BLACK ASH LITERATURE REVIEW

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TABLE OF CONTENTS

INTRODUCTION

The emerald ash borer (*Agrilus planipennisi*) is native to China, Korea, Japan, Mongolia, Taiwan, and eastern Russia where it exists in low levels and feeds on Manchurian ash (Haack et al., 2002). In 1998, Emerald Ash Borer (EAB) was accidentally introduced to Detroit, Michigan, likely as a stowaway in solid wood packing material (Poland & McCullough, 2006). From 1998-2006, EAB became established in North America, and the infestation advanced at a rate of approximately 20 kilometers per year, however the cause of ash decline was unknown (Prasad et al., 2010). In June 2002, five entomologists collected five iridescent green beetles while visiting a site exhibiting signs of significant ash decline (Cappaert et al., 2005). By July of 2002, the beetles from this site were identified as *A. planipennisi*, and quarantine measures were enforced in Michigan.

The rate of short-distance EAB dispersal in North America has been, and continues to be, a product of both insect flight and human activities such as moving firewood (Prasad et al., 2010). Human activity is also responsible for long-distance ash transportation that has spread EAB to new locations where they form satellite populations, which grow and eventually coalesce with existing populations, thereby accelerating the rate of spread (Herms & McCullough, 2014). There is typically little evidence of an EAB infestation for the first four years after establishment, which poses significant challenges for detection and management (McCullough & Mercader, 2012).

These non-native beetles appear to exclusively colonize species within the ash (*Fraxinus*) genus (Herms & McCullough, 2014). In early infested forests in North America, EAB ash mortality ranges from 80% to greater than 99% (Burr & McCullough, 2014; Herms, Gandhi, et al., 2009; Smith et al., 2015). Resistance is most often detected in white ash, occasionally detected in low quantities in green ash, and has yet to be detected in black ash. Studies on the spread of EAB and the susceptibility of North American *Fraxinus* species to EAB infestation indicate that EAB could functionally extirpate all native *Fraxinus* species from North America (Herms & McCullough, 2014).

EAB has become the most destructive invasive forest insect in the history of the United States (McCullough & Mercader, 2012). The impacts of ash mortality are complex, and have ecological, cultural, and economic implications (Herms & McCullough, 2014). Pests and pathogens, such as EAB, are biotic agents that can have dramatic effects on forests, carbon storage, and resilience to ongoing climate change (Flower & Gonzalez-Meler, 2015). Cultural effects are less amenable to quantification, but are deeply important to consider, as ash trees are a spiritual resource for many First Nations and Native American peoples (Herms & McCullough, 2014). A 2010 study simulated the spread of EAB through North America from 2009-2012, and estimated the cost associated with treatment, removal, and replacement for the infested trees on developed land – the experiment yielded a value of $10.7 billion dollars, a cost that warrants ongoing attempts to slow the spread (Kovacs et al., 2010).

EAB LIFECYCLE

Adult female EAB deposit eggs on ash bark, preferably in crevices or highly textured locations, in late June or early July (Bauer, Haack, et al., 2004; Wei et al., 2007). The eggs are approximately 1 mm wide, and are initially white before transitioning towards a more amber hue (Bauer, Haack, et al., 2004). After 9.0 ± 1.1 days, the eggs hatch into larvae (Wei et al., 2007).

EAB larvae have four instars, and remain in the larval stage for an average of 308 days or 673 days depending on whether EAB in that location exhibit a one- (univoltine) or two-year lifecycle (semivoltine). Two-year lifecycles are less common, but have been observed in both China and North America (Bauer, Haack, et al., 2004; Wei et al., 2007). When the larvae hatch, they tunnel into the ash bark in search of their food source, the cambium layer (Bauer, Haack, et al., 2004). Upon reaching the cambium, the EAB larvae tunnel up the tree in ever-widening switchbacks – the larger they grow, the larger the tunnel and the wider the path. This feeding pattern creates serpentine-like galleries in the phloem and sapwood of the tree, with nearly half of girdling occurring on the south quarter of the tree bole (Wei et al., 2007). An exception to this activity occurs in ash branches less than 2 cm in diameter, where EAB larva are unable to enter the xylem, possibly because smaller branches don't supply sufficient nutrients for EAB development.

At the end of the fall, the larvae tunnel into the bark and excavate an overwintering chamber (Bauer, Haack, et al., 2004). Come spring, the larvae pupate for approximately 62 days before emerging as adults from D-shaped exit holes (Bauer, Haack, et al., 2004; Wei et al., 2007). Adults live for an average of three weeks (Wei et al., 2007), are most active during warm and sunny days from 3-6 pm (Bauer, Haack, et al., 2004), and feed exclusively on ash foliage. EAB adults appear to prefer trees with high sun exposure and mature leaves, perhaps because of the reduced concentration of defensive compounds (Chen & Poland, 2009). Female adult EAB require at least one week of maturation prior to mating Bauer, Haack, et al., 2004). After mating, the females continue to feed for 5-7 days before laying their eggs. An initial study found that over half of EAB adults dispersed fewer than 50 meters in 24 hours (Bauer, Miller, et al., 2004), while a more recent flight mill study found that mated females dispersed farther than other EAB adults, with a median distance of more than three kilometers flown per day (Taylor et al., 2010). Each female EAB beetle can lay between 50-90 eggs in her lifetime (Poland & McCullough, 2006).

Several research teams have simulated wounds on ash trees to determine what factors attract EAB adults. In these experiments, freshly girdled ash trees yield the highest larval densities and highest counts of adult EAB beetles, indicating that EAB is most attracted to sick or weakened trees (McCullough, Poland, Anulewicz, & Cappaert, 2009; McCullough, Poland, & Cappaert, 2009). EAB capture was also highest in areas with full or nearly full sun (McCullough, Poland, & Cappaert, 2009).

As EAB feed on the phloem of an ash tree, the tree loses its capacity to draw water up the trunk (Flower et al., 2010). Over time, the tree becomes increasingly water stressed and takes up more carbon-13. Why Carbon-13? Carbon-12 and Carbon-13 both exist freely in the Earth's atmosphere, and most plants prefer Carbon-12. However, stressed plants don't discriminate between available carbon isotopes. There is significant positive correlation between Carbon-13:12 ratios in ash leaves, Carbon 13:12 ratios in EAB adults and prepupae, number and density of larval galleries, and canopy decline. In areas that are known to have an active EAB infestation, canopy assessments (a survey with values from 1-5) are a good analogue for EAB stress currently experienced by an ash tree. In both white and green ash, 10% canopy dieback equates to approximately 8-9 EAB larvae per meter (Anulewicz et al., 2007).

However, monitoring the spread of EAB is a challenging task, as infestations are difficult to detect in the first four years (McCullough & Mercader, 2012). This challenge underscores the importance of implementing trapping and other EAB detection strategies to track early arrival of EAB, and respond to the spread (Crook & Mastro, 2010). EAB beetles use volatile odors to differentiate between ash and other trees, and are attracted to some colors, but not to others (McCullough & Poland, 2009). These observations have led to the development of several effective trapping designs that combine these compounds and colors, including (Z)030hexenol (Z3-6LOH) in light green prism traps (Grant et al., 2010), and green leaf alcohol mixed with Manuka oil in double decker triangular purple traps (McCullough & Poland, 2009). (Z)-3-hexenol also elicits a strong response from EAB adults (Chen & Poland, 2009).

IMPACTS ON THE FRAXINUS GENUS

As of 2013, there were approximately 8.7 billion ash trees and saplings in the lower 48, comprising about 2.5% of the aboveground carbon (Flower et al., 2013). Forest Inventory and Analysis National Program (FIA) data from 2010 revealed that North America's *Fraxinus* population contained approximately 1.9 Pg of aboveground carbon, which contributed about 1.5% of the world's gross primary productivity (Flower et al., 2010).

