

Sprouting and seed production may promote persistence of green ash in the presence of the emerald ash borer

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Abstract. Invasive insects and pathogens have had major impacts on many forest tree species in North America that often affect forest structure and composition. Despite these effects, variation exists in the likelihood that some native species may persist following outbreaks and establishment of exotic insects and pathogens. Emerald ash borer (EAB; *Agrilus planipennis*) has killed millions of trees near its introduction point in southeastern Michigan, and several recent studies in the area have predicted functional elimination of green ash (*Fraxinus pennsylvanica*) from the landscape. Intensive management in yet unaffected stands that results from such predictions, however, demands data that examine the potential for persistence of the host species in the presence of the invasive. This study examined the potential for persistence of green ash in the presence of EAB by measuring surviving trees, regeneration, and seed rain characteristics in 17 small, near-pure stands of green ash in five consecutive growing seasons. Live trees experienced 58% mortality due to EAB, significantly less than that reported for ash in mixed stands. Approximately 20% of surviving trees exhibited signs of EAB, confirming that EAB mortality has slowed significantly but is ongoing. Sprouting was the dominant mode of ash regeneration in every year, and 27% of large sprouts produced seeds during a mast year in 2011. Advanced regeneration and new seedling establishment resulted in a sizable level of ash regeneration over the five years of the study even when sapling and seedling mortality was taken into account. Seed production was reduced considerably following EAB-caused mortality, but there was no evidence that seed dispersal limited seedling recruitment. These results suggest that the seed-producing ability of small trees and basal sprouts, as well as continued low-level mortality that will retain reduced host density, may allow green ash to persist in the presence of EAB. Although green ash populations and individual trees are unlikely to ever resemble the stature of those prior to EAB, their presence will continue to be an important component of forests on the landscape.

Key words: ash regeneration; disturbance; forest recovery; *Fraxinus pennsylvanica*; invasive insects; southeastern Michigan.

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INTRODUCTION

The near-elimination of forest tree species by non-native insects or pathogens has become increasingly common in recent decades (Gandhi and Herms 2010). Nearly every native woody plant genus in eastern North America is associated with at least one introduced species, some

of which have had significant impacts upon their host plant populations (Mattson et al. 2007). For example, beech bark disease (*Neonectria* spp.) is an exotic canker fungus spread by the beech scale (*Cryptococcus fagisuga* Lind.) in the northeastern United States that has killed up to 55% of stems and 92% of basal area of American beech (*Fagus grandifolia* Ehrh.) (Wieferich 2013). Perhaps

the most infamous tree species impacted by an invasive is the American chestnut (*Castanea dentata* (Marsh.) Borkh.), which was virtually eliminated from the landscape when chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) killed >3.5 million trees in the southeastern United States between 1900 and 1940 (Anagnostakis 1987). Today, surviving chestnut trees exist mainly as root-collar sprouts that are killed prior to reaching reproductive age (Jacobs et al. 2013). Sudden or selective mortality of major canopy species caused by invasive species epidemics in temperate forests may have major impacts on forest composition and structure (Gandhi and Herms 2010), and thus intensive management activities to avoid or mediate such impacts are not uncommon (Bond et al. 2010).

Despite major effects on some tree species, there is variation in the likelihood that some native species may persist following outbreaks and establishment of exotic insects and pathogens. In contrast to the American chestnut (Jacobs et al. 2013) which did not persist following invasive establishment, Barnes (1976) and Richardson and Cares (1976) documented the persistence of the American elm (*Ulmus americana* L.) after Dutch elm disease (DED; *Ophiostoma ulmi* (Buisman) Melin & Nannf) killed about 200 million mature elm trees in the northeastern United States between the late 1920s and the 1970s (Hubbes 1999). Despite heavy mortality, a reduction in life span, and markedly reduced basal area, succeeding cohorts of elm were not eliminated (Barnes 1976). Instead, elm populations were likely to remain as an important species though not a canopy dominant in hardwood-dominated lowland ecosystems (Richardson and Cares 1976). Clearly, identifying and documenting mechanisms by which host species might persist in the presence of an invasive agent is critical for mitigating potential impacts of future spread into unaffected areas, as well as future species introductions.

As the number of highly destructive invasive species continues to increase in North American forests, a perceived need to proactively manage an uninfected area assuming the inevitable arrival of the invasive has also increased (Bond et al. 2010). For example, management alternatives for beech bark disease include the removal of healthy beech from uninfected stands depending on their isolation from nearby infested stands

(Heyd 2005). Actions that follow the devastation of more harmful invasive agents may be even less conventional. Aftermath forests affected by chestnut blight (Jacobs et al. 2013) and hemlock woolly adelgid (*Adelges tsugae* Annand; Vose et al. 2013, Orwig et al. 2002) are often restored by planting non-native or hybridized species or by facilitating movement of native species to new habitats. Even forests affected by DED, despite the documented persistence of elm, may include management alternatives that encourage underplanting of disease-resistant cultivars or other species (Stipes 2000). Given the potential effects of such management alternatives on biodiversity or forest composition and structure, it is imperative to document the potential (or lack thereof) for a native species to persist in the presence of a destructive exotic species to appropriately guide proactive or aftermath management.

Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) is one of the most significant species introduced into eastern North America in recent years (Cappaert et al. 2005). EAB was introduced to southeastern Michigan from Asia and by 2009 caused nearly 100% mortality of ash trees (*Fraxinus* spp.) in mixed hardwood stands nearest its introduction point (Burr and McCullough 2014, Klooster et al. 2013, Kashian and Witter 2011). All North American species of ash are susceptible to EAB (MacFarlane and Meyer 2005). Seedlings and saplings <2.5 cm in diameter are least affected by EAB, making regeneration critical to the future of ash in this region. In southeastern Michigan and northeastern Ohio, ash regeneration is abundant in the understory of affected mixed hardwood forests but recent ash germinants are few or lacking, suggesting a depletion of the ash seed bank resulting from the elimination of parent trees by EAB (Klooster et al. 2013, Kashian and Witter 2011). Despite the presence of a few lingering live mature ash in forests of this region (Marshall et al. 2013, Knight et al. 2012a), ash has been suggested by some investigators to have completely ceased its regeneration (Herms and McCullough 2014, Klooster et al. 2013). Low-level, established populations of EAB remain in these forests (Burr and McCullough 2014, Klooster et al. 2013), certainly making the likelihood of ash persistence precarious. These data have begun to foster proactive, intensive management techniques in areas where EAB has not yet become established,

including drastic reduction in ash basal area via harvesting (Michigan Department of Natural Resources 2011, Petrice and Haack 2011) or rapid conversion of forest composition to other species (Slesak et al. 2014, Knight et al. 2012b).

