar maple seedlings were present in 17 sites.

DISCUSSION

A substantial number of white ash trees remain alive and healthy in the core of the EAB invasion in southeast and south central Michigan, despite the relatively long history of EAB presence in this region. More than 65% of the white ash basal area and 75% of the white ash stems tallied across the 28 sites I surveyed were alive and nearly all of those trees (95%) had less than 30% canopy dieback. I did survey sites where white ash mortality was similar to the catastrophic rates reported in previous studies (Gandhi and Herms 2010, Knight et al. 2013, Klooster et al. 2014, Smith et al. 2015). In one of my sites, every white ash tree was dead and more than half of the white ash trees in four other sites were dead. Nevertheless, the continued survival of white ash in sites spanning 11 counties is encouraging.

I originally hypothesized that the presence of green ash, a highly preferred and vulnerable EAB host (Cappaert et al 2005, Anulewicz et al. 2007, 2008, Rebek et al. 2008, Chen and Poland 2010, Limback 2010), could affect white ash survival, either positively or negatively. If green ash trees acted as a sink for EAB oviposition, the number of eggs laid on less attractive white ash might be reduced, particularly if intraspecific competition for phloem reduced larval survival on green ash trees. Conversely, if high numbers of EAB adults emerged from green ash trees, nearby white ash trees could be heavily colonized as the green ash declined and succumbed, a pattern previously observed with green ash and white ash landscape trees (Anulewicz et al. 2007). In addition, an abundance of green ash, which can grow in heavier soils or in ephemerally flooded areas, could indicate site conditions were less than optimal for white ash, which is more often found on upland mesic sites (Schlesinger 1990, NRCS 2017). In my survey, green ash trees were present in all but one site, although 90% of those trees had been killed by EAB. I included the density of green ash stems (live and dead), total green ash basal area and live green ash basal area as potential predictors of the proportion of white ash stems or basal area alive in the multiple regressions. None of the green ash-related variables, however, significantly entered either regression.

Differential survival of green ash and white ash trees in my sites is clearly consistent with previously observed interspecific variation in EAB host preference (Cappaert et al. 2005, Anulewicz et al. 2008, Rebek et al. 2008, Pureswaran and Poland 2009, Chen and Poland 2010, Tanis and McCullough 2012, 2015). Although both ash species appear to be highly suitable hosts for leaf-feeding adult beetles and larvae developing in phloem and cambium (Anulewicz et al. 2008, Pureswaran and Poland 2009, Chen and Poland 2010), green ash is consistently colonized sooner and at higher densities than white ash. For example, in a recent plantation study, 21 randomized blocks of four ash species were exposed to the local EAB population for a single season, then debarked in autumn. All 21 green ash trees were heavily infested, with an average of 220 ± 40 larvae per m^2. In comparison, three of the 21 white ash trees were heavily infested, while five white ash had no galleries and overall larval density on white ash averaged 41 ± 12 larvae per m^2 (Tanis and McCullough 2015). Although both green ash and white ash appear to be highly suitable hosts for leaf-feeding adult beetles and larvae developing in phloem and cambium (Anulewicz et al. 2007, 2008, Rebek et al. 2008, Pureswaran and Poland 2009, Chen and Poland 2010), host preference of ovipositing females appears to determine EAB attack densities and mortality rates.

Variation in white ash survival in my sites was at least partially attributable to the size and density of the white ash trees along with the basal area or density of co-occuring overstory species. Most white ash trees in the second-growth sites I surveyed were ≤ 30 cm in DBH and 75% of these trees were alive and healthy. Larger trees, however, did not fare as well; less than half of the trees > 30 cm DBH were alive and there was a negative relationship between DBH and survival. The underlying mechanisms driving this pattern are not clear. Landing rates of EAB adults on sticky bands affixed to tree trunks were higher on larger ash trees than on smaller trees in one study (Marshall et al. 2009), but tree size was not related to either EAB adult captures or larval densities in several other studies (Anulewicz et al. 2007, McCullough et al. 2009*a*, 2009*b*, Siegert et al. 2010, Jennings et al. 2014, Burr et al. 2018). Larger and presumably older white ash trees may have been less vigorous than smaller trees; numerous studies have shown EAB adults are attracted to and preferentially oviposit on stressed ash trees (McCullough et al. 2009*a*, 2009*b*, Tluczek et al. 2011, Mercader et al. 2013). Additionally, basal area of all species combined was negatively related to white ash survival rates, which further suggests competition with other hardwood species or less than ideal growing conditions for white ash corresponded to higher mortality.

The positive relationship between density of white ash stems and white ash survival combined with the negative relationship between the diameter of white ash trees and the proportion of white ash basal area that was alive could suggest that many of the white ash were too small to be colonized during the peak of the EAB invasion in the early to mid-2000's. This seems unlikely, however, given that EAB will oviposit and develop on trees ≥ 2.5 cm DBH (Cappert et al. 2005, Poland et al. 2006). Further, more than 50-60% of the live white ash trees in the pole-sized or medium DBH classes were colonized by EAB in previous years, as evidenced by the bark cracks over old galleries and woodpecker holes. While EAB attraction to stressed trees is well-accepted (McCullough et al. 2009*a*, 2009*b*, 2015, Mercader et al. 2013, 2015), further research, particularly in recently infested sites, would be useful to more fully understand how the size and relative abundance of white ash trees can affect EAB host selection and subsequent tree survival.

Distance between sites and the epicenter of the EAB invasion in North America was also a significant predictor of white ash survival in both multiple regression models. Three of the six sites where ≥ 90% of the white ash stems and basal area were alive are located more than 100 km west of the southeast Michigan suburbs originally invaded by EAB (Siegert et al. 2014). In a previous study, green ash mortality recorded in 2010-2011 generally decreased from the EAB core in southeast Michigan, where nearly all overstory trees were dead, to southwest Michigan where 9% to 17% of the trees had been killed in 2010 and 2011, respectively (Burr and McCullough 2014). Smith et al. (2015), who monitored three ash species and measured an array of stand-related variables in forested plots in southeast Michigan from 2004 to 2007, reported that distance from the EAB origin was the only variable significantly related to ash decline and mortality. Although EAB populations generally advanced outward from southeast Michigan, human transport of infested ash nursery trees, logs, and firewood established numerous satellite infestations in other regions of the state (Siegert et al. 2010, 2014). For example, one site I surveyed where more than 30% of the white ash were dead, was >150 km west of the EAB origin. Nevertheless, four of the five sites with less than 50% survival of white ash stems (and basal area) were within 60 km of the EAB origin.

I did not attempt to directly assess parasitism by sampling EAB eggs or debarking trees to expose EAB larvae, but there was no relationship between white ash survival and the distance to locations where Asian parasitoids were released or have been recovered. Native parasitoids such as *Atanycolus* spp. and the introduced *Tetrastichus planipennisi* can cause substantial larval mortality, particularly in heavily infested trees (Duan et al. 2011, Duan et al. 2013, Cappaert and

McCullough 2009, Bauer et al. 2015), I am aware of no evidence that parasitoids have slowed ash mortality rates (Abell et al. 2012, Bauer et al. 2015, Duan et al. 2015) in North America. Although *T. planipennisi* appears capable of dispersing a considerable distance, its small ovipositor (2-2.5 mm length) reportedly limits its ability to parasitize EAB larvae in branches and boles > 12 cm DBH (Liu et al. 2003, Abell 2012, Duan et al. 2012*a*, 2013*a*). Variation in the type and quality of records in the MapBioControl also varied considerably. Information on parasitoid recovery was lacking for many release sites and many recovery sites did not correspond to locations where parasitoids were released. Although I found no evidence that EAB parasitism affected white ash survival, a limited amount of sampling could be useful in assessing parasitoid presence and parasitism rates.

In previous studies, individual living ash trees in the midst of dead ash trees were occasionally observed in forested areas following EAB invasion (Knight et al. 2013). These “lingering” ash trees were assumed to exhibit at least some level of resistance to EAB (Knight et al. 2013, 2014, Koch et al. 2012, 2015). Efforts were undertaken to collect seeds or propagate tissue from these trees (Koch et al. 2012), although some of the lingering ash trees eventually succumbed (Knight et al. 2014). I did not encounter individual lingering white ash trees, which were defined by Knight et al. (2014) as an individual healthy ash tree (> 10 cm DBH) in a site where > 95% of the ash were killed by EAB. In the four sites with high ash mortality (e.g., 55 to 80% of the white ash trees were dead), I still tallied four to seven live trees in my plots. Moreover, on most of the live white ash, as well as the dead ash, I could readily observe evidence of past EAB colonization on the tree trunks, including holes left by woodpeckers preying on late instar EAB larvae, exit holes left by emerged EAB adults and bark cracks over larval galleries. This suggests that while most trees are suitable EAB hosts, larval densities have not been high enough to cause mortality.

The ability of white ash trees to tolerate some level of EAB colonization may be facilitated by the highly sectored xylem tissue that characterizes the genus (Zwieniecki et al. 2001, Tanis et al. 2012*b,* 2016). In previous studies, ash trees produced callus tissue around the perimeter of longitudinal wounds on the trunk (McCullough et al. 2009*a*, Tanis et al. 2016) or laid new wood over plastic plugs or wounds following trunk injections of insecticide (Herms et al. 2014, Tanis et al. 2016). In this study, approximately 90% of the live white ash trees had formed wound periderm around the perimeter of old EAB larval galleries, re-establishing phellogen and cambial integrity (Mullick and Jensen 1973, Mullick 1977, Biggs et al. 1984).

Whether white ash trees will continue to persist in areas of southeast and south central Michigan over the long term remains unknown. Nearly complete mortality of green ash trees in and near the sites were surveyed suggest current EAB populations are substantially lower than during the peak of the invasion when beetles would have been emerging from those trees, as well as the white ash trees. Populations of EAB remain present in all of the sites (Robinett et al. *in prep*.) and densities could presumably build to damaging levels, particularly if trees are severely stressed by drought or other problems.

White ash regeneration, however, was abundant in all sites I surveyed, suggesting these sites will retain a white ash component for some time. Mature white ash trees (≤ 20 years old) typically produce abundant seed one out of every three years (Schlesinger 1990) and while seedlings are fairly shade tolerant, saplings and recruits require substantial sunlight (Wright 1965, Schlesinger 1990, Griffith 1991, NRCS 2017). In previous surveys in southeast Michigan and Ohio, nearly complete mortality of white ash, green ash or black ash overstory trees corresponded to depletion of the relatively short-lived ash seeds in seed banks (Knight et al. 2013, Klooster et al. 2014, Smith et al. 2015). An “orphan cohort” of previously established ash seedlings and saplings remained in these sites, presumably because they were too small to be colonized by EAB. In contrast to the abundant white ash regeneration in my sites, green ash was not well-represented in any of the regeneration strata, despite sometimes abundant numbers of dead overstory green ash. While this partially reflects my plot locations, which were established in the midst of abundant white ash, the scarcity of live overstory or regenerating green ash suggests this species has been effectively lost in these areas. White ash dominated not only the seedling and sapling strata, but also the recruits (stems ≥ 3.0 and ≤ 9.9 cm DBH), which could potentially replace overstory trees that decline or die. The general health of most overstory white ash in most sites, along with the abundant white ash regeneration, is encouraging.

APPENDIX

APPENDIX

Table 1.1: Total number of trees (live and dead) (≥ 10 cm DBH), mean (± SE), minimum and maximum diameter at breast height (DBH) (cm), total basal area ($m^2 \cdot ha^{-1}$) (live and dead) for white ash trees and the five tree species with the highest relative importance values (RIVs)[1] recorded in 28 sites located in southeast and south central Michigan in 2015.

Species	**No. of stems**	**No. stems per ha^{-1}**	**DBH (cm) ± SE; min, max**	**Total basal area ($m^2 \cdot ha^{-1}$)**	**Relative importance value**
White ash	821	2016.4	15.3 ± 0.2; 10, 44	42.7	132.9
Green ash	373	916.1	17.8 ± 0.4; 10, 53	27.9	88.7
Black cherry	333	817.9	18.6 ± 0.5; 10, 65	26.9	79.5
American elm	296	727.0	17.1 ± 0.5; 10, 77	20.4	75.4
Sugar maple	354	869.5	18.3 ± 0.5; 10, 90	28.4	58.4
Red oak	215	528.1	26.1 ± 0.4; 10, 92	35.8	52.7

[1] Relative importance represents the sum of frequency, dominance, and density of a species relative to all other species, following Kent and Coker (1992).

Table 1.2: Number of live white ash and green ash trees (≥ 10 cm DBH) with signs of EAB, including holes left by woodpeckers feeding on EAB larvae, cracks in the bark over EAB larval galleries, and bark cracks categorized as healing by DBH class, and across all classes.

Live white ash trees				
	No. live trees	**Woodpecker holes**	**Bark cracks**	**Healing bark cracks**
Pole (10.0-20.0 cm)	534	279	367	333
Medium (20.1-30.0 cm)	69	40	44	42
Large (> 30.1 cm)	13	9	7	7
Total	616	328	418	382
Live green ash trees				
Pole (10.0-20.0 cm)	24	22	18	1
Medium (20.1-30.0 cm)	1	1	1	0
Large (> 30.1 cm)	4	4	3	1
Total	29	27	22	2

Table 1.3: Parameter estimates (± SE), *t* values and *P* values of variables in a multiple linear regression to predict percentage of white ash stems alive in 28 sites in Michigan in 2015 ($R^2 = 0.49$; F = 4.72; DF = 7,20; $P = 0.003$).

Stand-level predictor variables	**Estimate ± SE**	***t* value**	***P* value**
Basal area of all species ($m^2 \cdot ha^{-1}$)	-0.020 ± 0.006	-3.35	0.003
Distance to EAB core (km)	0.004 ± 0.001	3.13	0.005
White ash stem ha^{-1}	0.004 ± 0.001	2.65	0.015
White ash basal area ($m^2 \cdot ha^{-1}$)	-0.150 ± 0.066	-2.26	0.035
Green ash live basal area ($m^2 \cdot ha^{-1}$)	-0.869 ± 0.511	-1.70	0.104
Green ash basal area ($m^2 \cdot ha^{-1}$)	0.095 ± 0.065	1.46	0.159
Green ash stems (ha^{-1})	-0.0004 ± 0.002	-2.22	0.832

Table 1.4. Estimated (± SE) parameters, t values and *P* values ($\alpha < 0.05$) of variables in a multiple linear regression to predict the proportion of white ash basal area alive in 28 sites in Michigan ($R^2 = 0.61$; F = 7.09; DF = 7,20; $P < 0.001$) (N = 28 sites).

Stand-level predictor variables	**Estimate ± SE**	***t* value**	***P* value**
White ash stems (ha^{-1})	0.015 ± 0.003	4.916	< 0.001
Distance to EAB core (km)	0.010 ± 0.004	2.754	0.012
Green ash basal area ($m^2 \cdot ha^{-1}$)	0.186 ± 0.183	1.018	0.321
Basal area of all species ($m^2 \cdot ha^{-1}$)	-0.018 ± 0.020	-0.912	0.373
White ash dead stems (ha^{-1})	-0.009 ± 0.010	-0.906	0.376
Green ash stems (ha^{-1})	-0.003 ± 0.005	-0.510	0.616
Green ash live basal area ($m^2 \cdot ha^{-1}$)	-0.385 ± 1.403	-1.274	0.787

Table 1.5: Total number and mean (± SE) number of stems per hectare among sites, relative frequency and density[1] of the five most abundant recruits, saplings, and seedlings recorded in 28 sites located in the core region of the EAB invasion in southeast and south central Michigan.

RECRUITS	**White ash**	**American elm**	**Hawthorn**	**Sugar maple**	**Black cherry**
No. of stems·ha^{-1}	16,695	2,192	1,462	1,397	731
Mean (± SE) stems·ha^{-1}	596 ± 118.9	115 ± 38.2	112 ± 37.7	155 ± 45.1	60 ± 11.3
Mean relative frequency ± SE	79 ± 4.6	29 ± 5.5	19 ± 5.1	13 ± 4.5	15 ± 4.5
Mean relative density ± SE	59 ± 4.8	8 ± 2.0	5 ± 2.2	6 ± 2.8	5 ± 1.6

SAPLINGS	**White ash**	**American elm**	**Black cherry**	**Sugar maple**	**Hawthorn**
No. of stems·ha^{-1}	47,129	3,898	1,851	1,462	1,186
Mean (± SE) stems·ha^{-1}	458 ± 34.3	97 ± 22.5	74 ± 22.2	81 ± 22.4	66 ± 16.3
Mean relative frequency ± SE	90 ± 3.5	35 ± 6.5	22 ± 5.4	16 ± 5.6	16 ± 5.0
Mean relative density ± SE	74 ± 4.4	6 ± 2.4	3 ± 1.2	2 ± 0.8	1 ± 0.7

SEEDLINGS	**Ash**	**Sugar maple**	**Black cherry**	**Hawthorn**	**Elm**
No. of stems·ha^{-1}	1,079,813	118,861	92,584	38,310	35,609
Mean (± SE) stems·ha^{-1}	10,186 ± 1262.9	3,495 ± 1484.6	2,153 ± 329.4	2,253 ± 434.8	1,112 ± 279.8
Mean relative frequency ± SE	93 ± 3.0	30 ± 5.9	37 ± 7.0	15 ± 4.9	27 ± 5.0
Mean relative density ± SE	69 ± 4.4	6 ± 2.5	9 ± 2.7	2 ± 1.2	2 ± 1.0

[1] Relative importance represents the sum of frequency, dominance, and density of a species relative to all other species, following Kent and Coker (1992).