In North America, ash trees are often a minor component of forested ecosystems, with white, blue, and Oregon ash occurring in fertile uplands and floodplains (MacFarlane & Meyer, 2005). Green, Carolina, and pumpkin ash tend to occur in river bottoms and wetlands, and black ash is most frequently observed in bogs and swampy areas. Velvet and single-leaf ash occupy drier environments, like semi-deserts and canyons. Simulating EAB-inflicted disturbance in forested landscapes yields a reduction in forest productivity, a result that is most pronounced in forests with a larger *Fraxinus* component (Flower et al., 2013).

In North America, there are at least 282 arthropod species that associate with *Fraxinus* species (Gandhi & Herms, 2010). 43 of these arthropod species associate exclusively with ash, and are therefore threatened by widespread ash mortality. The 239 other arthropod species may transfer to other plants, increasing their feeding impact on those plant species or experiencing a reduction in arthropod population. There will be additional and cascading effects on fungal, bacterial, and invertebrate associates, as well as parasites, vertebrate, and invertebrate predators and mutualists.

Ash trees exist in communities with other trees, and herbaceous plants. Mortality has trickle down effects on the surrounding plant community (Bethel et al., 2014). These effects are expected to be most pronounced in areas with higher ash importance values, such as hydric environments. Hydric environments also have higher Simpson's diversity values, lower canopy cover, and higher ground cover than mesic or xeric sites. Density of invasives, however, did not correlate with ash importance value or the percent of study plots that contain canopy gaps.

Studies looking at the effects of EAB on populations of ash trees have generally found dire results. In the Huron River Watershed in southeast Michigan, more than 99% of ash >2.5cm in diameter have succumbed to EAB mortality (Herms et al., 2010). In sites nearest to the EAB epicenter in Michigan, mortality exceeded 99% by 2009 (Klooster et al., 2014). In Michigan and Ohio, there are sites that experienced 100% mortality of canopy ash trees, and low levels of EAB were still detected in 2012.

In a study of five different ash species, black and green ash were most susceptible to EAB (Tanis & McCullough, 2015). White ash was also highly susceptible, while blue ash exhibited moderate resistance, and Manchurian ash was relatively resistant. These trends have been documented in prior studies throughout the Great Lakes Region. In southeastern Michigan, there was significant EAB mortality in all stands across the study area (Smith, 2006). Black ash had more advanced die back, a higher percent morality, more infested stems, and more frequent EAB attacks than in white and green ash. Blue ash trees frequently exhibited tissue growth over the larval galleries, which likely contributes to their moderate resistance (Anulewicz et al., 2007). EAB seem to prefer green ash over white ash, but prefer white ash over blue ash. As infestations progress and available green ash phloem decreases, EAB switches to the less preferred trees.

Healthy ash stands infested with EAB can succumb to almost complete mortality within six years (Knight et al., 2013). More rapid declines occur in forests with lower densities of ash where EAB larvae become highly concentrated on the relatively fewer trees that are present. Shaded trees and trees that show early signs of canopy decline are also more likely to quickly succumb to EAB mortality. After EAB infestation, ash stands tend to progress from healthy to nearly complete mortality within 5-7 years (Knight et al., 2010). Ash decline tends to occur more rapidly in forested areas with lower concentrations of ash, as well as in more mesic sites (Knight, Herms, et al., 2012). Individual trees that show early canopy dieback are among the first trees to succumb to EAB-induced mortality, as are more shaded trees (Knight, Herms, et al., 2012). Some ash trees have succumbed despite a lack of exit holes (Anulewicz et al., 2007). When debarked, the trees were extensively girdled, but all larvae had died as second or third instars due to intraspecific competition (Anulewicz et al., 2007).

Despite increased stress from EAB, ash trees aren’t responding with bumper crops of ash seeds (Herms et al., 2010). After mature ash trees succumb to EAB, the seed bank is rapidly depleted. In ash stands that succumbed to complete mortality in Michigan and Ohio, there were no viable seeds found after 2007/2008 (Klooster et al., 2014). Seedling density also dropped precipitously – one study found only 0.1 ash seedlings per hectare after infestation, while a healthy ash stand boast 800-20,000 seedlings per hectare (Herms et al., 2010). Because ash as small as 2.5 cm diameter can be infested, it is unlikely that these seedlings and saplings will persist until seed-bearing age (Herms et al., 2010; Klooster et al., 2014). These findings predict functional extirpation of North American ash species, unlike elms which can still persist until flowering and seed-bearing age despite the presence of Dutch Elm Disease.

Three management options for slowing the spread of EAB include removing ash trees, girdling ash trees, and insecticide (Mercader et al., 2011). While removing ash trees reduces EAB population size, there is no impact on the rate of spread compared to a no-management scenario. Girdling trees attracts ovipositing female EAB, and the girdled trees are later destroyed before the growing larvae can complete development. This treatment slows the spread of EAB by approximately 15%. Systemic insecticide applications resulted in a 30% decrease in radial spread, the greatest impact of the three management options that were evaluated. Because ash decline tends to occur more rapidly in forested areas with lower concentrations of ash, there is little evidence that forest thinning will protect remaining ash trees (Knight, Herms, et al., 2012). However, when ash creates a management concern, those that are the most stressed should receive priority for removal.

Trees that exhibit positive responses to EAB infestations include species in the *Acer* and *Ulmus* genera (Flower et al., 2013). Despite positive responses to EAB infestations in some species, the overall effect is a significant net decline, which leads to reduced carbon storage of the system and decreasing soil respiratory fluxes (Flower et al., 2013).

Lingering ash, or ash persistence, can take several forms. Four mechanisms of persistence observed in green ash include: resistant canopy trees, advanced regeneration, basal sprouts, and new cohorts that arise from existing seed banks (Kashian, 2016). There is evidence that in some forests, green ash may be able to resist the EAB infestation (Knight, Herms, et al., 2012). If lingering ash do persist, remnant populations may represent elms after Dutch Elm Disease rather than American Chestnuts, as elms in the northern forest often reach reproductive age before becoming infected, while American chestnuts die before flowering and fruiting. Within studied locations, approximately 1% of ash trees remained healthy after all other ash trees had succumbed to EAB-induced mortality. Observations suggest that healthy trees have remained healthy throughout the infestation, while declining trees continue to decline until they succumb to mortality. In other locations, white ash exhibiting initial canopy decline persisted and then improved, despite ongoing detection of EAB within the stand (Robinett et al., 2021). These findings provide an opportunity to further investigate the observed ash resistance, and may eventually lead to ash reforestation efforts.

BLACK ASH NATURAL HISTORY & ECOLOGY

Freshwater ecosystems are threatened on a global scale (Dudgeon et al., 2006), and forested wetlands are among the most threatened ecosystems in the U.S. (Dahl, 2011). Black ash are slow growing trees of forested, depressional wetlands (Burns & Honkala, 1990). With no known resistance to EAB, black ash are at risk of functional extirpation (Herms & McCullough, 2014). As a foundation species, ecological roles of black ash include moderating forest composition, mediating hydrological regimes, contributing to nutrient cycling, and storing carbon (Ellison et al, 2005). When a foundation species is affected or removed, the system is knocked out of balance, and the existing state of equilibrium is dramatically altered. This has extensive repercussions for the rest of the natural community to which the foundation species is connected.

Indigenous people have observed a decline in black ash since before EAB arrived in North America (Costanza et al., 2017). Factors that might be contributing to black ash decline include: (1) Anthropogenic activities such as road building that changes hydrologic flow, runoff of road salt, car and truck emissions and pollutants (Ward et al., 2006); (2) Diseases such as leaf spots, cankers, powdery mildew, and rusts; (3) Pests including carpenterworm (*Prionoxystus robiniae*) and fall webworm (*Hyphantria cunea*) (Benedict & David, 2003). Today, EAB is the biggest threat to the future of black ash.

