1-1-2016

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Recommended Citation

Spei, Benjamin Adam, "An Analysis Of Blue Ash (fraxinus Quadrangulata) Regeneration In Southeastern Michigan In The Presence Of Emerald Ash Borer (agrilus Planipennis)" (2016). *Wayne State University Theses*. 477.
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AN ANALYSIS OF BLUE ASH (*FRAXINUS QUADRANGULATA)* REGENERATION IN SOUTHEASTERN MICHIGAN IN THE PRESENCE OF EMERALD ASH BORER (*AGRILUS PLANIPENNIS)*

by

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THESIS

submitted to the Graduate School

of Wayne State University,

Detroit, Michigan

in partial fulfillment of the requirements

for the degree of

MASTER OF SCIENCE

2016

MAJOR: BIOLOGICAL SCIENCES

Approved by:

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Advisor Date

DEDICATION

I dedicate this thesis to my family and friends, without whom I never would have begun nor finished my graduate studies.

ACKNOWLEDGEMENTS

I would like to thank my advisor and mentor Dr. Dan Kashian for his patience and support while helping me through every step of this process and for teaching me that hard work can be enjoyable when in good company. Additionally, I'd like to thank my committee, Dr. Donna Kashian for allowing me into her lab during my undergraduate studies and spurring my interest in ecology; and Dr. Tom Dowling for teaching me during my courses with him to not be too cynical when reading articles about climate change and habitat loss. Also, I'd like to thank Doug Putt and Jenna Merlo for their tireless work in the field, never once complaining about the sometimes brutal conditions of stinging bugs and plants, sweltering heat and thunderstorms. Finally, I would like to thank my lab mates, Maggie Tucker and Bill Dodge for talking me through ideas, statistics and gripes.

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Introduction

Species resistance is defined as the ability of a population to avoid displacement from initial measures (numbers, biomass, energy content, etc.) following biotic and abiotic disturbances (Harrison 1979). A great deal of research in terrestrial systems has focused on the resistance of plant species to phytophagous insects (Raffa and Berryman 1983; Simms and Rausher 1989; Marquis and Alexander 1992; Strauss and Agrawal 2007) and the increasing threat of invasive species (Byers and Noonburg 2003; Dunstan and Johnson 2006; Melbourne et. al 2007). Empirical evidence suggests that resistance to herbivory and plant-pathogen interactions is hereditary (Simms 1993; Schmid 1994; Montarry et. al 2006) and driven by selective pressures placed upon the host by the invasive herbivore. Variation is thus necessary for a continued coexistence of host and pathogen. Equally important to host species persistence in the presence of a new invader, however, is the ability of the host species to regenerate even while its populations are negatively impacted by the invader.

To persist, host tree species must regenerate and recruit to replace the susceptible adult cohort with new reproductively active adults capable of producing seed (Greene 1999; McEuen and Curran 2004). Both asexual and sexual regeneration are common and important in post-disturbance tree species persistence (Plotkin et al. 2013). Regeneration from seed may occur from immediate germination of viable seeds produced annually, dormant seed banks in the soil (Bakker et. al 1996), and slow-growing seedlings in the understory that established prior to (advanced regeneration) and after disturbance (Greene 1999). Dormant seed banks in the soil and seedlings in the understory provide a source of genetic variation and may buffer long periods of poor seed production (Levin 1989; Leckie 2000). Presence of a seed source and post-disturbance regeneration does not ensure replacement of canopy trees of the same species (McEuen and Curran 2004) because the new cohort will be subject to varying levels of competition depending on forest community composition, densities and demographics, and its response to changing site factors such as light, water and nutrient availability (Thompson 1993; Peterson and Carson 1996). Disturbances by phytophagous insects may produce a range of these conditions during and following attacks depending on host density, composition and mortality rates (Ghandi and Herms 2010). Thus, successful post-invasion regeneration depends heavily on advanced regeneration and post-disturbance seed rain (Greene et al. 1999).

Emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) is an invasive, phloem-feeding beetle native to Asia discovered in southeastern Michigan in 2002 (Cappaert et. al 2005). Based on dendrochronological evidence, EAB became established in southeastern Michigan in the early 1990s, with initial ash mortality occurring in 1997 (Siegert et al. 2007; 2014). Emerald ash borer attacks all native North American species of the ash genus (*Fraxinus spp.)*, often within two to five years of exhibiting symptoms of infestation (Knight et al. 2010; 2012). Within its native range of northeastern China, Korea, and eastern Russia, EAB primarily attacks stressed or dying ash trees (Haack et al. 2002; Liu et al. 2003). In North America, however, even healthy ash trees with a diameter at breast height (DBH) $\geq$ 1 cm are susceptible to exploitation by EAB (Wagner and Todd 2015). Since its introduction, EAB has killed millions of ash trees and projected economic costs of removal and replacement of dead ash trees is in the billions (Herms and McCullough 2014). Current and past management attempts to stop or slow the rate of spreading infestations and ameliorate their negative impacts have been unsuccessful, and the range of EAB continues to grow annually. Since the initial infestations in Michigan, EAB infestations have been confirmed in 26 states and 2 Canadian provinces (www.emeraldashborer.info 2016.).

In southeastern Michigan and northwestern Ohio, where EAB has had the longest residence time in North America, ash species such as white ash (*F. americana* L.), black ash (*F. nigra* Marsh.), and green ash (*F. pennsylvanica* Marsh.) have documented mortality rates of up to 99% within mixed deciduous forests (Kashian and Witter 2011; Klooster et al. 2014). Some researchers have proposed that such high mortality rates have nearly eliminated the seed source for these affected ash species, resulting in a depleted seed bank and thus a loss of potential regeneration (Kashian and Witter 2011; Knight et al. 2012). Declining advanced regeneration and post-EAB regeneration have also been reported (Kashian and Witter 2011; Klooster et al. 2014), and many researchers have suggested that ash species are likely to be extirpated as important canopy trees in eastern North American hardwood forests as EAB continues to spread.

The much rarer blue ash (*F. quadrangulata* Michx.) exhibits much lower EAB infestation rates (Anulewicz et al. 2007) and observed mortality rates between 20% and 40% (Tanis et al. 2012). Unfortunately, little is known about the regeneration ecology of blue ash, information necessary to predict its persistence in the presence of EAB. Southern Michigan marks the northern limit of blue ash distribution, which ranges south into Alabama, east into West Virginia, and west into Oklahoma and Kansas (Prasad 2007). Barnes and Wagner (2004) describe blue ash as slow-growing, shade tolerant, and preferring wet-mesic to mesic sites on fine-textured soils in southern Michigan. It is typically associated with black maple (*Acer nigrum* F. Michx.), sugar maple (*A. saccharum* Marsh.), white ash, bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch) and American elm (*Ulmus americana* L.) in all height classes. Black and sugar maple in particular are very strong competitors following small gap-forming disturbances (Canham 1988; Lei and Lechowicz 1998). If blue ash is not outcompeted in the understory by its associate species, then there is potential for canopy replacement at least in part by blue ash following EAB infestations.

Given these results, more information on the regeneration ecology of blue ash is critical for management of ash species. In particular, the role of life history differences among species may impact vulnerability to EAB, requiring a species-by-species assessment of impact as the range of EAB continues to expand. Blue ash persistence may provide a baseline for ash mortality and regeneration levels upon which future stressors of native ecosystems can be compared.

To study and document the regeneration ecology of blue ash, I asked the following three questions:

1. *What is the current condition of blue ash in the presence of EAB?*

Based largely on the literature, I hypothesized that blue ash currently persists as a dominant overstory species despite the reduction in health caused by EAB. I expected to find blue ash age and size class distributions to be more even across all sites than white ash (see *Methods*), with its mode and mean occurring at higher values than white ash. I also expected to find the average mortality rates of blue ash to be significantly lower than those observed for white ash across all sites.

2. *What is the regenerative capacity of blue ash relative to its associated species?*

Based on initial field observations, I expected to find blue ash seedling and sapling densities equal to or greater than all of its associated species within blue ash-dominated stands at all size classes. I expected annual growth rates of blue ash to be similar to those of white ash, but greater than those of its associated species within blue ash stands.

3. *Given the first two questions, what is the potential for blue ash to persist in the presence of EAB?*

I hypothesized that blue ash has the potential to persist as an important canopy species within its range in North American forests even in the presence of EAB. I expected blue ash to persist with a truncated life span and overall reduction in overstory density and diameter, but with regeneration and recruitment levels that are capable to eventually replace canopy mortality.

