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Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by emerald ash borer (*Agrilus planipennis*)

Kathleen S. Knight · John P. Brown · Robert P. Long

Abstract Emerald ash borer (*Agrilus planipennis*) (EAB), an Asian woodboring beetle accidentally introduced in North America, has killed millions of ash (*Fraxinus* spp.) trees and is spreading rapidly. This study examined the effects of tree- and site-level factors on the mortality of ash trees in stands infested by EAB in OH, USA. Our data show that ash populations in forested sites can progress from healthy to almost complete mortality of mature trees within 6 years. Although the end result of nearly complete mortality does not vary, survival analysis with 5 years of data showed that some factors affected the rate of mortality. We found more rapid mortality in stands with lower densities of ash trees. This finding supports an extension of the resource dilution hypothesis whereby concentration of EAB on few trees in low ash density areas leads to rapid decline of these trees. This contradicts an extension of the resource concentration theory that greater host density increases relative pest abundance and host mortality. Although reductions in ash density via diversification may be desirable for other silvicultural, conservation, and management objectives in preparation for EAB, our study shows that the management strategy of reducing ash density is unlikely to protect the remaining ash trees. Survival analysis also showed that mortality was more rapid for trees shaded by other trees and for trees initially exhibiting dieback. In management scenarios where hazard tree removal must be spread over several years due to budget constraints, focusing initial tree removal on stressed trees is recommended.

Keywords Host density · Pest · Insect · Forest · Resource concentration · Resource dilution

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Introduction

Introduced pests and pathogens are a threat to trees and forests worldwide. In eastern North America, introduced pests and pathogens cause significant mortality of host tree species, unleashing a cascade of effects on forest ecosystems, including shifts in species composition, changes in understory light, temperature, and moisture, increases in coarse woody debris, and effects on carbon and nitrogen cycling (Lovett et al. 2006; Gandhi and Herms 2010). The relationship between host plant density and effects of pests is key to both

understanding the ecology of plant-host interactions and making forest management recommendations.

Two general theories regarding the relationship between host plant density and specialist pests, the resource concentration hypothesis (Root 1973) and the resource dilution hypothesis (Otway et al. 2005) make opposite predictions that may give insight into the effects of invasive pests of trees. The resource concentration hypothesis states that specialist herbivore pests are more likely to find and stay on hosts and attain greater relative abundance (per host) in areas with greater host density (Root 1973). The theory was first applied to exotic pests in agricultural systems (Root 1973) and has since been applied to invasive pests in natural systems (Rand and Louda 2006). The resource concentration hypothesis has been extended to also encompass the effect of the pest on host populations, which may then affect the composition of the plant community (Carson and Root 2000, Long et al. 2003, Carson et al. 2004). Many examples of outbreaking specialist insects in areas of high host density support this hypothesis and play an important role in regulating plant community composition (Carson et al. 2004). In contrast, the resource dilution hypothesis states that greater herbivore loads occur in areas of lower host density (Otway et al. 2005), as seen in a grassland biodiversity experiment. Evidence for these hypotheses has been mixed, and the spatial scale at which the relationship is studied (Sperry et al. 2001), the identity of the host and insect species (Vehviläinen et al. 2007), as well as the biology of the insect species, especially the mechanism by which they locate hosts (Hamback and Englund 2005), may be important in the shape and direction of the relationship.

Studies of the relationship of mature tree density to pest-mediated mature tree mortality in pine species provide support for the extension of the resource concentration and resource dilution hypotheses to effects on host populations. A study of pinyon pine (*Pinus edulis*) attacked by three monophagous herbivores isolated the effect of host tree density and found support for the resource concentration hypothesis (Sholes 2008). Other evidence, also supporting the resource concentration hypothesis, comes from the mountain pine beetle on lodgepole pine (*Pinus contorta*) (Mitchell et al. 1983) and ponderosa pine (*Pinus ponderosa*) (Larsson et al. 1983; McCambridge and Stevens 1982). In these systems, tree density and vigor are closely correlated, and the latter is probably

ultimately responsible for increased mortality (Larsson et al. 1983; Mitchell et al. 1983). This is supported by experimental evidence that increasing tree vigor by thinning and fertilization results in decreased susceptibility to pest attack (Waring and Pitman 1985). Southern pine beetle infestations, which exhibit a wave-like dispersal pattern, have also been shown to follow the predictions of the resource concentration hypothesis (Showalter and Turchin 1993).

The mortality of trees exposed to native or exotic pests or pathogens is related to both tree and site characteristics. At the tree level, tree size, crown class, and vigor influence the survival of trees attacked by insect pests (Campbell and Sloan 1977; Haavic and Stephen 2010; Volney 1998). Additionally, a variety of site characteristics, including host tree density (Larsson et al. 1983; McCambridge and Stevens 1982; Mitchell et al. 1983), climate, and site index (He and Alfaro 2000; Robertson et al. 2008) alter tree survival patterns in areas infested by insect pests. Understanding the relationships among tree characteristics, site attributes, and tree survival facilitates the development of management strategies to protect forest health. For example, stand thinning and fertilization have been used to decrease mortality of lodgepole pine attacked by mountain pine beetle (*Dendroctonus ponderosae*) (Waring and Pitman 1985).

