Forest Ecology and Management 261 (2011) 480–488

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes

Daniel M. Kashian[a,*], John A. Witter[b]

[a] Department of Biological Sciences, Biological Sciences Building, 5047 Gullen Mall, Wayne State University, Detroit, MI 48202, United States
[b] School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109, United States

ARTICLE INFO

Article history:
Received 13 August 2010
Received in revised form 25 October 2010
Accepted 29 October 2010
Available online 24 November 2010

Keywords:
Emerald ash borer
Forest recovery
Disturbance
Fraxinus
Ash regeneration

ABSTRACT

The emerald ash borer (EAB) has killed millions of ash trees in Michigan and at least fourteen other states since its first detection near its introduction point in metropolitan Detroit in 2002. Despite overstory ash mortality near 100% in many areas, ash seedling and saplings remain unaffected and provide the potential for ash re-establishment into the canopy of deciduous forests of the region. We examined the potential for ash re-establishment in areas of heavy mortality by measuring the status and change of ash regeneration at 45 sites across southeastern Lower Michigan in 2007 and 2009. Ash regeneration was found to be abundant in all forest types, particularly in the smallest height classes, though it was more abundant in ash species of upland forests compared to those of lowland forests. New seedlings 1–2 years old were less common than other regeneration size classes, and declined substantially between 2007 and 2009, suggesting a depletion of the ash seed bank in these forests. Regeneration density was not explained well by the presence of overstory ash prior to EAB introduction, suggesting that competitive interaction with other tree species in higher canopy strata is an important driver of ash regeneration density. Regeneration is sufficient to replenish overstory ash to pre-EAB levels in upland forests, though ecological changes caused by overstory ash mortality in lowland areas may affect local hydrology in a way that reduces opportunities for tree regeneration. Despite abundant ash regeneration, it remains unclear whether ash will recover to the overstory of forests in southeastern Michigan because of uncertainties in the future dynamics of EAB in the region.

1. Introduction

In an era where rates of ecological change are unprecedented, understanding the effects of exotic plants and animals on native species is critical for predicting their consequences for native biodiversity. The emerald ash borer (Buprestidae*: Agrilus planipennis*; EAB) is a bark beetle native to Asia that kills >85% of healthy ash trees (genus *Fraxinus*) in a forest stand within 3–5 years of infestation outside its native range (Poland and McCullough, 2006; Wei et al., 2007). First detected in North America in 2002, EAB has spread from its introduction in metropolitan Detroit, Michigan (Siegert et al., 2007) to at least fourteen other states and the Canadian provinces of Ontario and Quebec despite aggressive quarantine and eradication efforts (Poland, 2007). EAB spread has occurred in both a wave pattern across the landscape consistent with the establishment of an exotic species as well as through long-range dispersal by humans along major roadways (Prasad et al., 2010). The potential for slowing EAB spread now lies with native and introduced parasitoid wasps (Gould, 2007), but already-extensive tree mortality in Michigan, Ohio, Indiana, and Illinois suggests that EAB may eliminate ash trees from forests across the eastern United States, at least as an important canopy species. Ecological research on EAB thus far has focused on biological control and surveillance (Castrillo et al., 2008; Liu and Bauer, 2008), dispersal modeling (BenDor et al., 2006; Murihead et al., 2006; Prasad et al., 2010), and monitoring of ash mortality (Anulewicz et al., 2007; Smitley et al., 2008). Few data exist, however, that describe the potential for ash to regenerate following EAB-induced mortality or that address broad uncertainties about the likelihood that ash will be restored and persist as a canopy tree species.

Ash trees represent a significant component of both natural woodlands and urban plantings in the Great Lakes region (MacFarlane and Meyer, 2005). Ash trees are common street plantings in urban areas whose extirpation may greatly reduce urban environmental quality (MacFarlane and Meyer, 2005). Several ash species also are common across many natural ecosystem types in

---

* Corresponding author. Tel.: +1 313 577 9093.
E-mail address: dkash@wayne.edu (D.M. Kashian).

0378-1127/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2010.10.033

this region, with white ash (*F. americana* L.) on dry-mesic and mesic upland sites, black ash (*F. nigra* Marsh.) on poorly drained (wet) sites in deciduous swamps, and green ash (also called red ash; *F. pennsylvanica* Marsh.) on mesic to wet-mesic river floodplains where soil is saturated during only part of the growing season (Barnes and Wagner, 2003). Of the three major ash species, black ash is most restricted in its distribution and limited to wet sites, while white ash and green ash have a much wider ecological amplitude. Two rarer species, blue ash (*F. quadrangulata* Michx.) and pumpkin ash (*F. profunda* (Bush) Bush), also are found in forests of the region; all five ash species are vulnerable to EAB. Ash were once relatively free of major disease and insect pests (Barnes and Wagner, 2003), but were experiencing ash yellows (an insect-transmitted pathogen) and an unexplained decline epidemic (Feeley et al., 2001; Woodcock et al., 1993) prior to the arrival of EAB. Many EAB spread models predict a rapid expansion of the beetle's range to other areas having an important ash component in the region (Murihead et al., 2006; Prasad et al., 2010), such that most ash trees east of the Great Plains are in danger of extirpation (BenDor et al., 2006). EAB is therefore one of the most significant exotic species introduced into North America in recent years (Cappaert et al., 2005; Liu et al., 2003), having already killed millions of trees since its introduction (Siegert et al., 2007). In quickly removing a canopy species, EAB outbreaks have or are likely to have dramatic impacts on forest stand dynamics (Beckage and Clark, 2003), timber production (Poland and McCullough, 2006), wildlife forage, and the regulation of moisture and light regimes in terrestrial systems (Schlesinger, 1990). Quantifying short-term responses of ash populations to widespread canopy tree mortality, therefore, is critical in predicting and managing long-term ecological impacts of EAB (Poland and McCullough, 2006).

The removal of a common canopy species from forested ecosystems is a relatively rare ecological event (Barnes, 1976), such that similarly significant impacts on other deciduous species that have occurred in the past may provide important insights for current trends. For example, American chestnut (*Castanea dentata* (Marsh.) Borkh.) once dominated upland forests in the eastern United States (Anagnostakis, 1987), but chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) killed about 3.5 billion chestnut trees in this region between 1900 and 1940. Today, surviving American chestnut trees exist mainly as root-collar sprouts that are again killed by the pathogen prior to reaching reproductive age (Anagnostakis, 1987); restoration of the species (or hybrids resembling it) is today approached using intensive breeding and planting of blight-resistant genotypes. Similarly, Dutch elm disease (*Ceratocystis ulmi*) killed about 200 million mature elm trees (genus *Ulmus*) in the northeastern United States between the late 1920s and the 1970s (Hubbes, 1999), and continues today to move westward after spreading nearly to the Great Plains. In contrast to chestnut blight, the main effect of Dutch elm disease on elm trees has been to reduce the lifespan of the genus rather than eliminate it from eastern forests (Barnes, 1976), and thus trees persist as sub canopy and understory species rather than as a canopy dominants. Compared to these significant mortality events, EAB has killed over 50 million trees in less than a decade and threatens the entire *Fraxinus* genus endemic to North America (Gandhi and Herms, 2010). Given that seedlings and saplings <2.5 cm in diameter are not yet affected by EAB, current ash regeneration represents the critical resource for ash recovery in natural areas. However, little or no published data exist to describe the potential for ash species to recover following significant EAB-caused mortality when these data are essential for management and/or restoration planning, particularly in light of the varying role of post-mortality regeneration of species subject to major mortality events in recent decades.