Methods

Study Area

I sampled a total of 18 blue ash stands at 6 sites in southeastern Michigan near the epicenter of the EAB introduction point (Figure 1). There are no blue ash stands in southeastern Michigan that have been unaffected by EAB and thus a proper blue ash control stand could not be established. For this reason, I also sampled 18 white ash stands across the 6 sites for reference. I chose white ash as a reference species because it was determined during preliminary field work to be the most commonly occurring associate ash species, and because much of the research describing ash resistance and regeneration associated with EAB has focused on white ash (Hausman et al. 2010; Kashian and Witter 2011; Palla and Pijut 2011; Klooster et al. 2014). White ash thus served as a base comparison for EAB susceptibility.

LaFurge Woods Nature Preserve (LaFurge), Lower Huron Metropark (Lower Huron), and Kosch Headwaters Preserve (Kosch) were sampled during July and August 2014. Conant Farm in Salem Township (Conant), Eberwhite Woods in Ann Arbor (Eberwhite Woods) and Portland State Game Area (Portland) were sampled the following July and August in 2015. The Conant Farm site is on privately owned property currently being managed for historic and ecological restoration; all other sites were on State, County, or municipal property designated for public use as park or gaming recreation areas. Blue ash was found growing most often on mesic to wet-mesic sites with clay-rich, dense soils on river banks or near streams or swamps. Three of the 18 stands occurred on well-drained upland areas with sandy-clay textured soils, with one stand at each of Eberwhite Woods, Lower Huron, and Kosch.

Stand Selection

All sites included at least a 0.1-ha area where blue ash dominated the overstory and represented > 50% of the basal area (50% relative density determined from DBH). Each site was sampled using three 10 x 30 m (300 m^2) plots placed randomly within each stand. Three stands at each site that are currently or were, prior to EAB, dominated by white ash were also sampled using the same methods as those used for the blue ash stands.

Current condition of blue ash

Current stand density was determined by counting stems of all living trees $\geq$ 1.5 cm DBH (0.5 cm larger than minimum size for EAB exploitation; Wagner and Todd 2015). All overstory (> 9.0 cm DBH) were measured and counted, and all understory trees (1.5 - 9.0 cm DBH) were grouped into 1-inch (1.5 - 4.0 cm DBH), 2-inch (4.1 - 6.6 cm), and 3-inch (6.7 - 9.0 cm) size classes for analysis. Tree age of overstory blue ash and white ash was estimated from increment cores sampled 30 cm above the ground. Prior to aging, increment cores were mounted and sanded per standard techniques (Speer 2010), and annual rings were counted and measured under a dissecting microscope. Presence of EAB was determined and evaluated using identification of external symptoms (EAB exit holes, epicormic sprouting, bark splitting, and/or woodpecker damage; Smith 2006). Crown condition for all living ash was rated by severity using standard techniques for assessing progressive degrees of ash health on a categorical scale of 1 – 5, where 1 is a healthy canopy and 5 is a dead tree (Smith 2006). All trees > 9.0 cm DBH killed by EAB were identified using the presence of EAB galleries (larvae tracks in phloem) and/or exit holes in bark of standing and fallen dead trees. Post-EAB mortality levels were estimated for blue and white ash by comparing current and pre-EAB densities of ash for each site, and pre-EAB stand density was reconstructed by combining living trees with dead trees determined to have been killed by EAB.

Differences in live/dead ratios between white and blue ash stands at each site were compared using Fisher's exact test and across all sites using hierarchical log-linear analysis to examine potential interaction between site and species. All statistical analyses were conducted using IBM SPSS statistics version 23 (IBM Corp 2015). Fallen trees that lacked evidence of EAB-caused mortality were considered to pre-date EAB infestation and were not used in calculations.

Crown conditions were compared among size classes using a Spearman rank correlation test to determine whether infestation rates varied with size. Spearman rank scores for each species were checked for significance using Fisher's Z test. Frequency distributions of crown condition class ratings for overstory blue ash and white ash were compared using skewness and kurtosis for assessment of histogram asymmetry and tested for significance using a Mann-Whitney U rank test for ordinal data.

The central tendency of living overstory trees was calculated using the quadratic mean diameter (Qm) across all plots for each site ($\sqrt{\frac{\sum D^2}{n}}$). Qm has a more direct relationship to basal area than the arithmetic mean diameter and assigns greater weight to larger trees in a forest stand (Curtis and Marshall 2000). Qm was not normalized and thus compared between white and blue ash stands across all sites using a non-parametric Mann-Whitney U test.

Mean age of overstory trees across all sites for white and blue ash was assessed for normality using the Shapiro-Wilk test and residual plots, and was compared between white and blue ash using Welch's t-test due to unequal variances (Welch 1938). Welch's t-test was chosen because sample sizes did not differ greatly (N=60 white, N=67 blue) and because the variable with the higher variance (blue ash) also had the higher sample size (Zar 1999). When compared at each site independently, difference in mean age was tested for significance using a non-parametric Mann-Whitney U test due to small sample sizes.

Regenerative capacity of blue ash relative to other tree species

Each 300 m^2 plot was subdivided into three 5 x 10 m (50 m^2) subplots established perpendicular to the long axis of the main plot. Within each subplot, all tree seedlings and saplings (< 1.5 cm DBH or shorter than breast height) were identified by species and recorded; non-ash tree species counted were pooled into a single category. Seedling and sapling densities were tallied by height classes per Kashian and Witter (2011): < 0.5 m, 0.5 - 1.0 m, and > 1.0 m tall. Ash seedlings in all height classes were characterized as advanced regeneration (established prior to EAB) or new seedlings (establishing post-EAB) by counting axillary bud scars (Kashian *in press*) and comparing to time since EAB infestation estimates presented by Prasad et al. (2010). Moreover, ash seedlings < 3 years old were tallied separately.

Five-year growth rates for seedlings and saplings for each size class were recorded by measuring the distance between axillary bud scars for white ash, blue ash and other species growing within blue ash stands. Differences between mean growth rates were used to determine the probability of blue ash being outcompeted or outcompeting its associated species.

Belt transects 1 x 10 m long were run perpendicular to a long axis of each plot (plot line chosen by coin flip) and all seedlings and saplings growing within the belt were measured. A new belt was run at 2-m intervals along the plot axis until 10 of each species (blue ash, white ash, other spp.) within each size class were measured. If 10 individuals of each species for each size class could not be found on the first randomly chosen long axis, then the method was repeated on the opposite length (Figure 2).

Light readings were recorded for each plot using a LI-250 light meter with a Li-190SA quantum sensor attached (Li-COR, Inc., Nebraska-USA). Light readings were taken between the hours of 12 p.m. and 2 p.m. during similar weather conditions (overcast) one meter above the ground from a flat surface. Three readings were recorded at each corner of each blue ash plot located at the outer edge and midpoint of each growth rate sampling area. These readings were then averaged for each plot at each site.

Seedling and sapling densities were computed as stems per hectare prior to statistical analysis and could not be normalized. Seedling and sapling densities were averaged for blue ash, white ash, and other species (independent variables) in each size class for each site and compared using the non-parametric Kruskal-Wallis test to assess whether differences in establishment with change in EAB overstory resistance (dependent variables) were significant. White ash seedling densities within the white ash stands were compared to its most abundant associate species using the non-parametric Mann-Whitney U test. The ratio of pre-EAB to post-EAB seedlings and saplings in each size class were compared between white and blue ash both within the blue ash stands and between the blue and white stands using a Chi-square test for independence to analyze relative establishment and recruitment. Densities of seedlings < 3 yrs old were averaged for each site and compared between white and blue ash using a non-parametric Mann-Whitney U test.

Growth rates were transformed using either a logarithmic or square root transformation to correct for normality and heteroscedasticity. The $\log_{10}(X+1)$ and $\sqrt[2]{X + 0.05}$ equations were used for transformations because many of the recorded values were between 0 and 1 making these forms of the equations more appropriate (Zar 1999). Growth rates for each species at each size class (independent variables) were compared between species with a repeated-measures analysis of variance (ANOVA) using a mixed linear model with plots (random independent variable) nested within site (fixed independent variable) and light readings applied as a covariate using an unstructured covariate structure to check for significance of differences in growth rates (dependent variable). I chose an unstructured covariate structure to minimize bias because it does not make assumptions about the relationships between observations and because it gave the lowest values for Akaike's information criterion (AIC) and Hurvich and Tsai's criterion (AICC) (see *Results*). When growth rates were found to be significantly different, a least significance difference (LSD) multiple comparison was used to determine which means differed.