Among the largest concerns regarding EAB in forested areas is potential infestation where ash is a major canopy dominant. Notably, most studies of EAB nearest its introduction point were conducted in forests where ash species constituted on average <25% of the canopy trees (Burr and McCullough 2014, Klooster et al. 2013, Kashian and Witter 2011) and competition among trees is largely inter-specific. Preliminary studies have suggested that high ash densities may have a dilution effect on EAB, such that ash mortality is lowest where ash trees occur at higher concentrations (Knight et al. 2013). Forests of higher relative density of ash, if they persist, may therefore be important source populations for re-colonizing the landscape in the presence of EAB. In southeastern Michigan, where EAB has been established longer than anywhere in North America, green ash (*Fraxinus pennsylvanica* Marsh.) forms small, relatively dense, nearly pure “groves” of trees regenerated from seed (Taylor 1972). Green ash has been predicted to be “functionally eliminated” by EAB from mixed-species forests (Burr and McCullough 2014, Herms and McCullough 2014, Klooster et al. 2013), but comprehensive studies or data are lacking where green ash relative density is high. Of particular interest are processes that may heavily influence post-outbreak recovery, such as the ecological role of surviving trees (Plotkin et al. 2013), seed production and dispersal (Turnbull et al. 2000), and recruitment limitation (Clark et al. 1998).

For five consecutive growing seasons, I examined small forest stands in southeastern Michigan where green ash was a canopy dominant to examine the potential for green ash to persist following heavy EAB-caused mortality. Similar to elm following DED and based on life history characteristics of green ash, I hypothesized that ash persistence is possible in the presence of EAB, though at relatively low abundance, if stands are able to maintain a cohort of trees that produce viable seed. I tested this hypothesis by asking: (1) What is the current condition of surviving ash trees in areas suffering heavy EAB-caused mortality? (2) What is the level of ash regener-

ation in heavily-EAB impacted stands? (3) How much viable ash seed is produced within these stands, how does it influence seed dispersion patterns, and does it limit seedling establishment in these stands?

METHODS

Study sites

Seventeen study sites were sampled in southeastern Lower Michigan, USA (42°25' N, 83°38' W; Fig. 1) and were located either on private land or within state or municipal park boundaries. All sites were flat and experienced standing water in the spring months (typically between March and May), likely explaining a notable lack of shrub and herbaceous vegetation. Sampled forest stands were 40–70 yr old, ranged in size between 0.08–0.5 ha, and were dominated (relative density >95%) in all strata by green ash (also called red ash (Barnes and Wagner 2004)). High ash dominance in this

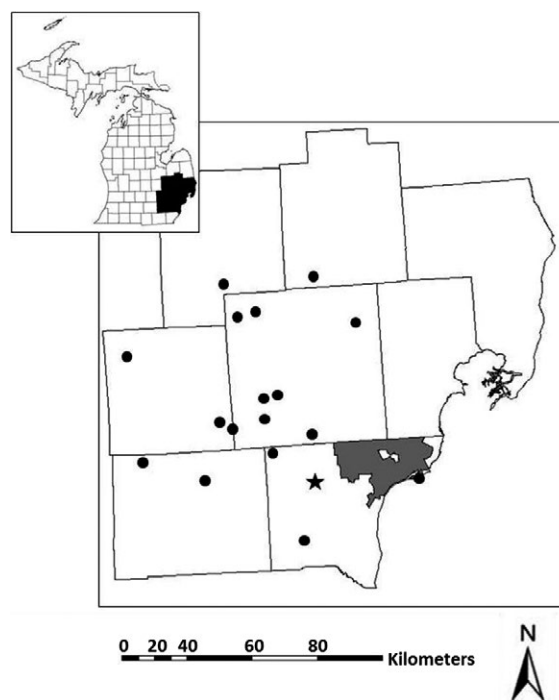


Fig. 1. Locations of 17 green ash stands across six counties in southeastern Michigan. The shaded area represents the City of Detroit for reference; the star represents the approximate introduction point of emerald ash borer.

Table 1. Structural characteristics of 17 stands dominated by green ash and infested by EAB in southeastern Michigan. Data shown were collected in 2012 for trees > 4 cm diameter at breast height.

Period of EAB attack	Area (m ²)	Ash relative density (%)	Pre-EAB density (trees/ha)	Post-EAB density (trees/ha)	Live ash BA (m ² /ha)	Dead ash BA (m ² /ha)	Pre-EAB Qm (cm)	Post-EAB Qm (cm)	Live ash with EAB (%)	Dead ash with sprouts (%)
1998–2000	823	96.5	963	475	8.84	7.63	12.7	11.1	23.7	66.7
1998–2000	1156	99.2	1445	464	9.06	20.09	13.1	9.2	19.6	80.6
1998–2000	2189	97.6	1595	676	5.59	26.34	9.8	7.4	33.8	73.6
1998–2000	1632	96.4	1913	900	8.12	19.65	8.7	7.9	16.0	78.4
1998–2000	842	95.3	1050	400	5.86	21.34	14.6	9.1	21.9	78.8
2001–2002	2573	96.8	848	372	0.49	16.39	16.6	5.7	15.1	45.4
2001–2002	3014	96.7	487	227	1.09	3.04	10.6	8.2	2.9	69.2
2001–2002	2100	99.6	1776	938	5.98	8.90	9.2	6.3	5.6	50.6
2001–2002	956	99.1	1158	442	5.85	14.31	11.2	8.5	11.9	60.3
2001–2002	3263	97.7	1753	897	6.02	25.99	15.2	10.2	29.3	63.1
2001–2002	2221	96.4	1995	832	8.26	14.35	12.3	9.4	23.0	64.1
2003–2004	2500	97.6	1356	592	6.83	1.31	8.4	6.3	14.9	96.9
2003–2004	1881	96.1	2528	933	6.98	18.90	11.4	7.6	36.3	47.4
2003–2004	4342	96.9	1186	498	7.23	28.36	10.8	8.1	26.6	49.0
2003–2004	5031	98.6	2314	724	8.59	29.96	9.5	6.7	16.9	45.2
2003–2004	2285	98.7	1509	709	5.24	18.17	13.3	11.5	5.1	35.8
2003–2004	1741	96.3	1576	718	8.61	16.37	9.5	7.6	13.1	45.2
Mean	2228	97.4	1497	635	6.39	17.12	11.6	8.3	18.6	61.8