We used repeated, landscape-scale field studies in southeastern Michigan to quantify the occurrence and distribution of ash regeneration where the impact of EAB has been the strongest and most prolonged to date, with the ultimate goal of examining the potential for ash killed by EAB to replace itself. We hypothesized that current ash regeneration is plentiful enough to replace canopy mortality, even with significant sapling and seedling mortality expected to occur prior to overstory recruitment. We tested this hypothesis with two specific questions: (1) What is the status and condition of ash regeneration in areas suffering heavy EAB-caused mortality in southeastern Michigan? (2) How did available ash regeneration change over two years of additional EAB infestation between 2007 and 2009?

2. Methods

2.1. Study sites

Study sites were selected in accordance with the Ash Plot Monitoring System (APMS), initiated in 2004 to detect the presence of EAB and monitor changes in the conditions of ash in natural areas across Michigan (Windfeldt, 2005). We sampled ash regeneration in 45 stands, including 23 within the Huron River Watershed that were previously sampled by Windfeldt (2005) to assess overstory ash conditions following EAB infestation. The 23 APMS sites were initially selected based on their representation of ash quantity in southeastern Michigan; the remaining 22 sites were selected in a manner similar to the APMS. Study sites were located in six counties in southeastern Michigan and included natural areas owned and/or managed by the Michigan Department of Natural Resources, various municipalities, and private landowners (Fig. 1). Elevation ranged between about 175 m on the lake plain nearest Lake Erie to the east to nearly 400 m on morainal features to the west (Albert et al., 1986).

Study sites were ecologically diverse but spanned the range of ash occurrence in the region. Upland study sites were characterized by white ash, though species composition and the proportion of ash varied by the soil moisture status at each site. Mesic sites averaged a basal area of 28.7 m^2/ha, dominated mainly by sugar maple (*Acer saccharum* Marsh., 36% of basal area), American elm (*Ulmus americana* L., 12%), and basswood (*Tilia americana* L., 9%), with white ash representing about 11% of the basal area prior to EAB infestation. Dry-mesic sites averaged a basal area of 21.6 m^2/ha and were dominated by oaks, particularly white oak (*Quercus alba* L., 23%) and northern red oak (*Quercus rubra* L., 16%), as well as black cherry (*Prunus serotina* Ehrh., 11%), with white ash representing only 7% of the basal area before EAB-caused mortality occurred. Green ash was not found at any upland site. Deciduous swamps sampled averaged a basal area of 11.5 m^2/ha; black ash represented on average about 15% of the basal area before EAB occurrence, which was dominated by red maple (*A. rubrum* L, 36%) and American elm (*Ulmus americana* L., 27%). Species composition was more variable in river floodplains, but on average these systems averaged a basal area of 27.6 m^2/ha, were dominated by silver maple (*A. saccharinum* L., 38%), eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall, 28%), and American elm (13%), with green ash representing on average 8% of the basal area and white ash 2% prior to EAB infestation.

2.2. Field sampling

Sampling occurred within belt transects located along either permanently marked transects sampled by Windfeldt (2005) or newly established in the field. When newly established, transect starts were located randomly within each selected stand and were not purposely limited to forests with a heavy ash component. Each stand included one of three possible transect configurations depending on the size and shape of the stand: (1) three parallel tran-

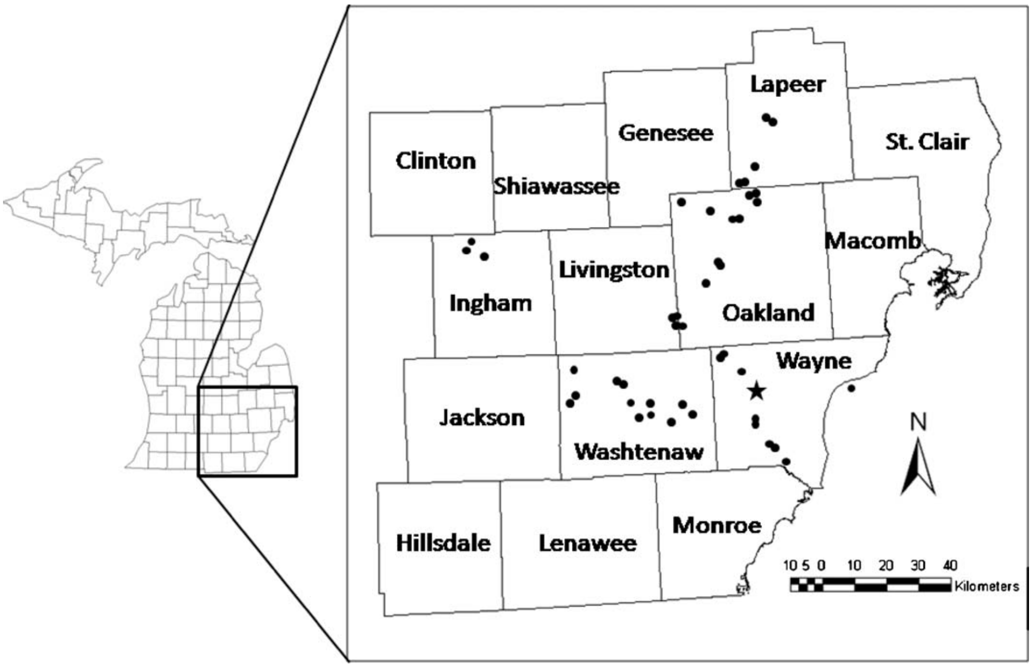

Fig. 1. Location of 45 sampling sites for ash regeneration in 6 counties of southeastern Lower Michigan. The star indicates the approximate introduction point of emerald ash borer in North America.

sects of equal length; (2) two parallel transects of equal length; or (3) a single transect. When more than one transect was used, transects were located a minimum of 40 m apart. Belt transects ranged from 250 to 500 m in length, depending on the size of the stand.

All ash seedlings and saplings (defined as stems <2.5 cm in diameter at breast height; DBH) were counted within 4 m of each side of the transect (8-m belt). All ash seedlings and saplings in uplands were assumed to be white ash because of the lack of other overstory ash species in these systems. Black ash regeneration was clearly identifiable because of its distinct placement of lateral leaf scars relative to the terminal bud compared to the other ash species. Green ash seedlings were distinguished from white ash seedlings in river floodplains using the shape of leaf scars, but the co-existence of white and green ash in these systems leaves the highest probability for measurement error. Ash seedlings and saplings were categorized into three height classes; <0.5 m; 0.5–1.0 m; and >1.0 m. New ash seedlings 1–2 years old were aged using bud scars and tallied separately within the 8-m belt transect. The current year's germinants were not counted to avoid a biased count that would likely be greatly reduced by mortality before the cohort reached its first year of age. Moreover, all live and dead trees >2.5 cm DBH were measured, converted to basal area, and tallied by species within a 10-m belt transect that encompasses the belts used for regeneration estimates. Trees of all species were measured in the belts; transects used for trees were wider than those used for seedlings to encompass a suitable number of ash stems for analysis. All dead trees were examined for previous EAB infestation; nearly all EAB-killed dead ash remained standing during the period of this study. Sampling was first conducted in summer 2007; ash regeneration counts and overstory ash mortality were re-sampled in summer 2009.