Results

Current condition of blue ash

Overstory white ash experienced higher EAB-caused mortality than blue ash at all sites (Figure 3). White ash overstory mortality ranged from 43.5% at Conant Farms to 83.3% at Eberwhite Woods, with an overall estimated mortality (all sites combined) of 56.1%. Blue ash mortality ranged from 7.1% at Portland to 31.6% at Conant Farm with an overall estimated mortality of 23% (Appendix 1). Blue ash mortality was consistently lower than that for white ash at all sites, and overall mortality differed significantly between white ash and blue ash ($p < 0.001$). The interaction between site and species and between site and mortality were not significant. Four of the six sites exhibited significantly different living and dead overstory stem ratios (Eberwhite Woods: $p = 0.005$, La Furge: $p = 0.001$, Lower Huron: $p = 0.037$, Portland: $p = 0.004$). Comparison of living stem densities of overstory trees between white ash and blue ash in their respective stands showed no consistent pattern and did not differ greatly when tallied across all sites.

The quadratic mean diameter (Qm) of surviving overstory trees was significantly larger for blue ash (30.6 cm) than white ash (15.6 cm) when compared across all sites ($U = 5.991$; $p < 0.001$). Blue ash Qm was larger than white ash at all sites and differed significantly at three sites, (Lafurge: $p = 0.0001$, Kosch: $p = 0.0001$ and Lower Huron: $p = 0.006$). Similarly, blue ash mean age (65 yrs) was more than double that of white ash (24 yrs), and the difference was significant when averaged across all sites ($t = 14.079$; $p < 0.001$). Mean age for blue ash ranged from 41 years (Conant Farm) to 75 years (Portland), and white ash mean age ranged from 19 years (Lower Huron) to 32 years (Eberwhite Woods) (Appendix 1). Blue ash was significantly older than white ash at all sites except Eberwhite Woods, which was more than likely due to an inadequate sample size for white ash at this site; only two living overstory white ash were present across all three stands sampled. Age distribution for blue ash followed a near perfect normal distribution ($W = .990$; $p = 0.869$) with minimal skewness (0.033, S.E. 0.295) and kurtosis (-0.309, S.E. 0.582). The white ash age distribution was normal at $\alpha = 0.05$ ($W = 0.962$; $p = 0.086$), but compared to blue ash was much more skewed (0.632, S.E. 0.327) with a tail extending towards higher age and kurtotic (2.113, S.E. 0.644) with most of the trees falling between 20 and 30 years old (Figure 4).

Much of the deviation of the white ash age distribution was due to one outlier tree at Eberwhite woods site estimated at 43 years. With the anomaly removed, the distribution was much more normal ($W = 0.986$; $p = 0.801$) with a severe reduction in skewness (-0.134, S.E. 0.330) adding more weight to the young trees, and kurtosis (0.056, S.E. 0.650).

Crown condition ratings were found to be positively correlated with size class for both blue ash ($\rho_s = 0.542$, $p < 0.001$) and white ash ($\rho_s = 0.341$, $p < 0.001$), such that larger crown ratings were associated with large-diameter (and thus older) trees. The correlation coefficient for blue ash was significantly greater than white ash ($Z = 2.72$, $p = 0.007$), meaning the correlation between tree size and crown dieback was stronger (i.e. more positive) for blue ash, with larger blue ash trees exhibiting higher levels of infestation and higher crown ratings than white ash for smaller size classes. Crown rating frequencies for overstory stems differed significantly between white and blue ash ($U = 3.407$; $p = 0.001$). White ash crown rating distribution was negatively skewed (-0.597, S.E. 0.291) and platykurtic (- 1.102, S.E. 0.574) with 64.7% of observed crown ratings > 3. Blue ash crown rating distribution followed a much more normal distribution with minimal skewness (.082, S.E. 0.279) and marginal kurtosis (-0.638, S.E. 0.552) with 31.2% of crown ratings > 3 (Figure 5).

Seedling and sapling densities and growth rates

Mean density for the < 0.5 m height class was by far the highest for non-ash species (35,833 stems/ha) and was lowest for white ash (604), but mean densities did not differ between species at any height class when averaged across all sites. Much of the error associated with non-ash species group was due to the Lafurge site, which was the only site with significant differences between average species densities ($H = 6.543$; $df = 2$, $N = 9$; $p = 0.033$). White ash and blue ash densities did not differ from each other, but both white and blue ash densities differed from non-ash species density. When Lafurge values were treated as an outlier and removed, the error dropped greatly with mean values of 2204 (± 882), 600 (± 363) and 1947 (± 634) stems/ha for blue ash, white ash and non-ash species respectively. Blue ash densities did not differ from white ash or non-ash densities, but white ash was significantly less dense than non-ash species ($p = 0.010$) (Figure 6a). Saplings 0.5 - 1.0 m or > 1 m tall did not differ between species. Mean density of new seedlings (< 3 yrs old) was greater for blue ash than white ash in their respective stands at all sites. Across all sites, mean densities differed significantly between blue ash (485 ± 104 stems/ha) and white ash (109 ± 47 stems/ha; $t = 3.289$; $p = 0.008$; Appendix 2).

White ash seedling densities within white ash stands occurred at higher average densities than within blue ash stands (Figure 6b). White ash seedling densities within white ash stands were higher than associated non-ash species at all height classes, and significantly higher for the 0.5-1 m height class ($p = 0.026$) and the > 1 m height class ($p = 0.002$). Blue ash seedlings were not present within any white ash dominated stand at any height class.

Mean growth rates for the < 0.5 m height class differed significantly between all species when averaged across all sites, with white ash having the fastest rate of growth (3.13 cm/yr; Appendix 3, Figure 7). The interaction between site and species was not significant. When compared at each site independently, blue ash mean growth rates for the < 0.5 m height class did not differ from or were significantly greater than non-ash species at all sites and did not differ from white ash at four of the six sites surveyed. Growth rates for blue ash were significantly less than those for white ash at Kosch (blue ash: 2.56 cm/yr, white ash: 3.29 cm/yr; $F = 3.931$; $p = 0.024$; Appendix 3) and Conant Farm (blue ash: 2.67 cm/yr; white ash: 36 cm/yr; $F = 4.551$; $p = 0.013$;

Appendix 3). Mean growth rates for the 0.5 - 1.0 m height class did not differ significantly between species across all sites (blue ash: 5.81 cm/yr; white ash: 5.86 cm/yr; Figure 7). The interaction between site and species was significant (F = 4.420; $p < 0.001$) which was likely due to variation in mean growth rates of non-ash species and white ash. When compared at each site independently, blue ash mean growth rate either did not differ from the species with the highest mean growth rate (5 sites) or had the highest mean growth rate (1 site) itself for the 0.5 – 1 m height class (Appendix 3, Figure 7).

Mean growth rates for saplings > 1 m differed between species (F = 12.725; $p < 0.001$), with blue ash (10.7 cm/yr) and white ash (10.8 cm/yr) differing from non-ash species (8.82 cm/yr) but not from each other (Figure 7) across all sites. There was a significant interaction between site and species ($p = 0.001$). When compared at each site, blue ash growth rates were greater than or equal to non-ash species but less than white ash growth rates with significant difference at one site, LaFurge, where mean growth rates were 7.54 and 10.55 cm/yr for blue ash and white ash respectively ($p = 0.022$; Appendix 3).

Ratios of pre-EAB to post-EAB seedlings did not differ significantly between species in their respective stands when pooled across all sites (Figure 8). The interaction between site, species and establishment was significant following a hierarchical log-linear analysis ($p < 0.001$), and analysis by site showed no discernable pattern (Appendix 1). Comparison of establishment ratios between blue and white ash seedlings growing within the same stands (blue ash stands) was also dependent on site with a significant interaction between site, species and establishment ($p < 0.001$); analysis by site was variable and showed no evident patterns.

Discussion

Blue ash mortality is far less than that of white ash at all sites despite the similarity in living overstory stem densities. Remaining overstory blue ash trees are almost double the diameter and more than double the age of white ash overstory, suggesting that blue ash is continuing to persist in the presence of EAB. In contrast, most of the remaining white ash overstory trees are young, small, and likely are individuals released from the subcanopy and understory following EAB-caused mortality of the larger and older trees and removal of the canopy. More than 90% of all overstory white ash stems sampled were < 30 years old while > 96% of blue ash stems sampled were >30 years old (Figure 4), suggesting that blue ash is being killed by EAB at a much lower frequency than white ash.