The native range of black ash reaches from eastern North Dakota to southeastern Manitoba to northwest Newfoundland to Delaware, where black ash is a slow growing tree of forested, depressional wetlands (Benedict & David, 2003; Burns & Honkala, 1990). While large old growth black ash stands exist in North America (>200 years old), they are uncommon (Costanza et al., 2017). These swamps and floodplains are poorly drained or seasonally inundated (Burns & Honkala, 1990), and are often characterized by muck and peat soils, but are occasionally in sandy or loamy soils underlain by clay or an impermeable layer (Eyre, 1980). Black ash can tolerate a pH ranging from 4.4 to 8.2 (Godman & Mattson, 1976). These small trees prefer hummocky sites (Benedict & David, 2003), and are generally classified as shade intolerant (Harlow et al., 1979).

Black ash rarely grow larger than 60 feet in height, and 12-20 inches in diameter (Wright & Rauscher, 1949). While black ash are generally slow growing trees, they exhibit the highest growth rates when there is spring flooding, followed by summer drying (Slesak et al., 2014). They are opposite branching, with pinnately compound leaves (Stephens, 1973). Most leaves have 7-11 leaflets, averaging 9 leaflets per leaf. Both male and female ash produce flowers in May or June, just before leaf out (Schopmeyer et al., 1974). The pollen from the male flowers is then dispersed by wind, and pollinates the female flowers (Wright, 1953). The fruits, single-seeded samaras borne in terminal or axillary clusters, mature from June to September (Schopmeyer et al., 1974). The seeds require cold stratification prior to germination. In the average natural cycle, seeds germinate two years after maturation, but may remain viable for up to 8 years. Good seed crops occur in intervals of approximately four years (Schopmeyer et al., 1974), and sexual reproduction is not correlated with flooding (Tardif et al., 1994). Black ash is also capable of asexual reproduction via vegetative sprouting (Burns & Honkala, 1990). Hypertrophied lenticles present on the stems of young black ash likely serve as an adaptation that allows young black ash to tolerate periods of soil inundation and associated soil anoxia.

Black ash has numerous ecological roles, including readily observable functions such as providing food for wildlife (Anderson, 2006). Numerous species consume black ash seeds, including wood ducks, quail, bobwhite, purple finches, pine grosbeaks, beavers, porcupines, white-footed mice, and turkeys. Ungulates, including moose and deer, browse on the young shoots of black ash seedlings and saplings.

However, not all ecosystem functions are as visible. Since the discovery of the North American EAB infestation in 2002, North American scientists have been testing the ecological functions of black ash. Their findings are summarized below.

Forest Composition

1. In Ottawa National Forest, there are extensive wetland complexes that offer unparalleled opportunities to study black ash response to EAB simulations (Davis et al., 2017). One such study compared three treatments: (1) control, (2) girdle, and (3) ash-cut. Girdling and ash cutting were meant to simulate short- and long-term effects of EAB infestation. All *Fraxinus* with diameters greater than 2.5cm were girdled/cut, and cut trees remained onsite.

   The results of the experiment indicated that retained canopy trees did not exhibit a significant response to thinning, despite the increase in resource availability (Davis et al., 2017). While there was an observed increase in sapling density in the girdle treatment, it was not a significant increase. There was no detectable change in sapling basal area in the ash-cut treatment. There was also no statistical change in overall large and small woody stems, but there was an observed increase in the density of red maple and yellow birch small woody stems in both the girdle and ash-cut sites. Black ash woody stems remained constant in the girdle and ash-cut sites, likely due to a reduction in seed material, while black ash woody stems increased in the control. The response exhibited by herbaceous species lagged two to three years post-treatment, but strong effects on herbaceous species were observed in both treatments. Notably, non-graminoid obligate wetland species were not observed before treatment, but were detected post-treatment. However, facultative wetland species did not exhibit a change in constituency. It is possible that this indicates a change in the hydrology of the system.

2. Noting the long-term (pre-EAB) decline of black ash in North America, Palik et al looked at stands across Michigan to determine what tree species were replacing black ash through the last several decades of black ash decline (Palik et al., 2012). They found little black ash regeneration or self-replacement, instead noting extensive crown dieback and dead black ash in stands. They found that stands with greater black ash canopy dieback and mortality correlated with stands experiencing black ash sapling dieback and mortality. In the studied stands, the most abundant woody species other than black ash was speckled alder, a species that does not reach canopy standards in these systems. These findings suggest a long-term conversion to open shrubland in historically black ash-dominated stands.

3. A study in Ohio looked at response of red and silver maples following EAB infestation in black ash wetlands (Costilow et al., 2017). The growth of both maple species increased by 72% after EAB infestation, with maples in the intermediate crown class responding most dramatically. Maples also experienced radial growth increases that coincided with ash canopy dieback due to EAB. Findings alluded to possible benefits of decreased below-ground competition in addition to reduced competition for light.

4. An EAB infestation simulation in black ash wetland forests examined the effect of decreasing black ash canopy cover on herbaceous species and ground cover (Looney et al., 2017). The study included four treatment groups: clearcutting, group selection, girdling, and control. They examined the effects of decreasing black ash canopy cover on herbaceous species and groundcover. The results, which are discussed below, indicate

that artificial regeneration is likely necessary to mitigate the impacts of EAB on black ash forests.

Tree regeneration was significantly higher in the clearcut treatment than in the other treatment and control groups (Looney et al., 2017). *Fraxinus nigra* had the highest seedling density, and *Ulmus americana* was the most abundant non-EAB host tree across all groups. Regeneration of other tree species varied by site and by existing tree community. *Quercus macrocarpa* was the third-most abundant species. The height of the herbaceous layer increased, which may contribute to suppression of tree regeneration. However, total ground cover was not significantly impacted. Species richness and diversity increased across treatments. The clearcut and group selection treatments led to an increase in graminoid cover. The control and girdling treatments led to an increase in wetland indicator species. The girdling treatment was associated with an increase in fern cover, which may also suppress tree regeneration.

5. A team examined old growth black ash stands, where black ash reach ages of 200-300 years old (Fraver et al., 2022). They found continuous recruitment every decade over the last 200 years, where recruitment coincided with fluctuations in height of water table. Throughout the last 200 years, there was relatively little disturbance to these stands, with occasional low to moderate severity disturbance events. These findings indicate that once established, black ash is able to maintain dominance in a stand. EAB is likely to have a dramatic impact on these old growth black ash stands.

Aquatic Community

1. Changes in canopy cover and composition, hydrology, and quantity and quality of leaf litter are likely to have impacts on the aquatic invertebrate community (Youngquist et al., 2017). Short term, the increase of downed woody debris may increase aquatic invertebrate diversity. However, in the long-term, changes in landscape composition are expected to negatively impact the aquatic community, and have cascading effects into terrestrial communities. Because insects and amphibians transport nutrients from aquatic into terrestrial environments, the two systems are inextricably connected.

Nutrient Cycling

1. After researching black ash leaf litter cycling in wetland ecosystems, researchers found that both upland and wetland species contributed leaf litter to these systems (Palik et al., 2006). The breakdown rate of black ash leaves was faster than upland leaves, and development of mosquito larvae that fed on black ash leaf litter was higher than for mosquito larvae that fed on upland leaves, specifically quaking aspen and sugar maple. These results indicate that wetlands that receive more upland leaf litter may be lower quality habitat for invertebrates that rely on leaf detritus for their development. Black ash litter breaks down more slowly because it has a lower carbon to nitrogen ratio than in the upland species, making it higher quality litter for leaf detritivores, and causing black ash to contribute more mineralized nitrogen to the ecosystem. Losing black ash from these systems will lead to lower quality conditions for detritivores, and likely impact their population and function.

Hydrology

1. Another study in the depressional wetlands of Michigan looked into the ecohydrological role of three species that often coinhabit these ecosystems, *Betula allegheniensis* (yellow birch), *Acer rubrum* (red maple), and *Fraxinus nigra* (black ash) (Shannon et al., 2018). They measured sap flux response to water level and atmospheric drivers, which are important factors when considering a replacement species for black ash in these ecosystems.