study is a significant departure from previous studies of EAB-affected ash. Other tree species occasionally present included box elder (*Acer negundo* L.), red maple (*A. rubrum* L.), silver maple (*A. saccharinum* L.), eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall), and American elm.

Study site locations were stratified based on time since EAB attack (TSA) as estimated by Prasad et al. (2010), including 1998–2000 ($n = 5$), 2001–2002 ($n = 6$), and 2003–2004 ($n = 6$; see Table 1), although tree mortality peaked prior to 2009 for all stands (Klooster et al. 2013, Kashian and Witter 2011). EAB was assumed to have established in each stand since its respective TSA. Dendrochronology was used to confirm the membership of each stand to its specific TSA group as estimated by Prasad et al. (2010). Tree ring series were obtained from cross-sections of all fallen dead ash trees in each stand and increment cores from standing dead ash, as well as increment cores obtained from live ash trees. Fallen dead trees were only counted when their former rooting location could be determined to be within the stand to ensure that fallen trees input into the stand from floodwater were not included in the

sample. Increment cores and cross-sections were mounted and sanded per standard techniques (Speer 2012), and annual rings were counted and measured under a microscope using a sliding bench micrometer. Seven to 10 of the largest (oldest) live ash trees in each stand were used to develop master chronologies (20–40 yr long) with assistance from the program COFECHA (Holmes 1983). TSA group was confirmed for a stand if >75% of the killed trees dated to the appropriate period of time. Trees whose death dated to 2010 were used to compare the number of trees lost to EAB in the five sampling years. Pre-EAB density was estimated by counting the number of trees >4 cm DBH prior to the first year of EAB attack; pre-EAB diameter of current live ash trees was estimated by subtracting the ring widths grown since EAB attack from the current diameters. Pre-EAB basal area was estimated by summing the basal area of ash trees determined to be alive prior to EAB attack minus the basal area grown since EAB attack, plus the basal area of dead trees.

EAB impacts and condition of surviving trees

Field sampling was conducted annually in 2010–2014; 2011 was a mast year for green

ash in southeastern Michigan. The perimeter of each stand was mapped using a global positioning system (GPS) unit to determine the stand shape and the area. Using methodology from McEuen and Curran (2004), circular plots (100-m²; 11.3 m diameter) were arranged along a 15-m staggered array in an east-west direction. Because of the small size of the 17 stands, sample plots within each stand were established systematically to maximize both the sampled area and the number of plots per stand. The number of plots increased with the stand area and ranged from 4 to 36 (total plots = 261). In each plot, the diameter of all live trees >4 cm were measured and tagged at breast height (DBH) and aged using an increment core sampled 30 cm above the root collar. EAB activity in live ash trees was noted in 2012 using EAB exit holes, woodpecker damage, bark splitting, or epicormic sprouting as indicators (Smith 2006). Crown condition was scored each year using standard techniques for assessing progressive degrees of ash health based on crown dieback on a 1–5 scale, where 1 is a healthy tree and 5 is a dead tree (Smith 2006). Changes in crown condition ratings over the five year duration of the study were assessed with transition matrices (Knight et al. 2008a). Seed-bearing trees were identified in each sampling year to account for potential inter-annual variation in seed production (see below). Pre-EAB conditions were estimated from standing and fallen dead ash trees using the presence of EAB galleries or exit holes and dendrochronological dating to determine the year of death. Differences in current ash tree density (natural log transformed), estimated pre-EAB ash tree density, current ash basal area, and the proportion of live trees exhibiting signs of EAB infestation were compared among TSA groups using analysis of variance (ANOVA). Number of ash trees and seed trees killed could not be normalized and were compared among the five field seasons using the Friedman test. Alpha = 0.05 for all analyses. For these and all analyses, the assumption of uncorrelated errors in statistical models (no spatial autocorrelation in the residuals) was tested using the Durbin–Watson statistic; no evidence of spatial autocorrelation was found for any analysis given that $d > 1.6$.

Ash regeneration

Living sprouts (originating from the root collar of top-killed ash) were counted at the end of each growing season. Sprouts were tagged, measured, and cored if they were >4 cm DBH. Seedlings and saplings (all ash <4 cm DBH that originated from seed) were counted in September of each year and classified as advanced regeneration (established prior to first year of EAB attack) or post-EAB seedlings (established after first year of attack) using bud scar counts (Clark and Hallgren 2004). A separate field trial of 50 destructively sampled ash saplings where bud scars were counted and compared with the number of annual growth rings suggested that this method was accurate with an error of ± 2 yr. Changes in densities of advanced regeneration and post-EAB seedlings (natural log transformed) and sprouts between 2010 and 2015 were examined using repeated-measures ANOVA, and one-way ANOVA was used to test for differences in regeneration densities based upon the time of EAB attack.

Seed production, dispersion, and seedling establishment

Seed traps with a surface area of 0.25 m² were located at the center point of each plot. In 2010, 50 traps were chosen at random from the total of 261 across the study area to test seed retention and seed predation from the traps. Ash samaras were marked and left in the 50 random traps for 30 d in June, August, and October; retention in the traps averaged 92%, 96%, and 91%, respectively. Samaras were collected monthly between May and November each year. Samara counts were standardized by seed trap area and expressed as m²/forest floor to represent seed production each year. Similar to McEuen and Curran (2004), seed dispersion was calculated as the proportion of traps in a stand that received samaras in a given year. Source dispersion was calculated as the proportion of plots in a stand having seed-bearing ash trees, and source density was calculated as the basal area of seed-bearing ash. Seed-bearing trees were identified specifically in each of the five sampling years because (1) ash trees are dioecious, such that not all mature trees are sources of seed, and (2) seed

production varied considerably for individual trees across the five years of this study.

