



Potential for persistence of blue ash in the presence of emerald ash borer in southeastern Michigan



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ABSTRACT

Since the introduction of the invasive bark beetle emerald ash borer (*Agilus planipennis* Fairmaire, EAB) to southeastern Michigan, most native ash (*Fraxinus* spp.) species such as white ash (*F. americana* L.), black ash (*F. nigra* Marsh.), and green ash (*F. pennsylvanica* Marsh.) have suffered mortality rates exceeding 99% after infestation in mixed stands. EAB-caused mortality has reduced or eliminated ash seed sources, resulting in a depleted seed bank and a reduced potential for regeneration that has led many researchers to predict a grim future for ash in North America. Blue ash (*F. quadrangulata* Michx.) is thought to be the most EAB-resistant of all North American ash species with observed mortality rates between 30% and 40%, but few data exist describing blue ash regeneration dynamics in the presence of EAB. We sampled blue ash-dominated stands at six different sites in southeastern Michigan, nearest the EAB introduction point. White ash stands at the same six sites were also sampled as the reference condition for ash in the presence of established EAB. Overstory mortality for blue ash ranged between 7 and 32% and was significantly lower than white ash across all sites. Post-EAB 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 that blue ash has not experienced the same seed bank depletion as white ash. Blue ash seedling growth rates were greater than or equal to associated non-ash tree 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. Our results suggest that blue ash is currently maintaining a relatively healthy and dominant position in the canopy of several forests in southeastern Michigan, and that blue ash is still regenerating in a capacity that shows a high probability of canopy self-replacement and thus persistence in the presence of EAB.

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1. Introduction

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, 1999) and the increasing threat of invasive species (Byers and Noonburg, 2003; Dunstan and Johnson, 2006; Melbourne et al., 2007). To persist in the presence of a destructive invasive species, however, host tree species must regenerate and recruit to replace the susceptible adult cohort with new reproductive adults capable of producing seed (Greene et al., 1999; McEuen and Curran, 2004; Kashian, 2016). Both asexual and sexual regeneration are common and important for persis-

tence of tree species following disturbances (Plotkin et al., 2013). Results of sexual regeneration may include immediate germination of viable seeds produced annually, dormant seed banks in the soil (Bakker et al., 1996), and/or slow-growing seedlings in the understory that established either prior to (hereafter “advanced regeneration”) or after the disturbance (Greene et al., 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, 1990; Leckie et al., 2000). However, presence of a seed source and post-disturbance regeneration does not ensure replacement of canopy trees of the same species (McEuen and Curran, 2004). In fact, the new cohort will be subject to varying levels of competition depending on forest community composition and structure as well as changing site factors such as light, water, and nutrient availability (Thompson et al., 1993; Peterson and Carson, 1996) potentially altered by phytophagous insects (Gandhi and Herms, 2010). Thus successful post-invasion

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regeneration and host species persistence depends heavily on advanced regeneration and post-disturbance seed rain (Greene et al., 1999; Kashian, 2016).

Emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) is an invasive, phloem-feeding beetle native to Asia that was discovered in southeastern Michigan in 2002 (Cappaert et al., 2005). EAB became established in southeastern Michigan in the early 1990s, with initial tree mortality occurring in 1997 (Siegert et al., 2007, 2014). Emerald ash borer attacks and kills all native North American species of the ash genus (*Fraxinus* spp.) with mortality often occurring within two to five years after exhibiting symptoms of infestation (Knight et al., 2010, 2012). In North America, healthy ash trees with a diameter at breast height (DBH) ≥ 2.5 cm are most 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 of dollars (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; EAB infestations thus far have been confirmed in 30 states and 2 Canadian provinces as of January 2017 (Fig. 1; www.emeraldashborer.info, 2017).

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 of affected ash species, resulting in a depleted seed bank and thus a loss of potential regeneration (Kashian and Witter, 2011; Knight et al., 2012). Declines in advanced regeneration and post-EAB regeneration have also been reported (Kashian and Witter, 2011; Klooster et al., 2014), and many researchers have suggested that *Fraxinus* is likely to be extirpated as an important canopy tree in eastern North America as EAB continues to spread (Anulewicz et al., 2007; Burr and McCullough, 2014; Herms and McCullough, 2014).