2.3. Data analyses

Sites were classified into major forest types (mesic hardwoods, dry-mesic hardwoods, river floodplain, deciduous swamp) based on the site factors and tree species composition described above. Ash regeneration tallies were computed as regeneration density on a per hectare basis for each height class within each forest type. Variables were transformed using logarithmic or square root transformations when data departed from assumptions of normality or heteroscasdicity. Regeneration density was compared within height classes across forest types using one-way analysis of variance, except for variables with many zero values whose distributions departed from normality which were examined using the nonparametric Kruskal–Wallis test. Changes in regeneration density between 2007 and 2009 were examined using repeated-measures analysis of variance.

Simple linear regression was used to examine relationships between the four regeneration height classes and distance from EAB introduction (introduction point based on that determined by Siegert et al. (2007)); basal area of ash prior to EAB infestation (basal area of EAB-killed ash + basal area of current live ash); basal area of current live ash; and ash relative density (number of ash stems/total number of stems for all tree species). Assumptions of linearity and heteroscasdicity were examined using plots of regression residuals, and normality was examined using histograms and skewness and kurtosis computations. Scatter plots were produced and compared for variables that did not meet the assumptions of linear regression. Finally, backwards stepwise regression was used to develop a linear model that would relate regeneration density of each height class to a subset of these variables. Alpha was set at 0.05 for all statistical analyses.

3. Results

3.1. Current condition of ash regeneration

Ash regeneration was abundant across the landscape, although it varied substantially within and among forest types and height classes. Regeneration density was heaviest for seedlings <0.5 m tall in all forest types, with averages ranging from 21,553 stems/ha in mesic hardwoods to 9062 in deciduous swamps (Table 1). Regeneration <0.5 m tall was the only height class that differed significantly among forest types, probably because of high variation in seedling density among sites within each forest type.

Table 1
Mean values of ash regeneration density (stems/ha) for height classes across four forest types in southeastern Lower Michigan measured in 2007. One standard error is shown in parentheses. Regeneration density differed only in the <0.5 m height class, and was significantly lower in wetlands compared to upland forest types (values having the same letter indicate a lack of significant difference at alpha = 0.05).

Seedling Size	Mesic Hardwoods	Dry-mesic Hardwoods	River Floodplain	Deciduous Swamp	*F*-Ratio	*p*-value
1–2 year	998 (254)	1158 (920)	892 (391)	770 (562)	0.865	0.467
<0.5 m	21553^A (7430)	17483^A (16139)	12654^B (4756)	9062^B (5895)	1.384	0.042
0.5–1 m	1696 (348)	777 (510)	1422 (440)	990 (208)	0.964	0.419
>1 m	1976 (1039)	392 (222)	904 (282)	489 (96)	1.181	0.329

There were significantly more seedlings <0.5 m tall in upland forest types (white ash on dry-mesic and mesic sites) than in river floodplains (green ash) and deciduous swamps (black ash; $F = 1.384$, $p = 0.042$; Table 1). The two larger height classes (0.5–1 m and >1 m) exhibited similar mean values across forest types, but mean values were much lower than in the <0.5 m height class (Table 1). Regeneration density of white ash decreased between the <0.5 m class and the 0.5–1 m class by 92–95% in the upland forest types, and green and black ash by 89% in the wetland forest types, suggesting that substantial mortality is likely to occur in the seedling cohort that currently fills the <0.5 m height class. New seedlings 1–2 years old did not differ among forest types ($F = 0.865$, $p = 0.467$), but mean values were much lower than the <0.5 m height class (Table 1). Identification of bud scars on a small subset of seedlings in the <0.5 m height class at each site suggested that seedlings in this class averaged 5–20 years old.

The density of new seedlings 1–2 years old exhibited a clear increase with increasing distance from the point of EAB introduction ($r^2 = 0.33$, $p = 0.001$; Fig. 2a). Seed availability likely increases with increasing distance from the introduction point because EAB-caused mortality of live ash also decreases further from this point. This trend was virtually eliminated by 2009, with almost all significant densities of new seedlings found >115 km from the introduction point (Fig. 2b). These trends in new seedling density are almost certainly related to mortality of overstory ash in 2007–2009. Mortality of overstory ash in 2007 was near 100% in most stands <90 km from the point of introduction (Fig. 3a). Stands located 90–115 km from the point of introduction were much more variable in the level of EAB-caused mortality, and at >115 km mortality was relatively low (<40%). By 2009, ash mortality was nearly 100% for all stands closer than 115 km from the introduction point, and all stands sampled showed some level of EAB-caused mortality (Fig. 3b).

Backward stepwise linear regression using distance to the EAB introduction point, current live ash basal area, pre-EAB ash basal area, and ash relative density identified several explanatory variables that differed across the seedling height classes. Distance to the EAB introduction point was found to be a useful explanatory variable only for density of new seedlings 1–2 years old ($r^2 = 0.33$, $p < 0.001$), although this model was the strongest of the five models presented here. All other regeneration height classes were best explained by amount or proportion of past and current ash in the overstory. Regeneration density of 0.5–1 m tall seedlings ($r^2 = 0.17$, $p = 0.035$) and total regeneration density across all height classes ($r^2 = 0.18$, $p = 0.032$) were best explained by current live ash basal area and pre-EAB ash basal area. Regeneration density of seedlings <0.5 m tall ($r^2 = 0.15$, $p = 0.022$) was best explained by current live ash basal area, and regeneration >1 m tall ($r^2 = 0.16$, $p = 0.029$) was best explained by pre-EAB ash basal area (Table 2). The overall weakness of these models suggests that seedling density depends somewhat on seed availability provided by the presence of overstory ash, but that long-term survival of established seedlings is probably more closely related to processes not measured in this study, such as competitive interactions with overstory or understory tree and shrub species or site factors (shade, presence of organic matter, soil texture, soil moisture status) that might affect young seedlings.