Patterns of sudden increase in annual growth ring widths observed in the 57 overstory white ash tree cores show evidence of a release in growth from the understory (19%) or groundcover (39%) over the past 7 – 13 years that correspond to the period of EAB-caused tree mortality. Also, several overstory individuals (11%) were $\leq$ 15 years old but exhibited rapid and steady growth characteristic of root collar sprouts (Kashian *in press*). Thus at least 68% of the current overstory sampled in white ash stands had not yet attained overstory stature prior to EAB; their placement in the overstory today likely resulted from a release of advanced regeneration following the disturbance. These data also suggest that much of the canopy within white ash stands is being replaced by white ash at these sites, such that the main effect of EAB-caused mortality is on stand structure rather than tree species composition or dominance.

The distributions in crown conditions for overstory blue ash shows evidence of a continuing resistance to EAB. A larger proportion of blue ash, though much older than white ash, maintain a lower crown rating (Figure 5). The majority (69%) of blue ash overstory had a canopy rating of 3 or less while the majority of white ash (> 60%) had a canopy rating of 4 or 5. Both white and blue ash showed an increase in higher crown rating frequency with increase in diameter size class meaning the larger and likely older trees of both species are experiencing higher levels of EAB infestation while younger and smaller ash trees of the understory and subcanopy remain with healthier crowns, poised for further canopy replacement. This trend was, as expected, much stronger for blue ash. Overall, blue ash overstory consistently exhibited lower stand mortality and a higher percentage of healthy individuals than white ash at all sites, consistent with reports of EAB-caused mortality in common garden experiments and forest settings (Herms 2015; Tanis and McCullough 2012; Anuliwicz et. al 2007).

Overstory trees in stands dominated by blue ash are clearly experiencing a reduction in health and moderate levels of EAB caused mortality. The severity of EAB-caused mortality appears to be related to the length of time since EAB infestation. Portland, in Ionia County, had the lowest blue ash mortality rates and did not have confirmed EAB infestation until 2005 while all other sites were infested by 2002, though dendrochronological reports suggest that EAB was probably present in these areas by the mid to late 1990s (Siegert et. al 2014; Siegert et. al 2007). It may be that simply not enough time has passed for overstory blue ash to reach the same stand-wide levels of mortality as other native ash species growing in the same areas as proposed by (Anuliczwicz et. al 2007). Tanis and McCullough (2012) reported mortality rates of < 40% at two sites surveyed for blue ash in southeastern Michigan, with the majority of surviving trees being relatively healthy (< 30% canopy dieback). Similarly, this study revealed that the majority (> 60%) of living blue ash in the five sites I sampled in southeastern Michigan had a crown rating of 3 or less which is equivalent to approximately 50% canopy dieback and 50% gallery cover or less

(Flower et. al 2013). Though slightly higher than those found by Tanis and McCullough (2012) prior to 2012, these crown conditions and mortality rates on their own do not suggest that a dramatic decline of overstory blue ash is imminent.

Regeneration

My results suggest that blue ash seedling densities are occurring at levels equivalent to or greater than all associate species within blue ash-dominated stands. Blue ash seedlings are most abundant and dominant in the < 0.5 m height class and become less dense and dominant in larger height classes, suggesting (1) there is a high level of blue ash seedling mortality rather than recruitment to larger height classes, and (2) potentially higher shade tolerance of associate species (which was most commonly sugar maple). Nevertheless, blue ash saplings are present at all height classes and do not differ significantly from other ash or non-ash species.

The presence of seedlings and saplings in the < 0.5 m class suggests that an input of new seeds (and thus seedlings) into the understory continues even after EAB infestation for both ash species. The majority of the seedlings counted for both ash species were new seedlings that established after EAB infestation (Figure 8), which suggests that viable seed production has persisted since EAB infestation for both species. It appears that higher EAB-caused mortality of overstory white ash has impacted the establishment of new white ash seedlings (< 3 yrs old) compared to blue ash; declining regeneration (and presumed seed rain) is not yet evident for blue ash.

The lower density of post-EAB and < 0.5 m white ash seedlings within the blue ash stands may be representative of a lag time in seed production, whereby the smaller and younger post-EAB overstory white ash did not produce seed before it was able reach the canopy. Within the white ash stands, white ash seedling densities showed some evidence of a rebound in seed production. Within these stands white ash seedlings dominate at all height classes, but the < 0.5 m height class had the highest amount of variation (Figure 6b). This dissimilarity of seedling densities and trends for white ash between the white and blue ash stands suggest seed dispersal range has narrowed in the time since before EAB.

Results for average annual growth rates support a similar conclusion that blue ash is not being outcompeted by associate species. Surprisingly, white ash showed some evidence of a competitive edge in relation to its growth rate. White ash appears to be the only associate species at any site or in any height class that showed higher growth rates than blue ash. Considering the high susceptibility of white ash to EAB and the ability of blue ash to resist and thus maintain a low population of EAB, blue ash is likely to outcompete white ash prior to or shortly after reaching the canopy within blue ash-dominated stands. This is reflected in the complete lack of living mature white ash trees juxtaposed with several fallen dead mature white ash stems within the blue ash stands.

Will blue ash persist in the wake of EAB?

Shortly after the discovery of EAB in 2002, efforts were initially aimed at control of the invasive pest with hopes of stopping or delaying its spread long enough to develop a means to reduce its impact on native forest ecosystems. Rapid spread of EAB and high ash mortality rates within its increasing range has quickly changed the direction of research to one aimed at understanding and predicting the future composition and function of North American forests as ash is removed from the canopy (Smith et al. 2014; Kashian and Witter 2011). Many researchers have suggested that black, white, and green ash will be removed from North American forests as a functioning dominant or co-dominant species (Herms and McCullogh 2014; Anulewicz 2007; but see Kashian *in press*). However, the same should not yet be predicted for blue ash given the reduced mortality of its overstory trees, the abundance of its regeneration, and its competitive growth rate in the understory relative to other species.

A caveat of this study is that all sites showed evidence of an active EAB population, and implications of this for blue ash in the future remains unclear. At the five sites in southeastern Michigan, 92.7% of all overstory blue ash stems showed some evidence of EAB infestation. However, the majority of these trees continue to maintain a healthy crown, suggesting they are not past a point of recovery even after an extended period of exposure. This shows evidence of a spectrum of resistance for blue ash, especially given the levels of EAB-caused mortality of other ash species in the region (Herms and McCullough 2014; Klooster et. al 2014; Knight et. al 2010; Anulewicz 2007). All sites contained ample regeneration at levels comparable to the most abundant species and growing at least as quickly. Finally, there remains evidence of viable seed inputs (based on the number of new ash seedlings across all plots) to maintain a genetically diverse input of further regeneration within all stands. All of these components are supportive of the potential for sustainable canopy replacement by blue ash, at least in part, within blue ash stands. All that is required for continued ash persistence is a constant input of viable seeds, which can be accomplished by the establishment of a new cohort if they grow to reproductive maturity quick enough to replace at least the majority of dying canopy trees. This new group of seed bearing adults need only maintain their position long enough to once again replenish the seed bank. If current trends of blue ash resistance and regeneration continue, it is likely blue ash will persist in southern Michigan forests.

This study was conducted at sites at or near the documented northern limit of blue ash on primarily dense, clay rich soils and slightly drier river banks. In the heart of its distribution (e.g. Kentucky and Tennessee), blue ash stands are more common on limestone soils of dry uplands (Prasad 2007). Blue ash has only relatively recently become infested with EAB even near its introduction point, and it remains to be seen how site factors and ecosystem differences will affect the impact of EAB on blue ash. Where blue ash is more common in the overstory, one would expect higher regeneration densities and thus higher probability of persistence, but differences in overstory composition will produce various competitive species with varying levels of regeneration. This study provides an initial description of blue ash regenerative potential, but continued studies over time across a diversity of forest types are needed for better predictions of the future of blue ash in North American forests.

Figure 1. Location of six blue ash sites sampled in southeastern Michigan. Star represents EAB introduction point near Canton, MI (Smith et. al 2015).