The rarer blue ash (*F. quadrangulata* Michx.) exhibits much lower EAB infestation rates compared to other ash species (Anulewicz et al., 2007) and observed mortality rates between 20% and 40% (Tanis and McCullough, 2012), but little is known about its regeneration ecology. Southern Michigan marks the northern limit of blue ash distribution, which ranges south into Alabama, into eastern Tennessee, and west into Oklahoma and Kansas (Fig. 1; Little, 1971; Prasad et al., 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, with a medium-sized tree averaging between 30 and 50 cm in diameter when mature. 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.) (Barnes

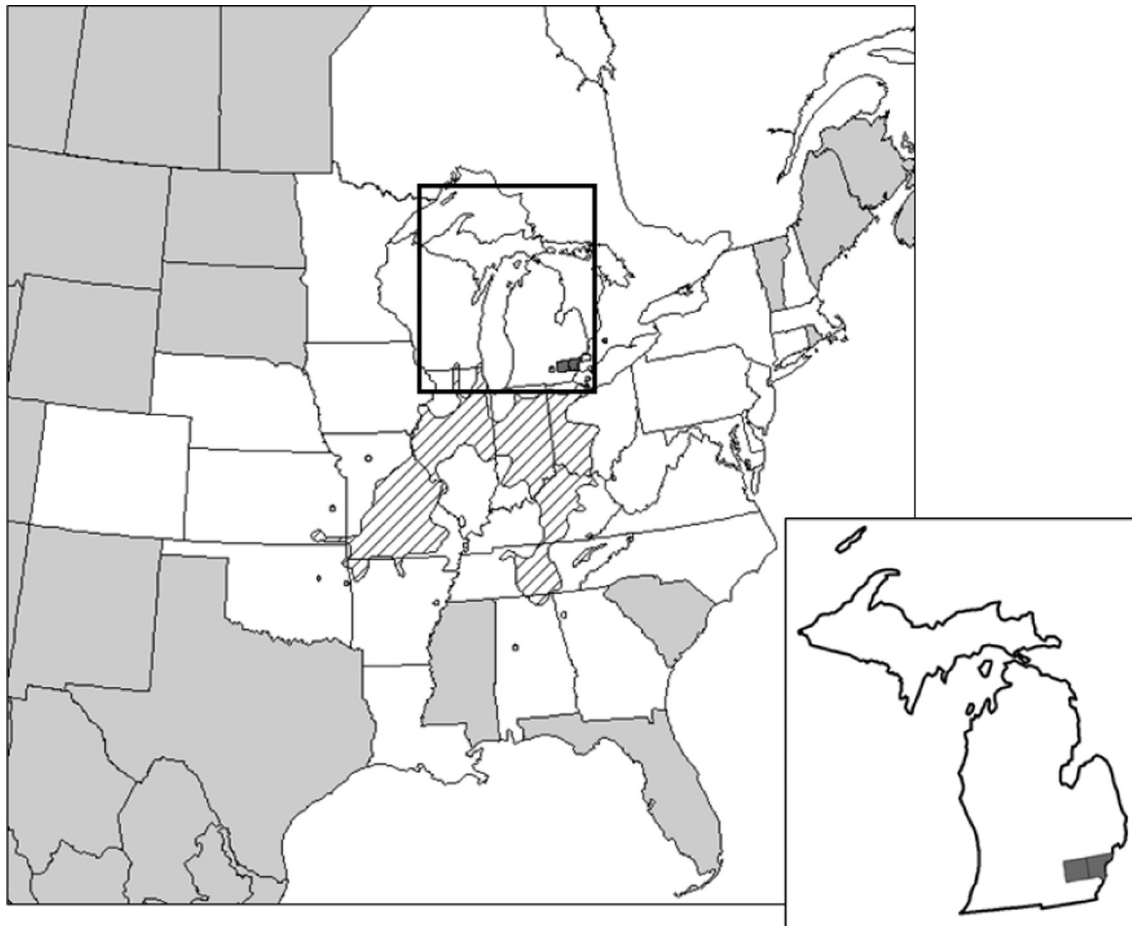


Fig. 1. Study site locations in relation to current distribution of emerald ash borer and blue ash in North America. Unshaded states and provinces represent areas where EAB presence has been confirmed. Cross-hatched area represents the distribution of blue ash according to Little (1971). Dark-shaded area in inset are counties that encompass the study area.

and Wagner, 2004). Blue ash persistence following EAB infestation relies heavily on its ability to compete with its associates and any other potentially invasive competitors in the understory; black and sugar maple are particularly strong competitors following small gap-forming disturbances (Canham, 1988; Lei and Lechowicz, 1998).