Seed collected from each seed trap was physically examined to determine its viability based on recommendations from the National Center for Genetic Resources Preservation (Ellis 2006). Samaras were examined for aborted embryos (mature fruit but soft or missing seed), the presence of seed insects or predation (presence of bore holes or misshapen seeds or fruits), or other damage to the seed coat. Only seeds considered viable upon physical inspection (sound seeds) were included in analyses of seed production. Sound seeds were air dried for storage prior to germination experiments (Ellis 2006). For germination trials, seeds were stored on moist filter paper and placed into cold storage (10 °C) for 90 d to ensure stratification. After stratification, 500 randomly selected seeds were subjected to germination trials in 2010, 2011, and 2012 by placing seeds on moist filter paper in germination boxes in groups of 100 seeds in a greenhouse in early May. Germinated seeds were recognized after 60 d as those seeds exhibiting at least an identifiable radicle that had emerged from the seed coat.

The rationale of McEuen and Curran (2004) was used to investigate the impacts of seed distribution on seedling recruitment within the 17 stands sampled. Seed dispersion should be low if seed was not universally or evenly available within a stand. Variation in seed dispersion (natural log transformed) that occurred with changes in source density (natural log), source dispersion (arcsine square root), and seed production (natural log) was tested using Pearson correlation coefficients (Spearman rank correlations when nonlinear). Significance values of correlation coefficients were adjusted using the Dunn-Sidak method to correct for potential inflation of Type I error. The spatial relationship between seeds and post-EAB seedlings was tested with Fisher's exact test to determine whether seed dispersal limits seedling recruitment, with the idea that seeds and recruits should be spatially correlated if seeds are limiting (McEuen and Curran 2004). The spatial relationship between seeds and advanced regeneration was also examined, since pre-EAB seed distribution from a heavier-than-current seed rain is even less likely to have been restricted if current seed dispersal patterns are uniform across the stand. Finally,

linear regression was conducted to predict seed dispersion patterns from source density, source dispersion, and seed production for each year. Candidate models included all combinations and subsets of the full, 3-variable model, and the best model was selected by minimizing the Akaike information criterion (AIC).

RESULTS

Condition of surviving trees

Live tree density varied across the 17 stands between 227 and 938 trees/ha, with an average of 635 (± 54) trees/ha; pre-EAB density for the same stands ranged between 487 and 2528 trees/ha with a mean of 1497 (± 128) trees/ha (Table 1). EAB caused a mean decrease of 57.6% in live tree density from 1497 (± 128) to 635 (± 54) trees/ha, a 62.7% decrease in mean basal area from 17.12 (± 2.02) to 6.39 (± 0.60) m²/ha, and a 28.4% decrease in mean quadratic mean diameter (Qm) from 11.6 (± 0.58) to 8.3 (± 0.4) cm (Table 1). Neither live tree density, basal area, nor quadratic mean diameter differed among the five TSA groups prior to EAB attack or after EAB attack, suggesting that EAB impact was similar regardless of when initial attack occurred, and that stands were similar in structure prior to EAB attack.

Approximately 18.6% (± 2.3) of the remaining live trees exhibited symptoms of EAB infestation, but did not differ among TSA groups. A mean of 54.7% (± 5.6) of seed-bearing trees were infested by EAB in 2012, and seed tree infestation was greater in stands attacked most recently (2003–2004) compared with those attacked earlier ($F_{2,14} = 6.896$, $P = 0.008$). There were significantly more trees killed by EAB in 2011, 2012, and 2013 compared to 2010 and 2014 (Friedman test: $\chi^2_4 = 10.81$, $P = 0.029$); the number of seed trees lost did not differ across the years. Significant differences were found mainly in stands attacked most recently, where there were more trees ($\chi^2_4 = 11.813$, $P = 0.019$) and seed trees ($\chi^2_4 = 9.733$, $P = 0.045$) lost between 2011 and 2013 compared to 2010 and 2014.

Across all sites, 1356 live ash trees were sampled beginning in 2010, 34% of which had healthy canopies (condition class 1). After five years (in 2014), only 11% of the original trees remained healthy and 347 (26%) had died, but 324 new

Table 2. Transition matrix of green ash canopy condition pooled for 17 green ash stands in southeastern Michigan between 2010 and 2014. Values represent the percentage of trees that were rated as a specific crown condition class in 2010 but changed to another specific crown condition in 2014.

Crown condition class in 2010	Crown condition class in 2014				
	1	2	3	4	5
1	26.1	25.0	18.4	30.3	0.2
2		18.5	22.1	46.0	13.4
3			4.7	12.1	83.2
4				5.8	94.2

overstory trees had recruited from the understory, such that the net loss of individual overstory trees was <2%. By 2014, the crown conditions of 19% of the original trees had not changed since 2010, but 56% of the trees had their crown condition worsen over the five years of the study (Table 2). Notably, 67% of the tree crown conditions remaining unchanged between 2010 and 2011, 63% between 2011 and 2012, 76% between 2012 and 2013, and 78% between 2013 and 2014. The most significant change between 2010 and 2014 was the movement of fairly healthy canopies (condition class 2) to unhealthy canopies without the onset of mortality (condition class 4) in 15% of the original trees.