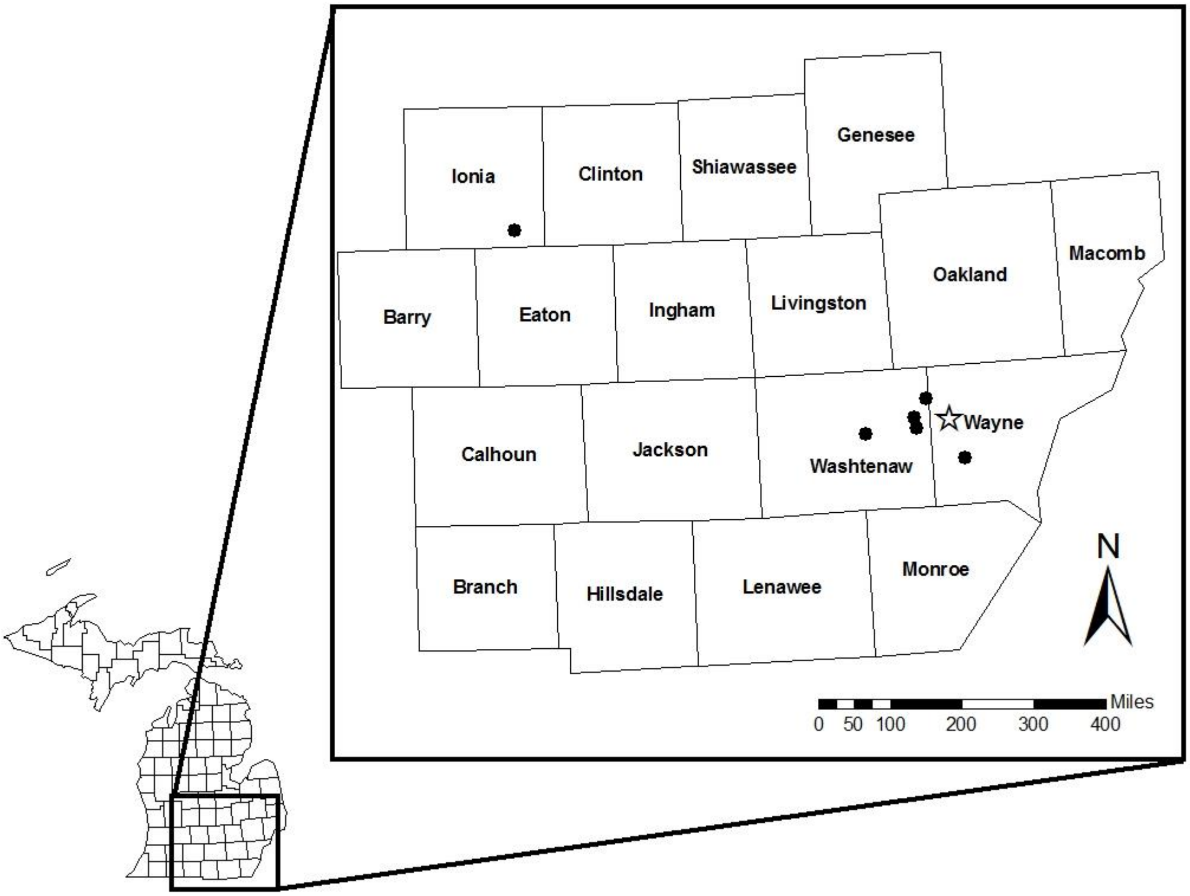


Figure 2. Diagram of 30 m x 10 m plot with 10 m belt. First belt was run 2 m in from 10 m side. A new belt was run every 2 m until 10 individuals of each species group at each size class was found.

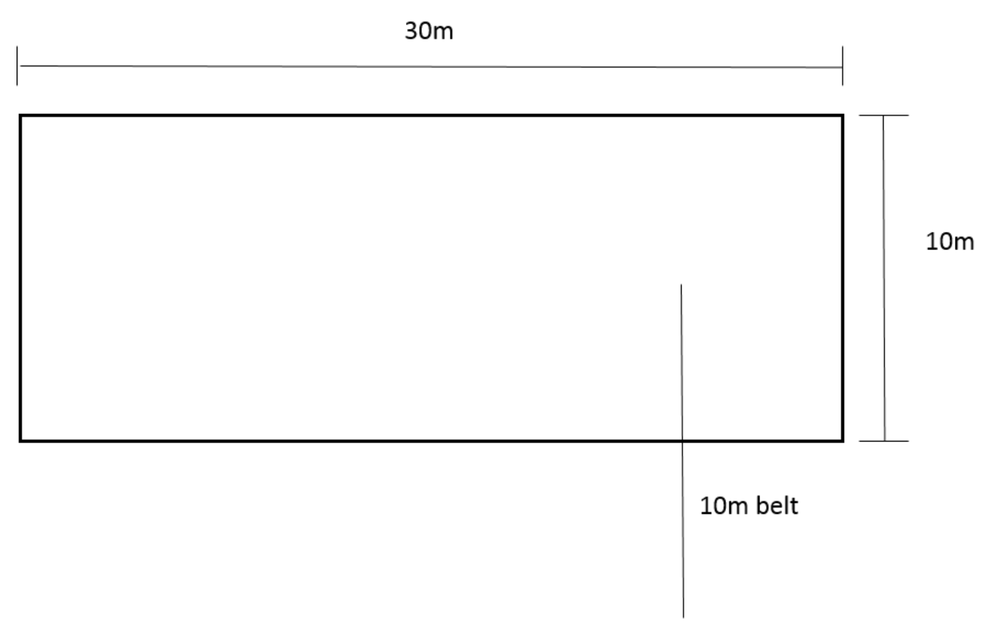


Figure 3. Comparison of living and dead overstory stem counts between blue ash and white ash in their respective stands, tallied across all sites.

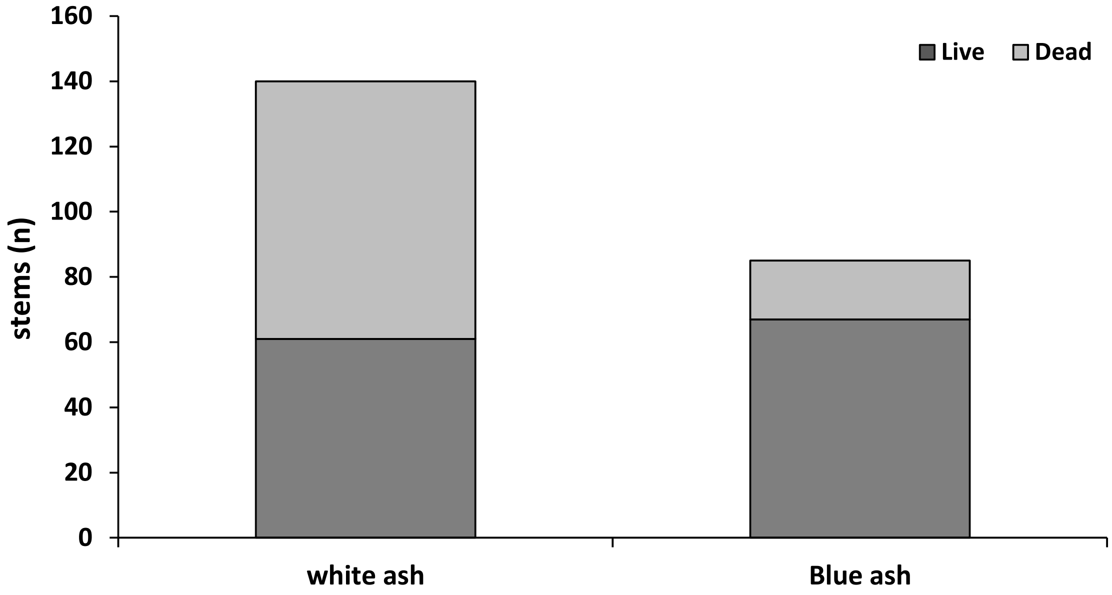


Figure 4. Histogram of age distribution for (A) blue ash and (B) white ash within their respective stands. Mean age differed significantly between stand types $p < 0.001$**.**