To study and document the regeneration ecology of blue ash in the presence of EAB, we asked the following three questions: (1) What is the current condition of blue ash in the presence of EAB? We hypothesized that blue ash currently persists as a dominant overstory species despite the negative impacts of EAB; (2) What is the regenerative capacity of blue ash relative to its associated species? We expected that blue ash seedling and sapling densities would be equal to or greater than all of its associated species at all size classes in stands where blue ash dominated the overstory; (3) Given the first two questions, what is the potential for blue ash to persist in the presence of EAB? We expected blue ash to persist with EAB, though with a truncated life span (eventually succumbing to premature death due to EAB) and overall reduction in overstory density and diameter, but with regeneration and recruitment levels that are capable to eventually replace canopy tree mortality.

2. Methods

2.1. Study area

We sampled blue ash-dominated stands between July 2014 and August 2015 using 18 plots at 6 sites in southeastern Michigan near the reported EAB introduction point. 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. 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 dominance determined from DBH). Each site was sampled using three 10 × 30 m (300 m²) plots placed randomly within each stand. Because virtually all blue ash stands in southeastern Michigan are affected by EAB, we also sampled white ash-dominated stands using an additional 18 plots at the same 6 sites to represent the “standard condition” of ash-dominated stands in the presence of EAB. Three plots at each site currently or formerly (prior to EAB) dominated by white ash were sampled using the same methods as those used for the blue ash stands. White ash was chosen as a reference species because it is the ash species most commonly occurring with blue ash, 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 in Michigan prior to EAB has been documented as moderately shade tolerant, moderately fast-growing, requiring high-nutrient soils, and tolerant of a range of moisture regimes. In southern Michigan it is common to find white ash growing on the edges of deciduous swamps and second bottoms of river floodplains as well as on nutrient-rich uplands (Barnes and Wagner, 2004).

2.2. Current condition of blue ash

Current stand density was determined by counting stems of all living trees ≥9.0 cm DBH. All overstory (>9.0 cm DBH) trees were measured and counted, and all understory trees (1.5–9.0 cm DBH) were grouped into three size classes for analysis: 1.5–4.0 cm DBH, 4.1–6.6 cm, and 6.7–9.0 cm. 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 under a dissecting microscope. Pres-

ence of EAB on a given tree 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 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 formerly rooted within the plot and killed by EAB were identified using the presence of EAB galleries and/or exit holes in bark of standing or 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; pre-EAB stand density was reconstructed by combining living trees with dead trees determined to have been killed by EAB. All sites were on land used for conservancy, restoration, or public use. All plots were established away from trails and other common use areas. The abundance of dead wood and the lack of evidence of cutting, trimming, or tree removal suggested that no trees living or dead were removed prior to or during EAB infestation years. Mortality of ash trees caused by EAB has occurred relatively recently, and thus dead ash trees have shown to provide a reasonable estimate of pre-EAB stand structure (Kashian and Witter, 2011; Kashian, 2016).

Statistical analyses were conducted using IBM SPSS statistics version 23 (IBM Corp, 2015). 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 the potential interaction between site and species. Pre-EAB and post-EAB tree densities were compared between blue ash and white ash stands using a *t*-test. Dead trees that lacked evidence of EAB-caused mortality were considered to pre-date EAB infestation and were not used in calculations. 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 diameter for living overstory trees was calculated using the quadratic mean diameter (Q_m) across all plots for each site ($\sqrt{\frac{\sum D^2}{n}}$). Q_m 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). Q_m was not normalized and thus was compared between white and blue ash stands across all sites using the 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). When compared at each site independently, differences in mean age were tested using the Mann-Whitney-*U* test.