Ash regeneration

Ash regeneration in the 17 stands occurred as three distinct types: sprouts originating from trees top-killed by EAB, advanced regeneration that established prior to EAB infestation, and seedlings that established since EAB infestation occurred (Fig. 2; Appendix S1). The degree of sprouting in the 17 stands was a surprising result given the lack of post-EAB green ash sprouting reported in the literature (Klooster et al. 2013). Sprouting was the dominant mode of ash regeneration in every year of sampling, ranging from a maximum of 57% of total regeneration in 2010 to a minimum of 40% in 2014 (Fig. 2). The percentage of trees top-killed by EAB that had sprouts across the 17 stands ranged from 36% to 95%, with a mean of 62% ($\pm 4\%$; Table 1), but sprout density did not increase significantly between 2010 and 2014 for the pooled data. There was a lag time between tree death by

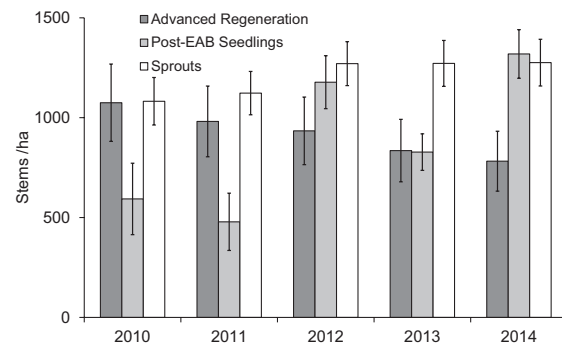


Fig. 2. Mean density for three regeneration types over five growing seasons for 17 green ash-dominated stands in southeastern Michigan. Regeneration types include advanced regeneration (seedlings and saplings established prior to EAB attack), post-EAB seedlings (seedlings established after EAB attack); and basal sprouts originating from trees killed by EAB. Values are means for pooled data across all TSA groups (see text for explanation).

EAB and the appearance of significant sprouting; sprout density was significantly higher for stands attacked early (1998–2000) compared to those attacked late (2003–04) in 2010 (ANOVA , $F_{2,14} = 8.82$, $P = 0.003$) and 2011 ($F_{2,14} = 6.06$, $P = 0.013$). When examined by TSA group, sprout density was higher in 2010 and 2011 for stands attacked early (1998–2000; repeated measures ANOVA , $F_{4,16} = 4.93$, $P = 0.009$), lower in 2010 and 2011 for stands attacked in 2001–02 ($F_{4,20} = 30.19$, $P < 0.0001$), and higher in 2013 and 2014 for stands attacked most recently (2003–04; $F_{4,20} = 51.79$, $P < 0.0001$).

Approximately 31% of all live trees >4 cm DBH originated as basal sprouts following EAB-caused mortality; 90% of these sprouts were <7 yr old when aged in 2012, and 50% were <5 yr old. Diameter growth of sprouts >4 cm DBH occurred at a much higher rate than either live trees or advanced regeneration; mean basal area increment for sprouts ($n = 767$) increased on average by 49% (compared to 36% for live trees) between the 3rd and 6th years of growth, then by 56% (compared to 36% for live trees) between the 7th and 10th years of growth (Fig. 3). Seed production by sprouts occurred across all sprout age classes almost proportionally to their occurrence; 27% of sprouts >4 cm at DBH produced seeds during the mast year in 2011 (24% in 2013); 89% of the

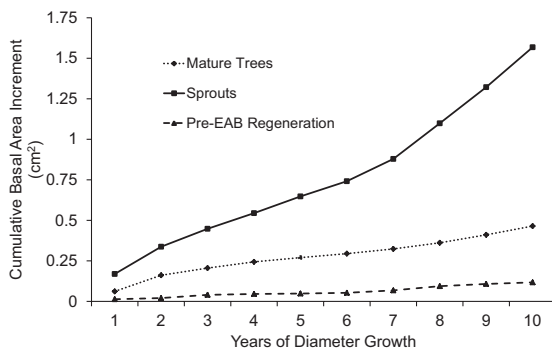


Fig. 3. Relative basal area increment for green ash basal sprouts and advanced regeneration in 17 stands in southeastern Michigan. Basal area increment for surviving trees is also shown for comparison.

sprouts that produced seeds were <7 yr old, but this age class represented almost 90% of the sprouts.

Across all stands, advanced regeneration density declined (repeated-measures ANOVA, $F_{4,64} = 26.14$, $P < 0.0001$) from 1075 (± 194) stems/ha in 2010 to 782 (± 50) in 2015, suggesting some mortality of pre-EAB established seedlings and saplings (Fig. 2). There was no difference between TSA groups in the amount of advanced regeneration. Advanced regeneration was a lower proportion of total regeneration than sprouts but more than post-EAB seedlings in 2010 (36% of regeneration) and 2011 (34%), and a lower proportion than both sprouts and seedlings in 2012 (24%), 2013 (25%), and 2014 (20%; Fig. 4). Seedlings that established following EAB attack across all stands was 593 stems/ha (± 179) in 2010 and 479 (± 143) in 2011, but then increased significantly to 1178 stems/ha (± 132) in 2012, 828 (± 91) in 2013, and 1319 (± 122) in 2014 (repeated-measures ANOVA, $F_{4,64} = 17.93$, $P < 0.0001$; Fig. 2). Post-EAB seedlings represented the lowest proportion of total regeneration across all stands in 2010 (18%) and 2011 (15%). Beginning in the year following the mast year, however, post-EAB seedlings exceeded advanced regeneration and represented 34% of all recruits in 2012, 28% in 2013, and 39% in 2014 (Fig. 4). The significant difference in the number of post-EAB seedlings beginning in 2012 shows a clear accumulation of post-EAB seedlings that occurred following a mast year. Post-EAB seedling density never differed between TSA groups in any sampling year.

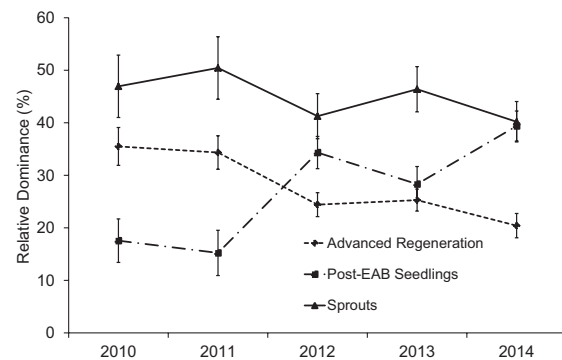


Fig. 4. Relative proportion of ash basal sprouts, advanced regeneration, and post-EAB seedlings for 17 green ash-dominated stands in southeastern Michigan. Values shown are relative dominance, or the percentage of total regeneration in a given year.