   They found that black ash had a 80-160% higher sap flux rate than non-black ash species at all water levels (Shannon et al., 2018). Another key finding revealed that black ash's sap flux rates increased about 45% as water levels decreased. Both black ash and red maple exhibited increased responses to vapor pressure deficit as water levels decreased. These findings indicate that losing black ash from depressional wetlands will lead to persistently higher water levels. Having too much water relative to average in an ecological system can deplete oxygen in the soil, and inhibit oxygen uptake in roots, thereby inhibiting plant growth (Armstrong & Drew, 2002). Neither red maple nor yellow birch have sap flux rates that can match the ecohydrological function of black ash (Shannon et al., 2018).

2. A six-year study in Chippewa National Forest in northern Minnesota monitored water levels throughout the snow free season (Diamond et al., 2018). The experimental design included six blocks, each with four 1.6 ha circular treatment plots: (1) control plot, (2) all black ash greater than 10 cm in diameter were girdled, which was meant to simulate an EAB infestation without any intervening management, (3) 20% of the black ash overstory in the plot was harvested via eight 0.04 ha gaps, and (4) all trees in the plot were harvested. The third and fourth plot designs were meant to represent possible management strategies for mitigating and adapting to the impacts of EAB.

   The results found that the girdling treatment caused the most impact to the black ash wetland, resulting in the highest water levels (Diamond et al., 2018). This was likely the result of a combination of decreased evapotranspiration and continued shading by standing dead trees, thereby preventing mitigation by sub-canopy evapotranspiration. In some cases, standing water persisted for several years after the initial girdling treatment. The plots where all trees were harvested resulted in a shift to wetter conditions, but results of this study indicated that a clearcut system recovers faster than in the no-management approach. Plots with 0.04 ha gaps recovered the most quickly, suggesting that removing about 20% of the black ash overstory might be a viable mitigation strategy.

3. A study was performed in Minnesota, where the growing season water balance is the result of precipitation and evapotranspiration, and there is little connection to greater groundwater systems, and no surface flow (Slesak et al., 2014). The study included four treatments: clearcutting, girdling, group selection, and a control treatment.

   Clearcutting in black ash wetlands led to delayed water table drawdown, and the average water table level was significantly higher than in the control treatment (Slesak et al., 2014). In sites that received a girdling treatment, which most closely simulates EAB mortality, there was little difference in the first year, but by the second year, the team measured similar results to the clearcutting, namely delayed water table drawdown, and a heightened average water table. In the first year, girdling allows xylem water transport to continue, so has limited effects on soil moisture for at least the first season after treatment (HoÈgberg et al., 2001). There was little change measured after group selection treatment where 20% of the canopy was removed (Slesak et al., 2014). The team attributes their results to reduced transpiration, and in the case of girdling, increased shading that reduced evaporation.

4. A study in the Upper Peninsula of Michigan's Ottawa National Forest measured hydrological changes after girdling and subsequent cutting of black ash trees in forested wetlands (Van Grinsven et al., 2017). The team looked at hydrologic and water table response after disturbance via simulated EAB infestation. The topography of the study areas was generally characterized by landform depressions, surrounded by upland sites and species.

   The scientists concluded that depressional black ash wetlands are well supplied with groundwater, based on results from hydrologic gradients, deuterium signatures, and an isotopic mixing model (Van Grinsven et al., 2017). This indicates the importance of considering the hydrologic regime in forested wetlands that are currently dominated by black ash – a strong groundwater interface and thick organic soils help to mediate the levels of the water table. Steady recharge is most pronounced during the spring, summer, and fall. Findings suggest that in sites with comparable hydrogeological conditions, loss of black ash won't prevent other woody vegetation from establishing, and as black ash is replaced by other species, the carbon storage of these systems will rebound. However, during dry years, because there won't be any black ash canopies shading wet areas, evaporation could increase, and lead to faster drawdown and a shorter hydroperiod.

5. Another study in Minnesota measured black ash sap flux, vapor pressure deficit, and soil moisture (Telander et al., 2015). The researchers found that higher sap flux density coincided with greater vapor pressure deficit, when moisture levels were at or near saturation. However, there was an opposite relationship when soil moisture content was lower than saturation. The greatest stand-level sap flux density occurred when soil moisture reached saturation.

   Black ash evapotranspiration varied considerably by site, indicating that the impacts of black ash mortality on hydrologic regimes will vary considerably depending on local context – Black ash sap flow density is greatly influenced by the local hydrologic regime, and therefore the hydrologic effects of black ash mortality will be most pronounced in the wettest stands (Telander et al., 2015).

Carbon & Greenhouse Gases

1. A lab experiment that simulated EAB mortality in black ash stands measured the associated changing gas fluxes (Toczydlowski et al., 2020). They found that black ash

EAB mortality will likely lead to increased fluxes of N_2O and CH_4, which are both potent greenhouse gasses.

CULTURAL SIGNIFICANCE OF BLACK ASH

Just as there are ecological keystone species, there are cultural keystone species (Garibaldi & Turner, 2004). These species are integral to the identity of a people, and are reflected in their spiritual and cultural practices. In conservation decisions, ecological and cultural keystone species are equally important to consider.

Black ash holds significant cultural value and is a keystone for many indigenous peoples in North America, and the perspectives of these peoples are essential to consider when managing for EAB (Willow, 2011). Today, scientists predict that the EAB infestation will lead to the functional extirpation of black ash (Herms & McCullough, 2014). This is deeply concerning for Native people who worry about the future of black ash and the ability to sustain a centuries-old tradition of basketry and black ash craftsmanship (Benedict, 2010a; Costanza et al., 2017). There is no ecological or cultural substitute for black ash in these cultural and ecological systems (D'Amato et al., 2018).

There are many recorded ethnobotanical uses of black ash, including lacrosse sticks, barrels, medicinal uses for rheumatism and loosening bowels, and black ash baskets made by the Abenaki, Ojibwa, Malecite, Meskwaki, and other tribes (Anderson, 2006). Black ash is also featured in a Wabanaki creation story (Costanza et al., 2017). Les Benedict of the Mohawks of Akwesasne has written and spoken extensively about black ash. For his people, he highlights the significance of black ash's medicinal properties (Benedict, 2010a), and the importance of black ash basketry for connecting the Akwesasne Kanienkehaka (Mohawk) from past to present (Benedict, 2010b). Black ash is also linked to Akwesasne Kanienkehaka language and ceremonies (Benedict, 2010a). For many Akwesasne Kanienkehaka, black ash is a form of medicine and cultural identity. The same is true for many indigenous peoples whose ancestral lands overlap with black ash trees.

In northeastern North America, the Wabanaki tribes in Maine (Aroostook Band of Micmac Indians, Houlton Band of Maliseet Indians, Passamaquoddy Tribe, and Penobscot Indian Nation) and the Saint Regis Mohawk Tribe in New York and Canada have a long-documented history of black ash basketry (Benedict & Frelich, 2008; Diamond & Emery, 2011). There are several types of black ash baskets, including larger utility baskets for hunting and gathering, and smaller decorative or ornamental baskets (Benedict, 2010a; Diamond & Emery, 2011). Black ash baskets are sometimes used ceremonially, such as in the exchange of baskets in wedding ceremonies (Benedict, 2010a). For some people, including Mohawk, black ash baskets are sold as a source of income.

The use of black ash wood in basketmaking traditions is due to its supple yet strong nature (Benedict & David, 2003). Black ash is also noted as being much easier to pound and to work with than white ash (Anderson, 2006). Black ash wood is ring porous, meaning that each annual growth ring has porous spring growth and dense summer growth (Anderson, 2006). When subjected to pounding, the wood splits along the soft spring growth and can be peeled into splints that are ideal for basketry, barrel hoops, snowshoe frames, canoe ribs, and material for woven chair seats (Anderson, 2006; Benedict, 2010a).