2.3. Regenerative capacity of blue ash relative to other tree species

Three 5 × 10 m (50 m²) subplots in each 300 m² plot were used to sample regeneration. The long axis of each subplot was established perpendicular to the long axis of the larger plot at the 0–5 m, 12.5–17.5 m, and 25–30 m marks. Within each subplot, all tree seedlings and saplings (<1.5 cm DBH or shorter than breast height) were counted by species; non-ash tree species 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 (established post-EAB) by counting axillary bud scars (Kashian, 2016) and comparing to time-since-EAB infestation estimates estimated by Prasad et al. (2010) and validated using

dendrochronological methods by Siegert et al. (2014). Ash seedlings <3 years old were tallied separately.

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 (1) blue ash, (2) white ash, and (3) all other tree species in each size class for each site and compared using the non-parametric Kruskal-Wallis 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 the Mann-Whitney-*U* test.

Five-year average height 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 tree species growing within blue ash stands. Belt transects 1 × 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. Growth rates were transformed using either a logarithmic or square root transformation to correct for normality and heteroscedasticity. The $\log_{10}(X+1)$ and $\sqrt[3]{X+0.05}$ transformations were used because many of the recorded values were between 0 and 1, making these forms of the equations more appropriate (Zar, 1999).

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 pm and 2 pm 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, then averaged for each plot at each site. Growth rates for each species at each size class were compared between species with a repeated-measures analysis of variance (ANOVA) using a mixed-linear model with plots nested within site, and light readings applied as a covariate using an unstructured covariate structure to examine differences in growth rates.

3. Results

3.1. Current condition of blue ash

Overstory blue ash mortality ranged from 7% to 32%, with an overall estimated mortality across all sites of 21%; white ash mortality ranged from 44 to 83% and averaged 59% (Table 1). Blue ash mortality was consistently lower than that for white ash at each site, and overall mortality was higher for white ash (Fisher's exact test; $p < 0.001$, $n = 87$ stems in blue ash stands and 139 stems in white ash stands). Interactions between site and species or between site and mortality were not significant. Pre-EAB tree density for white ash stands was higher than for blue ash stands ($t = 2.919$, $p = 0.03$), but current stand densities did not differ significantly (Table 1).

The quadratic mean diameter (Qm) of surviving overstory trees was larger for blue ash (30.6 cm) than white ash (15.6 cm) when compared across all sites ($U = 5.991$; $p < 0.001$); Qm of dead blue ash did not differ from those of white ash (15.2 cm vs. 19.5 for white ash). 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 ($t = 14.079$; $p < 0.001$; Table 1). Mean age for blue ash ranged from 41 to 75 years, and white ash

Table 1

Overstory, seedling and sapling density, and growth rate for blue ash, white ash, and other species across all blue ash stands (SE in parentheses). Values within the same row marked with different superscripts differed significantly at $p < 0.05$. Overstory characteristics are for blue ash stands compared to white ash reference stands.

	Blue ash	White ash	Other spp.
<i>Overstory (>9.0 cm)</i>			
Pre-EAB tree density (stems/ha)	157 (11.9) ^a	239 (25.8) ^b	–
Post-EAB tree density (stems/ha)	124 (7.8)	113 (24.9)	–
Mortality (%)	20.5 (3.7) ^a	59.2 (6.4) ^b	–
Qm (cm)	30.6 ^a	15.6 ^b	–
Age (yrs)	65 (2.8) ^a	24 (0.7) ^b	–
<i>Seedling/sapling density (stems/ha)</i>			
<3 yrs old	485 (118) ^a	109 (52) ^b	–
<0.5 m	2204 (882)	600 (363) ^a	1947 (634) ^b
0.5–1 m	633 (172)	1200 (453)	1707 (931)
>1 m	926 (270)	846 (337)	637 (321)
Pre/post EAB ratio	0.32	0.62	–
<i>Growth rate (cm/year)</i>			
<0.5 m	2.80 (0.06) ^a	3.13 (0.08) ^b	2.48 (0.06) ^c
0.5–1 m	5.81 (0.14)	5.86 (0.17)	5.33 (0.14)
>1 m	10.66 (0.28) ^a	10.83 (0.29) ^a	8.82 (0.30) ^b

mean age ranged from 19 to 32 years. Age distribution for blue ash followed a near perfect normal distribution ($W = 0.990$; $p = 0.869$) with minimal skewness (0.033 ± 0.295) and kurtosis (-0.309 ± 0.582). The white ash age distribution was also normal at $\alpha = 0.05$ ($W = 0.986$; $p = 0.801$), but was skewed toward younger trees ($-0.134 + 0.330$) compared to blue ash with most of the trees between 20 and 40 years old (kurtosis = $0.056 + 0.650$; Fig. 2).