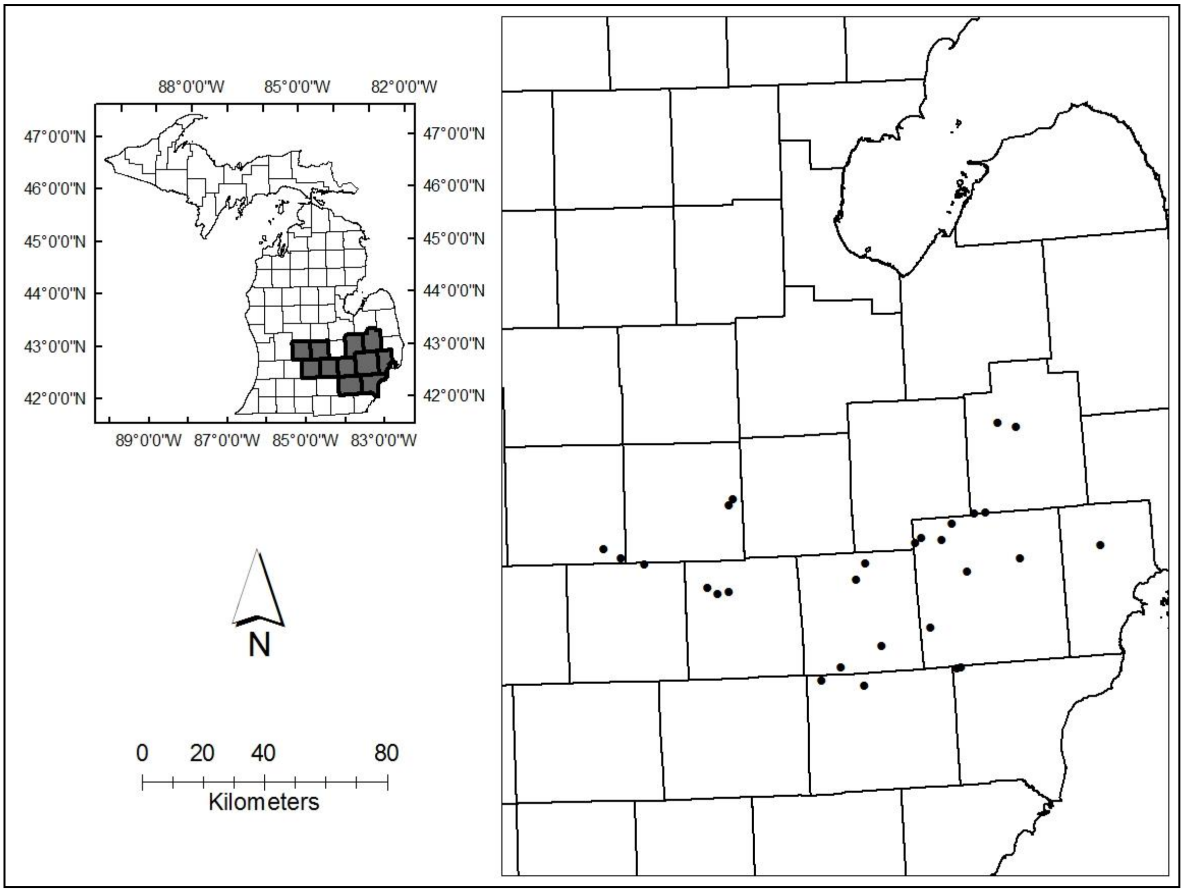


Figure 1.1: Location of 28 sites in 11 counties in Michigan dominated by white ash trees across southeast and south central Michigan.

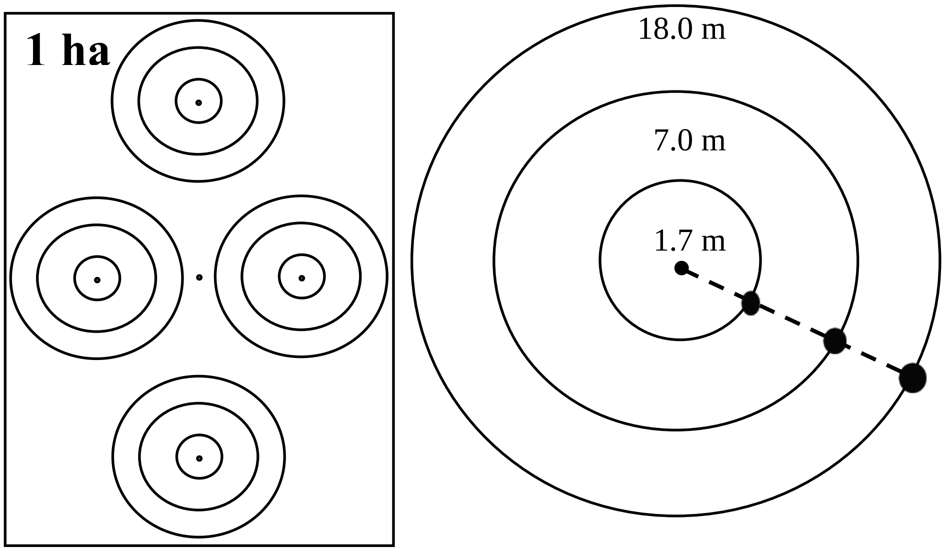


Figure 1.2: Within each site, white ash trees (≥ 10 cm DBH) were surveyed in four macroplots (18 m radius) in a 1 ha area. Seedlings were recorded in microplots (1.7 m radius), and saplings and recruits were recorded in subplots (7 m radius) centered in each macroplot.

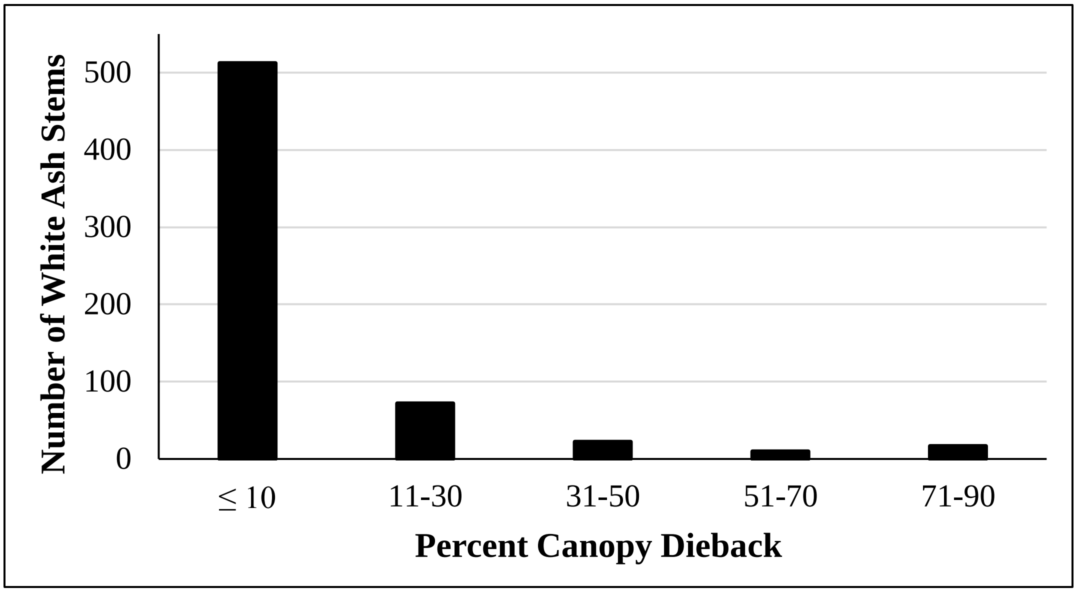


Figure 1.3. Number of white ash trees (≥ 10 cm DBH) by canopy dieback class, recorded in 28 sites in southeast and south central Michigan in 2015.

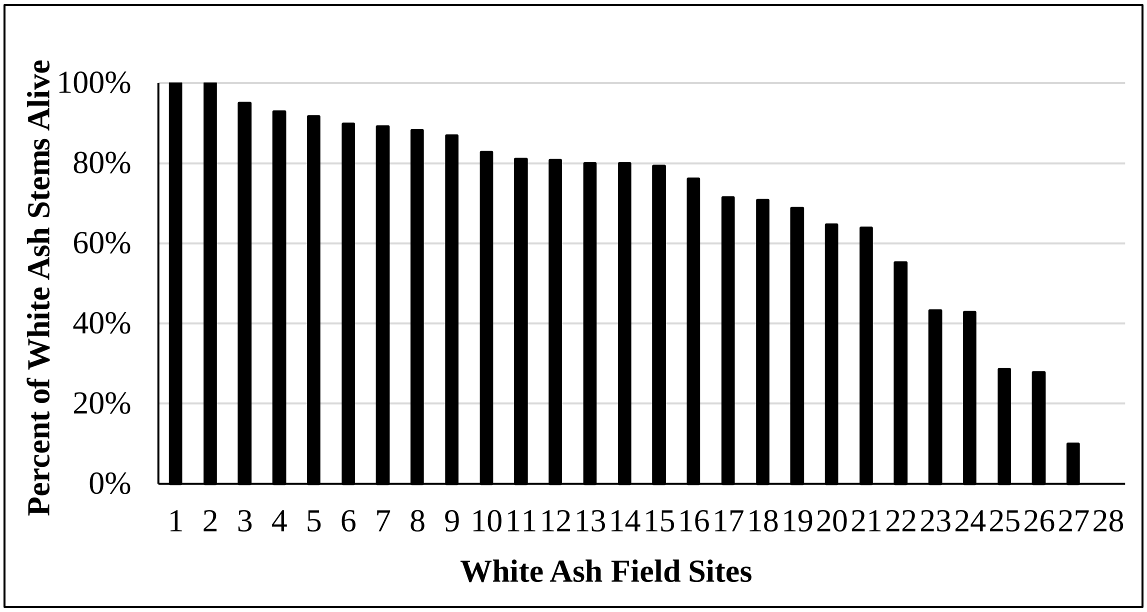


Figure 1.4: Percentage of white ash stems alive in 28 sites surveyed in southeast Michigan in 2015. Site order represents high to low percent white ash stem survival.

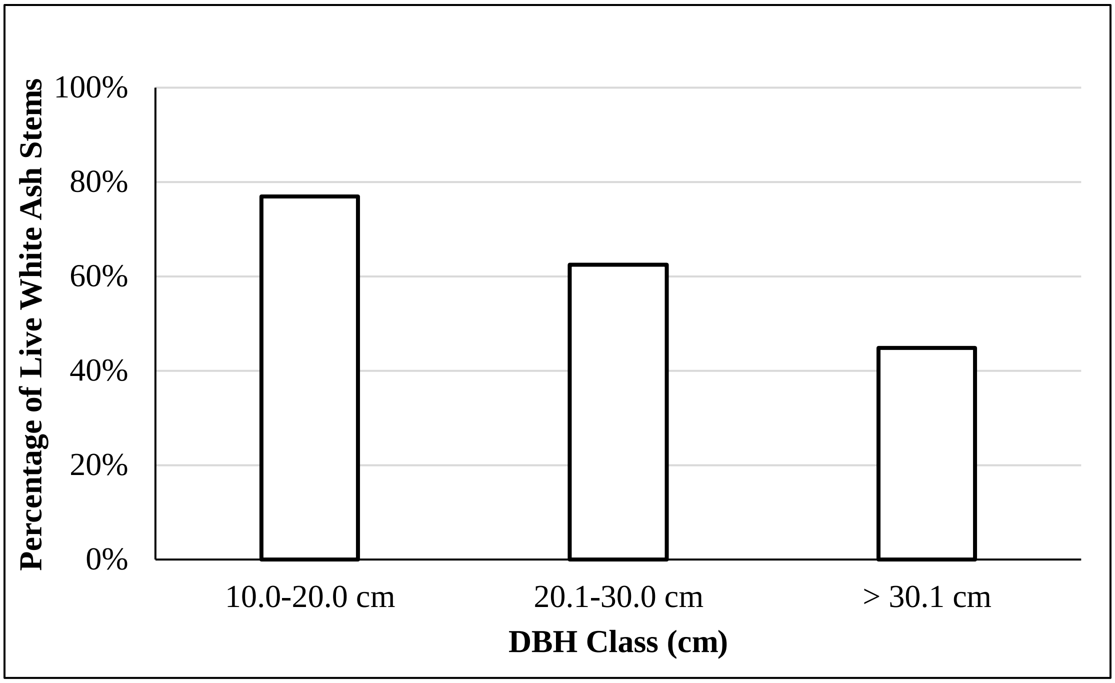


Figure 1.5: Percentage of white ash trees alive by DBH class recorded in 28 sites. A total of 685, 107 and 29 white ash trees were recorded in the pole-sized, medium, and large DBH classes, respectively.

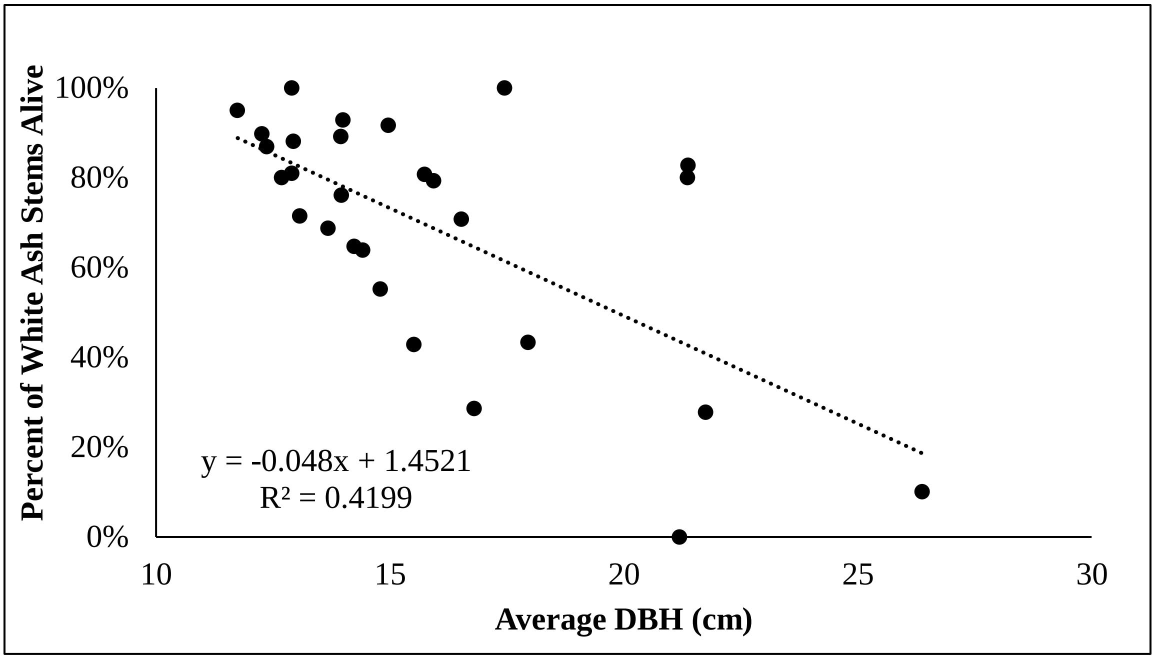


Figure 1.6. Average DBH (cm) of white ash trees calculated for 28 forested sites located in southeast and south central Michigan and proportion of live white ash trees.

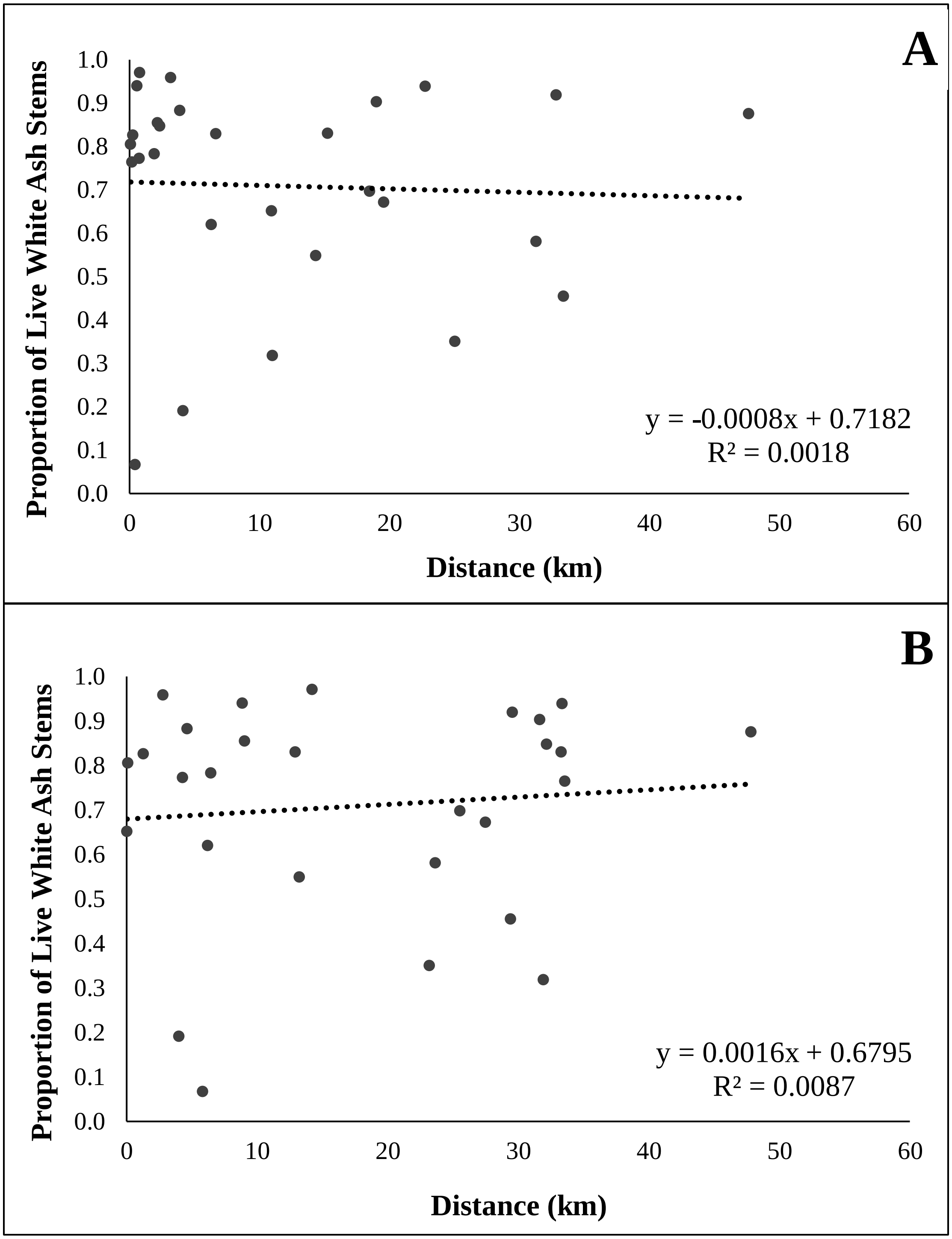


Figure 1.7: Linear distance (km) between the 28 white ash sites located in southeast and south central Michigan, and the nearest site where introduced EAB parasitoids were (A) released and (B) recovered.