The act of locating, felling, and processing black ash logs into usable splints is an intensively physical and variable process (Diamond & Emery, 2011). It's important to note that not all basket makers are basket-tree harvesters – many basket makers rely on "basket-tree harvesters," tribal members who have learned to identify basket quality black ash trees (Costanza et al., 2017). Many basket-tree harvesters and basktemakers have their own approach for black ash stand management and for processing black ash. After basket trees are identified and felled (seed trees are rarely harvested), some basket tree harvesters pound black ash logs in the woods where they were felled, while others transport the log before processing. A mallet or axe is used to pound the logs (Benedict, 2010a; Benedict & David, 2003). The logs split along the growth rings and are peeled from the log, processed, and used to weave baskets. Some pound by hand while other have mechanical processors (Diamond & Emery, 2011). Different parts of the tree are used for basket styles, functions, and components Benedict & David, 2003). The outer wood tends to be whiter and suppler and is used for more decorative and fancy baskets, while the heartwood which transitions towards brown and brittle, along with the branches, and lower quality trees, can be used for basket rims and handles (Benedict & David, 2003; Costanza et al., 2017; Diamond & Emery, 2011).

Through experience, basket makers have learned that only 5-20% of black ash trees are basket quality (Benedict & Frelich, 2008). While black ash preferences vary by basket maker (Costanza et al., 2017), basket quality trees typically have at least 20 years of 2-3-millimeter-thick growth rings, have a minimum DBH of 12.5 centimeters, and have at least 2 meters of trunk that is free of surface defects (Benedict & Frelich, 2008; Costanza et al., 2017; Diamond & Emery, 2011). The size of a harvested tree often depends on human or machine power available to transport the tree out of the woods (Diamond & Emery, 2011). Hand-harvested trees tend to be smaller, while folks who use tractors to extricate can harvest larger trees. Some harvesters use an increment borer before harvesting, others estimate expected growth ring thickness based on other characteristics. An increment borer can shed light on the variety of growth ring thicknesses within a single tree. Additional site and tree characteristics that influence basket quality are listed below.

Site hydrology: Sites with ponding water can slow and inhibit black ash growth, leading to smaller growth rings (Benedict & Frelich, 2008; Costanza et al., 2017; Diamond & Emery, 2011). Ideal sites have sufficient saturation to limit the growth of other tree species, but not so much water that black ash growth is suppressed. Some basketmakers have identified floodplains as locations where basket quality trees tend to grow (Costanza et al., 2017). Percolating groundwater has also been observed to co-occur with basket-grade trees, possibly indicating a relationship with mineral and calcium availability (Diamond & Emery, 2011).

Microtopography: Trees growing on slightly higher microsites in wetter environments help black ash to avoid saturated conditions that might curb growth rate (Costanza et al., 2017).

Lower percent herb cover: In locations that are water or nutrient limited, extensive herb cover appears to compete with black ash (Benedict & Frelich, 2008).

Greater light availability: Black ash from areas that have more available light, such as edge locations or areas without conifers, tend to produce higher quality ash (Benedict & Frelich, 2008; Costanza et al., 2017; Diamond & Emery, 2011). Dominant or co-dominant trees are generally preferred, with canopies that extend for approximately half of the tree's height (Costanza et al., 2017).

Height of the bole: The quality of the bole tends to deteriorate as wood is processed from higher up the tree (Diamond & Emery, 2011).

Rooting depth: Sites that are nutrient poor or have buttressed root growth often indicate a shallow water table, and saturation conditions that yield growth rings that are too narrow for basketry (Costanza et al., 2017).

Canopy: Healthy canopies are preferred, although sometimes dying trees will be harvested if the growth rings look promising (Costanza et al., 2017). Trees with epicormic activity are not desirable.

Bark texture: Trees with corkier texture are more desirable, possibly because corky bark indicates a thicker layer of xylem which produces thick layers of phloem, and translates to larger growth rings (Costanza et al., 2017). Yellow tinted bark has also been noted as more desirable than grayish bark.

Tree attributes: Stem defects such as cracks, knots, stubs, holes, and curves, can make a tree unusable and challenging to process. Good tree boles should have at least 4.5-6 feet of straight, clear wood.

Stand and species composition: Sites can yield both good and poor-quality black ash (Costanza et al., 2017). Black ash that grow in pure stands tend to be of higher quality, possibly because of the lower canopy cover associated with these sites. Some basket makers have noted a brittleness in black ash splints harvested from sites where coniferous trees are present. Red spruce, balsam fir, and northern white cedar can indicate poor soil drainage, which often yields narrow growth rings in black ash.

In the 1990s, the Maine tribes formed the Black Ash Task Force in response to concerns about the observed decline in black ash health and population (Costanza et al., 2017). The Black Ash Task Force includes tribal, university, and state and federal personnel, and is still active today, and has spoken about the importance of protecting black ash stands with high quality basket trees (Costanza et al., 2017). Additional precautionary steps to maintain a source of black splint material include harvesting and processing logs, storing splints, or establishing agroforestry black ash plantations, possibly in the Pacific Northwest (Benedict, 2010a; Costanza et al., 2017). Submerging recently infested black ash logs also provides a short-term opportunity for killing EAB larvae and preserving black ash logs (Poland et al., 2015; Siegert et al., 2014). While submergence times vary depending on season, Poland et al. (2015) found complete EAB mortality if logs were submerging in the winter or spring and then held underwater for an additional 13 weeks once the water temperature reached 10-13˚C (Poland et al., 2015). This submergence duration still preserved wood quality for basketmaking, with staining and waterlogging only occurring in the outermost layers. Ongoing research in collaboration with tribal partners is recommended to inform ash management and decision making (Costanza et al., 2017).

POPULATION CONTROL & BIOCONTROL

Prior to the arrival of EAB in North America, the ecology of EAB in its native region was not well understood (Liu et al., 2003). In an attempt to identify EAB's native parasitoids and patterns of infestation, studies were undertaken in China. Native *Fraxinus* species were less likely to be attacked than nonnatives like *Fraxinus pennsylvanica*. Due to natural tree resistance, native ash in China did not experience major die-off due to EAB infestations. Researchers suspect that a combination of inherent and co-evolved resistance combined with natural EAB population controls help to keep China's EAB population in check.

In total, EAB larvae were found in 5 of the 6 provinces studied, in 6 of the 11 study sites, and in 9 out of 29 plots (Liu et al., 2003). The distribution of EAB larvae was patchy, even within plots. Trees in urban or roadside environments were more likely to be infested, likely because of the increased stress of these environments. There were no predators or fungal pathogens detected. The detected rates of parasitism included 6.3% for *Spathius* sp. and 6.6% for *Tetrastichus sp.* (later identified as *Spathius agrili* and *Tetrastichus planipennisi* (Yang et al., 2005)). In 2005, two additional EAB parasitoids, both egg parasitoids, were identified in China: *Oobius agrili* sp.n. and *Avetiane Ua xystrocerae* sp.n. (Zhang et al., 2005). Further studies in China found a 74% reduction of the EAB population due to the impact of parasitism by *Tetrastichus planipennisi* and *Oobius agrili* (Liu et al., 2007). Parasitism by *T. planipennisi* was found to be 16% in July, increasing to 40% by August.

Similar results have been found in *Agrilus* species native to North America (Loerch & Cameron, 1983). Extensive studies on the Bronze Birch Borer (*Agrilus anxius* Gory)*,* a species native to the United States that feeds on white birch (Slingerland, 1906), have found that parasitism decreased the egg population by 7%, the larval population by 18%, and woodpecker activity added an additional 60% reduction in population (Loerch & Cameron, 1983).