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 skewed toward higher ratings (-0.597 ± 0.291) and flatter than normal (kurtosis = -1.102 ± 0.574), with 64.7% of observed crown ratings >3. Blue

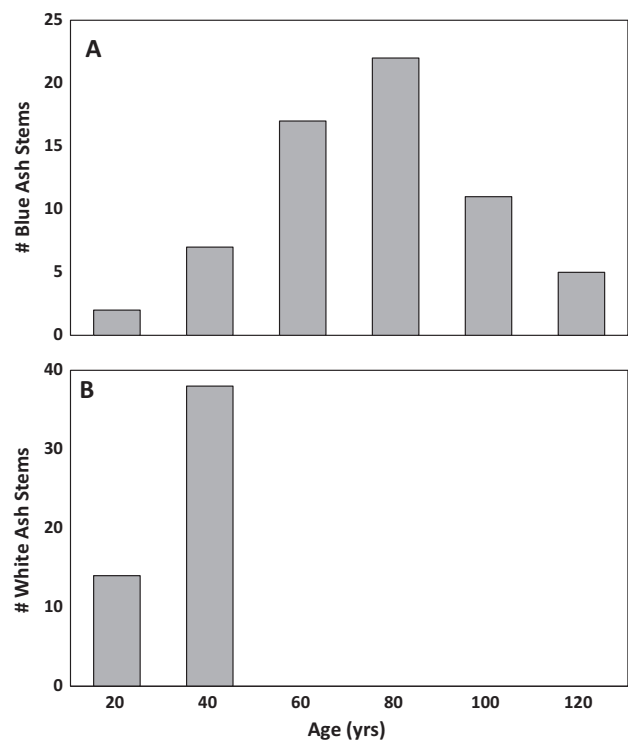


Fig. 2. Age distribution for (A) blue ash and (B) white ash within their respective stands. Mean age differed significantly between stand types $p < 0.001$.

ash crown rating distribution followed a much more normal distribution (skewness = 0.082 ± 0.279 , kurtosis = -0.638 ± 0.552) with 31% of crown ratings >3 (Fig. 3).

3.2. Seedling and sapling densities and growth rates

Mean density for the <0.5 m height class was lowest for white ash (600 stems/ha) compared to blue ash (2204) and non-ash species (1947), with a single outlier plot removed due to a dense carpet of sugar maple seedlings that skewed the results of the non-ash values (Table 1). Blue ash density did not differ from white ash or non-ash densities, but white ash was significantly less dense than non-ash species ($H = 9.210$; $p = 0.010$; Table 1). Mean density of 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 were significantly higher for blue ash (485 stems/ha) compared to white ash (109 stems/ha; $t = 3.289$; $p = 0.008$; Table 1).

Not surprisingly, white ash seedling densities within white ash stands were higher than within blue ash stands. White ash seedling densities within white ash stands were higher than associated non-ash species for the <0.5 m height class (1658 ± 703 vs. 640 ± 197 stems/ha), and significantly higher for the 0.5–1 m height class (1218 ± 231 vs. 458 ± 160 stems/ha; $Z = 2.162$ $p = 0.026$) and the >1 m height class (1267 ± 138 vs. 369 ± 131 stems/ha; $Z = 2.802$ $p = 0.002$). Blue ash seedlings were not present within any white ash-dominated stand at any height class, despite similarities in site.

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; Table 1). The interaction between site and species was not significant. Mean

growth rates for the 0.5–1.0 m height class did not differ significantly between species across all sites. The interaction between site and species was significant ($F = 4.420$; $p < 0.001$) but was likely due to variation in mean growth rates of non-ash species and white ash. 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 (Table 1) across all sites. There was a significant interaction between site and species ($F = 2.593$; $p = 0.001$).