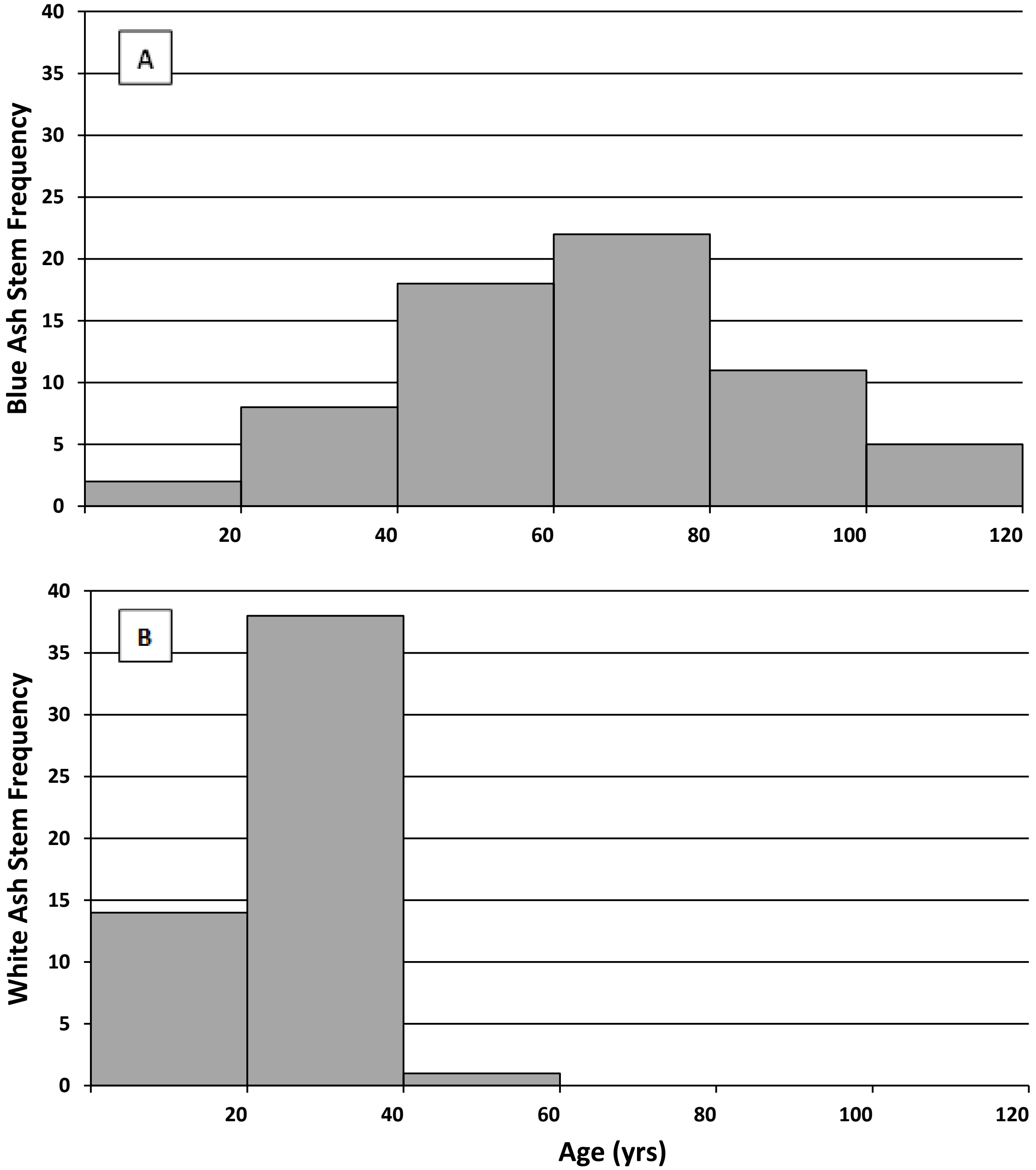


Figure 5. Frequency of crown rating for overstory stems for (A) blue and (B) white ash. Distributions for the two stand types were significantly different p = 0.007.

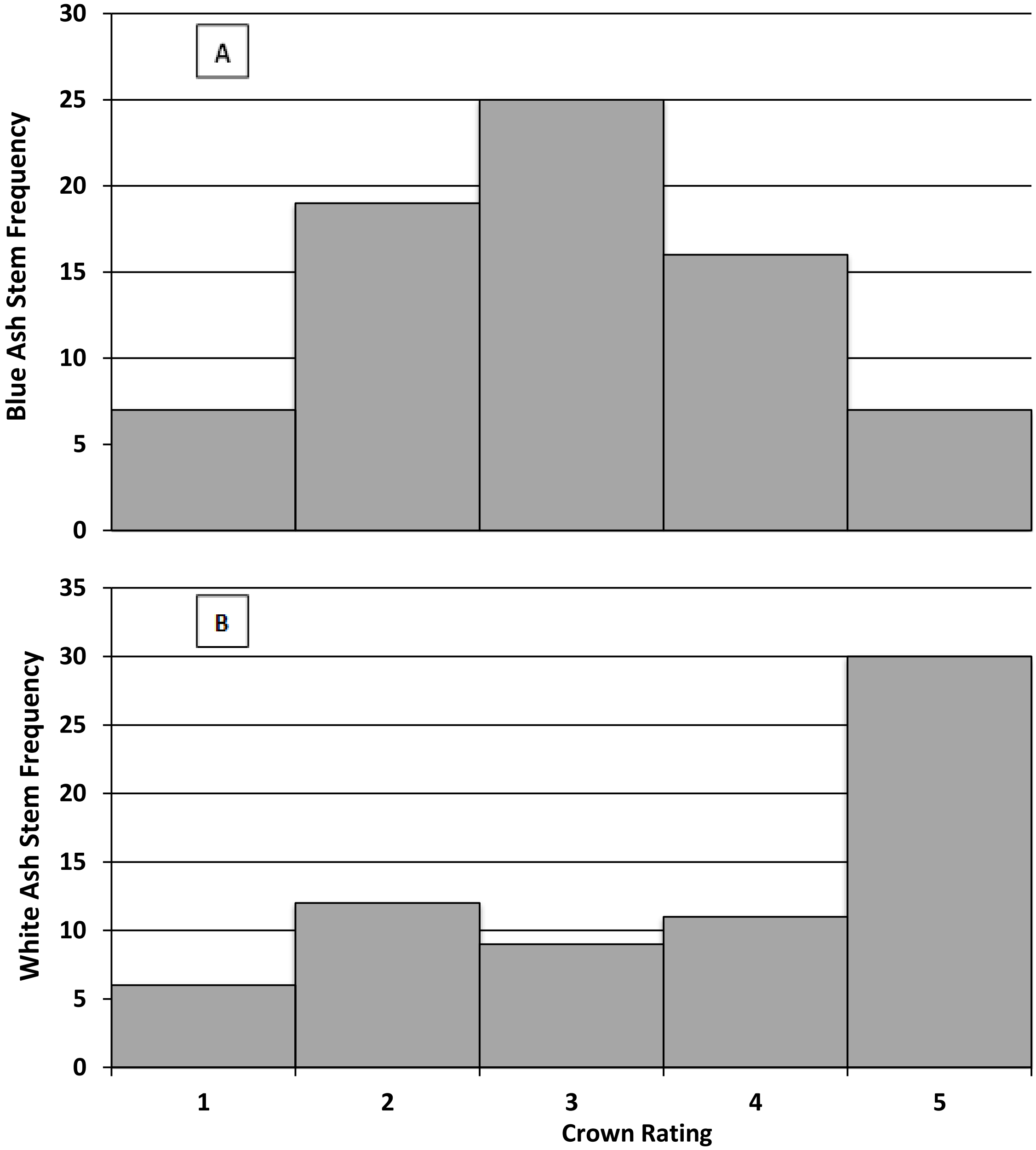


Figure 6. (A) Comparison of mean stem densities (stems/ha) of each species across all sites at each height class. Values for Lafurge were not included in the < 0.5 m height class. (B) Comparison of mean stem densities (stems/ha) of white ash and other species within white ash stands averaged across all sites at each height class. Error bars represent ± 1 SE.