In the early 2000s, there were parallel efforts to detect parasitoids of EAB in North America (Bauer, Liu, Haack, et al., 2004). After collecting around 6000 EAB individuals from sites throughout the Midwest, the samples were tested for fungus and parasitoids. While five fungi, a few parasitoids of immature EAB were detected, and mortality was observed due to starvation, cannibalism, desiccation, and woodpecker predation, levels were well below what's been documented in native *Agrilus* species. Only 1% of EAB larvae were parasitized by the detected parasitoids, *Atanycolus hicorae, Atanycolus simplex,* and *Spathius simillimus, Phasgonophora sulcate,* and *Balcha indica* (nonnative) (Bauer et al., 2008). Because these parasitism statistics are significantly lower than those observed in EAB's native range of China (Liu et al., 2007), as well as significantly lower than the rate of parasitism of the US native *Agrilus anxius* (Loerch &

Cameron, 1983), there was reason to pursue biocontrol efforts in North America (Bauer et al., 2008).

A team at the USDA and the University of Michigan developed laboratory rearing techniques, and determined life cycles for *Tetrastichus planipennisi, Oobius agrili, and Spathius agrili* (Bauer et al., 2008). Prior to release, there was extensive research on the likely impact of introducing these non-native wasps to North America (Bauer et al., 2008). It was determined that the non-native wasps were unlikely to perform a parasitism switch, and therefore were unlikely to affect non-EAB *Agrilus* species. Given the devastating effect of EAB to North American ash, and the potential for biocontrol to slow the spread of infestation, biocontrol was deemed a viable pursuit. In January of 2007, permit requests were submitted to the USDA Animal and Plant Health Inspection Service (APHIS). After six months of review by researchers, land managers, and a 60-day window for public comments, "Findings of No Significant Impact," led to a release permit being issued in July of 2007, at which time all three parasitoids were released in Michigan. Releases began in Michigan in the summer of 2007, and the research team began periodically monitoring the populations of the three parasitoids that were released (Bauer et al., 2010). Using tree inspections, traps, and dissections, the scientists kept tabs on reproduction, overwintering, dispersal, and populations. These observations were compared to ash in areas without biocontrol.

Additional follow up on biocontrol efforts in Michigan, where *Tetrastichus planipennisi* and *Spathius agrili* were released in 2009 found that *Tetrastichus planipennisi* was most abundant immediately following release (accounted for 93% of parasitoids collected in 2009), and 58% in 2010 (Duan et al., 2012). *T. planipennisi* accounted for 1-5% of EAB parasitism across survey sites, and appeared to disperse approximately 1 kilometer immediately after release. *S. agrili* was not detected, possibly because of smaller release (300 individuals). Additionally, parasitism of EAB larvae by a native Atanycolus spp., increased from 0.5% in 2009 to 19% in 2010. Other biotic factors, such as microbial activity and host tree resistance, accounted for 10-22% mortality of the observed EAB larvae.

Additional studies have searched for parasitism by native parasitoids, and determined if this activity has increased in years since EAB arrived in North America. Across a sample of 1041 EAB larvae (collected in Maryland and Pennsylvania), researchers found at least 10 hymenopterous parasitoids had attacked the immature EAB (*Balcha indica* (native to SE Asia), *Eupelmus pini*, *Atanycolus nigropyga*, *Atanycolus* sp., *Spathius laflammei*, *Dolichomitus vitticrus, Dolichomitus sp,Orthizema sp.*, *Cubocephalus sp*) (Fuester et al., 2010). Mortality from parasitism was approximately 4%, while fungal activity accounted for 59% mortality, (Fuester et al., 2010). While findings by Fuester et al. (2010) support ongoing biocontrol efforts, a 2009 study observed considerable parasitism of EAB by North American native *Atanycolus cappaerti* (Cappaert & McCullough, 2009). Parasitism rates of EAB by *A. cappaerti* ranged from 9-71%. These findings indicate that *A. cappaerti* could potentially augment existing EAB biocontrol efforts. Further research has documented the lifecycle of *A. cappaerti*, and developed lab rearing techniques (Duan & Schmude, 2016). The population of *A. cappaerti* and other native parasitoids continue to grow as the EAB infestation spreads, and contribute to EAB population control.

Finally, a note on woodpecker predation. Studies on woodpecker predation of EAB larvae are inconclusive, as there has been notable variability in the results (0-90% predation reported) (Herms & McCullough, 2014). One group of scientists detected that 35% of larval mortality was due to woodpecker predation (Anulewicz et al., 2007). In another study, woodpecker activity accounted for 12% of mortality (Fuester et al., 2010). In Michigan, woodpecker predation accounted for a 32–42% reduction of the immature EAB population in the sites (Duan et al., 2012).

INSECTICIDE & FUNGAL APPLICATIONS: RESEARCH & DISCOVERIES

Suppressing wood-boring pests is a difficult proposition (Bauer, Liu, & Miller, 2004). To address this challenge, there have been numerous efforts to control EAB through fungal and insecticide applications and injections (Herms, McCullough, et al., 2009). There are at least four different options for treating ash with insecticide: soil injections or drenches, trunk injections, lower trunk sprays, and protective cover sprays. The four insecticide options are described below (Herms, McCullough, et al., 2009).

*Soil Injections***.** Soil injections (or drenches) need to be applied when the soil is moist, but not saturated to allow for optimal uptake by the tree (Herms, McCullough, et al., 2009). Saturated conditions can lead to dilution, forming puddles of insecticide, and unnecessary runoff into local waterways. If there are flowering plants in the area, they either need to be destroyed (to avoid insecticide uptake by pollinators), or an alternative method of insecticide treatment should be considered. Existing studies have revealed varying efficacy of these treatments.

Injecting Insecticides. Another form of EAB control involves injecting insecticides into the trunks of ash trees (McCullough et al., 2005). The outcome of these injections is affected by the timing and method of injection, tree health and size, and existing EAB pressure. Trunk injections are a good choice for trees that are growing in wet or sandy soils, as direct injection constrains the insecticide to the injected tree (Herms, McCullough, et al., 2009). Injections typically require drilling into the base of the tree through the bark and into the outer sapwood. Studies have found that wounds sustained during drilling recover by the end of the growing season. The ideal timing for injection occurs after leaf out, but before EAB eggs hatch. Injected trees require a steady source of water to allow for uptake and translocation of the chemicals via transpiration. Emamectin benzoate provides protection for 2-3 years.

Emamectin Benzoate has previously been used to control pests in fish farming, veterinary medicine, and agriculture (McCullough, Poland, Anulewicz, Lewis, et al., 2009), and represents an econcomically viable management option for urban forests (McCullough & Mercader, 2012). By 2009, several states had granted special permissions for Emamectin Benzoate, in the form of TREE-äge, to be used as EAB control (McCullough, Poland, Anulewicz, Lewis, et al., 2009). Regardless of whether Emamectin benzoate is applied annually or biennially, this insecticide provides dramatic EAB control, resulting in more than 90% mortality of EAB larvae. There are at least two factors that contribute to higher ash survival: treating trees early or before an EAB infestation is present, and treating a higher density of trees per area (McCullough & Mercader, 2012).

Imidacloprid, another insecticide injected for EAB control, has also been well studied (McCullough et al., 2005). There are two different approaches for imidacloprid injections: 1. Imicide, where imidacloprid is injected using Mauget capsules. The release into the tree uses very little pressure, and requires passive uptake by the tree, sometimes taking several hours; 2. Pointer, which requires a wedgle for delivery. A wedgle looks like a hypodermic needle, and requires high pressures for a relatively quick injection procedure. Over a three year study, researchers found that while EAB continued to attack and cause decline in both control and treated trees, treated trees experienced significantly lower levels of dieback. Additionally, Imicide appeared to offer significantly more protection than Pointer. Injecticide-B is separate insecticide that is also used for EAB control (McCullough et al., 2005). After injection, Injecticide-B is translocated through trees more rapidly than imidacloprid does. However, additional benefits have not been found. After insecticide injections of Imidacloprid and Injecticide-B, EAB continues to attack and cause decline in both control and treated trees, but treated trees experienced significantly lower levels of dieback (McCullough et al., 2005; Rebek et al., 2008).