Seed production, dispersion, and seedling establishment

Only about 16% of seed collected from seed traps appeared to have visible damage that likely reduced or eliminated their viability. About 11% of total seed collected contained aborted embryos, while the remaining 5% showed evidence of insect damage. Percentage of germination of those seeds deemed viable upon inspection was relatively high for all years, with the highest value in 2010 (87%) and the lowest during the mast year in 2011 (79%). Percent germination was 83% in 2012.

Seed dispersion (proportion of traps receiving seed; Fig. 5a) was significantly higher during the mast year (2011) and in 2013 than in the other three years of the study (Friedman test: $\chi^2_4 = 42.8$, $P < 0.001$). Seed production (Fig. 5b) was significantly higher during the mast year in 2011 (100 ± 14.5 seeds $m^{-2} yr^{-1}$) and during a good seed year in 2013 (72.5 ± 10.6 seeds $m^{-2} yr^{-1}$), but was otherwise 15 seeds $m^{-2} yr^{-1}$ or less in the other three years of the study (repeated-measures ANOVA: $F_{4,64} = 43.9$, $P < 0.0001$). Likewise, source dispersion (proportion of plots with seed trees; Fig. 5c) and source density (basal area of seed trees; Fig. 5d) were highest in 2011 and 2013 (source dispersion: $F_{4,64} = 63.6$, $P < 0.0001$; source density: $F_{4,64} = 19.0$, $P < 0.0001$). Seed dispersion was best predicted in 2010 with a linear model using seed production alone (adjusted $R^2 = 0.39$, $P = 0.004$, AIC = 0.588), in 2011 using

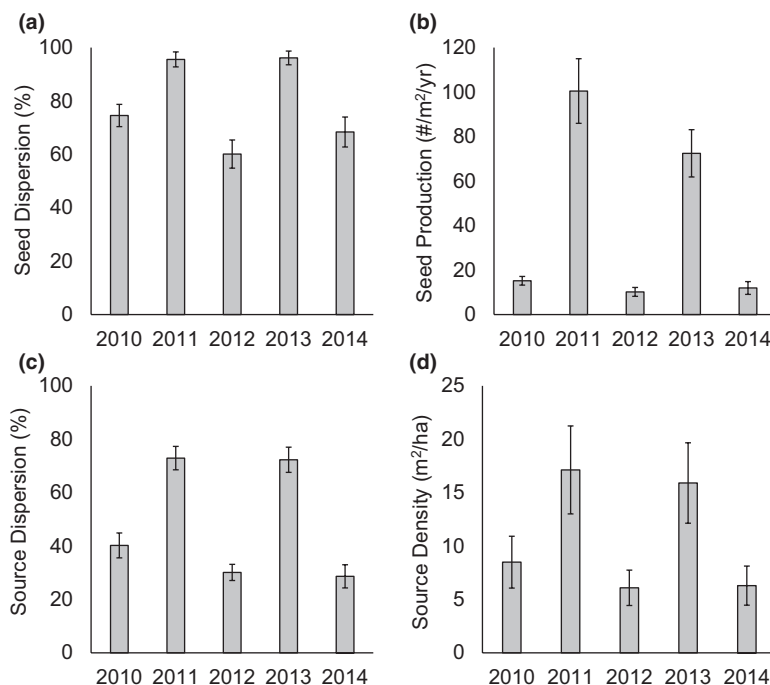


Fig. 5. Source and seed rain characteristics for 17 green ash stands over three growing seasons in southeastern Michigan. Data shown are for (a) seed dispersion (proportion of seed traps in a stand that received ash samaras); (b) seed production; (c) source dispersion (proportion of plots in a stand having seed-bearing ash); and (d) source density (basal area of seed-bearing ash).

source density alone (adjusted $R^2 = 0.5$, $P = 0.001$, $AIC = -32.742$), and in 2013 using source dispersion alone (adjusted $R^2 = 0.34$, $P = 0.015$, $AIC = -29.912$). Both seed production (partial $r^2 = 0.678$) and source density (partial $r^2 = 0.049$) were included in the model for 2012 ($P < 0.001$, $AIC = -7.689$), and seed production (partial $r^2 = 0.506$) and source density (partial $r^2 = 0.072$) were included in the model for 2014 ($P = 0.002$, $AIC = -9.125$).

Seed dispersion was positively correlated with seed production (2010: $r = 0.66$, $P = 0.004$; 2012: $r = 0.84$, $P < 0.001$; 2013: $r = 0.65$, $P = 0.004$; 2014: $r = 0.71$, $P = 0.001$) and source dispersion (2011: $r = 0.53$, $P = 0.03$; 2012: $r = 0.64$, $P < 0.05$; 2013: $r = 0.56$, $P = 0.019$) in years when seed production was low, and was related only to source dispersion in the most year (2011: $r = 0.53$, $P = 0.03$), suggesting that tree size (source density) was largely negligible in affecting seed distribution (Table 3). Correlations were inconsistent when analyzed by TSA. For stands attacked early (1998–2001), seed dispersion was unrelated to seed production, source dispersion, or source density in all

sampling years. For stands attacked in 2002–2003, seed dispersion was related to source density in 2010 ($P = 0.01$), source dispersion in 2012 ($P = 0.04$), and both source dispersion ($P = 0.02$) and source density ($P = 0.05$) in 2011. Stands attacked late (2003–2004) included positive correlations between seed dispersion and seed production ($P = 0.02$), source dispersion ($P = 0.002$), and source density ($P = 0.02$) in 2010, between seed dispersion and seed production ($P = 0.001$) and source dispersal ($P = 0.05$) in 2012, and between seed dispersion and seed production ($P = 0.004$) in 2014 (Table 3). Overall, there was no consistent pattern to suggest that the availability and distribution of parent trees affect seed dispersal within these small stands of ash. See Appendix S2 for stand-level values of seed dispersion, seed production, source density, and source dispersion.