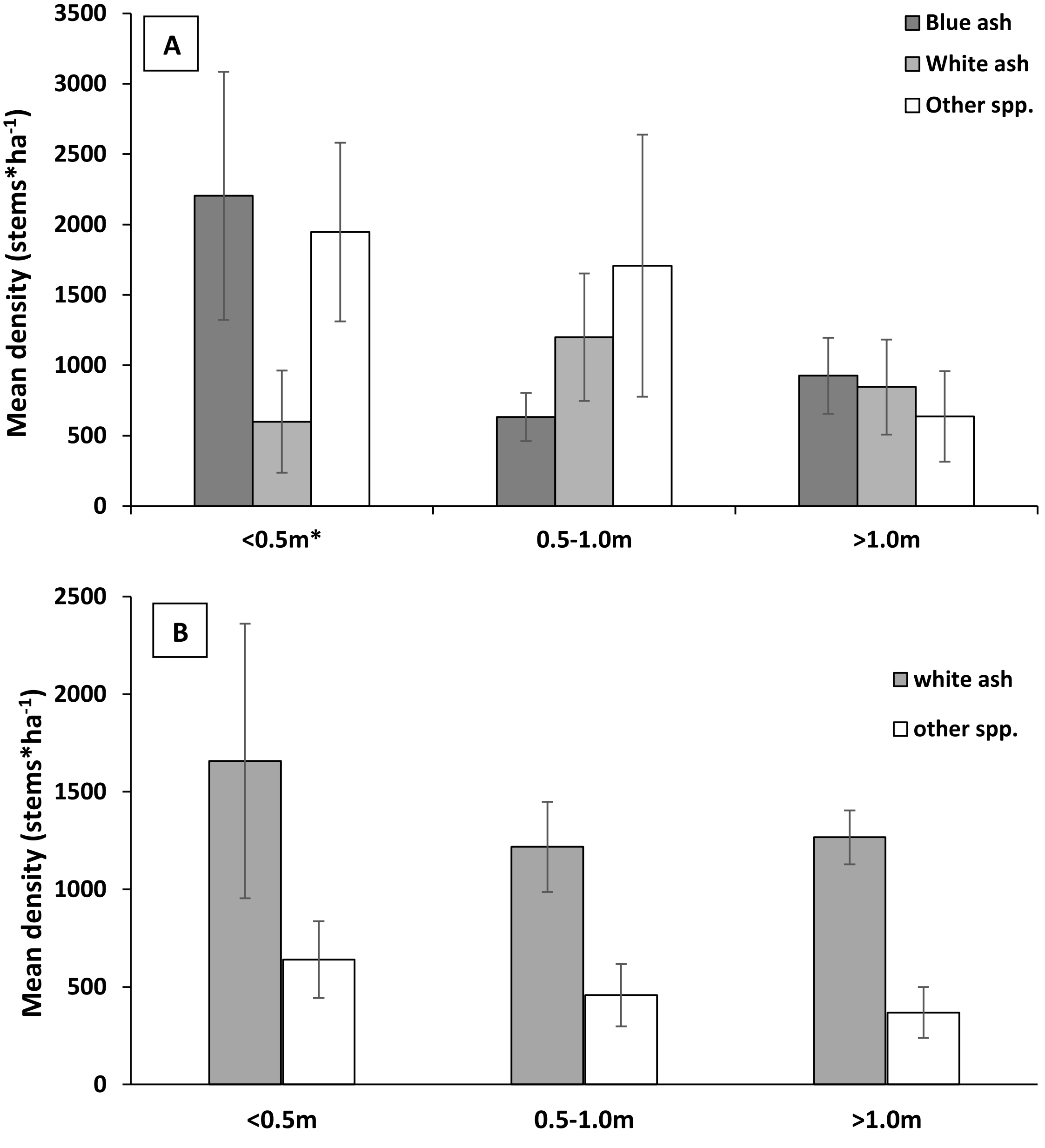


Figure 7. Comparison of mean annual growth rates (cm/yr) for each species across all sites at each height class. Error bars represent ± 1 SE.

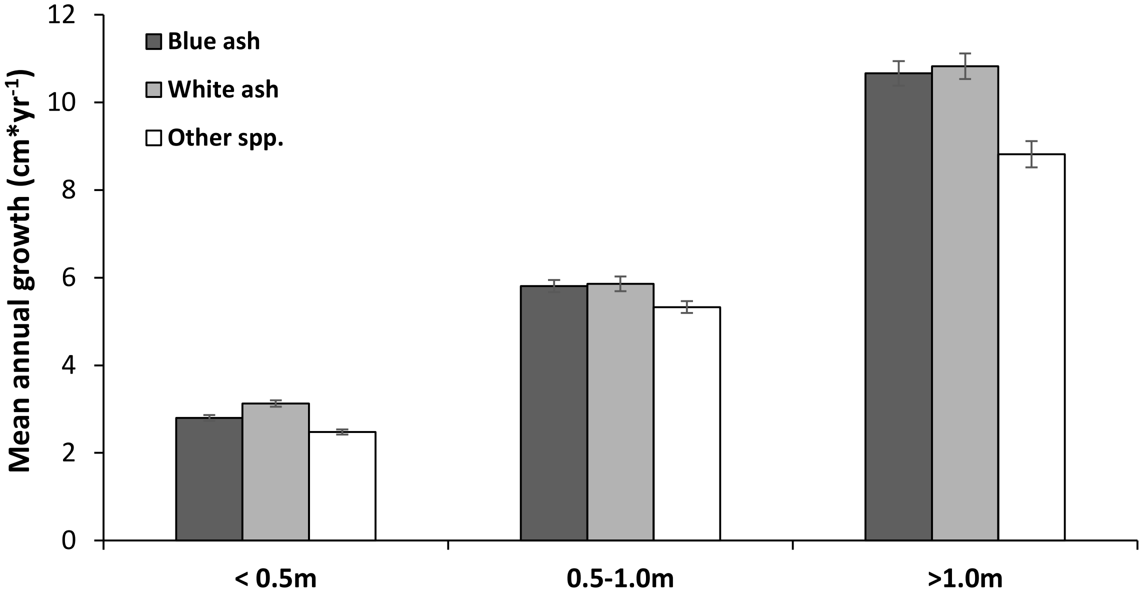
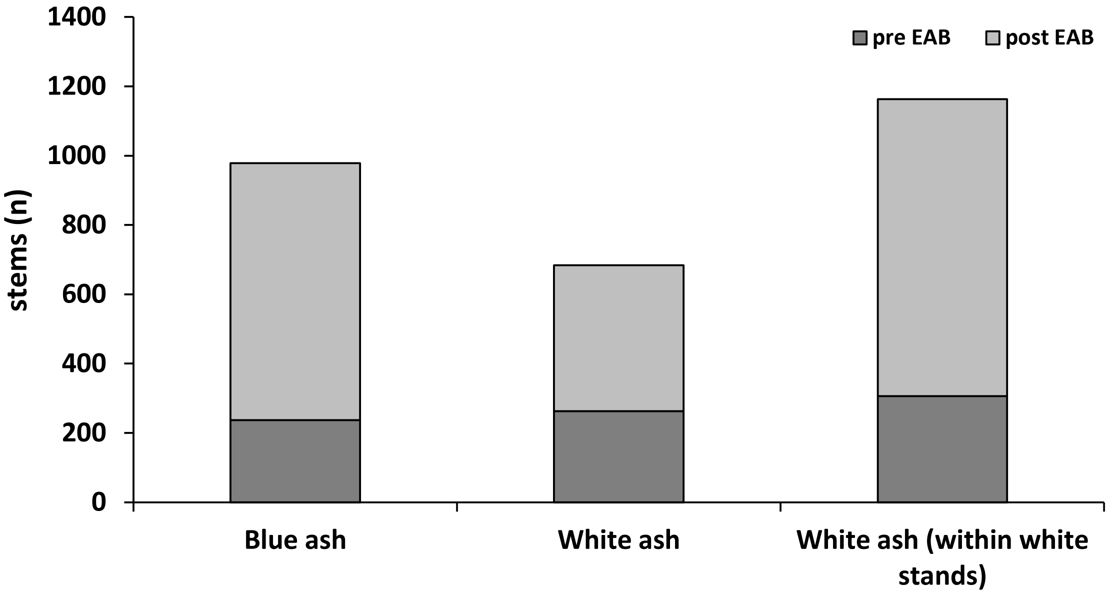


Figure 8. Comparison of counts of advanced regeneration (pre-EAB) and new seedlings (post-EAB) of blue and white ash tallied across all sites. Values are shown for white ash seedlings within blue ash and white ash stands. New seedlings are more abundant than advanced regeneration for all species categories. Ratios did not differ significantly between categories.



APPENDIX A

Comparison of number of stems (N), ratio of advanced regeneration to new seedlings, stand mortality, quadratic mean diameter (Qm) and mean age (± S.E.) between blue ash and white ash stands at each site and across all sites. Values in parenthesis show ratios for pre/post EAB established seedling counts for white ash within blue stands. *significant at $p < 0.05$; **$p < 0.001$.