Lower trunk sprays. Lower trunk sprays, such as Dinotefuran, are a non-invasive application of insecticide to the lower 5-6 feet of the tree (Herms, McCullough, et al., 2009). The insecticide penetrates through the bark, and is transported throughout the tree. Studies on EAB control have found similar results to soil injections.

Additional trunk sprays include two noenicitinoids, imidacloprid and dinotefuran, which are sprayed on tree trunks (McCullough, Poland, Anulewicz, Lewis, et al., 2009). When these two neonicotinoid mixtures are sprayed on the trunk, they move through the bark, into the xylem, and are transported into the foliage. To be effective, both imidacloprid and dinotefuran must be applied annually. While these trunk sprays reduce EAB larval densities, their efficacy is much lower than for Emamectin Benzoate.

Protective cover sprays. Protective cover sprays are a non-invasive application where insecticide is sprayed on the trunk, main branches, and sometimes on the foliage (Herms, McCullough, et al., 2009). These sprays directly affect EAB larvae as they hatch from eggs, as well as EAB adults. However, there is no effect on the larvae feeding below the bark.

Another study tested the efficacy of using fungal sprays for EAB control (Bauer, Liu, & Miller, 2004). When a fungal spray containing *Beauveria bassiana* strain GHA was sprayed on ash trees before EAB emergence, the application helped to suppress EAB populations. The fungus was able to permeate the larvae, having lethal effects. Fall sprays were less effective, as was the application of fungal bands.

Insecticide applications and injections have been widely assessed, mostly on trees between 7-14 inches in diameter (McCullough, Poland, Anulewicz, Lewis, et al., 2009). Application method, active ingredient, and timing of application varies by product, and some products have additional specifications, like the maximum amount that can be applied per acre per given year Herms, McCullough, et al., 2009). Additional detail and products can be found in the 2009 paper by Herms, McCullough, et al.

BREEDING EFFORTS

The *Fraxinus* genus includes approximately 40 temperate trees and shrubs in the Northern Hemisphere (Hinsinger et al., 2013). A dive into the phylogeny, or relatedness of this genus, reveals that while white ash *(Fraxinus americana)* and green ash *(Fraxinus pennsylvanica)* belong to the *Melioides s.s.* section, black ash *(Fraxinus nigra)* and Manchurian ash *(Fraxinus mandshurica)* belong to the *Fraxinus* section. The common ancestor of the *Meloides* and *Fraxinus* genera diverged around 44.2 mya, and the *Meloides s.s.* section diversified around 12.9 million years ago. In the *Fraxinus* section, divergence of European/Asian and North American *Melioides* ash occurred approximately 18.0 mya, and Manchurian ash subsequently diverged from European *Fraxinus* species approximately 15.3 mya. Put simply, black and Manchurian ash are more closely related than black ash is to green and white ash, and may have important implications for efforts to breed resilient ash trees. Despite these different phylogenetic histories, all North American ash trees display far greater mortality and yield higher populations of EAB adults than Manchurian ash (Rebek et al., 2008). EAB appear to prefer white, green, and black ash over blue and Manchurian ash (Pureswaran & Poland, 2009). This evidence indicates that EAB discriminates among host trees, and therefore must be interpreting a chemical signal that allows for differentiation between species.

In a comparison between the phloem chemistry of Manchurian ash, North American white ash (Fraxinus americana), and green ash (Fraxinus pennsylvanica), hydroxycoumarins were present in the phloem of Manchurian ash, but not in green or white ash (Eyles et al., 2007). These phenolic compounds have been previously correlated with deterrence of insect feeding. These findings may represent a mechanism of resistance against EAB. Additional preliminary analyses of genes expressed in the phloem of black, green, white, blue, and Manchurian ash revealed numerous genes of interest for future efforts to breed resistant ash (Bai et al., 2011). Several proteins have been identified in Manchurian ash that may contribute to resistance against EAB: a PR-10 protein, an aspartic protease, a phenylcoumaran benzylic ether reductase (PCBER), and a thylakoid-bound ascorbate peroxidase (Whitehill et al., 2011).

A study by Cipollini et al. (2011) compared EAB response across four varieties of ash (a wild-seeded lab grown green ash and three cultivars *F. mandshurica*, cv. Mancana, *F. americana*, cv. Autumn Purple, and *F. pennsylvanica* cv. Patmore). In the Manchurian ash, EAB larval gallery wounds underwent rapid browning, likely due to phenol oxidizing enzymes present in the phloem (Cipollini et al., 2011). The phloem was also observed to contain "a high soluble protein concentration, low trypsin inhibitor activities, and intermediate levels of peroxidase activity and total soluble phenolic concentration" (Cipollini et al., 2011, pg. 450). By comparison, white ash displayed "slow wound browning rate and low levels of peroxidase activity and total soluble phenolic concentrations" (Cipollini et al., 2011, pg. 450). Analyses of the wild green ash and the green ash cultivar revealed "high activities of peroxidase and trypsin inhibitor, a high total soluble phenolic concentration, and an intermediate rate of wound browning" (Cipollini et al., 2011, pg. 450).

The observed similarities between Manchurian ash and green ash -- high levels of inhibitors and phenolic concentrations -- were unexpected, and therefore indicate that peroxidase activity and trypsin inhibitor activity, as well as concentrations of phenolic concentrations are not characteristic of ash susceptibility to EAB (Cipollini et al., 2011). Therefore, specific compounds in Manchurian or green/white ash might be responsible for the differential response to EAB, as phenolics are often a major player in a plant's resistance to insects.

Subsequent phenolic analysis of the phloem contained within the four different ash revealed 33 compounds (Cipollini et al., 2011). Nine of the compounds were unique to Manchurian ash, and might yield some resistance. Four of the compounds were unique to the white and green ash, and could act as a feeding stimulant to the EAB. Of the nine compounds that were unique to Manchurian ash, there were several hydroxycoumarins, lignans, and phenylethanoids. Hydroxycoumarins have been suggested to retard insect development by indirectly limiting glucose availability (Silva et al., 2006). Lignans are also known to affect insect activities. The effects of the other compounds detected in this study have not yet been documented.

However, further inquiry into these compounds revealed that the hydroxycoumarins and two phenylethanoid compounds were present in high concentrations in the phloem of black ash trees (Whitehill et al., 2012). Because black ash is highly susceptible, it is highly unlikely that these compounds contribute to EAB resistance. This study also detected high levels of pinoresinol dihexoside in Manchurian ash relative to other *Fraxinus* species, which is a lignan and is known to suppress growth and feeding in several insect species, and might contribute to EAB resistance in Manchurian ash.

There are several trajectories for breeding resistant ash. The hybrid approach crossbreeds North American ash species with Asian ash species that have inherited resistance to EAB (Koch et al., 2012). Surprisingly, a hybrid offspring of *F. nigra* x *F. mandschurica* was also highly susceptible to EAB, indicating that it does not inherit the Manchurian ash's resistance (Rebek et al., 2008). A traditional approach identifies lingering ash (mostly green and white ash), preserves and replicates the genetic material through grafting and seed collection (Koch et al., 2012). The traditional approach also includes genetic analysis of lingering individuals to look for resistance phenotypes and genes that increase EAB tolerance. There has been little work documenting successful or ongoing efforts to breed resistant ash.

Alternative regeneration methods for black ash propagation have yielded exciting results. Because seed production in black ash is erratic, and seedbanks diminish quickly after EAB infestation, innovative regeneration has been another research focus (Lee & Pijut, 2017). "Adventitious shoot organogenesis in *F. nigra* using in vitro-derived leaf explants" is a successful type of plant propagation where leaflets are subjected to conditions that cause the leaflets to produce suckers/shoots, which can then be planted and used for plant regeneration.

UNDERPLANTINGS IN BLACK ASH STANDS

Several studies have simulated EAB infestations, and experimented with underplanting a variety of different species. These studies all occurred in the Midwest, and are summarized below.