CHAPTER TWO

Captures of emerald ash borer (*Agrilus planipennis*) adults in sites with varying amounts of white ash phloem

ABSTRACT

Emerald ash borer (EAB), (*Agrilus planipennis* Fairmaire), first identified in 2002 in southeast Michigan, is now established in 31 states and three Canadian provinces. Catastrophic rates of ash (*Fraxinus* spp.) mortality have been recorded in the core of the EAB invasion in southeast Michigan. While numerous studies have evaluated trap designs and lures for EAB detection, little is known about the persistence and densities of EAB populations in post-invasion sites after most ash trees have died. I monitored two baited double decker (DD) traps in the midst of white ash (*F. americana*) trees in 30 post-invasion sites in southeast and south central Michigan from 2014 to 2016. Traps consisted of (1) a dark green prism above a light purple prism, each baited with *cis*-3-hexenol, or (2) two dark purple prisms baited with *cis*-3-hexenol on the upper prism and Manuka oil on the lower prism. Size and condition of ash trees in an 18 m radius around each trap were surveyed in 2014 and again in 2016. Area of live white ash phloem was calculated and related to EAB adult captures. A total of 580, 585, and 932 EAB were captured in 2014, 2015, and 2016, respectively. Green-purple DD traps captured more EAB adults than traps with two dark purple prisms. Male beetles accounted for 69% to 77% of the captures each year and consistently preferred the green panels. Linear relationships between ash phloem area and EAB captures were not significant, indicating local phloem availability had little effect on beetle captures.

INTRODUCTION

Emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae), an invasive phloem-feeding beetle native to Asia, has been found in at least 31 U.S. states and three Canadian provinces to date (EAB.info 2017), along with western Russia (Baranchikov et al. 2008, Straw et al. 2013, Orlova-Bienkowskaja 2014). Hundreds of millions of ash (*Fraxinus* spp.) have been killed and more than 8 billion ash trees in U.S. forests are threatened (Poland and McCullough 2006, Pugh et al. 2011, Herms and McCullough 2014). In its native range in Asia, EAB is a secondary pest, colonizing severely stressed or declining ash trees (Baranchikov et al. 2008, Liu et al. 2003, Wei et al. 2004). In North America, EAB adults are attracted to and preferentially oviposit on stressed ash trees, but can also colonize and kill healthy ash trees (Cappaert et al. 2005, Poland and McCullough 2006, McCullough et al. 2009*a*, 2009*b,* Siegert et al. 2010, Tluczek et al. 2011, Herms and McCullough 2014).

Although EAB can likely develop on all North American ash species, interspecific variation in host preference has been documented (Cappaert et al. 2005, Anulewicz et al. 2007, Rebek et al. 2008, Chen and Poland 2010, Tanis and McCullough 2012, 2015). Of the four prominent ash species that occur in Michigan and much of the Great Lakes Region, green ash (*F. pennsylvanica* Marsh.) and black ash (*F. nigra* Marsh.) are highly preferred and vulnerable hosts, while blue ash (*F. quadrangulata* Michx.) is less preferred and/or more resistant (Anulewicz et al. 2007, Tanis and McCullough 2012, 2015). White ash (*F. americana* L.) appears to be an intermediate host (Limbeck 2010, Tanis et al. 2012, 2015). In some forested sites in southeast Michigan and northwest Ohio, i.e., the original “core” of the EAB invasion, all or nearly all white ash trees have been killed by EAB (Anuelwicz et al. 2007, Smith et al. 2010, Tanis and McCullough 2012, Klooster et al. 2014, Knight et al. 2014). In other forested areas in this region, however, a high proportion of white ash trees are alive and remain relatively healthy, despite the presence of EAB for at least ten years (McCullough, unpublished data).

Adult EAB generally emerge in late May or June in southern Michigan and feed on the margins of ash leaves throughout their 3-6 week life span. Larvae feed on phloem and cambium in serpentine galleries that often score the outer sapwood, disrupting translocation of water and nutrients. As larval densities build, canopies thin, branches die and eventually the entire tree succumbs (Cappaert et al. 2005, Poland and McCullough 2006, McCullough et al. 2009*a*, Herms and McCullough 2014). The number of EAB larvae that can successfully develop on a given ash tree, or within a specific area where ash trees occur, depends primarily on the availability of live phloem for larval development. McCullough and Siegert (2007) used DBH to estimate phloem area in 148 green ash and white ash trees ranging from 5.2 to 65.0 cm DBH, then determined that on average, 89 ± 4.6 EAB adults could potentially develop per m^2 of phloem. Empirical data collected from debarked trees indicated an individual EAB larva requires approximately 10.13 cm^2 of phloem for development (McCullough and Siegert 2007, Mercader et al. 2011). Thus, a large tree can produce more EAB adults than a small tree and the number of EAB adults that could potentially be produced in a specific area depends on the abundance and size of the ash trees.

Numerous studies in North America have evaluated survey methods, trap designs and lures for detection and delineation of recently established EAB infestations. Although a short range, female-produced pheromone appears to facilitate mating (Lelito et al. 2009, Pureswaran and Poland 2009, Silk et al. 2009, 2011, Ryall et al. 2012), EAB adults do not produce long range sex or aggregation pheromones (Otis et al. 2005, Pureswaran and Poland 2009). Instead, they rely on olfactory and visual cues to locate suitable hosts where they will presumably encounter potential mates (Rodriguez-Saona et al. 2007, Crook et al. 2009, Crook and Mastro 2010).

Methods to detect low-density EAB populations include visual surveys of ash trees to identify external signs of EAB infestation, girdled ash trees and artificial traps. External signs of EAB infestation such as holes left by woodpeckers preying on late instar EAB larvae, small D-shaped holes left by emerging EAB adults, declining canopies and epicormic sprouts are generally not apparent on recently infested trees with low densities of EAB. Girdling ash trees by removing a band of outer bark and phloem around the tree trunk in spring stresses the tree, which alters volatile profiles and increases EAB attraction (Crook et al. 2008) and attracting EAB adults (McCullough et al. 2009*a*, 2009*b*, 2011, Poland and McCullough 2010, Rauscher 2006, Tluczek et al. 2011, Mercader et al. 2013, 2015). Debarking girdled ash trees in fall to locate EAB larval galleries is the most effective method of detecting or monitoring low density populations (McCullough et al. 2009*a*, 2009*b*, 2011, 2015, Mercader et al. 2013, 2015), but locating suitable trees for girdling can be challenging, especially for multi-year surveys.

National EAB detection programs in the U.S. and Canada primarily employ artificial baited traps that incorporate visual and olfactory cues to attract EAB adults (USDA APHIS 2017, CFIA 2016). Most EAB detection programs currently use prism traps or funnel traps in specific shades of green or purple that are coated with clear insect glue and hung from a branch in an ash tree (Crook et al. 2009, 2012, 2014, Cook and Mastro 2010, Francese et al. 2010, 2013*a*, 2013*b*, 2014, Crook et al. 2014). A green leaf volatile, *cis*-3-hexenol, is most commonly used in the U.S. to bait EAB traps (de Groot et al. 2008, Grant et al. 2010, 2011, Poland et al. 2011). In past years, EAB traps were also baited with lures containing Manuka oil, an extract of the New Zealand tea tree (*Leptospermum scoparium* J.R. Forst and G. Forst), which contains sesquiterpenes associated with ash wood and bark that are attractive to EAB beetles (Crook et al. 2008, de Groot et al. 2008, Crook and Mastro 2010, Grant et al. 2010, Poland et al. 2011).

An alternate trap design, known as the double decker trap (DD), is comprised of two sticky prisms attached to a 2.4-m polyvinyl chloride (PVC) pipe that slides over a t post for support (McCullough and Poland 2009, 2017, Poland et al. 2011). These traps, which resemble the silhouette of a small tree, are intended to be placed within 5-10 m of ash trees but in an open area to exploit the preference of EAB for sunny conditions (McCullough et al. 2009, Poland et al. 2011) and to ensure visual and olfactory cues are not overwhelmed by live ash trees (McCullough et al. 2009*a*, 2009*b*, Poland et al. 2011, 2014, McCullough and Poland 2017). Multiple studies across dozens of sites have shown detection rates or EAB adult captures (standardized by trapping surface area) are higher on DD traps baited with *cis*-3-hexenol or a combination of *cis*-3-hexenol and Manuka oil than on baited purple or green prisms or funnel traps hung from ash branches (Marshall 2010*b*, McCullough et al. 2011, Poland et al. 2011, 2014, Poland and McCullough 2017, Wieferich et al. 2017)

Although nearly all trapping studies to date have focused on EAB detection, I was interested in evaluating the relationship between EAB captures and the availability of live ash phloem in post-invasion sites. I hypothesized that live ash phloem represents a critical but limited resource for EAB populations in post-invasion areas and that EAB adult captures would be higher in areas where phloem remains abundant, while few adults would be captured in sites where nearly all ash trees are dead. Conversely, the lack of a relationship between EAB captures and phloem area could suggest that traps attract EAB adults from beyond the vicinity of the traps or that local EAB populations are not limited by phloem availability and that other factors may be influencing densities. I monitored two double decker trap designs in 30 post-invasion sites over three seasons and evaluated relationships between EAB captures and live ash phloem.

METHODS

Site selection

I used a Michigan county atlas in April 2014 to identify 70 large, forested areas on state, county, or municipal property in southeast and south central Lower Michigan, then queried managers of each area to assess white ash tree presence and abundance. I visited 40 sites where white ash occurred and identified 30 areas where white ash trees, whether dead or alive, appeared to be relatively abundant (Fig 2.1). I recorded GPS coordinates in the midst of the white ash trees in each site.

Trapping

At each of the 30 sites, I set up two double decker (DD) traps, 36 to 50 m apart, between 24 May and 12 June in 2014 and recorded GPS coordinates. Traps were placed in the same locations in 2015 and 2016. Traps remained in place through mid-September each year. Traps were placed in full sunlight, 5-10 m from the edge of wooded areas or in open areas among scattered ash trees. Each DD trap consisted of two coroplast panels (36 × 60 cm panels) (Great Lakes IPM, Vestaburg, MI) folded into three-sided prism (36 × 60 cm on each side). Prisms were zip-tied to a 3 m tall PVC pipe (10 cm diam); the upper and lower prisms were 3.0 m and 1.8 m from the ground, respectively. The PVC pipe was supported by sliding the pipe over a t-post (McCullough and Poland 2017). Prism surfaces were coated with clear Pestick™ (Hummert International, Earth City, MO) when the traps were set up. One DD trap was comprised of an upper dark green prism and a lower light purple prism. Two *cis*-3-hexenol bubble caps (release rate of 3.7 mg/d per bubble cap for a combined release rate of 7.4 mg/d; Contech Enterprises Inc., Delta, BC) were attached to the lower edge of both prisms. The second DD trap was comprised of two dark purple prisms. The top prism was baited with two *cis*-3-hexenol bubble caps while the lower prism was baited with a Manuka oil pouch (release rate of 50 mg/d, Synergy Semiochemicals, Corp.). Lures were replaced mid-season to ensure consistent volatile release and Pestick™ was re-applied mid-season. The same trap designs were placed in the same locations in all three years.

Captured EAB beetles were collected at two to three week intervals from early June to mid-September each year. Beetles were typically collected from multiple sites on a given day but it required approximately a week to check traps at all 30 sites. Beetles on each prism of the two traps were bagged separately and returned to the Michigan State University (MSU) Forest Entomology Lab. Beetles were soaked in Histoclear II (National Diagnostics, Atlanta, GA) to remove Pestick™ and examined under a microscope to confirm species and sex.

I acquired cumulative growing degree days (GDD) (base 50 °F/10 °C) for each site from the nearest MSU Enviro-weather station (Enviroweather.msu.edu). The Euclidean distance between each site and nearby weather stations were determined using ArcMap 10.3 and ranged from 5 to 43 km. I recorded the cumulative GDDs (base 50 °F /10 °C) for each collection period.

Fixed radius plots

I centered a circular plot with an 18 m radius around each of the two DD traps and recorded DBH of white ash trees (≥ 6 cm DBH). I visually estimated canopy dieback in increments of 10%, where < 10% indicated a full, healthy canopy and ≥ 80% indicated severe decline (Zarnoch et al. 2004). Ash trees were assigned to dieback classes (0-20%, 21-40%, 41-60%, 61-80%, 81-100%) for some analyses. Each ash tree was examined for signs of EAB infestation, including holes left by woodpeckers preying on EAB larvae and D-shaped adult EAB emergence holes. Trees were re-surveyed from early July to mid-August in 2016.

Density of white ash stems and white ash basal area ($m^2 \cdot ha^{-1}$) were calculated for each plot and summed for each site in 2014 and 2016. White ash trees were assigned to four DBH classes (6.0-13.0 cm, 13.1-25.0 cm, 25.1-42.0 cm, 42.1 to 60.0 cm). Area of phloem (m^2) in live and dead white ash trees was calculated using DBH for trees recorded in 2014 and 2016 following methods of McCullough and Siegert (2007). I also adjusted the area of live phloem to account for canopy dieback in individual trees. When dieback estimates were > 10%, I multiplied the estimated phloem area by the percentage of the canopy that remained healthy, e.g., the estimated live phloem area was reduced by the proportion of the canopy that was dead. I also estimated live phloem area for trees assigned to the five canopy dieback classes, using the midpoint of each dieback class.

Statistical analysis

Adult male and female beetles captured per trap (both prisms) and per prism were tallied for each collection period and summed by year. Differences in numbers of EAB captured per trap or per prism were compared among years and trap types, and among prism colors or lures within trap types using separate generalized linear mixed models (PROC GLIMMIX). In separate models, the main effects of trap type, year, prism color, position (upper or lower), and lure were tested as fixed effects. Site was a random effect in all models. To account for collinearity among years, an autoregressive order one covariance structure was used for all models, with the Kenward-Rogers modification of the denominator degrees of freedom (Alnosaier 2007). Because the response variable was count data, the negative binomial distribution was used with the log link function (Hilbe 2011). Differences among years, trap types, prism color within trap types, and lure within trap types for the separate models were tested with the Tukey-Kramer means comparison procedure. Residuals were tested for homogeneity of variance assumption using Levene’s test and models were adjusted if needed.

Simple linear regression was used to assess whether the area of live ash phloem (m^2) significantly predicted EAB adult captures within sites (PROC REG). Captures of EAB in 2014, 2015, and 2016 were compared to total area of live phloem measured in 2014 and EAB captures in 2016 were regressed on phloem area measured in 2016. Cumulative GDD for collection dates each year were plotted to identify when EAB adult captures peaked. All analyses were conducted using the SAS 9.4 for Windows statistical package (SAS Institute, 2012) with an α-level of 0.05.

RESULTS

Trapping

Overall, 580, 585, and 932 EAB adults were captured on the 60 DD traps in 2014, 2015, and 2016, respectively. Significantly more beetles were captured in 2016 than in either 2014 or 2015 (F = 6.08; df = 2, 42; $P = 0.0048$) (Fig 2.2). In 2014, no EAB adults were captured in two sites, while one to 61 beetles were captured in the other 28 sites. On average, 19 ± 2.8 beetles were captured per site in my first year of trapping. In 2015, EAB beetles were captured in 29 sites; the site with zero EAB captures in 2015 also had no EAB captures in 2014. Total beetles captured per site ranged from one to 64, with an average of 19 ± 3.0 per site. Between 2014 and 2015, EAB captures increased by ≥ 50% in 12 sites, remained consistent in four sites and decreased by ≥ 50% in five sites. In 2016, EAB adults were captured in all sites and number of captured beetles increased by approximately 60% in 14 of the 30 sites from 2014 to 2016 (Fig 2.2). I captured 191 and 194 more EAB adults in 2016 than in 2014 and 2015, respectively. Total captures ranged from one to 127 EAB adults per site and averaged 31 ± 5.3 beetles per site.

The cumulative number of EAB adults captured throughout the season differed between trap types (F = 24.91; df = 1, 178; $P < 0.0001$) and among years (F = 8.86; df = 1,14; $P = 0.0034$), but the interaction was not significant ($P = 0.636$). Overall, the PG trap caught significantly more EAB adults than the PP trap, accounting for 73%, 68%, and 67% of total captures in 2014, 2015, and 2016, respectively. The green prisms on the PG traps accounted for 40% and 35% of the total EAB captures in 2014 and 2015, respectively. On average, 7.7 ± 1.3 and 6.9 ± 1.3 EAB adults were captured on the green prisms in 2014 and 2015, respectively, while captures on the lower light purple prisms averaged 6.4 ± 1.1 in both years. In 2016, however, the light purple prisms on the PG traps caught an average of 11.2 ± 2.2 EAB adults, which accounted for 36% of the total beetle captures (Table 2.1). On the PP traps, the upper prisms accounted for 14%, 19%, and 20% of total EAB captures, while the lower prisms captured for 12%, 13%, and 12% of the beetles in 2014, 2015, and 2016, respectively. On average, 2.8 ± 0.7, 3.8 ± 0.9, and 6.3 ± 1.2 EAB adults were captured on the upper prisms, while 2.4 ± 0.8, 2.5 ± 0.6, and 3.9 ± 0.9 EAB adults were captured on the lower prisms in 2014, 2015, and 2016, respectively.