Data were pooled across all 17 stands to test for spatial correlation between seed and recruit presence at each sampling point for each year. For post-EAB regeneration, only 2010 showed a significant association of recruit presence with seed presence (Fisher's exact test: recruitment

Table 3. Pearson and Spearman rank correlation coefficients (Spearman in bold, used when relationships were nonlinear) between seed dispersion and seed production, source dispersion, and source density for 17 stands in southeastern Michigan in each year sampled; stands were also analyzed by time of EAB attack (early = 1999–2000, middle = 2001–2002, or late = 2003–2004).

Year	Group	# plots	Seed production	Source dispersion	Source density
2010	Pooled	17	0.66*	0.43	0.44
	Early	5	0.87	0.28	-0.12
	Middle	6	0.51	0.65	0.92*
	Late	6	0.89*	0.97**	0.87*
2011	Pooled	17	0.33	0.53*	0.39
	Early	5	n/a	n/a	n/a
	Middle	6	0.52	0.88*	0.82*
	Late	6	n/a	n/a	n/a
2012	Pooled	17	0.84**	0.64*	0.36
	Early	5	0.83	0.15	0.19
	Middle	6	0.80	0.84*	0.76
	Late	6	0.97**	0.81*	0.73
2013	Pooled	17	0.65*	0.56*	0.41
	Early	5	n/a	n/a	n/a
	Middle	6	0.78	0.79	0.85*
	Late	6	0.66	0.39	0.39
2014	Pooled	17	0.71**	0.47	0.28
	Early	5	0.70	0.18	-0.41
	Middle	6	0.60	0.58	0.81
	Late	6	0.95*	0.77	0.68

* Significant at alpha = 0.05.

** Significant with Dunn–Sidak correction.

presence with seed (R_s) = 67%, recruitment presence without seed (R_{ws}) = 14%, $n = 260$, $P = 0.007$). The lack of spatial correlation between seeds and recruits in 2011–2014 suggests that seed dispersal did not limit seedling recruitment (no seed limitation) in those years. For advanced regeneration, seed limitation was evident in 2012 ($R_s = 65\%$, $R_{ws} = 29\%$, $n = 258$, $P = 0.041$), 2013 ($R_s = 89\%$, $R_{ws} = 3\%$, $n = 260$, $P = 0.049$), and 2014 ($R_s = 58\%$, $R_{ws} = 32\%$, $n = 253$, $P = 0.045$).

DISCUSSION

This study corroborates others that have illustrated the severity of EAB impacts on ash in mixed stands (Burr and McCullough 2014, Klooster et al. 2013, Kashian and Witter 2011), but it highlights a remarkable consistency of the mode of green ash regeneration in pure stands over five years. Four mechanisms have maintained green ash regeneration and its recruitment to the overstory for at least 11 yr after EAB introduction: (1) post-infestation survival of canopy trees; (2) basal sprouts from

top-killed trees; (3) seedlings and saplings established prior to heavy mortality caused by the introduction (advanced regeneration); and (4) new cohorts of regeneration developing from seeds produced by surviving canopy trees and basal sprouts. At least for the small stands of ash sampled in this study, green ash has a strong potential to persist even in the continued presence of EAB, though with a very different ecological role than it held prior to the introduction of this highly destructive invasive species. Although the relatively short duration of this study and the small size of the stands examined leaves much uncertainty regarding green ash persistence, the data show no evidence of a physical or functional elimination of green ash as a species from the landscape in southeastern Michigan.

Negative impacts of EAB on canopy ash at the 17 sites were severe, as expected, with an average of 58% of canopy ash killed, 62% of basal area removed, and a dramatic reduction in the quadratic mean diameter of ash. Despite severe negative effects of EAB, however, survival of some canopy

ash trees was notable after 12 yr and consistent with studies of ash in mixed stands in southeastern Michigan (Marshall et al. 2013, Klooster et al. 2013, Knight et al. 2012a, Kashian and Witter 2011). Surviving ash may result from a patchy distribution of EAB (Burr and McCullough 2014), a potential resistance of some trees to survive EAB attack (Marshall et al. 2013, Knight et al. 2012a), and/or heavy ash dominance that dilutes the concentration of attacking EAB per tree and reduces tree mortality (Knight et al. 2013). Even ~ 40% survival of canopy ash in the small stands studied here may be important for post-EAB seed rain (see below). Green ash may be particularly poised to have resistant individuals given its high potential for genetic diversity (Koch et al. 2015, S.M. Taylor *personal communication*), and resistant survivors may eventually establish new resistant populations.

Sprouting as a mechanism of ash persistence

Vegetative reproduction via basal sprouting from top-killed ash trees was the most important mode of regeneration in this study in terms of post-EAB persistence, occurring on average on 62% of trees killed by EAB. Green ash (and the *Fraxinus* genus in general) is reported to be a prolific sprouter (Barnes and Wagner 2004, Del Tredici 2001). Re-sprouting of canopy trees may have immediate as well as long-term effects on forest recovery and composition (Loehle 2000, Cooper-Ellis et al. 1999, Putz and Sharitz 1991), particularly because the sprouts may form adventitious roots and with survival will eventually become autonomous from the top-killed tree (Del Tredici 1998). The high growth rate of sprouts also provides ash with an important competitive advantage compared with other established species, including invasive woody plants (Knight et al. 2008b).

The incidence of sprouting in this study was consistent with other studies of green ash in post-EAB mixed forests (Burr and McCullough 2014), but contrasted with Klooster et al. (2013), who noted no sprouting of ash following EAB mortality. Differences in deer browsing intensity among the study areas are not likely to explain this difference, since this study area overlaps significantly with that of Klooster et al. (2013) and is known for extensive deer activity in wooded areas. Instead, the discrepancy in the sprouting response in ash may be explained in part by tree

age and corresponding size, because deciduous trees <15 cm in diameter are most likely to sprout, and those >30 cm in diameter are least likely due to physiological factors that limit the life span of suppressed buds at the root collar (Del Tredici 2001). Species such as green ash that grow on stressful or low-quality sites are also more likely to sprout more vigorously (Del Tredici 2001). In addition, 2010 sprouting in this study was higher for stands attacked early, but by 2014 sprouting was highest for stands attacked most recently. These data suggest a delayed sprouting response after trees were top-killed by EAB, and illustrate that analyses of sprouting responses require multiple years of observation (Del Tredici 2001). Differences in post-EAB sprouting response in ash may lead to very different conclusions about the fate of ash in the presence of EAB, but it also suggests that older, larger ash stands on high-quality sites – those most valued as a timber resource – may be more strongly affected by EAB than stands where ash is smaller and less valuable.