3.2. Changes in regeneration between 2007 and 2009

The two-year change in ash regeneration across the landscape that occurred with EAB spread was marked and considerable. Each height class of total regeneration density averaged across all forest types decreased significantly between 2007 and 2009 (Fig. 4). The greatest change occurred in the <0.5 m height class, which decreased from an average of 17,908 stems/ha in 2007 to 11,485 stems/ha in 2009 ($F = 2.149$, $p = 0.028$), a decrease of 36%. Regener-

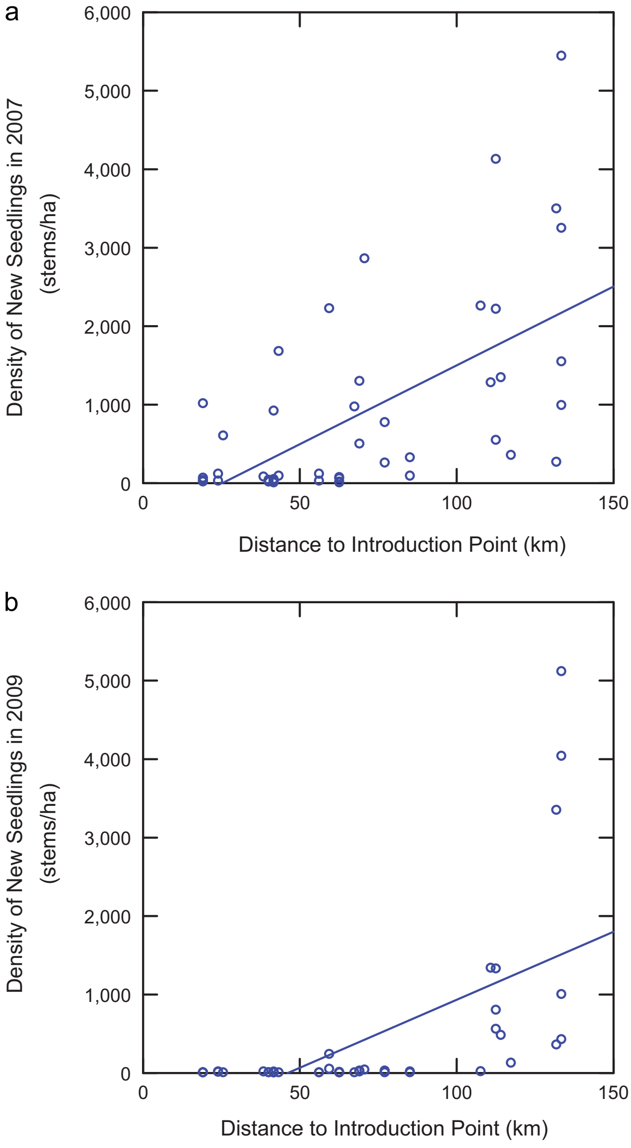

Fig. 2. Relationship between the density of new seedlings 1–2 years old (stems/ha) and distance from the introduction of emerald ash borer (km) in 45 stands sampled in southeastern Lower Michigan in 2007 (a) and 2009 (b). The clear trend of increasing seedling densities with distance was virtually eliminated by 2009.

Table 2
Backward stepwise regression results examining variation within regeneration height classes explained by ash basal area prior to EAB infestation, ash relative density prior to EAB infestation, current basal area of live ash, and distance to the EAB introduction point for 45 forest stands in southeastern Lower Michigan.

Height Class	Pre-EAB BA	Pre-EAB Ash RD	Live Ash BA	Distance to Intro	Full Model		
					r^2	F	p
New seedlings	Ns	ns	ns	0.33^{***}	0.33	23.01	***
<0.5 m	Ns	ns	0.15^{*}	Ns	0.15	7.03	*
0.5–1 m	0.11^{*}	ns	0.06^{*}	Ns	0.17	6.35	*
>1 m	0.16^{*}	ns	ns	Ns	0.16	5.19	*
All seedlings	0.10^{*}	ns	0.08^{*}	Ns	0.18	9.89	*

ns: not significant.
* $p < 0.05$.
*** $p < 0.001$.

ation density for seedlings 0.5–1 m tall decreased from an average of 1475 to 1253 stems/ha ($F = 1.545$, $p = 0.046$), and regeneration density for seedlings >1 m tall decreased from an average of 1436 to 1349 stems/ha ($F = 4.25$, $p = 0.039$). The reduction in regeneration <0.5 m tall without an increase in the larger height classes suggests that mortality, not recruitment to larger size classes, is causing the reduction in the smallest size class and therefore in the density of seedlings overall. New seedlings 1–2 years old decreased from an average of 998 stems/ha in 2007 to 438 stems/ha in 2009, a decrease of 56% (Fig. 5; KW = 1677, $p < 0.001$). These are overestimates for the EAB outbreak region because they include the larger landscape, including areas not yet attacked by EAB. Notably, 19 of the 47 sampled stands had no seedlings 1–2 years old in 2009.

The general distribution of seedling densities among forest types and height classes in 2009 was similar to that in 2007, with <0.5 m tall regeneration exhibiting the only significant differences among forest types (Table 3). As in 2007, <0.5 m tall regeneration density in upland forests was significantly higher than in deciduous swamps in 2009 ($F = 3.868$, $p = 0.016$), although river floodplains were not significantly different from upland forests as they were in 2007. More notable, however, was the decrease in regeneration density across all height classes and forest types between 2007 and 2009. Seedlings 1–2 years old decreased by 99% in dry-mesic hardwoods, 93% in river floodplains, 90% in mesic hardwoods, and 72% in deciduous swamps (Tables 1, 3). Regeneration <0.5 m tall decreased

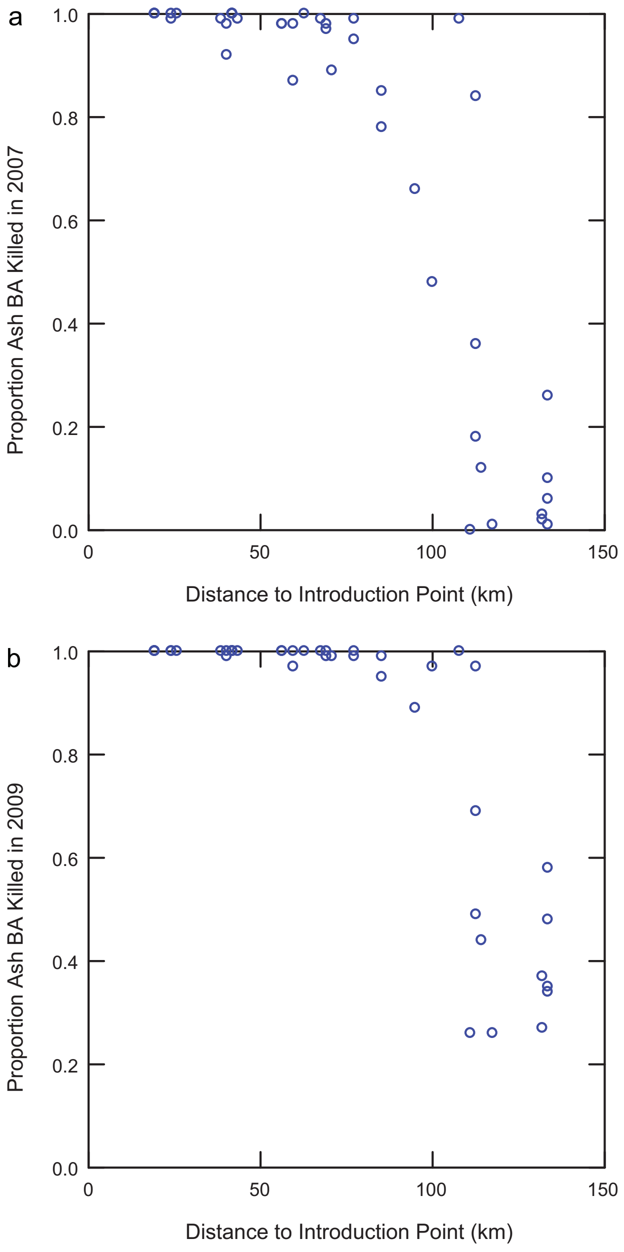

Fig. 3. Relationship between the percent of ash basal area killed by emerald ash borer and distance from the introduction of EAB (miles) in 45 stands sampled in southeastern Lower Michigan in 2007 (a) and 2009 (b). Mortality was near 100% in all stands closer than 115 km from the introduction point by 2009.