Overall, individual prisms baited with *cis*-3-hexenol lures captured more EAB adults than prisms baited with Manuka oil (F = 15.50; df = 3, 87; $P < 0.001$) and green prisms and light purple prisms baited with *cis*-3-hexenol captured more beetles than the dark purple prisms baited with either *cis*-3-hexenol or with Manuka oil. The trap designs and lures represented operational trapping regimes (USDA APHIS 2017), but prism colors, position and lures were confounded, making it difficult to fully determine which factor was most relevant to beetles. Results do suggest the PG trap was more attractive than the PP trap given that the *cis*-3-hexenol was more attractive than the Manuka oil lure on the PG trap, whereas *cis*-3-hexenol and Manuka oil captured similar numbers of beetles on the PP traps.

Male beetles dominated captures on both trap designs in all three years. Overall, 70%, 69%, and 77% of the EAB adults captured in 2014, 2015, and 2016, respectively were males. Male captures increased in 21 of the 30 sites from 2014 to 2016. Number of males captured increased by ≥ 50% in 13 sites and decreased by ≥ 50% in four sites, while two sites stayed the same. Two sites increased from zero males captured in 2014 to one captured in 2016, while one site increased from zero males captured in 2014 to eight sites in 2016. Females captured increased in 18 sites and remained stable in 2 sites from 2014 to 2016 (Fig 2.2). Number of females captured increased by ≥ 50% in 16 sites and decreased by ≥ 50% in three sites. One site increased from zero females captured in 2014 to one captured in 2016, while one site increased from zero females captured in 2014 to five captured in 2016. Green prisms caught significantly more males than the light purple prisms or either of the dark purple prisms (F = 15.50; df = 3,87; $P < 0.0001$). Significantly more female EAB adults were captured in 2015 and 2016 than in 2014 (F = 4.57; df = 2,58 $P = 0.014$). Total number of females captured differed among years and prisms, but were not affected by the interaction ($P = 0.837$). Light purple prisms on the PG traps caught significantly more EAB females than either of the dark purple prisms on the PP traps or the upper green prisms on the PG traps (F = 11.7; df = 3,87; $P < 0.0001$) (Table 2.1).

EAB adult captures and growing degree days

I began collecting EAB from the DD traps on 10 June each year. Sites were visited to collect captured beetles following the same order used when I set up the traps. Cumulative growing degree days (GDD) (base 50ºF/10ºC) associated with the first trap checks in each site ranged from a minimum of 654 to 941 DD_{50} (Table 2.2). Peak EAB activity occurred in late June to early July each year, with EAB captures accounting for 54%, 52%, and 62% of the total EAB captured in 2014, 2015, and 2016, respectively. Following this peak in 2016, EAB adults captured during my third check occurring in August decreased by 85%, whereas in 2014 and 2015, EAB adults captured decreased by 48% and 39%, respectively. Across all three years, I caught ≤ 21 EAB during my final check in September (ending on September 17, 11, 23 in 2014, 2015, and 2016, respectively).

White ash phloem

Abundance and condition of white ash trees in the plots centered on the two traps in each site varied substantially. In 2014, a total of 1,109 white ash trees (≥ 6 cm DBH) were measured, including 477 trees with ≤ 10% canopy dieback and 657 trees with ≤ 50% canopy dieback.

Conversely, 44 white ash trees were severely declining with ≥ 80% canopy dieback and an additional 373 trees are dead. External signs of EAB infestation were apparent on 58% of the 736 live white ash trees recorded, while 98% of the dead white ash trees were killed by EAB. Of the 304 white ash trees showing 10% to 50% canopy dieback, external signs of EAB infestation were apparent on 78%, while 98% of the 44 white ash trees showing 80% to 90% canopy dieback had external signs of EAB infestation (Table 2.3).

In 2016, number and condition of white ash trees were similar to those in 2014. There was a slight increase in the number of white ash trees recorded from 2014 to 2016 because of young, healthy trees that were > 6 cm DBH in 2016 but not in 2014. In 2016, I measured a total of 1,187 white ash trees, including 662 white ash trees with ≤ 10% canopy dieback, and 726 trees with ≤ 50% canopy dieback. There were seven white ash trees that were heavily infested and severely declining with ≥ 80% canopy dieback, and an additional 430 that are dead (Table 2.3). External signs of EAB infestation were apparent on 71% of the 757 live white ash trees, and 99% of the dead white ash trees. Of the 118 white ash trees showing 10% to 50% canopy dieback, external signs of infestation were apparent on 94%, while all 15 white ash trees in severe decline showing 80% to 90% canopy dieback were infested with EAB.

Estimated area of live white ash phloem within sites was similar in 2014 and 2016. In 2014, I recorded a total of 3,627.2 m^2 of phloem, of which, 1,832.5 m^2 was alive. A total of 684.8 m^2 of phloem recorded was alive in the small DBH class (6.0 to 13.0 cm), while 279.1 m^2 of phloem recorded was alive in the two large DBH classes combined (25.1 to 42.0 and 42.1 to 60.0). Based on the trees recorded in 2014 and phloem area, potentially 10,761 ± 1,558.4 EAB could have emerged across the sites, ranging from a minimum of 1,673 to a maximum of 37,466 within sites. When adjusting phloem to account for canopy dieback, total phloem decreased to

1,566.0 m^2, and the total live phloem decreased to 1,382.8 m^2. In the small DBH class, the amount of live adjusted phloem recorded was 557.3 m^2, and 195.4 m^2 in the two large DBH classes combined.

In 2016, I recorded a total of 3,569.1 m^2 of phloem, of which 1,732.1 m^2 was alive. The small DBH class (6.0 to 13.0 cm) accounted for 728.6 m^2 of the live phloem recorded, while the two large DBH classes combined (25.1 to 42.0 and 42.1 to 60.0 cm) accounted for 259.2 m^2 of the live phloem. Based on the trees recorded in 2016 and phloem area, potentially 10,881 ± 1,434.9 EAB could have emerged across the sites, ranging from a minimum of 2,095 to a maximum of 36,567 within sites. When adjusting phloem to account for canopy dieback, total phloem decreased to 1,641.1 m^2, while the total live phloem recorded decreased to 1,457.4 m^2. Live phloem adjusted for canopy dieback decreased to 635.9 m^2 for the small DBH class, and 201.4 m^2 for the two large DBH classes combined.

The level of infestation and condition of white ash trees varied from nearly all trees alive and in relatively good condition, to $\geq$ 90% mortality. In my third year of trapping, I captured EAB in all sites using baited DD traps, even where nearly all trees were dead. Relationships between the area of live white ash phloem derived from the 2014 surveys and the number of EAB adults captured were weak in 2014 and 2015 (Fig 2.3). Despite the notable increase in EAB captures in 2016, the area of live white ash phloem available for EAB larval development explained relatively little variation in EAB adult captures in 2016 ($P = 0.166$), or when comparing 2016 EAB captures to 2014 phloem area ($P = 0.189$) (Fig 2.3). I re-ran each regression excluding the one outlier site with the highest amount of live phloem. This resulted in a significant relationship between 2014 white ash phloem and 2015 EAB captures ($y = 0.695x + 27.003$; $R^2 = 0.16$; $P = 0.032$).

When I adjusted the area of live white ash phloem (m^2) measured in 2014 to account for canopy dieback, the relationship with EAB captures remained weak in 2014, as well as 2015 and 2016. Similarly, EAB captures in 2016 were not strongly related to the adjusted area of live phloem calculated from the 2016 survey ($P = 0.241$) (Fig 2.4). After re-running the regression excluding the outlier site, the relationship between adjusted 2014 live phloem and 2015 EAB captured was significant ($y = 0.707x + 27.765$; $R^2 = 0.16$; $P = 0.031$).

DISCUSSION

Populations of both EAB and white ash trees continue to persist in these post-invasion sites. I found that white ash phloem was not a limiting factor for EAB larval development. While EAB are likely to colonize ash trees within 200 m of their point of emergence when phloem is abundant (Siegert et al. 2010), it is likely captured EAB dispersed from parent trees outside my surveyed plots. Across the 30 sites, the level of infestation and condition of white ash trees varied from nearly all trees alive and in relatively good condition, to ≥ 90% mortality. However, the condition of ash trees recorded in my plots was similar in 2014 and 2016, despite capturing significantly more EAB adults in 2016 compared to the previous two years. This may be a result of larvae developing in two years rather than one, or from beetles dispersing from ash trees surrounding these sites. I found that green-light purple (PG) traps lured with *cis*-3-hexenol captured significantly more EAB adults than the purple-purple (PP) traps.

While the availability of ash phloem for larval development would be a limiting resource if it was related to EAB captures, I found this not to be the case. In both 2014 and 2016, one of the 30 sites had low EAB captures with roughly 175 m^2 of live white ash phloem area available. When excluding this site to compare total EAB adults captured and live white ash phloem, there was a significant relationship between phloem and adjusted phloem calculated from 2014 trees and EAB adult captures in 2015. However, when comparing total EAB adult captures in 2016 to white ash phloem available in both 2014 and 2016, the relationship was weak. Despite the abundance and availability of phloem in many of the sites, trees continue to persist and remain in relatively good condition.

Most EAB females will select ash tree hosts close to their point of emergence to oviposit their eggs (Mercader et al. 2009). In a simulation study conducted by Mercader et al. (2011), mortality rates and the relationship between the proportion of EAB larvae that develop in one or two years and larval density for a site were found to likely be affected by the diffuse distribution of ash phloem. Siegert et al. (2010) reported a significant bias in the dispersal of EAB towards areas where ash phloem was relatively abundant within 200 m of their emergence point, however, larvae were also reported up to 650 m from the origin. Mercader at al. (2009) reported 70% of larval galleries were on trees within 100 m of the point of emergence, while a single larvae was reported 750 m from the point of emergence. I focused only on white ash trees recorded within radius plots extending out 18 m from each trap. Since live white ash trees were abundant in many of the sites I surveyed, it is possible EAB adults captured on my traps emerged from live white ash trees present beyond my 18 m plots.

Determining the amount of total and live phloem (m^2) for an individual tree, or for multiple trees, allows us to estimate the area of phloem available for EAB development on ash trees of varying diameter classes. McCullough and Siegert (2007) found that, on average, roughly 89 EAB could successfully develop and emerge per m^2 of phloem surface area, and that EAB production averaged 68.8 ± 5.9 beetles per m^2 on small trees (2.5-13 cm DBH) and 105.3 ± 5.7 beetles per m^2 on larger trees (DBH $>$ 13 cm). Based on the trees recorded and phloem area calculated, I found on average 10,761 ± 1,558.4 and 10,881 ± 1,434.9 EAB could have potentially emerged across the sites in 2014 and 2016, respectively. The DBH of live white ash trees recorded in sites ranged from 6.0 to 40.6 cm, with 80% having a DBH of $\leq$ 13 cm. Young white ash trees generally have relatively smooth bark on the branches and much of the trunk. When young trees are attacked by EAB, females are likely to lay most eggs on the trunk of the tree, both because branches are too slender and because females usually prefer rough-textured bark near the base or around branch crotches (Anulewicz et al. 2006. Larval feeding on tree trunks and its effects on water and nutrient translocation can result in rapid mortality. Despite this, many of the white ash trees recorded in the sites remain in good condition from my initial plots conducted in 2014 to when I repeated these plots in 2016. Additionally, many show signs of previous infestation, but are still persisting.

Development of an efficient and effective artificial trap for capturing and monitoring EAB adults has proven to be a challenging task. Poland et al. (2011) found significantly more EAB were captured on DD traps that are designed to imitate the silhouette of a tree compared to canopy traps hung in infested ash trees. Poland and McCullough (2014) found both green and purple double decker traps were the most successful trap design in capturing EAB adults when compared to canopy traps. Multiple studies have shown males to be consistently attracted to dark green panels, while females are attracted to the purple (light and dark) panels (Crook et al. 2009, Grant et al. 2009, Francese et al. 2010). In my study, the PG trap which combines both green and purple panels captured significantly more beetles than the PP trap. I found the green panels of the PG traps captured significantly more males, while the light purple panels captured significantly more females. Males tend to hover near the canopy of ash trees (Rodriguez-Saona et al. 2007), resulting in higher proportions captured on green traps, while females are captured in higher proportions on purple prisms that imitate a tree trunk or branches where they oviposit their eggs (Crook and Mastro 2010, Francese 2010, Grant et al. 2011, Poland and McCullough 2014). Additionally, EAB adult activity is greatest in full sun (Yu 1992). Field studies showed higher numbers of EAB adults are captured on trap trees that are exposed to sunlight compared those growing in a shaded canopy (McCullough et al. 2009*a*, 2009*b*). Chen and Poland (2009) found EAB adults preferentially feed on ash leaves grown in sun over leaves grown in shade (Chen and Poland 2009). In contrast to traps hung on a branch in the shaded canopy of ash trees, double decker traps are placed in full sun, making them visually apparent to EAB adults (McCullough and Poland 2009, McCullough et al. 2011, Poland et al. 2011), giving this design an advantage.

In addition to color, lure type is also important in the success of the trap (Poland and McCullough 2014). Both the top and bottom panels of the PG trap and the top panel of the PP trap were baited with *cis*-3-hexenol, which is a lure that imitates volatiles released by stressed ash trees. Males are specifically attracted to *cis*-3-hexenol, and are often hovering the canopy of ash trees feeding on foliage (Lelito et al. 2008, Rodriguez-Saona et al. 2007), which may explain the abundance in male captures on panels baited with this lure. Poland et al. (2014) compared DD traps of different colors and found dark green-light purple DD traps lured with *cis*-3 hexenol to be the most effective DD trap, with a detection rate of 90%, while dark purple-dark purple DD traps lured with *cis*-3 hexenol and Manuka oil, or *cis*-3-hexenol on both the top and bottom prisms were the least attractive of the DD trap color combinations, with detection rates of 70% and 60%, respectively. I also found the use of both dark green and light purple panels, both lured with *cis*-3-hexenol, to be significantly more attractive to EAB adults than DD traps with dark purple top and bottom panels lured with both *cis*-3-hexenol and Manuka oil.

Emergence of EAB typically begins in mid-May when accumulated growing degree days (GDD) (base 50 ºF/10 ºC) reach 450 in southern Michigan. As in previous studies, EAB adult activity peaked in late June and early July in all three years (McCullough et al. 2009*a*, Poland et al. 2011). In 2016, however, the proportion of EAB adults captured during my first check beginning June 10 was double that of the previous two years, despite similar accumulation of GDD during this time across all three years. While this is notable, it could be a reflection of differences in sun or daily temperatures during this time that resulted in greater EAB adult emergence. Though EAB generally has a one-year life cycle, development in healthy ash has been found to take two years (Cappaert et al. 2005, Siegert et al. 2010, Tluczek et al. 2011). Based on conclusions from these previous studies, abundance of EAB emerging earlier in 2016 may be explained by the completion of a two-year life cycle in these sites due to the vigor of the surviving white ash trees reflecting the low population densities (Cappaert et al. 2005, Wei et al. 2007, Tluczek et al. 2011). Destructive sampling or bark windows of ash trees within these sites would have to be conducted to verify life stages to identify and quantify density of two-year galleries. Based on the difference in the population trend of EAB when comparing captures from 2014 and 2015 to 2016, it is difficult to determine whether populations will continue to build in these sites. Additional years of trapping would be beneficial to project the future condition of these stands.

While phloem is readily available for EAB development in these sites located in the core EAB invasion area, white ash trees seem to be coexisting with EAB populations. Natural enemies of EAB larvae, including woodpeckers (Cappaert et al. 2005, Duan et al. 2010 Lindell et al. 2008,), native parasitoids (Cappaert and McCullough 2009, Duan et al. 2012) and introduced parasitoids native to Asia (Yang et al. 2005, Yang et al. 2006, Bauer et al. 2008) could be keeping EAB populations below carrying capacity within these sites. Destructive sampling would have to occur to know for sure. Monitoring of these trees should continue in the future.

APPENDIX

APPENDIX

Table 2.1: Mean (± SE) number of adult emerald ash borer (EAB) males and females captured per prism in 2014, 2015, and 2016 in 30 sites in Michigan.

	Prisms			
	Green Upper	Light Purple Lower	Dark Purple Upper	Dark Purple Lower
2014				
Males	7.1 ± 1.2	4.5 ± 0.9	2.2 ± 0.5	1.6 ± 0.6
Females	0.7 ± 0.2	1.9 ± 0.4	0.6 ± 0.2	0.7 ± 0.3
2015				
Males	5.5 ± 1.1	4.1 ± 0.8	2.3 ± 0.6	1.3 ± 0.4
Females	1.4 ± 0.3	2.3 ± 0.4	1.4 ± 0.3	1.1 ± 0.3
2016				
Males	8.7 ± 2.0	7.9 ± 1.6	4.6 ± 0.9	2.8 ± 0.8
Females	1.0 ± 0.2	3.3 ± 0.7	3.9 ± 0.8	1.0 ± 0.3

Table 2.2: Number of male and female emerald ash borer adults captured by month and year. Accumulated growing degree days (base 50 ºF/10 ºC)[1] from the nearest MSU Enviro Weather station were compiled for each date.

N = 30 sites **Trap Check**	**Min; Max GDD**	**Male**	**Female**	**Total**
2014				
June	625.3; 812.6	62	17	79
July	938.0; 1114.8	263	53	316
August	1256.0; 1483.9	123	42	165
September	1861.0; 2335.6	13	7	20
2015				
June	669.5; 941.5	61	15	76
July	968.2; 1392.7	212	96	308
August	1475.9; 1964.3	119	69	188
September	2006.5; 2489.0	7	6	13
2016				
June	654.3; 856.6	232	38	270
July	1045.7; 1302.8	141	438	579
August	1710.7; 2036.2	37	25	62
September	2308.7; 2891.3	15	6	21

[1] Accumulted growing degree days base (50ºF) is the heat accumulation above the minimum threshold of 50ºF, beginning on January 1.

Table 2.3: Number of white ash (*F. americana*) trees, estimated total and adjusted area of phloem (m^2) recorded in fixed radius plots (18 m radius) in 30 sites in Michigan in 2014 and 2016. Phloem area was calculated following methods of McCullough and Siegert (2007), then adjusted to account for percent canopy dieback class.