A surprising result was that post-EAB basal sprouts as young as seven years old, as well as surviving trees, were important contributors to seed rain both during the mast year (2011) and in 2013. Ash sprouts (and surviving trees) therefore have significant roles as placeholders in stands attacked by EAB when they are able to maintain ash in the canopy and provide a seed source for new regeneration. Bleak predictions of ash persistence are largely based on the inability of ash to provide future inputs to the seed bank, given the likelihood that a high proportion of ash recruits will suffer mortality by EAB before they attain reproductive age (Burr and McCullough 2014, Klooster et al. 2013, Kashian and Witter 2011). Where sprouting is present and abundant, however, it represents an essential mechanism of ash persistence.

Ash seed production and regeneration dynamics

Trends over the five years of this study show a stability of ash regeneration density with occasional high seed years, even when accounting for sapling and seedling mortality (Fig. 2). Advanced regeneration exhibited a 27% decrease over the five years of the study; such a decline is not unexpected as sapling and seedling mortality occurs. Post-EAB seedlings were common

in 2012 (following the mast year in 2011) and 2014 (following the good seed year in 2013), suggesting that seed sources have not been completely extirpated (Herms and McCullough 2014, Klooster et al. 2013, Kashian and Witter 2011). Storage of seeds in a soil seed bank is an important mechanism for regeneration of deciduous species (Barnes et al. 1998) and would be advantageous in an instance when seed-bearing overstory trees are killed (e.g., Tryon et al. 1983), but green ash seeds typically germinate in the first spring after dispersal (Taylor 1972). Although green ash does not form a seed bank, its regeneration should continue as long as seed sources are available and mast years occur relatively frequently (1–5 yr; Bonner 2008).

The highest level of seed production in this study was during the mast year (2011), when ash produced an average of 101 seeds/m²/yr with average basal area of 6.27 m²/ha (Fig. 5b). McEuen and Curran (2004) found seed production for green ash to average 60 seeds m⁻² yr⁻¹ in five fragments in southeastern Michigan with average basal area 3.01 m²/ha, slightly higher than seed production measured in this study given fewer seed-bearing trees. Seed production by the 17 stands in this study was low in the years following heavy seed years (2012, 2014) probably because of resources expended on the mast during the previous growing season (Kelly 1994). These results confirm considerable post-EAB reduction in seed production, but also a substantial amount of seed produced during mast years that will likely contribute to future ash regeneration.

Overstory dominance by a species is highly dependent on the effectiveness of its seed dispersion (Ribbens et al. 1994), and the seed was not spatially restricted within the small stands in this study. The universal availability of seed across a given stand indicates that seed limitation does not occur and that seed is readily available at most microsites, maximizing potential establishment opportunities for seedlings (McEuen and Curran 2004). Lack of spatial correlation between seeds and recruits implies that seed dispersal does not limit recruitment even after substantial EAB-induced mortality. Seed and recruitment limitation promote species co-existence in temperate forests (Clark et al. 1998) by allowing competitors of a given species to occupy sites that

could not receive seeds from that species (Hurt and Pacala 1995).

Implications for post-EAB ash persistence

The results of this study suggest that green ash—due to its physiology, regeneration ecology, and site relationships—may be able to persist in the presence of EAB despite heavy mortality and significantly altered ash population dynamics. Persistence of green ash in the aftermath of EAB may arguably better resemble American elm after DED than American chestnut after chestnut blight, for example, given its propensity for sprouting and stable levels of seed production and seedling establishment after heavy EAB infestation. Understanding species persistence in the presence of an invasive should therefore be illustrative and create caution at the onset of new highly destructive invasives in forests when management or mitigation alternatives would need to be drastic to be effective at restoration.

Much like the response of American elm to DED (Barnes 1976), post-EAB green ash populations are unlikely to ever reach their pre-EAB condition neither in individual tree size nor stand-level productivity and health. EAB remain in southern Michigan and the study area at low population densities (Burr and McCullough 2014, Klooster et al. 2013), presumably because of the now-low density of post-EAB ash. Ash mortality due to EAB, even when populations are low, is clearly ongoing as evidenced by signs of infestation at the 17 study sites and other studies (Marshall et al. 2013). Moreover, sapling and seedlings that recruit to the overstory are likely to be eventually attacked by EAB when they grow large enough to be colonized (Burr and McCullough 2014, Klooster et al. 2013). Permanent establishment of EAB in the study area should restrict ash densities at low levels, however, creating a negative feedback that should also help to suppress EAB population densities. The ability of green ash to retain a reproductive cohort via sprouting and seed production even at highly reduced post-EAB tree densities, as well as persistence of green ash up to 16 yr after EAB infestation, provides some evidence that green ash may persist.

Persistence of green ash in the wake of EAB is to some degree a matter of interpretation, and its

management and/or remediation will depend strongly on our ability to accept the notion of highly altered population dynamics of a once-dominant species. Although this study purports a variety of mechanisms by which green ash may persist with EAB, it does not contradict the idea that the future condition of green ash as a timber resource is perilous (Pugh et al. 2011, MacFarlane and Meyer 2005). However, ash contribution to ecosystem function remains likely even if mature ash trees are unlikely to reach large sizes. For example, the sprouting response of green ash should mediate significant hydrological changes in lowland areas compared to near-complete elimination of canopy trees where ash is dominant (Slesak et al. 2014). In addition, the continuous, long-term presence of ash saplings and seedlings, as well as quickly growing basal sprouts, should provide host resources for the 44 high-risk insect species that use ash as a host tree (Gandhi and Herms 2010). Thus green ash persisting with EAB has been transformed from a canopy dominant to a species with a reduced but still important ecological niche rather than being functionally eliminated from the landscape. Understanding that highly altered tree species populations may still provide important contributions to ecosystem function is critical as additional invasive species inevitably become established in North American forests.

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