The emerald ash borer (*Agrilus planipennis*) (EAB), a specialist pest insect that feeds on ash (*Fraxinus* spp.) provides an opportunity to test the factors that affect the mortality of trees exposed to pests. EAB, a buprestid beetle native to east Asia (Haack et al. 2002), was accidentally introduced near Detroit, Michigan, USA in the 1990s (Siegert et al. 2007a) and discovered in 2002. Since its introduction, it has been detected in 15 US states and two Canadian provinces (http://emeraldashborer.info), and has killed millions of ash trees in the core infestation zone of Michigan and Ohio (Cappaert et al. 2005; Herms et al. 2004; Poland and McCullough 2006). EAB has also spread westward from its native Asian range through Russia where it has killed many ash trees and is a threat to ash in Europe (Baranchikov et al. 2008). EAB larvae live beneath the bark of ash trees and consume phloem tissue, creating feeding galleries that eventually cut off the transport of carbohydrates in the phloem tissue, girdling the tree.

Ash is an important component of many North American ecosystems. There are 16 species of ash in

the USA (USDA Plants Database 2010), five of which occur in Ohio. Blue ash (*F. quadrangulata*) inhabits calcium-rich sites (Braun 1961). Black ash (*F. nigra*) and pumpkin ash (*F. profunda*) occur in swamps and wet woods, with the former more prevalent in northern areas (Gleason and Cronquist 1991) and the latter more prevalent in the south (McCormack et al. 1995; Penskar 2004). White ash (*F. americana*) occurs in moist upland hardwood forests, often in mixed stands with other tree species. Green ash (*F. pennsylvanica*) exhibits broad habitat tolerance, and occurs in swamps, riparian areas, and moist upland areas (Gleason and Cronquist 1991). In swamps and riparian areas, ash may be the dominant tree species (K.S. Knight, personal observation). As early-successional species, ash trees may occur at high densities in disturbed sites.

The objective of this study was to determine the stand-level and tree-level factors that affect the mortality of ash trees in stands infested by emerald ash borer. In particular, we tested the relationship between host density and the rate (speed) of host mortality.

Methods

Field data collection

Stands (N = 31) were located in forested areas on both public and private lands in counties infested by EAB (Fig. 1). In some large parks, multiple stands were selected. A stand is defined as a forested area with homogeneous species composition, landscape position, and hydrology. Stands were chosen to represent a range of ash densities as well as different habitats to encompass the five ash species present in Ohio. A minimum of three plots were placed in each stand, with up to three additional plots in areas where each plot contained few ash. Plot placement depended on the shape and size of the stand and the abundance of ash. In large stands with abundant ash, the plots were placed 50–100 m apart along a transect located in the forest interior. In stands where ash was not abundant, plots were positioned by pacing 50 m and placing a plot at the end of the pacing distance if at least two ash trees ≥10 cm DBH were present. If no ash were present at that point, then pacing continued to the first location where the required ash trees were present. In
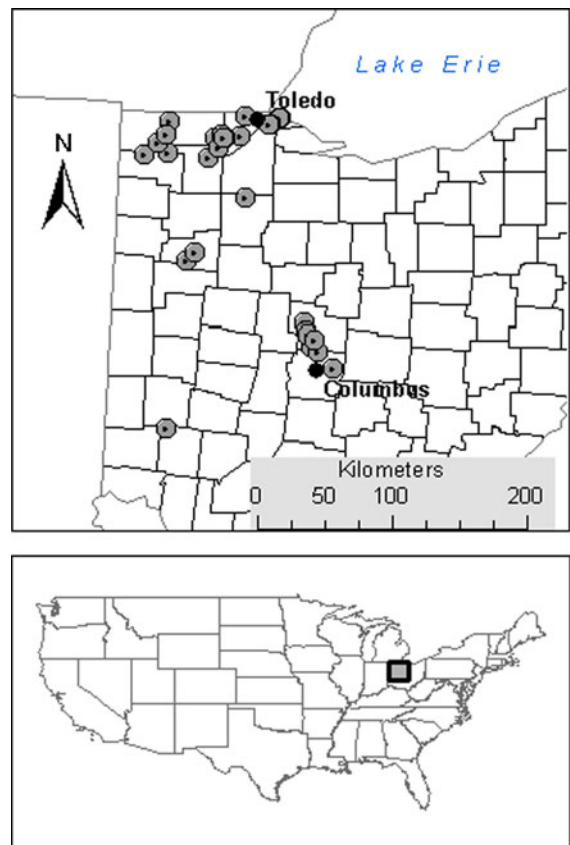

Fig. 1 Map of site locations in Ohio, USA

small stands, plots were placed to include at least two ash trees >10 cm DBH in each plot, to be away from forest edges and trails, and to be at least 20 m from other plots. These plot placement methods are not random and probably overestimate the abundance of ash in stands where ash is sparse.