Percent Canopy Dieback Class	**No. Trees**	**Total Phloem**	**Adjusted Live Phloem**
2014			
0.0-20.0%	555	1243.1	1118.8
20.1-40.0%	86	254.4	178.1
40.1-60.0%	31	91.7	45.9
60.1-80.0%	39	97.1	29.1
80.1-100.0%	398	1940.9	194.1
2016			
0.0-20.0%	693	1503.7	1353.3
20.1-40.0%	22	76.9	53.8
40.1-60.0%	20	65.0	32.5
60.1-80.0%	15	45.7	13.7
80.1-100.0%	437	1877.8	187.8

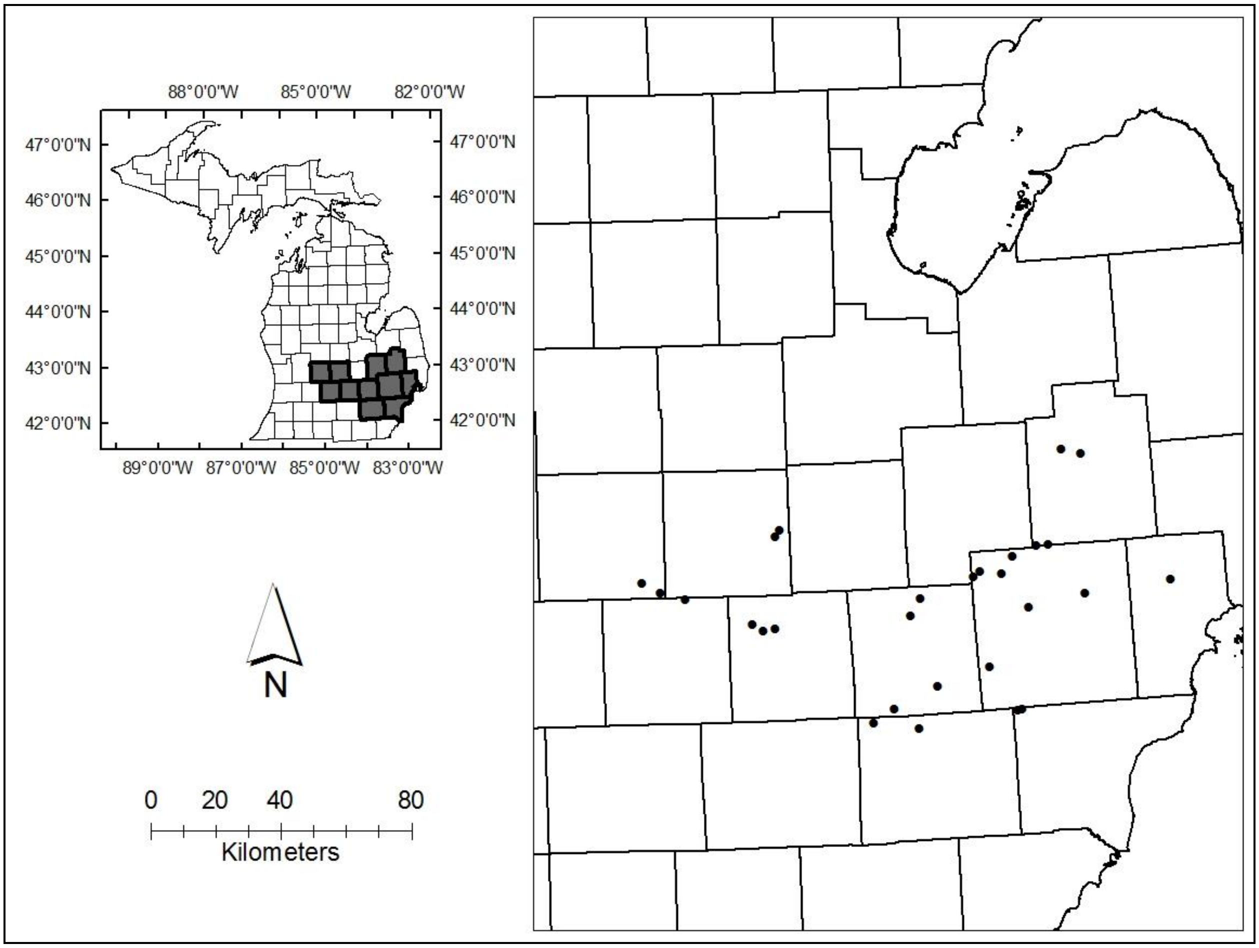


Figure 2.1: Distribution of 30 white ash sites in southeast and south central Lower Michigan.

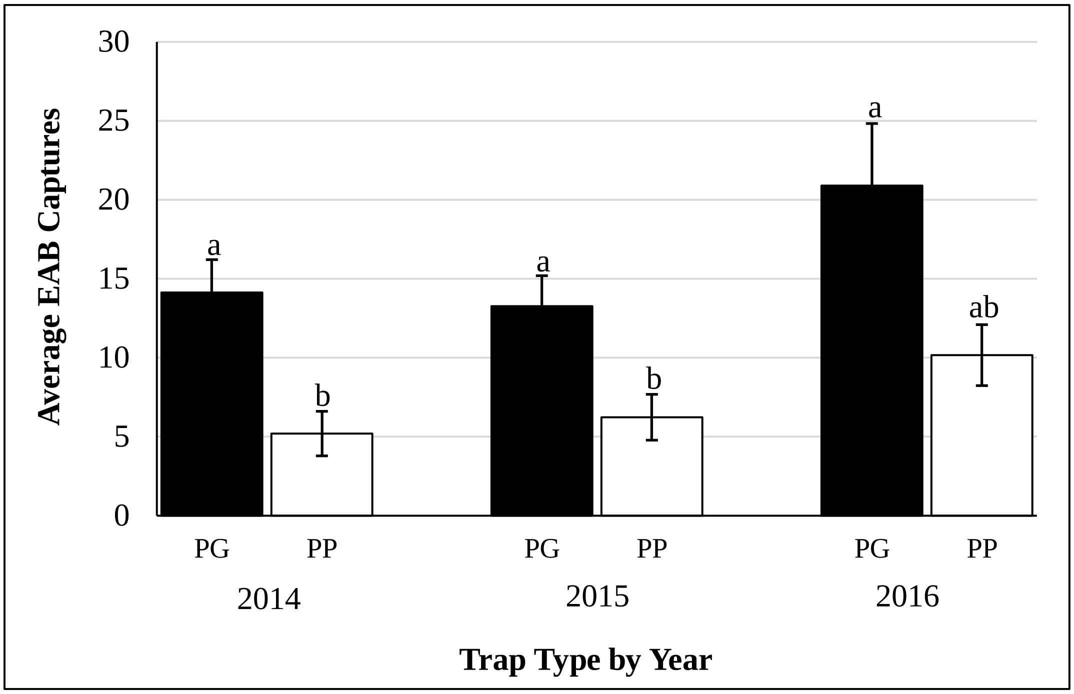


Figure 2.2: Total adult emerald ash borer captured in 2014, 2015, and 2016 on purple-green double decker traps (PG) and purple-purple double decker traps (PP). Bars topped by the same letter are not significantly different, $P > 0.05$.

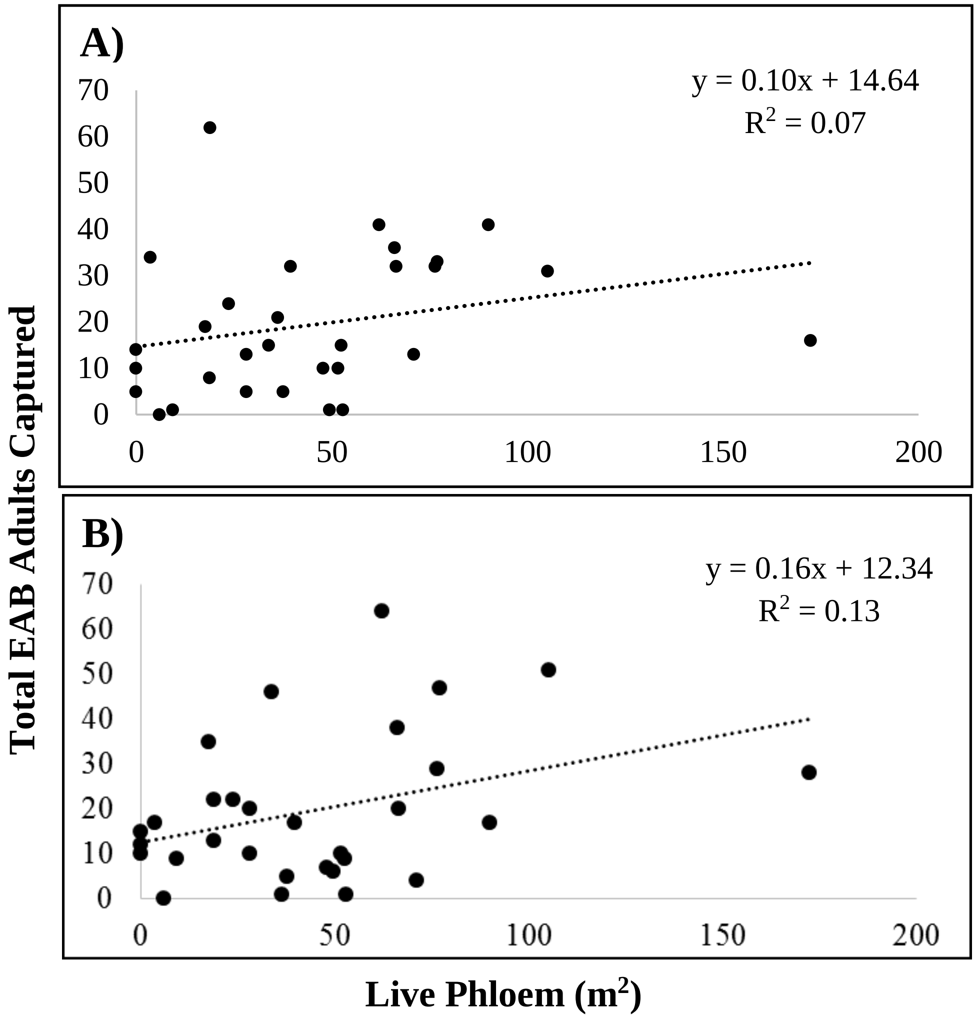
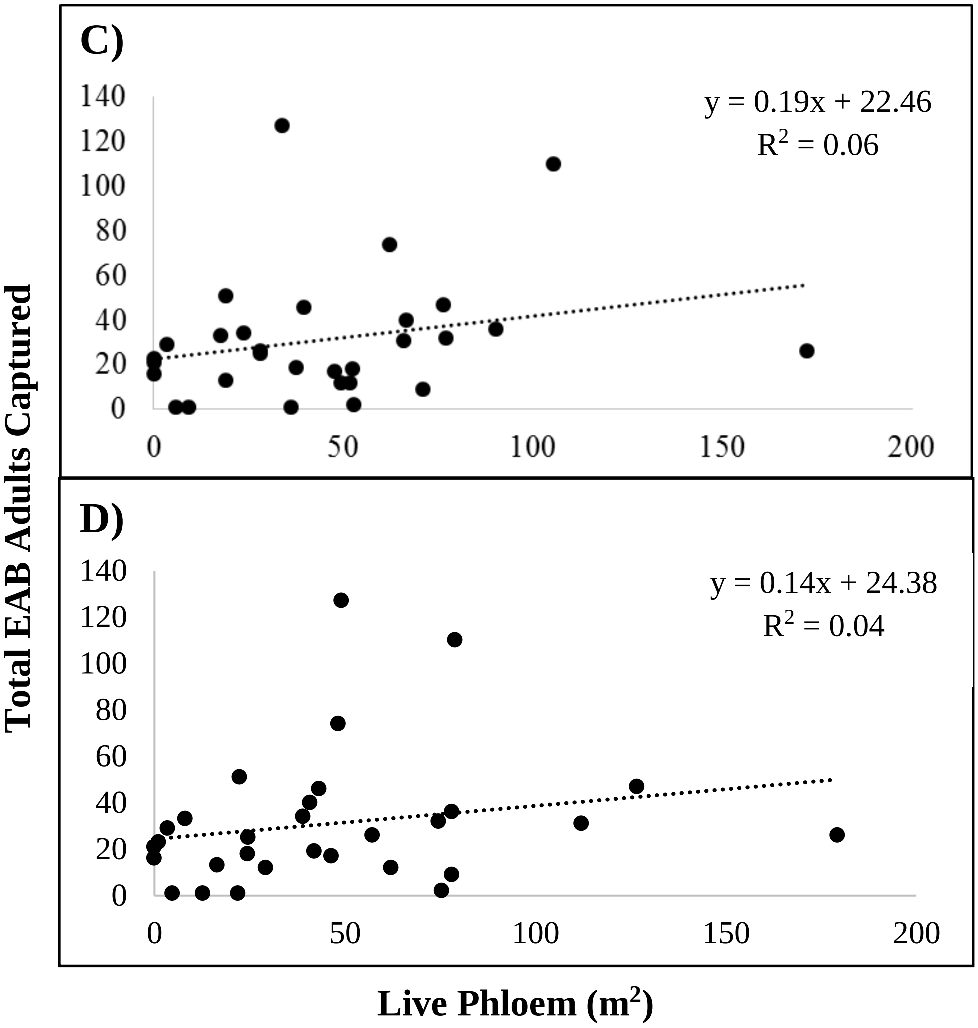


Figure 2.3: Linear relationship between total emerald ash borer adult captured in 2014-2016 and estimated area live white ash phloem (m^2) surrounding traps (18 m radius) in 30 sites in Michigan. Area of live white ash phloem (m^2) calculated from 2014 plot data is compared to adult emerald ash borers captures in (A) 2014, (B) 2015 and (C) 2016. Area of live white ash phloem (m^2) calculated from 2016 plot data is compared to 2016 EAB captures in 2016 (D). Live white ash phloem area (m^2) was estimated following the methods of McCullough and Siegert (2007) in 2014 and again in 2016.

Figure 2.3 (cont'd)



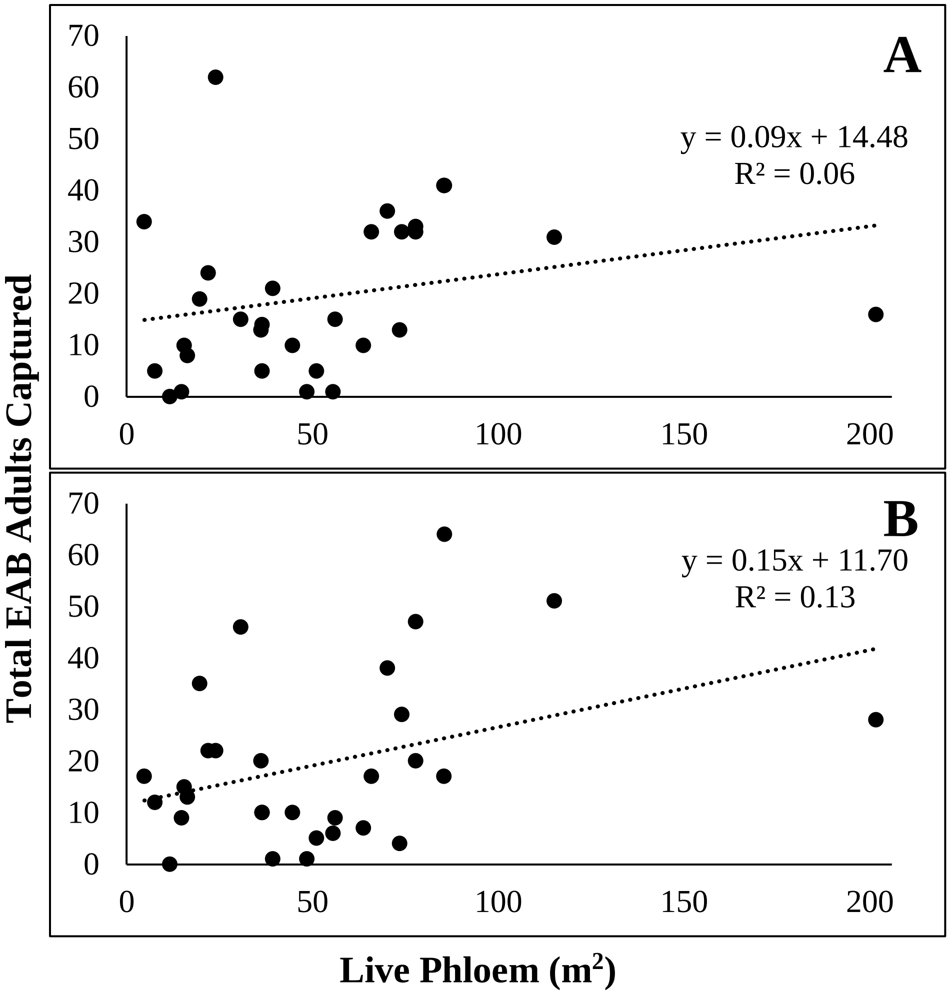
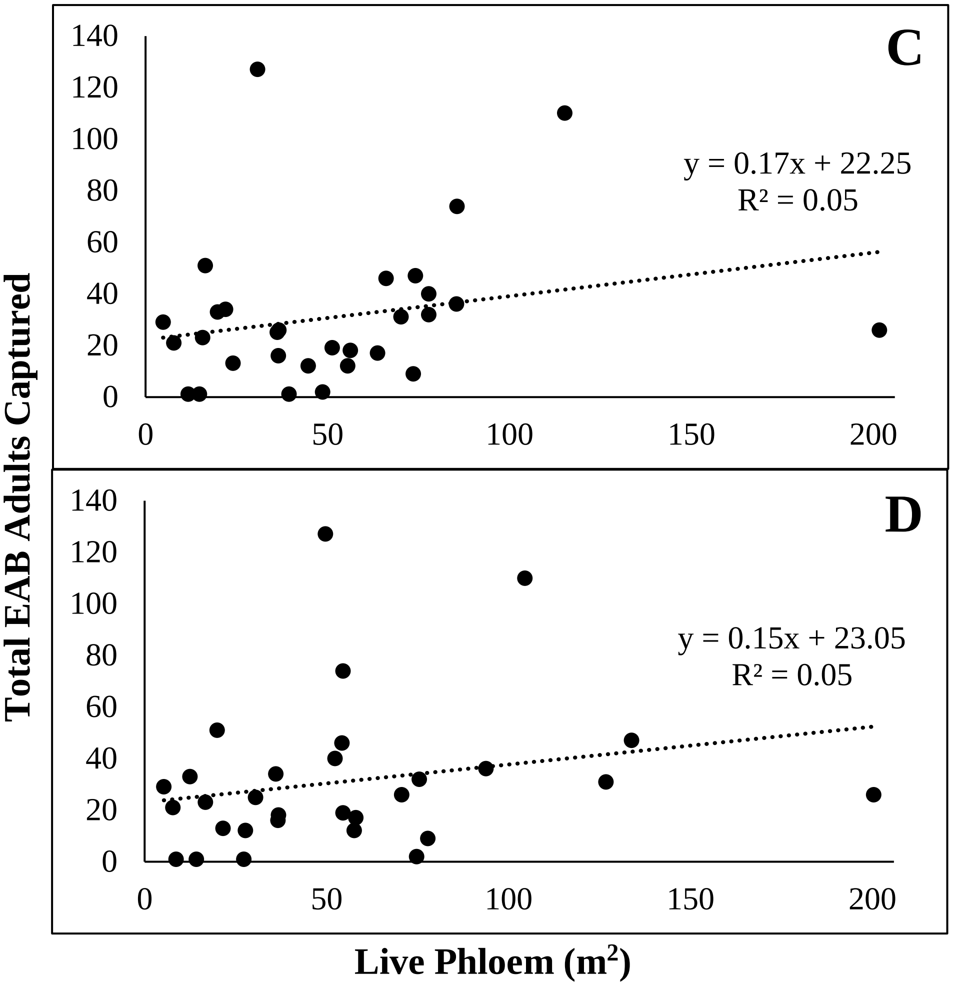


