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The Persistence of Blue Ash in the Aftermath of Emerald Ash Borer May Be Due to Adult Oviposition Preferences and Reduced Larval Performance

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The persistence of blue ash in the aftermath of emerald ash borer may be due to adult oviposition preferences and reduced larval performance

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Abstract

1. We examined the health of mature blue ash, *Fraxinus quadrangulata*, in two forests in southwestern Ohio in relation to that of mature white ash, *F. americana*, and examined the potential importance of oviposition preferences and larval resistance in the persistence of blue ash.
2. Both blue ash and white ash were largely unaffected by emerald ash borer in 2012. By 2018, nearly 90% of the blue ash trees observed in these forests had full or nearly full canopies, as opposed to less than 20% of the white ash encountered in our studies. In 2021, blue ash maintained a similar degree of canopy health as in 2018, but no standing live mature white ashes remained.
3. Bark removals revealed no current or past larval feeding attempts in blue ash in 2018 or 2021, except for one attacked and killed tree in 2018. All white ash trees examined were attacked. In a laboratory bioassay with cut stems, emerald ash borer larvae fed less and grew significantly more slowly on blue ash than on white ash.
4. Both reduced larval performance and reduced adult oviposition likely contribute to the persistence of blue ash in forests devastated by emerald ash borer.

KEYWORDS
Buprestidae, emerald ash borer, larvae, oviposition, tree resistance

INTRODUCTION

Persistence of a plant species in the face of rapidly-spreading invasive insects is associated with the degree to which it attracts or deters oviposition by adults, as well as resists and tolerates attack should adults choose to oviposit on it. Emerald ash borer (*Agrilus planipennis* Fairmaire, EAB) (Coleoptera: Buprestidae) is an Asian wood-boring beetle that is invasive in North America that has killed hundreds of millions of ash trees (*Fraxinus* spp.) (Herms & McCullough, 2014). Relative to its primary Asian host species, Manchurian ash (*Fraxinus mandshurica*), EAB shows increased adult and larval performance on North American ash species and is consequently more damaging to them (e.g., Rebek et al., 2008). Adult feeding rates and survival on foliage and their oviposition preferences generally correlate with larval performance of this beetle in the phloem across species. The order of oviposition preference and adult and larval feeding performance for major eastern *Fraxinus* species by EAB (from best to worst) appears to be green ash (*F. pennsylvanica* Marshall) and black ash (*F. nigra* Marshall), white ash (*F. americana* L.), and, finally, blue ash (*F. quadrangulata* Michx.) (Anulewicz et al., 2006, 2008; Tanis & McCullough, 2012, 2015).

Blue ash appears to be surviving in the aftermath of EAB throughout the Midwestern United States at a much higher rate than other ash species. In Michigan, survival and health of blue and white ash trees were examined over several years throughout an EAB infestation. Significantly fewer white ash survived the infestation over the course of 3 years than did blue ash, and 60% of surviving blue ash trees were considered 'healthy' (Tanis & McCullough, 2012). Another study in Michigan found that blue ash trees had higher survival rates, fuller canopies, and were larger and older, on average, than the white ash in the study because most of the older and larger white ash trees succumbed to attack (Spei & Kashian, 2017).