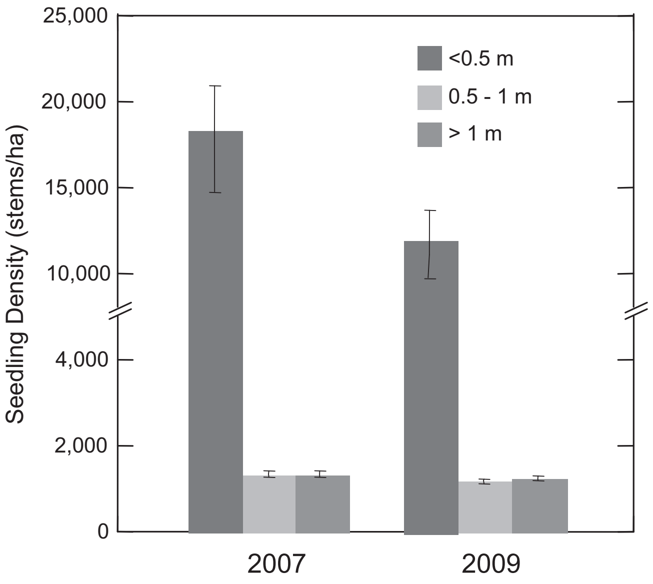

Fig. 4. Comparison of ash regeneration densities (stems/ha) in three height classes across all forest types for 45 stands sampled in southeastern Lower Michigan in 2007 and 2009. All height classes exhibited a significant decrease over the two-year period. Error bars represent ± 1 SE. Note change of scale for values >4000 on Y-axis.

Table 3
Mean values of ash regeneration density (stems/ha) for height classes across four forest types in southeastern Lower Michigan measured in 2009. One standard error is shown in parentheses. As in 2007, regeneration density differed only in the <0.5 m height class, and was significantly lower in wetland- compared to upland forest types (values having the same letter indicate a lack of significant difference at alpha = 0.05).

Seedling Size	Mesic Hardwoods	Dry-mesic Hardwoods	River Floodplain	Deciduous Swamp	*F*-Ratio	p-value
1–2 year	100 (51)	17 (11)	63 (40)	56 (55)	0.879*	0.831
<0.5 m	13712^A (4208)	10913^A (10488)	9842^A (3683)	3943^B (2370)	3.868	0.016
0.5–1 m	1405 (298)	605 (417)	1348 (385)	835 (167)	1.183	0.327
>1 m	1852 (1001)	385 (220)	829 (246)	430 (85)	1.075	0.370

* 1–2 year old regeneration was analyzed with the Kruskal–Wallis test.

less dramatically than new seedlings, but still decreased by 78% in river floodplains, 62% in dry-mesic hardwoods, 44% in deciduous swamps, and 36% in mesic hardwoods. Regeneration densities in the larger height classes – representing well-established regeneration – also decreased, but by far smaller margins averaging 11%. Repeated measures analysis revealed that seedlings <0.5 m tall decreased significantly for all forest types (within subjects; $F = 91.094$, $p < 0.001$) between 2007 and 2009, with a significant interaction term that suggests a greater change for dry-mesic hardwoods and river floodplains compared to mesic hardwoods and deciduous swamps (between subjects; $F = 6.034$, $p = 0.002$). Regeneration 0.5–1 m tall also decreased significantly over the two-year time period for all forest types ($F = 8.028$, $p = 0.007$), as did regeneration >1 m tall ($F = 13.65$, $p = 0.001$). The interaction term was not significant for either of the larger regeneration height classes. New seedlings 1–2 years old could not be analyzed with repeated measures analysis because they violate the assumptions of normality, but they clearly decrease dramatically between 2007 and 2009 (Tables 1 and 3).

4. Discussion

The introduction of emerald ash borer to the forests of southeastern Lower Michigan and the surrounding region has decimated the overstory ash components of its deciduous forests, and thus ash regeneration is critical for its recovery to the overstory of these ecosystems. Ash of reproductive age has now experienced upwards of 90–95% mortality near the origin point of the current range of EAB with the expectation that outlying areas will soon experience similar levels of mortality. Survival and establishment of current regeneration into the overstory are therefore necessary for future cohorts of ash and for ash to remain in forests of this area. It is not currently clear whether EAB-caused mortality will resume at the center of the EAB distribution once current ash seedlings and saplings there obtain a suitable diameter for infestation. In any case, understanding the response of ash dynamics to EAB attacks in southeastern Michigan – where ash mortality is highest and has occurred for the longest time in North America – is key to making effective EAB and ash management decisions in areas soon to be infested by EAB.

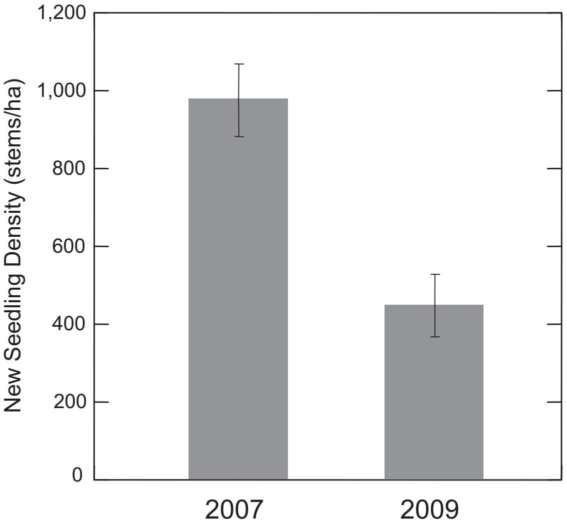

Fig. 5. Comparison of ash regeneration densities (stems/ha) for new 1–2 year old seedlings across all forest types in 45 stands sampled in southeastern Lower Michigan in 2007 and 2009. All height classes exhibited a significant decrease over the two-year period. Error bars represent ± 1 SE; data was analyzed using the Kruskal–Wallis test.