Species / Site	# Stems	Pre/post EAB ratio	Mortality (%)	Qm (cm)	Mean age (years)
La Furge					
Blue Ash	12	1.2	14.3*	42.5**	74 ± 4.2*
White Ash	7	0.92 (0.19)	72.0	10.9	29 ± 2.0
Kosch					
Blue Ash	10	1.0	28.6	31.4**	66 ± 4.1**
White Ash	17	0.65 (0.028)	45.2	14.1	25 ± 0.8
Lower Huron					
Blue Ash	9	0.21	18.2*	33.8*	63 ± 6.8**
White Ash	12	0.21 (0.51)	57.1	13.0	19 ± 1.3
Conant					
Blue Ash	13	0.065	31.6	18.5	41 ± 4.2*
White Ash	13	1.2 (0.29)	43.5	15.0	23 ± 1.1
EBW					
Blue Ash	10	0.59	23.1*	27.0	72 ± 4.7
White Ash	2	0.4 (0.49)	83.3	12.5	32 ± 11.5
Portland					
Blue Ash	13	0.013	7.1*	27.0	75 ± 9.1*
White Ash	8	1.0 (0.56)	57.9	25.0	28 ± 1.4
All Sites					
Blue Ash	67	0.32	23.0**	30.6**	65 ± 2.8**
White Ash	61	0.62 (0.36)	56.1	15.6	24 ± 0.7

APPENDIX B

Mean (± S.E.) number of stems for each species at each height class averaged across all blue ash stands for each site and across all sites. Values shown for "Other spp." represents value of most abundant non-ash species at each site.

Species/Site	**Density of seedlings < 3 yrs (stems/ha)**	**Density of saplings < 0.5 m (stems/ha)**	**Density of saplings 0.5 – 1m (stems/ha)**	**Density of saplings > 1m (stems/ha)**
La Furge				
Blue ash	289 (113)	1533 (885)	1311 (757)	2000 (1155)
White ash	22 (22)	622 (359)	2133 (1232)	1267 (731)
Other spp.	-	205266 (118510)	6044 (3490)	378 (218)
Kosch				
Blue ash	744 (495)	356 (205)	822 (475)	1444 (834)
White ash	495 (300)	333 (192)	2733 (1578)	2244 (1296)
Other spp.	-	2111 (1219)	2356 (1360)	1956 (1129)
Lower Huron				
Blue ash	767 (167)	2178 (1257)	711 (411)	822 (474)
White ash	111 (80)	2000 (1155)	1511 (872)	867 (500)
Other spp.	-	2311 (1334)	511 (295)	244 (141)
Conant				
Blue ash	556 (506)	4022 (2322)	311 (180)	378 (218)
White ash	189 (78)	556 (321)	689 (398)	533 (308)
Other spp.	-	511 (295)	289 (167)	-
EBW				
Blue ash	122 (40)	133 (77)	111 (64)	533 (308)
White ash	22 (22)	-	67 (26)	167 (64)
Other spp.	-	756 (436)	1022 (590)	1222 (706)
Portland				
Blue ash	433 (33)	4333 (2502)	533 (308)	378 (218)
White ash	11 (11)	111 (64)	67 (38)	-
Other spp.	-	4044 (2336)	22 (13)	22 (13)
All Sites				
Blue ash	485 (118)	2093 (728)	633 (172)	926 (270)
White ash	109 (52)	604 (296)	1200 (453)	846 (337)
Other spp.	-	35833 (33891)	1707 (931)	637 (321)

APPENDIX C

Mean (± S.E.) growth rates of each species at each height class averaged across all blue ash stands at each site and across all sites, and mean (± S.E.) light readings averaged across all blue ash stands. Means having different superscripts differed significantly at $p < 0.05$.

Species / Site	**< 0.5m Height Class mean ± SE growth rate (cm/year)**	**0.5 – 1m Height Class mean ± SE growth rate (cm/year)**	**> 1m Height Class mean ± SE growth rate (cm/year)**	**mean ± SE light (lux)**
La Furge				
Blue Ash	2.97 ± 0.17^{1}	5.04 ± 0.27	7.54 ± 0.54^{1}	120.3 ± 18.0
White Ash	3.52 ± 0.20^{1}	5.64 ± 0.34	10.55 ± 0.72^{2}	
Other Spp.	2.08 ± 0.09^{2}	4.23 ± 0.29	7.30 ± 0.61^{1}	
Kosch				
Blue Ash	2.56 ± 0.17^{1}	5.42 ± 0.40^{12}	11.98 ± 0.73^{1}	149.4 ± 12.0
White Ash	3.29 ± 0.16^{2}	7.06 ± 0.51^{1}	13.21 ± 0.69^{1}	
Other Spp.	2.59 ± 0.17^{1}	4.30 ± 0.24^{2}	6.93 ± 0.43^{2}	
Lower Huron				
Blue Ash	2.34 ± 0.12	4.67 ± 0.29	13.73 ± 0.86^{1}	372.3 ± 65.4
White Ash	2.50 ± 0.15	4.19 ± 0.24	8.64 ± 0.58^{2}	
Other Spp.	2.52 ± 0.16	6.37 ± 0.39	13.84 ± 1.09^{1}	
Conant				
Blue Ash	2.67 ± 0.14^{1}	7.79 ± 0.38^{1}	12.49 ± 0.70	190.6 ± 24.1
White Ash	3.36 ± 0.20^{2}	5.68 ± 0.32^{2}	11.61 ± 0.80	
Other Spp.	2.39 ± 0.14^{1}	5.62 ± 0.50^{2}	8.89 ± 1.25	
EBW				
Blue Ash	3.55 ± 0.19	6.36 ± 0.38^{1}	10.10 ± 0.61^{12}	190.4 ± 33.0
White Ash	3.99 ± 0.24	7.87 ± 0.51^{2}	12.96 ± 0.82^{1}	
Other Spp.	2.92 ± 0.15	5.5 ± 0.26^{1}	8.99 ± 0.48^{2}	
Portland				
Blue Ash	2.66 ± 0.13	5.53 ± 0.25	8.15 ± 0.47	249.3 ± 20.4
White Ash	2.31 ± 0.13	5.09 ± 0.42	7.99 ± 0.52	
Other Spp.	2.37 ± 0.14	6.00 ± 0.29	7.02 ± 0.47	
All Sites				
Blue Ash	2.80 ± 0.06^{1}	5.81 ± 0.14	10.66 ± 0.28^{1}	N/A
White Ash	3.13 ± 0.08^{2}	5.86 ± 0.17	10.83 ± 0.29^{1}	
Other Spp.	2.48 ± 0.06^{3}	5.33 ± 0.14	8.82 ± 0.30^{2}	

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ABSTRACT

AN ANALYSIS OF BLUE ASH (*FRAXINUS QUADRANGULATA)* REGENERATION IN SOUTHEASTERN MICHIGAN IN THE PRESENCE OF EMERALD ASH BORER (*AGRILUS PLANIPENNIS)*

by

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May 2016

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Major: Biological Sciences

Degree: Master of Science

Since the introduction of the invasive bark beetle emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) to southeastern Michigan, most native ash species (*Fraxinus spp.*) such as white ash (*F. Americana),* black ash (*F. nigra*), and green ash (*F. pensylvanica)* have suffered mortality rates exceeding 99% after infestation. This has led to the loss of seed sources resulting in a depleted seed bank and thus a loss of potential future regeneration. These trends suggest that these species will soon no longer function as important canopy species in North American hardwood forests as EAB continues to spread. Blue ash (*F. quadrangulata*) is thought to be the most resistant of all native ash species to EAB with observed mortality rates between 30% and 40%. This reduced mortality may be sufficient for mature blue ash trees to persist and maintain a seed bank robust enough to evolve even higher resistance to EAB. While several studies have quantified declining regeneration of other ash species, little research exists describing blue ash regeneration in the presence of EAB. A total of 18 blue ash stands were sampled at 6 different sites in southeastern Michigan near the EAB introduction point. For reference, 18 white ash (*F. Americana*) stands within the same 6 sites were also sampled.

Observed overstory mortality for blue ash ranged between 7.1% and 31.6% and was significantly lower than white ash across all sites. Overstory blue ash was on average significantly older and larger than white ash across all sites and maintained a higher frequency of healthier crowns. Blue ash regeneration densities were found to be abundant at all sizes within all stands. New seedlings (< 3 yrs old) were significantly more abundant for blue ash than white ash across all sites suggesting blue ash has not experienced the same depletion of its seed bank as white ash. Blue ash seedling growth rates were equal to or significantly greater than associate non-ash species at all size classes and at all sites; and equal to white ash seedling growth rates at the majority of sites and size classes with few exceptions. My results show blue ash maintaining a relatively healthy and dominant position in the canopy of several forests in southeastern Michigan. Furthermore, my results suggest that blue ash is still regenerating in a capacity that shows a high probability of canopy replacement by blue ash and thus its continued persistence in the presence of EAB.

AUTOBIOGRAPHICAL STATEMENT

We are all in the gutter, but some of us are looking at the stars.

-Oscar Wilde, *Lady Windermere's Fan*