Figure 2.4: Total adult emerald ash borer captures compared to total live white ash phloem area (m^2) adjusted for percent canopy dieback in 30 sites located in southeast and south central Michigan. Area of live white ash phloem (m^2) calculated from 2014 plot data adjusted for percent canopy dieback is compared to total adult emerald ash borer captured in 2014 (A), 2015 (B), and 2016 (C). Area of live white ash phloem (m^2) calculated from 2016 plot data adjusted for percent canopy dieback is compared to total EAB captures in 2016 (D). Live white ash phloem area (m^2) was estimated using diameter at breast height (DBH, cm) of white ash trees in two plots (18 m radius) surrounding each trap in each site, and was adjusted to incorporate percent canopy dieback by multiplying the percentage of the canopy not showing dieback. Phloem area was calculated following the methods of McCullough and Siegert (2007) in 2014 and again in 2016.

Figure 2.4 (cont'd)



CHAPTER THREE

Variables related to white ash survival rates in forested sites in the core emerald ash borer invasion area

ABSTRACT

The invasive emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) has caused catastrophic mortality of ash (*Fraxinus* spp.) trees since its arrival in the Detroit-metro area of southeast Michigan in the 1990’s, and currently threatens over 8 billion ash trees in U.S. forests. Despite previous studies reporting nearly 100% mortality of prominent ash species in Michigan following the initial wave of EAB infestation, an abundance of surviving white ash trees have been recorded in sites located in this area. Determining site-level variables associated with relatively high rates of white ash survival could be valuable, particularly for forest managers. I collected data in intensive plots, variable radius plots, and driving surveys in 2014 and 2015 in 28 sites in southeast and south central Michigan. I downloaded land type satellite data to fit models at five scales to determine whether any recorded variables consistently predict white ash stem survival rates. Results showed that as distance increased from intensive plots with abundant white ash, green ash presence, specifically those growing along roads, negatively affected white ash survival. The proportion of area classed as woody wetlands and the presence of white ash trees, specifically those along roads, are also important variables. These variables should be considered in decisions related to white ash management.

INTRODUCTION

The emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) has caused catastrophic damage in U.S. forests (Aukema et al. 2011, Herms and McCullough 2014) following its arrival in southeast Michigan during the mid-1990's (Cappaert et al. 2005, Siegert et al. 2014). Currently, EAB populations are found in 31 states and three Canadian provinces (EAB.info 2017). Hundreds of millions of ash (*Fraxinus* spp.) trees have died, and more than 8 billion ash trees across U.S. forests are threatened by this Asian, phloem-feeding beetle native to Asia (Poland and McCullough 2006). Projections suggest an estimated 10.7 billion USD will be spent by 2019 for removal or treatment of roughly half of the ash landscape trees likely to be affected (Kovacs et al. 2010). This widespread ash mortality caused by this invasive beetle has resulted in cascading effects through forested ecosystems, altering species composition, understory light, temperature, and moisture availability, increasing coarse woody debris, and affecting carbon and nitrogen cycling (Knight et al. 2013, Flower et al. 2013*a*, Burr and McCullough 2014, Klooster et al. 2014).

Spread of EAB is characterized by stratified dispersal, represented by short-distance adult flights (i.e., natural dispersal), while human-transport of infested ash material can result in long-distance spread (Mercader et al. 2011*a*, 2011*b*, Mercader et al. 2012, Siegert et al. 2014). Field studies based on systematically felling and debarking ash trees to locate larval progeny from beetles that emerged from a known point of origin have helped with the understanding of EAB dispersal (Mercader et al. 2009, Siegert et al. 2010). While some portion of female EAB adults likely have long range dispersed flights and colonize trees more than 800 m from their point of emergence (Mercader et al. 2012), multiple field studies have shown 90% of eggs laid by females are within 800 m of their emergence point, with most ovipositing on trees within 100 m (Mercader et al. 2009, 2012, 2015, Siegert et al. 2010).

In North America, EAB preferentially colonize stressed ash trees, but will attack healthy trees (Cappaert et al. 2005, Poland and McCullough 2006, McCullough et al. 2009*a,* 2009*b,* Siegert et al. 2010, Flower et al. 2013, Herms and McCullough 2014). Feeding and development of EAB can likely occur on all ash species in the U.S., including the four prominent species occurring in Michigan (Anulewicz et al. 2007, Tanis and McCullough 2012, 2015). Interspecific differences in ash resistance or EAB host preference among species have been observed (Cappaert et al. 2005, Anulewicz et al. 2007, 2008, Rebek et al. 2008, Pureswaran and Poland 2009, Chen and Poland 2010, Tanis and McCullough 2012, 2015). Green ash (*Fraxinus pennsylvanica* Marsh.) and black ash (*F. nigra* Marsh.) are consistently highly preferred and vulnerable hosts of EAB (Cappaert et al 2005, Anulewicz et al. 2007, 2008, Rebek et al. 2008, Chen and Poland 2010), while blue ash (*F. quadrangulata* Michx.) is relatively resistant to EAB (Anulewicz et al. 2007, Tanis and McCullough, 2012).

White ash (*F. americana* L.) is considered an intermediate host for EAB (Anulewicz et al. 2007, Tanis and McCullough 2012, 2015). Previous studies showed green ash trees are preferentially colonized in multi-species plantations and in landscapes where green ash and white ash trees co-occur (Anulewicz et al. 2007, Limback 2010, Tanis and McCullough 2015). While substantial white ash mortality has occurred in many areas in southeast Michigan (Gandhi and Herms 2010, Knight et al. 2013, 2014, Klooster et al. 2014, Smith et al. 2015), evidence to date suggests interactions between white ash trees and EAB may be relatively complex. We have observed live white ash trees in some forested sites in areas of southeast Michigan despite the presence of EAB in these sites for at least 10-12 years (McCullough, unpublished data).

Identification of variables associated with relatively high or low survival could have important management implications for the future of white ash trees as a functional component of forest systems.

Both tree and site characteristics play a role in tree mortality caused by native or exotic pests. Clark et al. (2015) developed decision models to predict the probability of ash tree mortality using tree health assessments and signs of infestation, specifically for management of hazardous trees in residential areas. This study focused on tree-level data, rather than data collected across a forested stand, and did not incorporate variables such as land use. Knight et al. (2013) evaluated relationships between site and tree-level factors and ash tree mortality in EAB-infested stands. They reported crown class, hydrology, ash canopy health class, and the number of ash trees per hectare were significant variables in models to predict ash survival rates. In contrast, Smith et al. (2015) reported no relationship between site and stand attributes including overstory species composition, ash density, basal area, and importance, and mortality rates of white, green, or black ash.

Factors that promote EAB dispersal should also be considered. A study by Jenkins et al. (2016) quantified ash mortality risks using “detection tree” data collected in Ohio from 2005 to 2007, while also incorporating distance to existing ash stands, campgrounds, roads, and railways that are corridors for EAB dispersal. They found ash trees growing along riparian corridors are at high relative risk of EAB-induced mortality. In heterogeneous sites with urban, residential, and wooded areas, EAB preferentially colonized open-grown ash trees rather than shaded trees in wooded areas, similar to findings from other studies (Siegert et al. 2010, McCullough et al. 2009*a*, 2009*b*).

I investigated site-level variables associated with white ash survival in southeast and south central Michigan forests where EAB has had the longest history of invasion in North America. I surveyed an array of variables in 28 sites located in this region to quantify site characteristics potentially associated with rates of white ash survival. My primary objectives were to document overstory species composition and condition in forested stands with a substantial component of white ash varying in survival and at least 10-12 years of EAB presence. I evaluated site-level variables within a 1.5 km radius from the center of each site, and hypothesized EAB colonization or population growth rates could be related to abundant white ash, abundant green ash, or land usage type. Since green ash is a highly preferred, vulnerable host of EAB (Anulewicz et al. 2007, 2008, Rebek et al. 2008), I hypothesize its presence could attract EAB, having a negative impact on white ash survival. However, if this preferred host is absent, some white ash trees may be alive and continue to persist. If the presence of open-grown ash trees growing in sunny-conditions, such as along roads around sites consisting of living white ash are scarce or absent, white ash trees may have a higher rate of survival. I developed models using survey results and spatial datasets to determine if any variables were consistent predictors of white ash survival. These variables could then be used to develop white ash survival prediction models where resource managers could prioritize harvest of white ash trees in forested areas projected to be susceptible to the infestation of EAB, while white ash trees projected to survive EAB infestation could be left to persist as a functional component within our forests.

METHODS

Site selection

I identified 70 large areas of public forestland (state, county, or municipal property) distributed across 11 counties in southeast and south central Michigan using a county atlas in 2014. Emerald ash borer is known to have invaded this area at least 10 to 12 years earlier (Pugh et al. 2011, Marshall et al. 2013, Burr and McCullough 2014, Klooster et al. 2014, Siegert et al. 2014). I contacted managers of each area to acquire information about the presence of white ash trees on the property. Based on forest inventory records and my visual observations, I eliminated areas with few or no white ash trees from further consideration. Remaining areas were further scouted to assess distribution and condition of white ash trees. I established a center point and recorded GPS coordinates in the midst of abundant white ash trees in 28 sites (Figure 3.1).

White ash condition

In August 2015, I delineated a 1 ha area around the center point of each site, divided the area into four equal quadrants, and established a fixed radius plot (18 m) in each quadrant. I recorded DBH (cm) of all tree species (≥ 10 cm DBH) and visually estimated percent canopy dieback of white ash trees and green ash trees ≥ 10 cm DBH when present. Sites were then classed as high survival if (≥ 85% of the white ash trees were alive, low survival if ≤ 60% of the white ash trees were alive, or moderate survival if > 60% but ≤ 84% of the white ash trees were alive.

Variable radius plots

I delineated a 1.5 km radius around the center point of each site using satellite imagery and ArcMap 10.3, then delineated forested areas within the 1.5 km radius. A 200 x 200 m grid was overlaid on each map and grid cells falling within each forested polygon were numbered.

Grid cells were selected for field surveys using systematic random sampling based on the polygon area. I surveyed a minimum of two grid cells in polygons < 8 ha and up to 20 cells in polygons > 81 ha.

I established a variable radius plot (10 baf prism) in the center of each selected grid cell and recorded species and DBH of all dead and live trees ≥ 10 cm. I visually assessed canopy dieback of live trees in increments of 10%, where 10% indicated a nearly full, healthy canopy, and 90% indicated a nearly dead canopy (Zarnoch et al. 2004). The total number of live and dead white ash trees recorded in variable radius plots were summed for each site. When ash trees were present, I recorded signs of EAB infestation, including holes left by woodpeckers feeding on EAB larvae, adult EAB exit holes, and bark cracks above larval galleries.

Driving surveys

I conducted additional surveys within the area defined by the 1.5 km radius in August 2015 to assess presence and abundance of white ash trees and green ash trees along roads, in open fields, hedgerows, and residential areas. A waypoint was taken when ash trees were present. I recorded the ash species and visually estimated DBH and canopy dieback. In locations where clusters of > 5 white ash trees or green ash trees were present, I counted or visually estimated the number of ash trees, and estimated the average DBH and canopy dieback for trees by species.

Geographic data

Land cover data were downloaded from the National Land Cover Database (NLCD 2011) and clipped to each 1.5 km radius. I calculated total area (km^2) of each land cover type with the area bounded by each radius in each site, and the proportion of area represented by deciduous forest, mixed forest, woody wetland, shrubland, cropland, grassland, and pasture. I summed the total area of deciduous forest and mixed forest within the four areas defined by the radii, then classified this variable as “forest” for analyses. I similarly summed the area of cropland, grassland, shrubland, and pasture for each radius and classified this variable as “open” for analyses.

Road shapefiles were downloaded from the Michigan Geographic Data Library (MiGDL) and clipped each to the areas as above. Using ArcMap 10.3, I calculated the length (km) of roads within each 1.5 km radius, and calculated the density of white ash and green ash trees (≥ 10 cm DBH) by summing the count of each species and dividing by the determined area of roads within the areas defined by the radii.

Statistical analysis

I summed the number of variable radius plots where white ash and green ash trees were tallied for each site. Average DBH (cm) and average percent canopy dieback were calculated for white ash and green ash trees (≥ 10 cm DBH) in the variables radius plots and driving surveys.

I fit a general linear model to variables within the areas defined by the 0 to 400, 400 to 800, 800 to 1200, and 1200 to 1500 m radii, and to a cross-scale model defined by the outer 1500 m radius. The response variable was the percentage of white ash trees (≥ 10 cm DBH) that were alive in the fixed radius plots. I began my analyses with 16 potential predictor variables I hypothesized could influence white ash tree survival, including counts, average DBH (cm) and canopy dieback estimates for white ash and green ash trees recorded in driving surveys and variable radius plots, number of plots with white ash or green ash trees present, proportion of woody wetlands, open area (area of crops, grass, shrubs, and pasture summed), forested area (summed mixed and deciduous forest), and densities of white ash and green ash trees along roads.

To address multicollinearity among potential predictor variables, I calculated Pearson's correlation coefficients, and excluded variables with a correlation coefficient > 0.40 for a conservative model (Elith et al. 2006, Wisz and Guisan 2009). Generalized Variance Inflation Factors (VIFs) were calculated and considered for the remaining predictor variables (Brunsdon et al. 2012, Neter et al. 1996) and competing variables with the highest VIF values were eliminated until all VIF values were < 2. Multicollinearity diagnoses were conducted using R statistical software (R Core Development Team, http://www.R-project.org)

I fit a set of competing models to my data and applied multi-model inference (Burnham and Anderson 2002) to assess the fit. I used the Akaike information criterion (AICc) corrected for small sample sizes (AICc; Shono 2000), as recommended when the ratio between n (the number of observations used to fit the model) and K (the number of parameters in the largest model) is < 40 (Shono 2000, Burnham and Anderson 2002). To optimize model strength, I applied a multi-model dredging function in R's MuMin package (dredge – MuMIn R package; available at http://r-forge.r-project.org) to assess valid combinations of variables to predict the percentage of white ash trees alive in the sites. All competing models with a delta AICc of < 2.0 were selected, as recommended by Burnham and Anderson (2002). Model averaging was used for the competing parameter coefficient estimates in the model following methods of Buckland et al. (1997), and the relative importance of variables were calculated (Burnham and Anderson 2002). Diagnostics for the competing models were assessed for normality of residuals and homoscedasticity by evaluating plots of fitted values vs. residuals, Q-Q plots and Cook's Distance plots. Model selection and residual diagnostics were conducted using R statistical software (R Core Development Team, http://www.R-project.org) at α of $P < 0.05$.

RESULTS

White ash condition

Overall, 74% of the 821 white ash trees (≥ 10 cm DBH) recorded in the fixed radius plots in the 28 sites were alive. There were 33 white ash trees with 70-90% canopy dieback that were classed as “dead”. White ash survival rates, i.e., the percent of stems ≥ 10 cm DBH alive, varied considerably among sites, ranging from 0% in one site up to 100% in two sites (Fig 3.2). In 14 of the 28 sites, ≥ 80% of the white ash stems were alive, and at least 50% of the white ash stems were alive in 22 sites. Nine sites were classified as high survival (≥ 85% of the white ash trees alive), seven sites were classified as low survival (≤ 60% of the white ash trees alive), and twelve sites were classified as moderate survival (> 60 % to 84% of the white ash trees alive).

Variable radius plots

White ash trees were present in a total of 98 of the variable radius plots established in forested areas. I recorded 240 white ash trees total and survival rates within plots ranged from 0% in three sites to 100% in nine sites. Overall, 75% of the white ash trees were alive and all had < 50% canopy dieback. In 15 sites, ≥ 80% of the white ash trees were alive and at least 60% of the white ash trees were alive in 23 of the 28 sites. In contrast, of the 214 green ash trees encountered in 91 variable radius plots, only 3% were alive in four of the 28 sites.