A restoration experiment in Ohio looked at viability of different species in floodplains that have been historically occupied by ash trees (Knight, Slavicek, et al., 2012). The team planted a mixture of Dutch Elm Disease-tolerant American elm, sycamore, and pin oak before, during, and after EAB infestation. Observed damage to the planted seedlings was mostly due to flooding (caused wilting of leaves, but many seedlings then resprouted), and insect herbivory. Herbivory was higher in the site that did not experience flooding. Overall mortality of seedlings was low, and DED-tolerant elm seedlings performed as well or better than the sycamore and pin oak seedlings.

A study in Minnesota tested planting tree species in *F. nigra* wetlands, after applying different treatments to those wetlands: clearcutting, group selection, girdling, and control (Looney et al., 2015). Results indicated that clear-cutting negatively impacted nine of the twelve species tested, while the control, girdling, and group-selection treatments yielded similar survival rates for the first few years. Group selection created a variety of light conditions, and maintained the hydrologic conditions. The highest seedling performance was detected in *Ulmus americana*, *Quercus bicolor*, and *Fraxinus mandshurica*, which are recommended as potential nurse crops to mediate the effects of black ash mortality. In control sites, the study found highest survivability in seedlings that were planted during the fall season.

Because EAB causes widespread ash mortality, stands that were once dominated by black ash may not be forested in the future, instead transitioning to shrub-dominated wetlands (Iverson et al., 2016). This complicates the task of underplanting, and necessitates considering what shrub species might colonize these wetlands, including: Alnus incana, red osier dogwood (Cornus sericea), mountain maple (Acer spicatum), bluejoint (Calamagrostis canadensis), fowl manna grass (Glyceria striata), and lake sedge (Carex lacustris), and non-natives including: glossy buckthorn (Frangula alnus) and reed canarygrass (Phalaris arundinacea). The authors of this paper recommend referencing the tree species list provided in the Looney et al (2015) paper and ongoing study.

Simulating the short and long-term effects of emerald ash borer in black ash wetlands in the Great Lakes Region, a team attempted to determine how alternative species performed in these sites (Bolton et al., 2018). The team began their efforts in three study sites, all located depressional wetlands in Ottawa National Forest. Attempting to mimic the effects of EAB, the treatments in each site included girdling trees, cutting ash, and leaving some areas as controls. In 2013, the team experimented underplantings with10 alternative species: American elm (*Ulmus Americana* L.), Basswood (*Tilia americana* L.), Burr oak (*Quercus macrocarpa* Michx.), Red maple (*Acer rubrum* L.), Silver maple (*Acer saccharinum* L.), Yellow birch (*Betula alleghaniensis* Britton*)*, Balsam fir (*Abies balsamea* (L.) Mill), Black spruce (*Picea marina* (Mill.) Britton), Northern white cedar (*Thuja occidentalis* L.), and Tamarack (*Larix larcinia* K. Koch). In 2015, based on preliminary observations, the team added a fourth site in Superior Municipal Forest. Located along a riparian corridor, there was no simulation of EAB infestation in this location. Instead, the researchers focused on the impacts of microtopography and herbivory on regeneration of three species: hackberry, northern white cedar, and red maple. Depending on the species, planting stock type varied in age from 2-4 years, and was either bare root or plugs. The study found highest survivability in silver maple, American elm, basswood, hackberry, red maple, and northern white cedar. The team recommends planting these species in an effort to mediate the impacts of EAB in ash-dominated wetlands. In addition, they found significantly higher survival when seedlings were planted on hummocks or in elevated seedbeds.

To determine what would occur if black ash wetlands were left unmanaged, a team studied natural replacement in black ash stands (Palik et al., 2021). In their research sites, the team documented 36 woody species, only 14 of which are capable of achieving canopy positions. Five of the 14 are facultative wetlands species, yet each of these five has a specific associated challenge. *Larix laricina* is being aggressively attacked by the eastern larch beetle. *Thuja occidentalis* is preferred browse by deer, and over browsing limits regeneration potential. *Abies balsamea* is relatively short lived and is severely impacted by spruce budworm outbreaks. *Populus balsamifera* has a range that is seriously limited by climate change. *Ulmus americana* rarely reaches overstory or maintains canopy position due to Dutch elm disease, which often kills elm trees before they reach dominant canopy positions. Therefore, there is little evidence to support that other species will naturally step in to replace black ash following EAB mortality.

Using a group of previously identified black ash replacement species, another research team tested seedling survivability to flooding (Keller et al., 2023). Their results about flooding tolerance hold important implications for the viability of replacement species in black ash wetlands. Species that survived and grew during flooding for up to 15 weeks were bald cyprus (*Taxodium distichum* (L.) Rich), American elm (*Ulmus americana* L.), and black birch (*Betula nigra* L.). Species that survived and grew during flooding for up to 6 weeks were northern white cedar (*Thuja occidentalis* L.), red maple (*Acer rubrum* L.), larch/tamarack (*Larix laricina* (Du Roi) K. Koch), swamp white oak (*Quercus bicolor* Willd.), and yellow birch (*Betula alleghaniensis* Britton). Species that performed poorly when subjected to any flooding were eastern black walnut (*Juglans nigra* L.), and sugar maple (*Acer saccharum* Marshall).

BLACK ASH SEED COLLECTION & PROPAGATION

Black ash trees are mostly diecious, although some bear both male and female flowers (Benedict & David, 2003). The flowers mature just before leaf emergence and can be differentiated based on form: female flowers are loose panicles, while male flowers are densely packed. Black ash pollen is disseminated by wind, and after fertilization, female flowers mature into single-seeded samaras that hang from the branches in clusters. Depending on conditions and location, the seeds can mature anytime between July-October. Recommendations for seed collection and propagation have been thoroughly researched, implemented, and shared by Les Benedict and Richard Benedict (2003). Their findings are summarized below.

Prior to seed collection, it is important to accurately differentiate between black, green, and white ash. Because the ranges of these three *Fraxinus* species often overlap, cues such as leaf structure, bark, and bud scars can be helpful in species identification.

The St. Regis Mohawk seed collection program has used three different methods of seed collection: 1) using pruning poles and ladders; (2) setting up canvas tarps below seed-laden trees and shaking the trees to collect seed; (3) leaving a tarp on the ground as a longer-term catchment. Promising seeds are fully elongated, starting to turn yellow-brown, and have a white endosperm. It is important to note that if branches are being sawed off for seed collection, the seeds should be assessed before cutting.

After collection, ash seeds need to be cleaned, and their stems can be removed. The seeds should then be dried until moisture levels reach 7-10%, which yields approximately 8,100 seeds per pound. These collected and dried seeds can be stored for up to 8 years in sealed containers at 5˚C.

Prior to germination, the ash seeds must undergo stratification (Schopmeyer et al., 1974). In New York, a successful stratification period included a 90-day warm stratification at 16-20˚C, followed by 90 day cold stratification at 5˚C. During stratification, the seeds were kept in sphagnum moss, contained in an aerated container.

When planting the seeds, seed beds should be prepared with 150 pounds per acre of fertilizer (15N:15P2O5:15K2O). Ideal conditions include a smooth surface before sowing, a pH between 6.0-6.5. Stratified seeds should be sown in May, or alternatively freshly collected seeds can be planted in mid-October to early November and subsequently undergo natural stratification. Seeds should be sown 1 inch apart, and topped with ¼ to ¾ inches of topsoil, and 3 inches of bark mulch. Germination typically occurs during the first and second years after planting. Because seedlings are susceptible to damping off diseases, or soil-borne fungal diseases, successful maturation requires sufficient soil aeration, intentional irrigation, and/or fungicide.

When planting black ash seedlings in forests, seedlings should be spaced 10-15”. Because black ash is shade intolerant, any surrounding or competing trees and plants should be thinned. Additional considerations include manual weeding, and fencing to prevent browse.

Further information about seed collection, seedling care, pruning, lifting, and harvesting can be found in Benedict and David’s 2003 publication.

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