Our hypothesis that available ash regeneration is plentiful enough to replace EAB-caused canopy mortality was generally supported, assuming that at least some of the current regeneration will survive to reach the overstory. Although ash is likely to be replenished in the canopy of upland forests, however, its restoration in wetland forests is more tenuous because of less regeneration that results from lower seedling establishment in these ecosystems. Nonetheless, all forest types examined in this study are currently well-stocked with seedlings that could easily restore ash into the canopy to levels prior to EAB introduction. Comparing regeneration height classes quantitatively within forest types is not an appropriate proxy for changes in seedling densities over time because of annual differences in seed availability, but qualitative assessments are probably indicative of broad trends. Mesic hardwoods, dominated by sugar maple, red maple, and American beech (*Fagus grandifolia* Ehrh.) on well-drained soils, had the highest initial ash seedling density (<0.5 m height class). Even with expected significant seedling mortality, these high initial densities likely led to the highest density of larger (and presumably older) ash regeneration (>1 m tall) of the forest types examined in this study. As soils in these ecosystems are mesic and typically favorable for seedling survival, the sharp reduction in seedling density between the <0.5 and 0.5–1 m height classes is probably indicative of competitive exclusion by other shade-tolerant species in mesic hardwood forests, particularly those in the understory, subcanopy, and overstory layers. In contrast, dry-mesic hardwood forests, typically dominated by white oak, northern red oak, black walnut (*Juglans nigra* L.), and red maple, also have high initial ash densities but also the lowest regeneration density in the >1 m class, probably because of drier surface soils that limit long-term survival of ash seedlings. Regeneration density of larger seedlings and saplings in lowland forests (river floodplains and deciduous swamps) is far less than that of upland forest types, probably reflecting a lower probability of consistent establishment due to inter-annual variations in flooding or saturated soil conditions. It is difficult to make inferences about ash species-specific differences in regeneration ability (e.g., black ash vs. white ash) because differences in this study are at least equally affected by site differences as by species' regeneration ecology. Qualitative assessment of lowland forests, for example, suggests that regeneration of all tree species (including ash species) is relatively low compared to that found in uplands, probably related more to difficulty of seedling establishment on wet or seasonally wet sites than the regenerative ability of black (swamps) or green (floodplain) ash.

Despite the abundance of ash regeneration, the relative lack of new seedlings (defined in this study as 1–2 year old seedlings) and their marked reduction between 2007 and 2009 suggests the depletion of the ash seed bank as a result of near-extirpation of new seed sources that have occurred with overstory ash tree mortality. Average new seedling densities across all forest types decreased to fewer than 450 stems/ha between 2007 and 2009 (Fig. 5), indicating a near elimination of the seed bank that will persist at least until the largest seedling class (>1 m tall) reaches reproductive age. Near-exhaustion of the seed bank is further evidenced by the reduction in small regeneration density (<0.5 m tall) between 2007 and 2009 without a concomitant increase in larger height classes—suggesting that seedling mortality, not recruitment to larger height classes, and a lack of new seedling establishment is causing the reduction in regeneration density overall. Seedling mortality of ash, particularly germinants, is not atypical (Kennedy, 1990; Schlesinger, 1990; Wright and Rauscher, 1990), but sustained lack of new ash seed is not historically common and will create a gap in the age structure of ash for many years. Moreover, 1–2 year old seedlings sampled in 2009 germinated from seeds in 2007 and 2008, and seedlings germinated in 2009 and 2010 are likely to be even fewer. Current regeneration density on the landscape will therefore be the only available input for ash restoration into forest canopies in the region over at least the next decade, and may be the final cohort of ash seedlings if EAB returns to attack and kill the maturing saplings before they reach reproductive age.

New seedling density shows a clear increase that occurs with distance from the point of EAB introduction (Fig. 2). New seedling density closer to the introduction point – areas without a seed source for a longer period of time – was lower in 2007, and approached zero by 2009. This pattern is consistent with overstory ash tree mortality, which decreases with distance from the point of introduction of EAB (Fig. 3). Distance from EAB introduction thus functions as a surrogate for time, with the closest sites attacked by EAB the longest time ago. For example, sites located 15–30 km from the introduction point were likely infested by 1998, whereas sites >80 km from the introduction point were probably infested in 2006 (Prasad et al., 2010). In this study, all sites within about 90 km of the point of introduction had experienced >90% mortality by 2007, where tree mortality became much more variable among sites and mortality beyond 115 km was very low, suggesting that this was the "front" of EAB-caused mortality at that time (Fig. 2). By 2009, this distance moved from 90 to about 115 km and among-site variation in mortality at that distance became much more variable than it had been in 2007. Together, the relationships of new seedling density and tree mortality with distance confirm that heavy ash mortality will greatly reduce the density of new seedlings – as well as overstory ash trees themselves – as EAB spread continues across Lower Michigan and the Midwestern U.S.

We found little evidence in our data to support the idea that regeneration densities are determined simply by the presence and abundance of overstory ash. We measured variables including current ash basal area, basal area of ash prior to EAB infestation, and ash relative density, none of which resulted in a strong predictive model of seedling density in our study. As all of these variables are closely related to seed availability, these results indicate that current regeneration densities of established seedlings (>1–2 years) are probably shaped more strongly by factors that drive seedling mortality, such as competition and site factors, rather than seed availability, at least over the last several decades when the current regeneration established. Both intraspecific and interspecific competition likely affect ash seedling survival, though we did not observe ash seedling regeneration to occur at high enough densities in the mixed hardwood stands sampled in this study for self-thinning of ash seedlings to occur. An important caveat of this study is that we did not measure ash seedling survivorship, which undoubtedly differs based on the density and competitive ability of neighboring non-ash seedlings and saplings and higher canopy strata. For example, despite the relatively high shade tolerance of ash seedlings, the higher shade tolerance and competitive ability of species such as sugar maple and beech in mesic hardwood forests – rather than simple ash seed availability – can largely influence the density of ash seedlings. Similarly in dry-mesic hardwood forests, dry surface soils and lower nutrient availability may make ash less competitive than drier-site species. Notably, the effects of simple seedling mortality due to competitive effects have likely been intensified as a driving factor behind ash regeneration once EAB eliminated the ash seed source and thus the "supply" of new seedlings within the affected area.

Despite heavy overstory mortality, EAB is unlikely to create overwhelming compositional changes in forests in southeastern Lower Michigan because of the low relative dominance and relative density of ash (see Appendix A). Ash in southeastern Lower Michigan typically occurs as scattered individuals across a forest or as a canopy dominant in small patches rather than as a widespread canopy dominant, particularly in upland forests, although the death of entire patches of overstory trees where ash dominates is certainly dramatic. In contrast to other forest insects that may cause widespread mortality of a large fraction of the overstory, the lower occurrence of ash in the region will probably cause a more tempered successional response to EAB, depending on the ecosystem and regardless of regeneration density. For example, the loss of overstory ash is unlikely to create a major change in most mesic or dry-mesic hardwoods because ash is typically scattered except for a few sites where ash relative density is high. Ash tree mortality may have a larger impact on the composition of lowland forests, as subsequent reduction in evapotranspiration may cause water tables to rise or increase draw-down time of flooded soils in the spring, creating seasonably more difficult conditions for germination and establishment of ash and other woody species. Future research is necessary to determine the degree to which exotic insect disturbances such as EAB may be the catalyst for major changes in forest ecosystem structure in forests such as in the river floodplains and deciduous swamps in southeastern Michigan and especially throughout the range of black ash.