Ratios of pre-EAB to post-EAB seedlings did not differ significantly between species in their respective stands (white ash ratios are from seedlings growing in white ash reference sites) when pooled across all sites. 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 (Table 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 ($p < 0.001$) and a significant interaction between site and establishment ($p < 0.001$).

4. Discussion

4.1. Current condition

The current condition of blue ash appears to be far less perilous compared to white ash in southeastern Michigan. Blue ash mortality was far less than that of white ash at all sites and living overstory blue ash trees were almost double the diameter and more than double the age of white ash overstory at the same sites. In addition, $>90\%$ of all overstory white ash stems sampled were <30 years old while $>96\%$ of blue ash stems sampled were >30 years old (Fig. 2). A larger proportion of blue ash maintained healthier crowns compared to white ash despite being much older (Fig. 3). 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 (Anulewicz et al., 2007; Tanis and McCullough, 2012; Herms, 2015). 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, $>60\%$ of living blue ash sampled in southeastern Michigan had a crown rating ≤ 3 which is equivalent to approximately 50% canopy dieback and 50% gallery cover or less (Flower et al., 2013). Although mean age and size of pre-EAB blue ash were probably older and larger than pre-EAB white ash in the stands that we sampled (based on the size of dead wood measured for each species), lower mortality rates and higher overall crown ratings in blue ash suggest that blue ash is less susceptible to EAB compared to white ash.

Though heavily affected by EAB, it is notable that white ash (as well as blue ash) in southeastern Michigan continue to persist and even dominate on some mesic sites. Most of the remaining white ash overstory trees were young, small, and likely were individuals released from the subcanopy and understory following EAB-caused mortality and partial removal of the canopy of the larger and older trees. We noted a sudden increase in annual growth ring widths observed in the 57 overstory white ash tree cores we sampled that suggest a growth release from the understory over the past 7–13 years that correspond to the period of EAB-caused tree mortality. Moreover, 11% of overstory individuals were ≤ 15 years old but exhibited rapid and steady growth characteristic of root collar sprouts (Kashian, 2016). Thus at least 68% of the current overstory sampled in white ash stands had not yet attained overstory stature

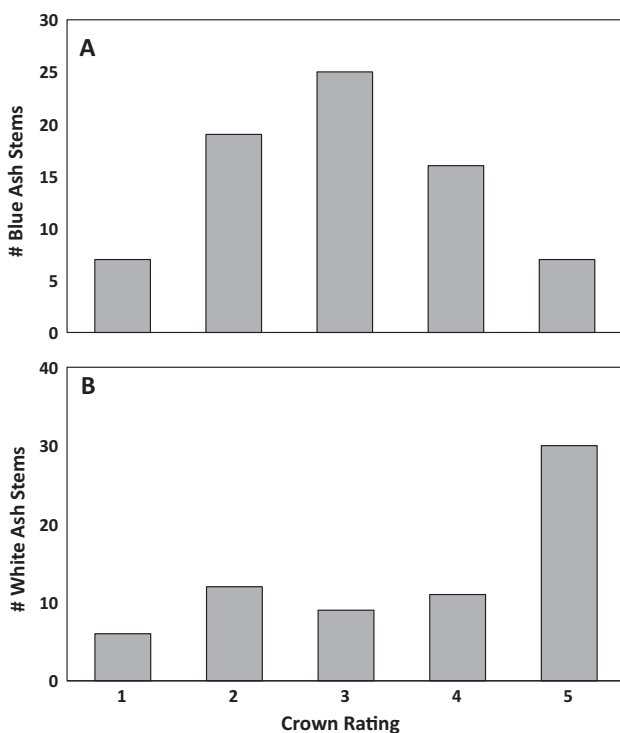


Fig. 3. Frequency of crown rating for overstory stems for (A) blue and (B) white ash. Distributions for the two stand types were significantly different (Mann-Whitney-U; $p = 0.001$).

prior to EAB; their placement in the overstory today likely resulted from a release of advanced regeneration following the disturbance or the survival and recruitment of root sprouts into the overstory. These data also suggest that much of the canopy within the white ash stands we sampled is being maintained as white ash, such that the main effect of EAB-caused mortality thus far is on stand structure in these stands rather than tree species composition or dominance where the relative density of ash is high.