The persistence of blue ash in the face of EAB attack could be due to several factors, including being less attractive to adults for oviposition, being a poorer substrate for adult foliar feeding, possessing increased larval resistance in the phloem, and exhibiting a higher tolerance of damage after attack. In the only study to address adult attraction to blue ash, blue ash bolts received fewer EAB eggs in the field than bolts of other more susceptible ash species in early host range tests in North America (Anulewicz et al., 2008). In terms of larval performance, Anulewicz et al. (2006) found that EAB larvae established a similar density of feeding galleries on blue ash as on black, white, and green ash in no-choice bioassays using adults caged on stems. Peterson et al. (2015) found that a similar proportion of EAB larvae from inoculated eggs developed and reached the prepupal stage on cut blue ash stems as on cut green ash stems, but they took much longer to do so. This indicates that blue ash is a poorer substrate for larvae although significant damage can still be accumulated across a season. In a similar vein, Olson and Rieske (2019) found that EAB larvae survived at a lower rate and fed slightly less on cut stems of blue ash than on cut stems of white ash. In the same study, field-grown blue ash trees produced a much higher level of callous tissue around artificial wounds than field-grown white ash, which suggests a heightened ability to repair phloem damage by this species. Finally, Tanis and McCullough (2015) found that young blue ash trees exposed to wild EAB in a plantation in Michigan harboured substantially fewer feeding galleries and live larvae than that observed in black, green, or white ash of similar age, which may have resulted from either oviposition preferences, host resistance, or both.

In this study, we sought to determine if there would be similar patterns in the persistence of blue and white ash trees in two 'EAB aftermath' forests in Ohio as has been observed in Michigan, and to assess the potential for adult oviposition preferences and larval resistance to be possible explanations for the persistence of blue ash. We first compared the canopy health ratings of mature white and blue ash trees in Glen Helen Nature Preserve in Yellow Springs, OH in 2018 and again in 2021. Ash trees in this preserve were first infested by EAB in ~2011 (Cipollini, 2015), and a survey in 2012 at this site indicated that most of the mature white and blue ash trees present in this preserve were healthy at that time on the basis of a standard ash tree canopy rating system (e.g., Knight et al., 2014; D. Cipollini, personal observation). We hypothesized that by 2018 and persisting in 2021, blue ash trees would continue to survive and maintain their health better than white ash trees, in accordance with other studies. We conducted a similar study of tree health of mature blue versus white ash trees in the Wright State University Woods in 2018 and again in 2021 and also examined larval feeding gallery densities as a proxy for comparative attack rates. We expected to observe greater persistence of blue ash and less historical evidence of feeding galleries in blue ash than in white ash. Lastly, we compared EAB larval performance on blue and white ash trees in cut stem bioassays using stems cut from trees in the Wright State University Woods. We predicted that performance of EAB larvae on cut stems would be poorer on blue ash than on white ash.

METHODS

White and blue ash were historically very abundant in Southwestern Ohio, including in the two natural areas that we studied. We first assessed the canopy health of mature blue ash and white ash trees in June 2018 in Glen Helen Nature Preserve in Yellow Springs, OH (39.8041°N, 83.8817°W). This 1100-acre preserve is primarily a mature, deciduous forest with predominantly oak, sugar maple, walnut, and, previously, ash trees inhabiting it prior to the invasion of EAB. Trees were examined that were growing in the vicinity of the Talus Trail, Lower Birch Creek Trail, and Inman Trail in a ~5-acre area. We haphazardly selected 31 standing blue ash and 30 standing white ash trees, with a minimum size of 10 cm DBH, throughout this area to examine. Canopy health of each tree was rated on a scale from 1 to 5, based on the Knight et al. (2014) canopy health condition rating system. A tree with a canopy rated as 1 has a full and healthy canopy, a canopy rating of 2 has leaf thinning, but no significant dieback, a rating of 3 has less than 50% of dieback, a rating of 4 has more than 50% dieback, and a rating of 5 is a completely dead tree with no leaves, but it may still have epicormic sprouts on the trunk. The DBH was measured for each tree as well. As part of the survey in 2018, we reassessed five marked trees of each species from a similar survey done in 2012 when EAB was first confirmed in this area and when none of the blue and white ash trees were yet exhibiting any dieback (Thiemann et al., 2016). These trees were among the 61 trees examined in 2018. The measured blue ash trees averaged 86.4 ± 47.7 cm in DBH while white ash trees averaged 78.0 ± 45.5 cm in DBH. We repeated this study in July 2021 with 33 blue ash trees and 8 white ash trees. Trees were not tagged in 2018, so trees examined in 2021 included a few but not all of the trees in the 2018 survey. The measured blue ash trees averaged 52.1 ± 27.2 cm in DBH while white ash trees averaged 42.4 ± 26.9 cm in DBH. Importantly, the majority of the white ash meeting our criteria that were formerly present in the area had died and had fallen since our last survey, reducing the number of white ash that could be examined in 2021.