Regardless of the conditions of current ash regeneration, it remains highly uncertain whether ash will re-establish into the overstory of southeastern Lower Michigan because of the relatively unknown future dynamics of EAB in North America. Specifically, it remains to be seen if EAB can sustain a population large enough within the area of heavy ash mortality to persist until the largest ash regeneration reaches a diameter large enough to be attacked and killed again by EAB. Extirpation of the genus *Fraxinus* may occur from the current and expanding range of EAB if EAB somehow persists or returns to attack maturing ash regeneration, but the EAB population would need to be sizable enough to quickly locate and kill newly mature ash trees before they reach reproductive age. Maturing ash regeneration that is able to produce seed before being killed provides the potential for restoration and maintenance of a long-term ash seed bank, albeit greatly reduced compared to pre-EAB levels. That regenerating ash reaches reproductive age is certainly possible, given that the "front" of EAB spread continues to move outward from the metropolitan Detroit area, with far more live host trees available outside the front than within it, such that the majority of the EAB population may be attracted away from the center of the affected area rather than towards it. However, despite <5% of overstory ash trees remaining nearest the introduction point, EAB individuals continue to be detected near the center of the EAB distribution (Kathleen Knight, personal communication), suggesting that individual insects remain in the area even as ash nears extirpation while the species spreads elsewhere. Moreover, reproductive success of ash, which is wind-pollinated and dioecious, is a function of the number of individual ash trees remaining, because the pollen produced by male trees must be abundant to be successfully delivered to flowers on female trees. Thus even regenerating ash that reach reproductive age may not successfully reproduce if the population of reproducing ash is low within the range of heavy EAB-caused mortality. EAB population dynamics are therefore key in determining whether North American ash will follow the model of Dutch elm disease, where individual trees experience a reduced life span but are able to reproduce, or American chestnut, where individual trees are killed before they are able to reproduce, or whether it will follow an entirely different, unprecedented model for native tree species heavily impacted by invasive insects or pathogens.

Acknowledgements

We would like to acknowledge the dutiful field assistance of Lena Cicchelli, Guadalupe Cummins, Bill Dodge, John Niedermiller, Tori Schneider, and John Stewart, in collecting the data in often jungle-like conditions of heat, humidity, thick undergrowth, and insects. Bill Dodge was instrumental in supervising the field crews, and in entering and summarizing field data. This project was funded by a University Research Grant at Wayne State University and by the Wayne State Department of Biological Sciences.

Contributions: DMK and JAW conceived the study and developed the experimental design; DMK performed field research, analyzed data, and wrote the manuscript.

Appendix A.

Site	Forest Type	Relative Density	Major Overstory Species
Bird Hills Natural Area	Mesic Hardwoods	2.7	*Quercus alba, Q. rubra, Tilia americana*
Belle Isle Park	River Floodplain	37.8	*Populus deltoides, Acer rubrum, Ulmus americana*
Bald Mountain Recreation Area 1	Mesic Hardwoods	15.3	*A. rubrum, Acer saccharum*
Bald Mountain Recreation Area 2	Mesic Hardwoods	10.7	*U. americana, Prunus serotina*
Cherry Hill Nature Preserve	Mesic Hardwoods	6.8	*Q. rubra, A. saccharum, U. americana*
Delhi Metropark	River Floodplain	32.9	*A. rubrum, Acer saccharinum, U. americana*
Dexter-Huron Metropark	River Floodplain	68.5	*T. americana, Quercus macrocarpa*
Dolph Park Natural Area	Mesic Hardwoods	30.8	*A. saccharum, U. americana, P. serotina*
Dansville State Game Area	River Floodplain	28.6	*P. deltoids, A. saccharinum, A. rubrum*
Highland Recreation Area	Mesic Hardwoods	31.6	*T. americana, Q. alba, P. serotina*
Huron Meadows Metropark 1	Mesic Hardwoods	14.2	*Q. alba, Q. rubra, A. saccharum*
Huron Meadows Metropark 2	River Floodplain	27.6	*Q. macrocarpa, T. americana, U. americana*
Holly Recreation Area	Mesic Hardwoods	17.4	*Q. rubra, U. americana, P. serotina*
Island Lake Recreation Area 1	Deciduous Swamp	46.0	*A. rubrum, U. americana*
Island Lake Recreation Area 2	Dry-mesic Hardwoods	3.0	*Q. alba, Quercus velutina, Carya ovata*
Island Lake Recreation Area 3	Mesic Hardwoods	10.3	*Q. alba, C. ovata*
Island Lake Recreation Area 4	Mesic Hardwoods	6.0	*Q. rubra, P. serotina*
Lower Huron Metropark 1	Deciduous Swamp	12.8	*Quercus palustris, Q. rubra, A. rubrum*
Lower Huron Metropark 2	River Floodplain	31.2	*Platanus occidentalis, U.americana*
Lower Huron Metropark 3	Deciduous Swamp	5.3	*Q. palustris, A. rubrum, U.americana*
Lower Huron Metropark 4	Mesic Hardwoods	21.9	*A. saccharum, T. americana, Carya cordiformis*
Lapeer State Game Area 1	Mesic Hardwoods	27.9	*T. americana, U. americana*
Lapeer State Game Area 3	River Floodplain	27.6	*P. deltoids. U. americana, A. rubrum*
Lapeer State Game Area 4	Mesic Hardwoods	34.6	*Q. rubra, A. saccharum, T. americana*
Lapeer State Game Area 2	River Floodplain	15.6	*P. deltoides, A. rubrum*
Maybury State Park 1	Mesic Hardwoods	7.8	*A. saccharum, Fagus grandifolia*
Maybury State Park 2	Mesic Hardwoods	5.7	*A. saccharum, Q. rubra*
Maybury State Park 3	Mesic Hardwoods	3.6	*A. saccharum*
Maybury State Park 4	Mesic Hardwoods	8.5	*T. americana, A. saccharum, Q. rubra*
Metamora-Hadley Recreation Area	Mesic Hardwoods	47.6	*A. saccharum, F. grandifolia, Q. rubra*
Ortonville Recreation Area 1	Mesic Hardwoods	39.6	*U. americana, A. saccharum, P. serotina*
Ortonville Recreation Area 2	Mesic Hardwoods	44.4	*Q. rubra, P. serotina, U. americana*
Ortonville Recreation Area 3	River Floodplain	13.4	*A. saccharinum, P. deltoides, U.americana*
Oakwoods Metropark	Mesic Hardwoods	7.8	*Q. rubra, C. ovata, T. americana*
Pinckney Recreation Area	Mesic Hardwoods	14.8	*Q. rubra, U. americana*
Proud Lake Recreation Area 1	Dry-mesic Hardwoods	21.6	*Q. alba, Q. rubra, P. serotina*
Proud Lake Recreation Area 2	Mesic Hardwoods	19.9	*Q. rubra, A. saccharum, P. serotina*
Parker Mill Park	Mesic Hardwoods	13.7	*T. americana, A. saccharum, U. americana*
Rose Lake Wildlife Area 1	Deciduous Swamp	14.7	*U. americana, Q. bicolor*
Rose Lake Wildlife Area 2	Mesic Hardwoods	22.3	*A. saccharum, P. serotina*
Seven Lakes State Park	Mesic Hardwoods	56.7	*Q. rubra, U. americana, A. rubrum*
U-M Botanical Gardens	Deciduous Swamp	49.2	*T. americana, U. americana*
U-M Nichols Arboretum	Dry-mesic Hardwoods	24.1	*P. serotina, Q. alba*
Waterloo Recreation Area 1	Dry-mesic Hardwoods	35.2	*Q. alba, Q. rubra, P. serotina*
Waterloo Recreation Area 2	Mesic Hardwoods	18.8	*Q. rubra, A. saccharum, T. americana*
Willow Metropark 1	Deciduous Swamp	22.9	*A. rubrum, Populus tremuloides*
Willow Metropark 2	Mesic Hardwoods	16.7	*A. rubrum, A. saccharum, U. americana*