Though slightly higher than those found by Tanis and McCullough (2012) prior to 2012, crown conditions and mortality rates for blue ash on their own do not suggest that a dramatic decline of overstory blue ash is imminent. Negative impacts of EAB on blue ash continue to occur, however, with overstory trees clearly experiencing a reduction in health and moderate levels of EAB-caused mortality still occurring. It remains unclear whether the resistance of blue ash to EAB will eventually be overcome with additional time, as proposed by Anulewicz et al. (2007), but the slower rate of mortality for blue ash compared to white ash may better position the species to persist because it provides a longer window for seed dispersal and subsequent regeneration to occur (see below).

4.2. Regeneration

Blue ash regeneration is occurring at levels equivalent to or greater than all associated species within blue ash-dominated stands. Blue ash seedlings were most abundant and dominant in the <0.5 m height class, becoming less dense and dominant in larger height classes. These trends suggest that there is (1) a high level of blue ash seedling mortality that reduces recruitment to larger height classes, and (2) potentially higher competitive ability of associate species (most commonly sugar maple). Nevertheless, blue ash saplings are present at all height classes and abundance does 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) continues even after EAB infestation for both blue and white ash (see Kashian and Witter, 2011 for comparison). The majority of the seedlings counted for both species established after EAB infestation, which suggests that viable seed production has persisted for both species even after EAB infestation occurred. Higher EAB-caused mortality of overstory white ash has more heavily impacted the establishment of new white ash seedlings (<3 yrs old) compared to blue ash, as declining regeneration was not yet evident for blue ash at the time of this study. Within the white ash-dominated stands, the size distribution of white ash seedlings suggests some evidence of a rebound in seed production, with dominance by white ash at all height classes.

4.3. 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 ash in forest ecosystems. Rapid spread of EAB and high ash mortality rates within its increasing range have 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 (e.g., Kashian and Witter, 2011; Smith et al., 2015). Many researchers have suggested that black, white, and green ash will be removed from North American forests as a functional dominant or co-dominant species given the much higher documented mortality rates of these ash species in earlier reports (Anulewicz et al., 2007; Marshall et al., 2013; Burr and McCullough, 2014; Herms and McCullough, 2014; but see Kashian, 2016). However, we suggest that 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. The mechanism of blue ash resistance is currently unknown and remains an important area of future research. Adult EAB have been observed feeding preferentially on white and green ash relative to blue ash in common garden experiments (Pureswaran and Poland, 2009) and may explain, in part, the continued persistence of blue ash. Blue ash have also anecdotally been observed to heal over bark galleries created by larval EAB (S. Taylor, *pers. comm.*).

A caveat of this study is that most overstory blue ash showed evidence of an ongoing EAB infestation (93% of overstory stems), and implications of this for blue ash in the future remains unclear. However, the majority of these trees continue to maintain a healthy crown and do not appear to be past a point of recovery even after an extended period of exposure. The presence of healthy canopy trees after at least 12 years of EAB presence provides some evidence of resistance for blue ash, especially given the levels of EAB-caused mortality of other ash species in the region (Anulewicz et al., 2007; Knight et al., 2010; Herms and McCullough, 2014; Klooster et al., 2014). All sites contained ample blue ash regeneration at levels comparable to the most abundant species and growing at least as quickly. Finally, the number of new blue ash seedlings provides evidence of continued viable seed inputs that will maintain a genetically diverse input of further regeneration. All of these components are supportive of the potential for sustainable canopy replacement by blue ash, at least in part, within blue ash-dominated stands. Continued blue ash persistence requires a constant input of viable seeds, which can be accomplished by the establishment of a new cohort if they grow to reproductive maturity quickly 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 southeastern 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. Indiana, Ohio, and Kentucky), blue ash stands are more common on limestone soils of dry uplands (Prasad et al., 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 (Kashian, 2016), 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 its geographic range are needed for better predictions of the future of blue ash in North American forests.

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