We were unable to sample the bark of trees in Glen Helen Nature Preserve, thus tree health and larval feeding gallery densities were also observed in October 2018 and in July 2021 in the Wright State University Woods. The Wright State University Woods (39.7853°N, −84.0549°W) is a 225-acre woodlot approximately 20 km west of Glen Helen with a similar tree composition and that has exhibited a similar EAB attack dynamic (Rigsby et al., 2014; D. Cipollini, personal observation). In 2018, five mature white ash and 10 blue ash trees

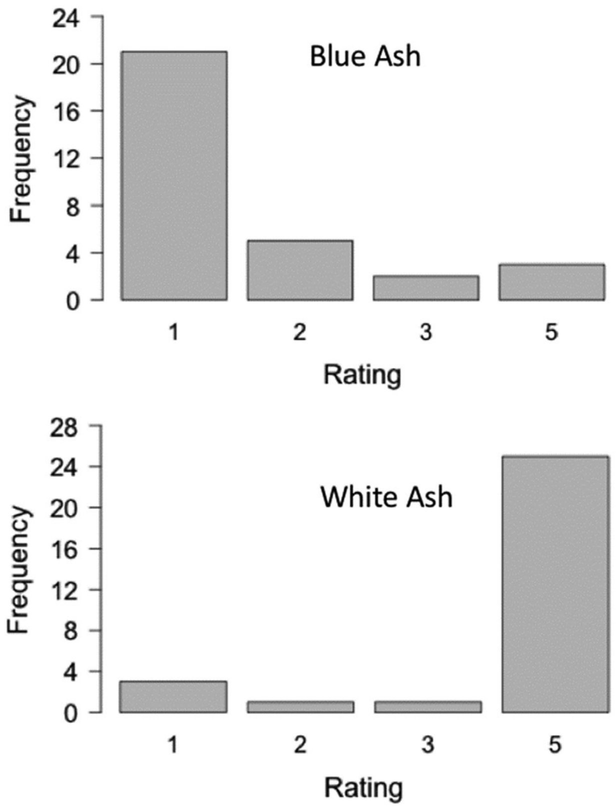

FIGURE 1 Frequency distributions of health canopy ratings of blue and white ash trees in an EAB aftermath forest in Glen Helen Nature Preserve in 2018. $N = 31$ blue ash, $N = 30$ white ash. Trees were rated as described in the methods section: trees with a rating of 1 had an intact canopy and 5 was a dead tree.

were haphazardly selected, measured for DBH and given a canopy rating, as above. The measured blue ash trees averaged 48.6 ± 17.7 cm in DBH, while white ash trees averaged 54.5 ± 19.9 cm in DBH. In addition, a rectangular 567 cm^2 area on each tree was debarked at breast height to expose EAB larval feeding galleries in the phloem and xylem. The 'frame' of the bark window was first cut with a wood chisel down to the cambium layer and then the bark was gently peeled from the tree (see Figure 2). The presence of feeding galleries in the bark window was recorded for each tree, and the percentage of the revealed bark area covered by feeding galleries was visually estimated. In 2021, we surveyed the health of 21 blue ash trees and nine white ash trees, and did bark explorations on five blue ash trees, as above. Trees were not tagged in 2018, so this included a few but not all of the trees examined in 2021. The measured blue ash trees averaged 40.6 ± 19.6 cm in DBH, while white ash trees averaged 59.7 ± 18.9 cm in DBH. As for Glen Helen, there were few white ash still standing that met our criteria for examination at the time of the 2021 survey.