References

Albert, D.A., Denton, S.R., Barnes, B.V., 1986. Regional landscape ecosystems of Michigan. School of Natural Resources, University of Michigan. 32 pp., 1 map.

Anagnostakis, S.L., 1987. Chestnut blight: the classical problem of an introduced pathogen. Mycologia 79, 23–27.

Anulewicz, A.D., McCullough, D.G., Cappaert, D.L., 2007. Emerald ash borer (*Agrilus planipennis*) density and canopy dieback in three North American ash species. Arb. Urb. For. 33, 338–349.

Barnes, B.V., 1976. Succession in deciduous swamp communities of southeastern Michigan formerly dominated by American elm. Can. J. Bot. 54, 19–24.

Barnes, B.V., Wagner Jr., W.H., 2003. Michigan Trees: Revised and Revisited. University of Michigan Press, Ann Arbor, MI.

Beckage, B., Clark, J.S., 2003. Seedling survival and growth of three forest species: the role of spatial heterogeneity. Ecology 84, 1849–1861.

BenDor, T.K., Metcalf, S.S., Fontenot, L.E., Sangunett, B., Hannon, B., 2006. Modeling the spread of the emerald ash borer. Ecol. Mod. 197, 221–236.

Cappaert, D., McCullough, D.G., Poland, T.M., Siegert, N.W., 2005. Emerald ash borer in North America: a research and regulatory challenge. Am. Entom. 51, 152–165.

Castrillo, L.A., Griggs, M.H., Vandenberg, J.D., 2008. Quantitative detection of *Beauveria bassiana* GHA (Ascomycota: Hypocreales), a potential microbial control agent of the emerald ash borer, by use of real-time PCR. Biol. Control 45, 163–169.

Feeley, C.J., Hart, E.R., Thompson, J.R., Harrington, T.C., 2001. Occurrence, associated symptoms, and potential insect vectors of the ash yellows phytoplasma in Iowa, U.S. J. Arb. 27, 331–340.

Gandhi, K.J.K., Herms, D.A., 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol. Invasions 12, 389–405.

Gould, J., 2007. Proposed release of three parasitoids for the biological control of the emerald ash borer (Agrilus planipennis) in the continental United States. Environmental Assessment, April 2007. United States Department of Agriculture Plant Protection and Quarantine. Otis ANGB, MA.

Hubbes, M., 1999. The American elm and Dutch elm disease. For. Chron. 75, 265–273.

Kennedy, H.E., 1990. *Fraxinus pennsylvanica* Marsh.: Green ash, in: Burns, R.M., Honkala, B.H. (Tech. Coords.), Silvics of North America, volume 2: Hardwoods. Agriculture Handbook 654. USDA Forest Service, Washington, DC, pp. 348–354.

Liu, H.P., Bauer, L.S., 2008. Microbial control of emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae) with Beauveria bassiana strain GHA: Greenhouse and field trials. Biol. Control 45, 124–132.

Liu, H., Bauer, L.S., Gao, R., Zhao, T., Petrice, T.R., Haack, R.A., 2003. Exploratory survey for the emerald ash borer, Agrilus planipennis (Coleoptera: Buprestidae) in China. Great Lakes Entom. 36, 191–203.

MacFarlane, D.W., Meyer, S.P., 2005. Characteristics and distribution of potential ash tree hosts for emerald ash borer. For. Ecol. Manag. 213, 15–24.

Murihead, J.R., Leung, B., van Overdijk, C., Kelly, D.W., Nandakumar, K., Marchant, K.R., MacIsaac, H.J., 2006. Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. Divers. Distrib. 12, 71–79.

Poland, T.M., 2007. Twenty million ash trees later: Current status of emerald ash borer in Michigan. Newslett. Michigan Entomol. Soc. 52, 10–14.

Poland, T.M., McCullough, D.G., 2006. Emerald ash borer: Invasion of the urban forest and the threat to North America's ash resource. J. For. 104, 118–124.

Prasad, A.M., Iverson, L.R., Peters, M.P., Bossenbroek, J.M., Matthews, S.N., Syndor, S.D., Schwartz, M.W., 2010. Modeling the invasive emerald ash borer risk of spread using a spatially explicit cellular model. Land. Ecol. 25, 353–369.

Schlesinger, R.C., 1990. *Fraxinus americana* L.: White ash, in: Burns, R.M., Honkala, B.H. (Tech. Coords.), Silvics of North America volume 2: Hardwoods. Agriculture Handbook 654. USDA Forest Service, Washington, DC, pp. 333–338.

Siegert, N.W., McCullough, D.G., Liebhold, A.M., Telewski, F.W., 2007. Resurrected from the ashes: a historical reconstructions of emerald ash borer dynamics through dendrochronological analyses, in: Mastro V., Reardon R., Parra G. (Comps.), Proceedings of the Emerald Ash Borer/Asian Longhorned Beetle Research and Technology Development Meeting. FHTET-2007-04, USDA Forest Service, Morgantown, W.V., pp. 18–19.

Smitley, D., Davis, T., Rebek, E., 2008. Progression of ash canopy thinning and dieback outward from the initial infestation of emerald ash borer (Coleoptera: Buprestidae) in Southeastern Michigan. J. Econ. Entom. 101, 1643–1650.

Wei, X., Wu, Y.U.N., Reardon, R., Sun, T.-H., 2007. Biology and damage traits of emerald ash borer (*Agrilus planipennis* Fairmaire) in China. Insect Sci. 14, 367–373.

Windfeldt, K., 2005. Conditions of Ash in the Huron River watershed. MS Thesis. University of Michigan, Ann Arbor.

Woodcock, H., Patterson III, W.A., Davies Jr., K.M., 1993. The relationship between site factors and white ash (*Fraxinus americana* L.) decline in Massachusetts. For. Ecol. Manag. 60, 271–290.

Wright, J.W., Rauscher, H.M., 1990. *Fraxinus nigra* Marsh.: Black ash, in: Burns, R.M., Honkala, B.H. (Tech. Coords.), Silvics of North America volume 2: Hardwoods. Agriculture Handbook 654. USDA Forest Service, Washington, DC, pp. 344–347.