Driving surveys

Both white ash and green ash trees were abundant along roads running through all 28 sites. Density of ash trees along roads ranged from 1.6 to 37.7 trees per km, averaging 12.3 ± 4.4, 14.8 ± 3.1, and 17.1 ± 3.8 trees for the sites with high, moderate, and low white ash survival, respectively. Density of ash along roads ranged from 73 per km to 472 per km, averaging 210 ± 23.3 trees per site. On average, there were 223 ± 52.0, 227 ± 38.4, and 178 ± 34.9 ash street trees in the high, moderate, and low survival sites, respectively. Survival of the ash street trees in the high, moderate, and low survival site classes was 46%, 46% and 26%, respectively. White ash trees accounted for 50%, 54%, and 26% of the street trees, while green ash accounted for 50%, 46%, and 74% of the total recorded in high, moderate, and low survival site classes, respectively.

Geographic data

Land use data was analyzed across the 1.5 km radius. For the high, moderate, and low white ash survival sites, forested area accounted for 34% to 40% of the total area. Open land comprised 30% of the total area in sites with high white ash survival. Woody wetlands were the least abundant land class, comprising 12% of the area in the low and moderate survival sites, to 19% in the high survival sites (Table 3.1).

Cross-scale model

A total of 29 competing models with a delta AICc < 2.0 (Table 3.2) had a ≤ 4% chance of being the best model to predict white ash survival recorded in the four fixed radius plots in the center of the sites. No single strongly weighted ($w_i > 0.9$) model could be identified. Variables in the top model (delta AICc = 0.00) with an AICc value of -8.79 included average DBH of green ash recorded in driving surveys, green ash density along roads, proportion of area classed as open, and white ash road density. Other variables included in competing models (delta AICc < 2.0) were average DBH of green ash and white ash recorded in variable radius plots, average DBH of white ash recorded in driving surveys, and the proportion of area classed as open (Table 3.2).

Based on the cross-scale full-averaged model, there were no variables that significantly affected white ash survival (Table 3.2). Density of white ash trees along roads had the highest value of relative importance (0.91) compared to all other variables (Figure 3.3). Average DBH of green ash trees along roads had a relative importance of 0.77, while green ash road density, the proportion of area classed as open, and the proportion of area classed as woody wetlands had importance values of 0.73, 0.67, and 0.53, respectively (Figure 3.3).

400 m model

Five competing models were identified for areas bounded by the 400 m radius. No single strongly weighted ($w_i > 0.9$) model could be identified. The intercept had an AICc value of 3.12 and was considered the top model (delta AICc = 0.00), with a weight of 0.30. Average DBH of white ash trees along roads had the second lowest AICc value of 4.40, but only had a 16% chance of explaining white ash survival.

The full-averaged model for the area within the 400 m radius showed the proportion of area classed as woody wetlands, green ash density along roads, and the proportion of area classed as forest were negatively related to white ash survival, but the parameters were not significant ($P = 0.83$, 0.85, and 0.95, respectively) (Table 3.3). Average DBH of white ash recorded during driving surveys, proportion of area classed as woody wetlands, and average DBH of green ash recorded in variables radius plots had the highest relative importance (0.16, 0.12, and 0.12, respectively) (Figure 3.3).

800 m model

Two competing models had a delta AICc < 2.0 (Table 3.4), but none were identified as the best model ($w_i > 0.9$). Variables in the top model (delta AICc = 0.00) with an AICc value of -1.16 included average DBH of green ash trees from the driving surveys and white ash tree density along roads. This model, however, only had a 36% chance of being the best model to explain white ash survival. The remaining model included average DBH of green ash recorded in driving surveys, green ash tree density along roads, and white ash tree density along roads, with a 19% chance of being the best model.

Based on the full-averaged model, average DBH of green ash trees recorded in driving surveys was the only significant variable negatively related to white ash survival ($P = 0.02$). The proportion of area classed as forest was also negatively related to white ash survival, but was not significant ($P = 0.90$) (Table 3.4). Average DBH of green ash trees recorded in driving surveys had the highest relative importance of 1.00 followed by white ash tree density along roads, having a relative importance of 0.90 (Figure 3.3). Green ash density along roads which had a relative importance of 0.19, while the remaining variables had a relative importance of ≤ 0.09 (Figure 3.3).

1200 m model

There were 23 competing models with a delta AICc < 2.0 in the 1200 m model, all of which had < 5% chance of being the best model to explain white ash survival (Table 3.5). The top model (delta AICc = 0.00) with an AICc value of 2.67 included average DBH of green ash trees recorded in variable radius plots, green ash tree density along roads, and proportion of area classed as forest. The second model with an AICc value of 2.72 included average DBH of green ash recorded in variable radius plots and proportion of area classed as open. Other variables included in the competing models were average DBH of green ash trees recorded in driving surveys, average DBH of white ash trees recorded in driving surveys and variable radius plots, and the proportion of area classed as woody wetlands (Table 3.5).

The full-averaged model for the 1200 m radius showed average DBH of green ash in variable radius plots, green ash density along roads, the proportion area classed as forest, the proportion of area classed as woody wetlands, and average DBH of green ash recorded in driving surveys negatively affected white ash survival, but none were significant (*P* = 0.36, 0.47, 0.66, 0.72 and 0.83, respectively) (Table 3.5). Average DBH of green ash recorded in variables radius plots had the highest relative importance of 0.61 while green ash tree density along roads had a relative importance of 0.48. The proportion of area classed as open and forest, and average DBH of white ash trees recorded in driving surveys had a relative importance of 0.34, 0.25, and 0.24, respectively. The remaining variables had a relative importance of ≤ 0.20 (Figure 3.3).

<u>1500 m model</u>

There were only two competing models with a delta AICc < 2.0 within the 1200 to 1500 m radius, but none were clearly the best ($w_i > 0.9$) (Table 3.6). The top model (delta AICc = 0.00) included green ash tree density along roads and the proportion of area classed as woody wetlands, which had a 36% chance of being the best model of the candidate set. The next model included green ash tree density along roads, average DBH of white ash in variable radius plots, and the proportion of area classed as woody wetlands with a 16% chance of being the best model (Table 3.6).

Green ash tree density along roads and the proportion of area classed as woody wetlands had a significant negative affect on white ash tree survival (*P* = 0.02) (Table 3.6). Average DBH of white ash trees recorded in driving surveys and average DBH of green ash trees recorded in variables radius plots both negatively affected white ash survival, however, this effect was not significant (*P* = 0.83 and *P* = 0.99, respectively). Green ash density along roads and the proportion of area classed as woody wetlands had the highest importance (1.00) of all variables in the 1200 to 1500 m model. Average DBH of white ash trees recorded in variables radius plots and driving surveys, and the proportion of area classed as open had a relative importance of 0.16, 0.12, and 0.11, respectively, while the remaining variables had a relative importance of < 10 (Figure 3.3).

Competing models with a delta AICc value of < 2.0 are considered to be essentially as good as the best model. When considering many models, the delta AICc value can become problematic because models strongly competing with the best model (delta AICc < 2.0) may differ very little structurally (Burnham and Anderson 2002, Symonds and Moussalli 2010). Although many site-level variables were tested in the models, the sample was limited to 28 sites. This resulted in model uncertainty, with many competing models at each scale. However, the variables that were consistently of high importance across the models are notable and deserve future exploration with a more abundant data set.

The presence of green ash was consistently important in predicting white ash survival at four different scales (400 to 800 m, 800 to 1200 m, 1200 to 1500 m, and cross-scale), having a negative effect on white ash survival. White ash tree presence along roads was also important in multiple models (400 to 800 m and cross-scale), while the proportion area classed as woody wetlands was one of two variables with the highest importance (1.00) in the 800 to 1200 m model, and had a negative effect on white ash survival in all models but the 800 to 1200 m model.

DISCUSSION

White ash trees are native forest species in 38 states and two Canadian provinces, are landscape trees in all 48 states, and are a component of 26 unique forest cover types in North America (NLCD 2017). Determining site-level variables associated with white ash tree survival in areas with the longest history of EAB invasion could provide direction for the management and information about the future of this species as a functional component of forest systems.

I hypothesized the presence of green ash, a highly preferred and vulnerable EAB host (Anulewicz et al. 2007, 2008, Rebek et al. 2008) could impact white ash survival. Previous studies have shown that EAB preferentially colonizes green ash trees over white ash trees where these species co-occur (Anulewicz et al. 2007, Limback 2010, Tanis and McCullough 2012, 2015). I found green ash trees present along roads in the areas surrounding the concentrations of white ash was negatively related to white ash survival. Additionally, the proportion of the area bounded by the 1.5 km radius that was classed as woody wetlands had a negative effect on white ash survival. Green ash is commonly found along rivers and streams, and can be abundant on land subject to flooding (NRCS 2017). Area of woody wetlands may, therefore, reflect conditions favorable and likely to support green ash trees. In this study, nearly all (97%) green ash trees recorded in variable radius plots were dead while the majority (75%) of white ash trees were alive and persisting. Continued monitoring to evaluate white ash persistence in these sites would be useful to assess whether EAB populations may eventually kill most of these trees, or if an equilibrium will eventually be reached with EAB functioning as a secondary pest, affecting primarily stressed and low vigor trees.

Green ash presence along roads was an important variable in most of the models. Clark et al. (2015) reported ash trees growing along riparian zones are at high relative risk of EAB induced mortality. In this study, my focus was on ash trees growing within a forested stand or along roads. While the area of railroads and streams within the area bounded by the 1.5 km radius was low in all sites, these linear corridors may be of importance if their presence was more abundant in the areas I studied. While we did not test for these variables in the models, they should not be excluded as potential variables in future models. Assessing ash abundance and condition along different types of corridors could yield more information about potential effects of streams, roads, or other linear corridors on ash survival.

Past studies in sites with a mix of urban, residential, and wooded areas showed EAB preferentially colonized open-grown ash trees exposed to sun compared to shaded trees (Siegert et al. 2010). The proportion of open area that was present in three of the five models was not of high importance. In the future, plots should be established in open areas based on the acreage of each, as I selected variable radius plot locations. Ash trees in open-grown areas could assist in the dispersal of EAB between forested areas where white ash are present. While the proportion of area classed as open was an important variable in multiple models, surveying ash trees growing in these open areas would give a better representation of the influence open-grown ash trees potentially have on white ash survival.

Ash trees along roads were abundant in all 28 sites. Most of these trees were growing in full sunlight, which is preferred by EAB (McCullough et al. 2009*a*, 2009*b*). Both white ash and green ash trees are prolific seed producers, contributing to their abundance along roads (NRCS 2017, Gucker 2005, Griffith 1991). This data was valuable in determining whether the density, size, and condition of white ash and green ash trees growing in the near proximity of abundant white ash trees influence their survival. The abundance of ash trees along roads resulted in a representation of the influence this corridor, and the density of roadside ash has on white ash survival. Like ash trees present in open areas, roadside ash could also promote EAB dispersal between forested areas.

Variables related to site nutrition were strongly related to white ash health in a study conducted by Knight et al. (2012). Soil moisture is an important factor in the distribution of white ash (NRCS 2017, Griffith 1991). White ash trees grow best on moderately well drained soils where roots can penetrate to a depth of 40 cm or more (NRCS 2017, Hosie 1969). Green ash trees grow best on fertile, moist, well-drained soils, and are most commonly found along rivers and streams and on land subject to flooding for as long as 40% of the growing season (NRCS 2017, Boerner and Brinkman 1996). Stress can alter volatiles emitted by ash trees, increasing their attraction to EAB adults (Rodriguez-Saona et al. 2006, McCullough et al. 2009*a*, 2009*b*, Chen and Poland 2009). If green ash trees experienced poorer growing conditions than white ash trees, survival rates could reflect EAB attraction to stressed versus healthier trees. This should be tested in future modeling approaches. While the majority (97%) of green ash trees were dead across the sites, I cannot state whether that is due to site-level variables, genetics, or a combination of the two based on the results from this study.

Although many site-level variables were tested in the models, model uncertainty was high as evidenced by the many competing models at each scale (Burnham and Anderson 2002). By averaging the covariate data collected and extracted at the different scales, I condensed the available information to enable these variables to be tested in models of white ash survival. Because of the high model uncertainty, however, whether or not the mean representations of these variables accurately reflect components of the true process of white ash survival requires further inquiry. The spatial distribution of a measured environmental variable will certainly affect whether a mean value adequately represents the factor in a model. For example, taking the average of data points collected across space may be a defensible solution if the variable is homogeneously distributed. But it is difficult to determine whether this is true in all cases; further investigation of the variables found in competing models of this study is necessary to determine which variables may actually be affecting white survival and at what scale. Rather than averaging data across areas bounded by different radii, extracting and analyzing data at the plot-level could influence, and potentially lead to, greater confidence in my results. This data would be more fine-scale, focusing on where they are both measured and where white ash trees are present. This might provide a larger sample size to analyze, and remove some of the observational uncertainty that comes with representing variables by the mean value, or other transformations.

High rates of white ash survival could result from infrequently occurring phenotypes that cause the trees to be less preferred or more resilient to EAB attack (Knight et al. 2012, Marshall et al. 2013). Knight et al. (2014) defined "lingering ash" as an individual tree that is alive in areas where more than 98% of the ash trees have been killed by EAB (Knight et al. 2014, Marshall et al. 2010). Bioassays suggest multiple aspects of the host-insect interaction are important for increased resistance to EAB (Koch et al. 2015). In my study, white ash tree populations were abundant within sites, therefore, they are not "lingering ash". Including these abundant white ash tree populations in selection and breeding programs could potentially assist in determining what drives resistance to EAB to eventually yield resistant ash hybrids or cultivars.

Results from this study are useful in identifying variables that could be considered in future models to understand the driving factors of this unexpected white ash survival. Based on my findings, it is important to consider land use type and the presence of green ash in models to predict white ash survival. Understanding why white ash survives EAB in some sites but not in other sites could have management implications. Ideally, resource managers could prioritize harvest of white ash trees in areas that are projected to be vulnerable to EAB infestation, and leave white ash that are unlikely to be killed, allowing white ash to persist as a functional component within forest systems.

APPENDIX

APPENDIX

Table 3.1. Average (± SE) proportion of area classified as forested, open area, or woody wetlands within the 1.5 km radius (706.8 ha) of the 28 sites located in southeast and south central Michigan separated into high survival (≥ 85%), moderate survival (> 60.0% to ≤ 84.0%), or low survival (≤ 60%) survival sites based on proportion of white ash stems live at the center of the sites in 2016.

	Forested area	**Open area**	**Woody wetland**
High survival sites (N = 7)			
Average proportion ha ± SE	0.34 ± 0.11	0.30 ± 0.04	0.12 ± 0.03
Min, max	0.08, 0.93	0.14, 0.44	0.01, 0.27
Moderate survival sites (N = 12)			
Average proportion ha ± SE	0.37 ± 0.05	0.25 ± 0.03	0.12 ± 0.02
Min, max	0.05, 0.62	0.01, 0.56	0.03, 0.23
Low Survival sites (N = 9)			
Average proportion ha ± SE	0.39 ± 0.07	0.24 ± 0.02	0.19 ± 0.03
Min, max	0.03, 0.67	0.02, 0.34	0.04, 0.30

Table 3.2. Competing models with a delta AICc < 1.0 for variables recorded across all four areas bounded by 400 m, 800 m, 1200 m, 1500 m, and cross-scale models. [1]Full-model averaging results from the cross-scale model.

Competing models

Variables	**df**	**logLik**	**AICc**	**delta**	**weight**
Average DBH of green ash along roads + green ash road density + proportion open land + white ash road density	6	10.79	-8.79	0.00	0.04
Average DBH of green ash along roads + green ash road density + proportion open land + white ash road density + proportion woody wetlands	7	11.84	-8.61	0.18	0.03
Average DBH of green ash along roads + green ash road density + average DBH of white ash + white ash road density + proportion woody wetlands	7	11.75	-8.43	0.36	0.03
Average DBH of green ash along roads + proportion open land + white ash road density	5	9.38	-8.19	0.60	0.03
Average DBH of green ash along roads + green ash road density + proportion open land + average DBH of white ash + white ash road density + proportion woody wetlands	8	12.79	-8.19	0.60	0.03
Average DBH of green ash along roads + green ash road density + proportion open land + average DBH of white ash + white ash road density	7	11.62	-8.16	0.62	0.03
Average DBH of green ash along roads + green ash road density + proportion of forested land + average DBH of white ash + white ash road density + proportion woody wetlands	8	12.75	-8.11	0.68	0.03
Average DBH of green ash along roads + green ash road density + proportion of forested land + white ash road density + proportion woody wetlands	7	11.56	-8.04	0.75	0.02
Average DBH of green ash along roads + green ash road density + white ash road density + proportion woody wetlands	6	10.37	-7.94	0.85	0.02
Average DBH of green ash along roads + proportion of open land + white ash road density + proportion woody wetlands	6	10.35	-7.91	0.88	0.02
Average DBH of green ash along roads + green ash road density + proportion of open land + proportion of forested land + white ash road density	7	11.47	-7.87	0.92	0.02

Table 3.2 (cont'd)

Average DBH of green ash along roads + proportion of forested land + average DBH of white ash + white ash road density	6	10.32	-7.84	0.92	0.02
Average DBH of green ash along roads + green ash road density + proportion of open land + proportion of forested land + white ash road density + proportion of woody wetlands	8	12.59	-7.78	1.00	0.02
Average DBH of green ash along roads + proportion of forested land + average DBH of white ash + white ash road density + proportion of woody wetlands	7	11.43	-7.78	1.01	0.02
Green ash road density + proportion of open land + white ash road density	5	9.15	-7.73	1.06	0.02
Green ash road density + proportion of forested land + white ash road density + proportion of woody wetlands	6	10.22	-7.64	1.15	0.02
Green ash road density + proportion of open land + proportion of forested land + white ash road density	6	10.22	-7.64	1.15	0.02
Green ash road density + proportion of open land + proportion of forested land + white ash road density + proportion of woody wetlands	7	11.31	-7.55	1.24	0.02
Green ash road density + proportion of open land + white ash road density + proportion of woody wetlands	6	10.15	-7.51	1.28	0.02
Green ash road density + proportion of forested land + average DBH of white ash + white ash road density + proportion of woody wetlands	7	11.24	-7.40	1.38	0.02
Average DBH of green ash along roads + average DBH of white ash + white ash road density + proportion of woody wetlands	6	10.10	-7.39	1.40	0.02
Average DBH of green ash along roads + green ash road density + average DBH of white ash + white ash road density	6	10.09	-7.39	1.40	0.02
Average DBH of green ash along roads + green ash road density + proportion of open land + proportion of forested land + average DBH of white ash + white ash road density + proportion of woody wetlands	9	13.47	-7.17	1.61	0.02
Average DBH of green ash along roads + green ash road density + proportion of forested land + white ash road density	6	9.98	-7.15	1.63	0.02

Table 3.2 (cont'd)

Average DBH of green ash along roads + green ash road density + proportion of forested land + average DBH of white ash + white ash road density	7	11.09	-7.11	1.68	0.02
Average DBH of green ash along roads + green ash road density + proportion of open land + proportion of forested land + average DBH of white ash + white ash road density	8	12.23	-7.07	1.72	0.02
Average DBH of green ash along roads + green ash road density + white ash road density	5	8.80	-7.03	1.75	0.02
Green ash road density + proportion of open land + average DBH of white ash + white ash road density	6	9.82	-6.85	1.94	0.02
Average DBH of green ash along roads + proportion of open land + average DBH of white ash	5	8.69	-6.82	1.97	0.01

Parameters of predictors[1]

Variables	**Estimate**	**Std. Error**	**Adjusted SE**	**z value**
Intercept	0.745	0.080	0.080	9.324
Average DBH of green ash along roads	-0.003	0.003	0.003	1.200
Green ash road density	-0.7e-03	0.7e-03	0.7e-03	1.132
Proportion of open land	0.173	0.174	0.176	0.987
White ash road density	0.002	0.9e-03	0.9e-03	1.668
Proportion of woody wetlands	-0.153	0.199	0.200	0.764
Average DBH of white ash	0.001	0.002	0.002	0.685
Proportion of forested land	-0.049	0.095	0.096	0.511
Average DBH of green ash	-0.3e-04	0.3e-03	0.3e-03	0.098
Average DBH of white ash along roads	-0.2e-04	0.5e-03	0.6e-03	0.039

[1] Parameters were derived from full-model averaging. This approach is recommended by Burnham and Anderson (2002) when high model uncertainty exists, where each averaged parameter estimate is weighted to reduce the influence of variables with low Akaike parameter weights (w_i).