In July 2018, one segment from each of 8 young healthy blue ash and white ash trees was cut from forest-grown trees in the Wright State University Woods for bioassays of EAB larval performance, conducted largely as in Cipollini and Rigsby (2015). Segments were approximately 5 cm in diameter and were cut into 35 cm lengths. The segments were surface disinfected with a 10% bleach solution for 10 min, thoroughly rinsed with distilled water, and dried in front of a fan for 30 min. Each segment was inoculated with five EAB eggs acquired from USDA APHIS PPQ EAB Biocontrol Facility in Brighton, MI, where adult EAB laid eggs on coffee filters in rearing containers. Each egg on the coffee filter was placed on the bark of the branch segment egg side out and wrapped in parafilm to hold it in place. Eggs were spaced 5 cm apart on the stems and 10 cm above the bottom of the segment, so the bottom end of each segment could be submerged in a tub of water. The segments were placed in a 25°C incubator on a 16:8 light: dark cycle and rotated periodically within the incubator to minimize microenvironmental effects. Hatch rates were checked 1 week later. Stems were debarked, and larval performance was measured in terms of gallery width and mass of recoverable larvae 6 weeks after egg placement. Some larvae were damaged and unmeasurable in the debarking process, so we emphasize larval feeding gallery width in our analyses. The maximum width of a feeding gallery produced by an EAB larvae correlates strongly with the mass of the larva making that gallery (Peterson et al., 2020). While it is possible that some tree defences are hampered in cut stems relative to live trees such that insect performance may be enhanced, numerous studies have shown that expected constitutive differences in the degree of resistance expressed by different host species for EAB are retained in this assay (Cipollini & Rigsby, 2015; Peterson et al., 2015; Peterson & Cipollini, 2020).

Statistical analysis

Differences in the distribution of canopy health ratings for blue and white ash trees during 2018 were assessed with Chi-Square analyses using JASP (Site). Since so few white ash survived, health rating distributions were not statistically compared between species in 2021. Given the lack of attack on blue ash recorded in the field at Wright State Woods, gallery densities on white and blue ash were also not statistically compared. Differences in hatch rate, larval survival, gallery width, and larval mass in blue and white ash trees were each examined using one-way ANOVA with tree species as the main effect.

RESULTS

Glen Helen-The distribution of trees in different categories of canopy health differed significantly between blue and white ash trees ($X^2 = 33.778$, $p < 0.001$) sampled at Glen Helen in 2018. Approximately 87% of blue ash trees in the survey were considered healthy (categories 1 or 2) whereas only about 16% of white ash trees were considered healthy (Figure 1). Conversely, only 12% of blue ash trees were unhealthy or dead (rating of 4 or 5) while 86% of white ash trees were unhealthy or dead (Figure 1). By 2021, all of the 33 blue ash trees surveyed were in the healthy categories (ratings 1 and 2) in Glen Helen, with an overall canopy health rating of 1.2. Two blue ash trees had external signs of EAB attack, but still had canopy ratings of 1. All

FIGURE 2 Typical degree of feeding by emerald ash borer larvae on white ash (left) and blue ash (right) observed in the Wright State University Woods in Fall 2018. Bark sections were removed at breast height to reveal feeding galleries.

eight mature white ash trees surveyed were dead and all had been severely impacted by EAB attack.

Wright State University woods-There were substantially more larval feeding galleries found in white ash than in blue ash in the Wright State University Woods in 2018, and all five standing mature white ash trees examined that year were dead. All five white ash trees examined possessed larval feeding galleries in the section of bark that we assessed, whereas only one out of 10 blue ash trees possessed any evidence of larval feeding galleries (Figure 2). The larval galleries exposed on white ash trees covered between 40% and 85% of the bark area exposed, while the single blue ash tree with galleries had 30% coverage. The single blue ash that was attacked by EAB was killed, but the other nine averaged 1.7 in canopy health ranking. Similar patterns were observed in 2021. All of the 21 blue ash trees sampled were in the healthy categories, with an overall average of 1.3 in canopy rating. The five trees in which bark explorations were made revealed no evidence of larval feeding galleries. Only one blue ash tree had external signs of EAB attack (but did not have the bark explored), but it remained in the highest canopy health category. All nine mature white ash trees examined in 2021 were dead (and many trees were down) and all had been severely impacted by EAB attack.

Larval bioassays-There was no significant difference in the average hatch rate of EAB eggs on white and blue ash in the bioassay ($F_{1,7} = 0.548$, $p = 0.471$). There was also no significant difference in the proportion of larvae that established a feeding gallery on white and blue ash ($F_{1,7} = 0.105$, $p = 0.471$). The average mass of the larvae recovered at harvest on white ash was 33.2 ± 5.3 mg, which was significantly greater than that of the larvae recovered at harvest on blue ash (9.7 ± 4.1 mg) ($F_{1,7} = 11.025$, $p = 0.016$). Larvae also produced significantly wider galleries on white ash than on blue ash: 3.57 ± 0.6 mm versus 2.72 ± 0.37 mm, respectively ($F_{1,7} = 17.585$, $p = 0.002$).

DISCUSSION

In 2012, healthy mature blue and white ash were abundant in forests throughout southwestern Ohio, which was true for the areas that we surveyed in this study (D. Cipollini, personal observation). By 2018, there was a four-fold higher proportion of mature blue ash considered healthy than white ash among the trees we sampled at Glen Helen Nature Preserve, which is consistent with previous studies conducted in EAB-aftermath forests in Michigan (Spei & Kashian, 2017; Tanis & McCullough, 2012). By 2021, that percentage remained high for blue ash, but most of the white ash that met our criteria for examination were dead. These patterns were similar in trees examined in the

Wright State University Woods in 2018 and 2021 and are commonly observed in other forests and woodlots throughout southwestern Ohio (D. Cipollini, personal observation). Finding mature white ash (or other susceptible ash species) healthy enough to produce a good seed crop is increasingly rare in this part of Ohio, while finding large mature blue ash within the historic range of this species in the state is still common (D. Cipollini, personal observation). While long-term trends are still unclear, these findings indicate that blue ash can generally survive the onslaught of extremely high densities of EAB that can occur at the peak in the invasion wave and that it continues persist in a healthy state well after the peak densities have passed. Significant reductions in EAB densities and reduced pressure on hosts that followed the loss of preferred ash species further benefit their persistence.

We found EAB larval performance to be poorer on blue ash than on white ash, which is consistent with previous studies (Peterson et al., 2015; Olson and Rieske, 2019). In a study using cut stems by Peterson et al. (2015), larvae developed more slowly on blue ash than on white ash, but a similar proportion made it to the fourth instar. Olson and Rieske (2019) found poorer survivorship and slightly reduced feeding of larvae on blue ash compared to white ash. In our study, we found more drastic differences, including significantly smaller gallery widths, far fewer live larvae and larvae with much smaller mass on blue ash than on white ash. This was true despite there being similar hatch rates and initial gallery establishment on the cut stems. While never directly compared in the same study, performance of EAB larvae on blue ash across several studies appears to be better than that usually observed on Manchurian ash, the ancestral host of EAB (Rigsby et al., 2019), but generally worse than that observed on black, green, and white ash. The source of variation in EAB larval performance among different ash hosts is not yet clear, especially involving blue ash, although a number of biochemical mechanisms have been suggested (e.g., Villari et al., 2016).