Table 3.3. Competing models and parameters calculated for variables and used to predict percent white ash survival (delta AICc < 2.0) in the center of areas bounded by a 400 m radius in 28 sites in southeast and south central Michigan. [1]Full-model averaging results from the 0 to 400 m model.

Competing Models

Predictors	df	logLik	AICc	delta	weight
Intercept	2	0.68	3.12	0.00	0.30
Average DBH of white ash along roads	3	1.30	4.40	1.28	0.16
Proportion of woody wetlands	3	1.02	4.96	1.84	0.12
Average DBH of green ash	3	1.01	4.98	1.86	0.12
Green ash road density	3	0.95	5.10	1.98	0.11

Parameters of Predictors[1]

Variables	Estimate	Std. Error	Adjusted SE	z value
Intercept	0.703	0.072	0.075	9.361
Average DBH of white ash along roads	0.9e-03	0.003	0.002	0.297
Proportion of woody wetlands	-0.027	0.123	0.127	0.213
Average DBH of green ash	0.3e-03	0.001	0.001	0.211
Green ash road density	-0.2e-02	0.001	0.001	0.191
Average DBH of white ash	0.3e-02	0.001	0.001	0.183
Proportion of forested land	-0.004	0.059	0.062	0.062

[1] Parameters were derived from full-model averaging. This approach is recommended by Burnham and Anderson (2002) when high model uncertainty exists, where each averaged parameter estimate is weighted to reduce the influence of variables with low Akaike parameter weights (w_i).

Table 3.4. Competing models and parameters calculated for variables and used to predict percent white ash survival (delta AICc < 2.0) in the center of areas bounded by an 800 m radius in 28 sites in southeast and south central Michigan. [1]Full-model averaging results from the 400 to 800 m model.

Competing models

Predictors	df	logLik	AICc	delta	weight
Average DBH of green ash along roads + white ash road density	4	5.45	-1.16	0.00	0.36
Average DBH of green ash along roads + green ash road density + white ash road density	5	6.33	0.07	1.23	0.19

Parameters of predictors[1]

Variables	Estimate	Std. Error	Adjusted SE	z value
Intercept	9.396e-01	1.323e-01	1.390e-01	6.758
Average DBH of green ash along roads	-1.603e-02	6.650e-03	6.974e-03	2.299
White ash road density	7.597e-03	4.470e-03	4.626e-03	1.642
Green ash road density	1.279e-03	3.516e-03	3.600e-03	0.355
Average DBH of white ash along roads	1.442e-04	1.085e-03	1.133e-03	0.127
Proportion of forested land	-8.631e-03	6.911e-02	7.221e-02	0.120
Average DBH of green ash	9.139e-05	9.147e-04	9.582e-04	0.095
Average DBH of white ash along roads	4.197e-05	1.554e-03	1.636e-03	0.026

[1] Parameters were derived from full-model averaging. This approach is recommended by Burnham and Anderson (2002) when high model uncertainty exists, where each averaged parameter estimate is weighted to reduce the influence of variables with low Akaike parameter weights (w_i).

Table 3.5. Competing models and parameters calculated for variables and used to predict percent white ash survival (delta AICc < 2.0) in the center of areas bounded by a 1200 m radius in 28 sites in southeast and south central Michigan. [1]Full-model averaging results from the 800 to 1200 m model.

Competing models

Variables	**df**	**logLik**	**AICc**	**delta**	**weight**
Average DBH of green ash + green ash road density + proportion of forested land	5	5.03	2.67	0.00	0.05
Average DBH of green ash + proportion of open land	4	3.51	2.72	0.04	0.05
Average DBH of green ash + proportion of open land + average DBH of white ash along roads	5	4.93	2.86	0.19	0.04
Green ash road density + proportion of woody wetlands	4	3.33	3.08	0.40	0.04
Average DBH of green ash	3	1.94	3.11	0.44	0.04
Intercept	2	0.68	3.12	0.45	0.04
Average DBH of green ash + green ash road density + proportion of forested land + average DBH of white ash along roads	6	6.39	3.22	0.55	0.04
Average DBH of green ash + green ash road	4	3.25	3.23	0.56	0.04
Green ash road density	3	1.82	3.36	0.69	0.03
Proportion of woody wetlands	3	1.59	3.81	1.14	0.03
Proportion of open land	3	1.58	3.84	1.16	0.03
Green ash road density + proportion of forested land	4	2.87	4.00	1.32	0.02
Average DBH of white ash	3	1.37	4.26	1.59	0.02
Average DBH of green ash + green ash road density + proportion of open land + average DBH of white ash along roads	6	5.87	4.26	1.59	0.02
Average DBH of green ash + green ash road density + proportion of open land	5	4.23	4.27	1.59	0.02
Average DBH of green ash + green ash road + average DBH of white ash along roads	5	4.21	4.31	1.73	0.02
Average DBH of green ash + proportion of forested land	4	2.69	4.35	1.68	0.02
Average DBH of green ash + Average DBH of green ash along roads	4	2.67	4.41	1.73	0.02
Average DBH of green ash + green ash road density + proportion of woody wetlands	5	4.13	4.46	1.79	0.02

Table 3.5 (cont'd)

Average DBH of green ash along roads	3	1.26	4.47	1.8	0.02
Average DBH of green ash + proportion of open land, average DBH of white ash + average DBH of white ash along roads	6	5.68	4.63	1.96	0.02
Average DBH of green ash + average DBH of white ash	4	2.55	4.64	1.97	0.02
Average DBH of green ash + average DBH of white ash along roads	4	2.55	4.65	1.97	0.02

Parameters of predictors[1]

Variable	**Estimate**	**Std. Error**	**Adjusted SE**	**z value**
Intercept	0.755	0.151	0.154	4.885
Average DBH of green ash	-0.002	0.003	0.003	0.916
Green ash road density	-0.5e-03	0.7e-03	0.7e-03	0.723
Proportion of forested land	-0.096	0.217	0.221	0.434
Proportion of open land	0.161	0.294	0.300	0.536
Average DBH of white ash along roads	0.002	0.004	0.004	0.423
Proportion of woody wetlands	-0.164	0.441	0.450	0.364
Average DBH of white ash	0.7e-03	0.003	0.003	0.284
Average DBH of green ash along roads	-0.4e-03	0.002	0.002	0.211

[1] Parameters were derived from full-model averaging. This approach is recommended by Burnham and Anderson (2002) when high model uncertainty exists, where each averaged parameter estimate is weighted to reduce the influence of variables with low Akaike parameter weights (w_i).

Table 3.6. Competing models and parameters calculated for variables and used to predict percent white ash survival (delta AICc < 2.0) in the center of areas bounded by a 1500 m radius in 28 sites in southeast and south central Michigan. [1]Full-model averaging results from my 1200 to 1500 m model.

Competing models

Variables	**df**	**logLik**	**AICc**	**delta**	**weight**
Green ash road density + proportion of woody wetlands	4	6.54	-3.34	0	0.36
Green ash road density + average DBH of white ash + proportion of woody wetlands	5	7.23	-1.73	1.61	0.16

Parameters of predictors[1]

Variables	**Estimate**	**Std. Error**	**Adjusted SE**	**z value**
Intercept	9.013e-01	8.674e-02	9.095e-02	9.911
Green ash road density	-5.417e-03	2.285e-03	2.404e-03	2.253
Proportion of woody wetlands	-1.241e+00	5.011e-03	5.273e-01	2.353
Average DBH of white ash	5.408e-04	1.737e-03	1.783e-03	0.303
Average DBH of white ash along roads	-4.050e-04	1.810e-03	1.871e-03	0.217
Proportion of open land	1.922e-02	1.012e-01	1.049e-01	0.183
White ash road density	1.864e-04	1.956e-03	2.050e-03	0.091
Average DBH of green ash along roads	4.208e-05	1.079e-03	1.135e-03	0.037
Average DBH of green ash	-5.174e-06	9.253e-04	9.743e-04	0.005

[1] Parameters were derived from full-model averaging. This approach is recommended by Burnham and Anderson (2002) when high model uncertainty exists, where each averaged parameter estimate is weighted to reduce the influence of variables with low Akaike parameter weights (w_i).

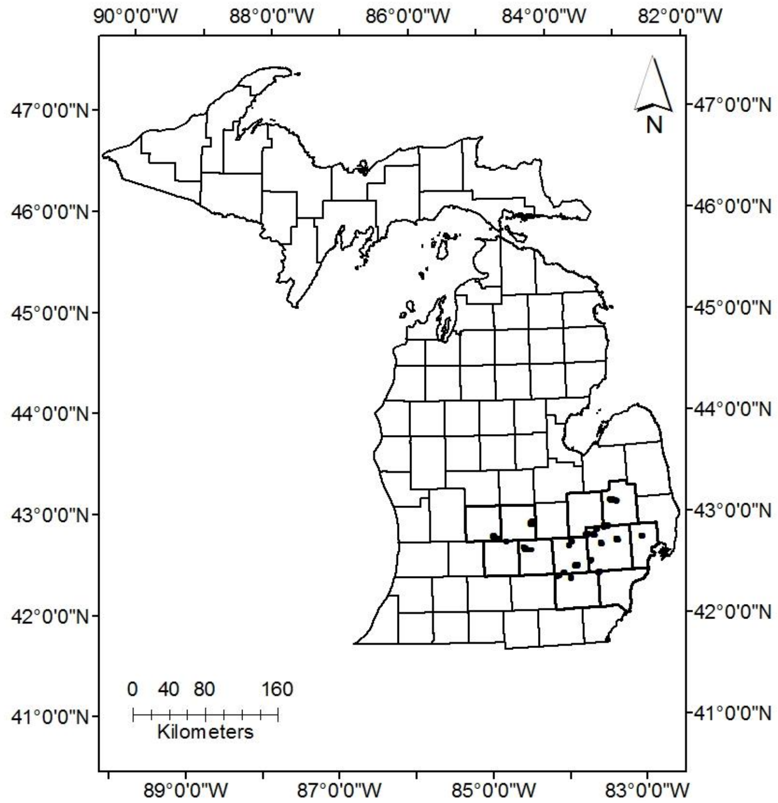


Figure 3.1. Location of 28 white ash sites in southeast and south central Michigan.

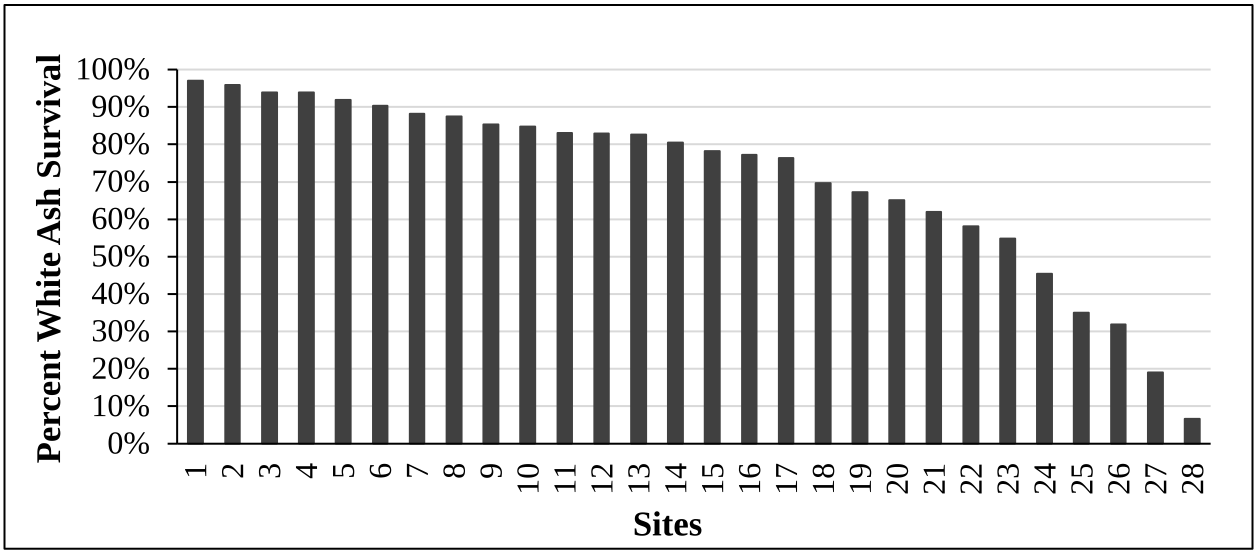


Figure 3.2. Percentage of live and dead white ash stems alive in 28 sites surveyed in southeast Michigan in 2016.

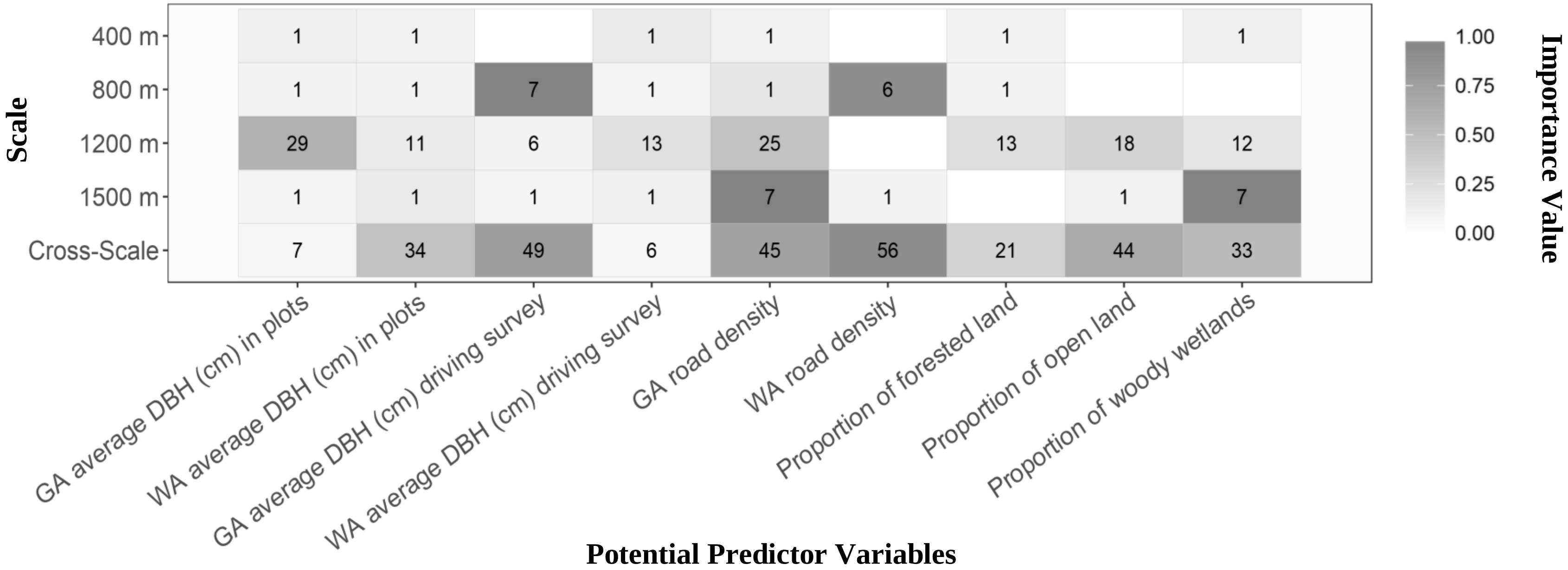


Figure 3.3: The relative variable importance for models developed to predict white ash survival rates in areas bounded by 400 m, 800 m, 1200 m, 1500 m, and cross-scale models. Radii and the cross-scale model for the entire 7.1 km^2 area bounded by the 1.5 km radius. Variables with a relative variable importance of 1.00 are of high importance in predicting white ash survival rate.

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