The one blue ash tree in which we confirmed EAB attack in the Wright State Woods in 2018 was killed and it is well known that EAB can kill blue ash in the field (Tanis & McCullough, 2012, 2015). Therefore, the level of phloem-based resistance shown by blue ash does not always protect them from mortality by EAB should adults choose to oviposit on it. Rigsby et al. (2014) found that EAB exhibit behaviours consistent with the 'mother knows best' hypothesis, whereby adult females preferentially lay eggs on species on which their larvae will perform best. For example, across 2 years at two common garden sites in Michigan and Ohio, adult EAB showed strong oviposition preferences for black, green and white ash, while its resistant ancestral host, Manchurian ash, was almost universally rejected as an oviposition site (Rigsby et al., 2014). Manchurian ash becomes much more attractive to adults and exhibits hampered resistance to larvae when it is stressed (Chakraborty et al., 2014; Showalter et al., 2018; Rigsby et al., 2019; D. Cipollini, personal observation). In a study examining interspecific variation in attack rates and larval success in the bark of ash trees, Anulewicz et al. (2008) found significantly lower egg deposition and lower gallery densities on blue ash than on white ash, although adult EAB would readily lay eggs and larvae would establish galleries on blue ash when adults were caged on the stems (Anulewicz et al., 2006). In our study in the Wright State Woods, we saw no historical evidence of EAB attack on mature blue ash in nine of the 10 trees that we examined with bark explorations in 2018 and in none of the five additional trees we explored this way in 2021. This entailed even less apparent attack on blue ash by EAB than seen by other researchers (e.g., Tanis & McCullough, 2012). In contrast, nearly all mature white ash trees had been attacked and killed in these woods by EAB by 2021 and it is not uncommon to find attacked and killed white or green ashes located within a few meters of completely healthy blue ash trees (D. Cipollini, personal observation). It is possible that we were not able to observe small, failed feeding attempts in our debarking process, but almost none of the blue ash trees in our surveys showed signs of even partially successful feeding galleries. There may also have been larval feeding galleries found higher in the canopy of the blue ash trees where EAB typically first attacks a tree that we were unable to observe, but in contrast, all white ash trees examined had readily observable galleries at breast height, as well as others dispersed throughout the entire tree. If EAB had attempted establishment in blue ash at points higher in the tree canopies, it had little observable impact on the trees during the time of our surveys. Variation in attraction of adults to hosts for feeding and oviposition is typically attributed to differences in the quality and quantity of the volatiles produced by ash trees (Peterson et al., 2020; Pureswaran & Poland, 2009; Rigsby et al., 2017). Blue ash trees vary to some degree in the composition and concentration of volatiles from more preferred ash tree species (Peterson et al., 2020; Pureswaran & Poland, 2009), which may explain the apparent reduced adult preference for blue ash. Regardless of the mechanism, we conclude that reduced attraction of EAB adults to blue ash (or active avoidance of it) and limited oviposition on this species is likely an important factor responsible for the persistence of blue ash through the invasion wave of EAB. For EAB, 'mother knows best' (sensu Rigsby et al., 2014) in terms of the reduced larval performance that would be expected on this species.

As the majority of the white ash and other preferred ash species have been decimated in Midwestern forests, EAB could respond in several ways. EAB still exists at low densities in these forests, persisting on younger ash trees that had previously escaped being killed during periods of higher EAB densities. These trees have subsequently benefited from a growth period with low EAB densities in recent years, but they will provide food for growing EAB populations in the future until their health is significantly affected and EAB densities decline again. EAB seems to have continued to largely find blue ash trees unattractive throughout this population dynamic and may not substantially affect populations of this species. By reducing competition from other susceptible ash species, EAB could conceivably benefit populations of blue ash in forests where multiple species had existed, as long as blue ash continues to reproduce (Spei & Kashian, 2017). While it seems that EAB could turn increasingly to blue ash when populations of more preferred ash species are completely wiped out, observations in the field do not support this pattern as of yet (D. Cipollini, personal observation). Tree stress may alter the relationship of EAB with blue ash as well, since stresses such as drought and wounding are known to make even relatively resistant species attractive and to increase their susceptibility to larval feeding (Chakraborty et al., 2014; Peterson & Cipollini, 2020; Rigsby et al., 2019; Showalter et al., 2018; Tluczek et al., 2011).

AUTHOR CONTRIBUTIONS

Don Cipollini: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review andediting. **Emily Morton**: investigation; formal analysis; visualization; writing - original draft; writing - review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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