Data collection began in 2005 in stands in the Toledo, Ohio area, which was infested the earliest. Additional stands were added in 2006 and 2007 in other parts of Ohio, for a total of 98 plots and 1,160 ash trees ≥10 cm DBH in stands infested by EAB by 2007. Yearly data collection continued through 2009, providing 3–5 years of data for each site. Circular plots 400 m^2 were used to collect data for ash trees ≥10 cm DBH and nested 200 m^2 plots were used to collect data for ash trees 0.1 cm to 10 cm DBH. Individual ash trees were tracked through time by matching plot position and tree diameter. Trees with two trunks that divided below breast height (1.4 m), less than 5 % of the total number of stems, were counted as separate trees. In summer (June–August) each year through
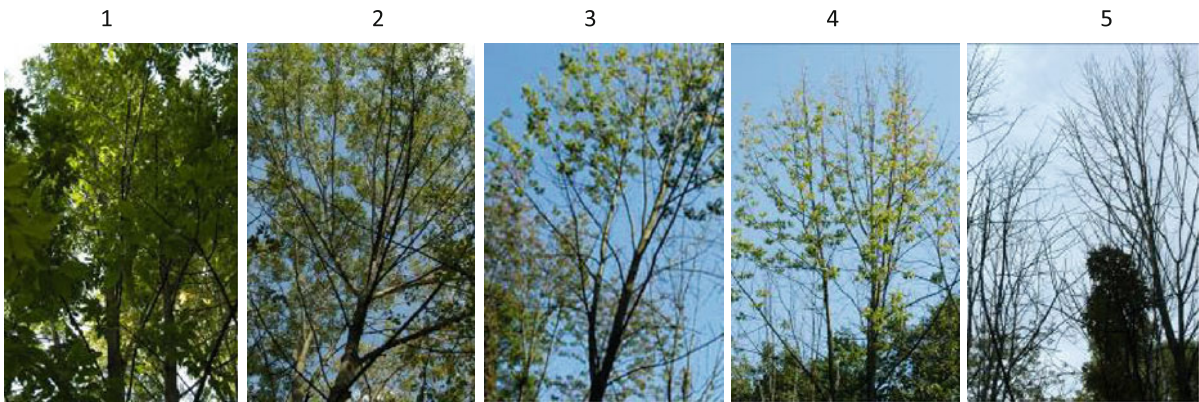
Fig. 2 Ash canopy health condition rating scale from Smith (2006)

2009, all ash trees were rated on an ash canopy health condition scale of 1–5 (Fig. 2) using protocols developed by Smith (2006) which are modifications of protocols developed for bronze birch borer (Ball and Simmons 1980). The rating scale has been correlated with EAB gallery cover and tree water stress (Flower et al. 2010), as well as with FIA canopy health rating methods (unpublished data).

The rating scale is defined as follows:

1. Ash tree with a full, healthy canopy.
2. Ash tree with a thinning canopy but no dieback.
3. Ash tree with dieback, defined as dead twigs or branches near the top of the tree, exposed to sunlight. Dead branches that are low and shaded were not rated and considered a normal part of branch senescence.
4. Ash tree with less than 50 % of a full canopy, which could occur through a combination of dieback and thinning.
5. Ash tree with a dead canopy, defined as no foliage in the canopy portion of the tree. The canopy is counted as dead even if live epicormic sprouts low on the trunk or stump sprouts are present.

In addition to the canopy health condition rating, for each ash tree the diameter at 1.4 m height was measured (DBH), the canopy class was classified as dominant, codominant, intermediate, or suppressed (Smith et al. 1996), EAB exit holes between 1.25 and 1.75 m height on the trunk were counted, and the ash species was identified. Black ash is easily identified by its corky bark (Leopold et al. 1998) and sessile leaflets (Gleason and Cronquist 1991), while blue ash is easily

identified by its shaggy bark and square twigs (Braun 1961; Leopold et al. 1998). White ash, green ash, and pumpkin ash are more difficult to distinguish in natural areas, and we used seed morphology and habitat characteristics to identify these species. Beginning in 2007 and continuing through 2009, researchers searched the ground for 5 min in each plot to collect samaras. Pumpkin ash samaras are distinct due to the large calyx (>2 mm) and often large size (>5 cm) (Gleason and Cronquist 1991). Green ash samaras generally have long narrow seeds with the wing decurrent for half of the length of the seed body, and white ash samaras generally have cigar-shaped seed bodies with very little of the seed enclosed by the wing (Gleason and Cronquist 1991). Stands were classified as xeric, mesic, or hydric environments based on observations of standing water and plant species composition. Xeric sites were defined as upland sites that very rarely experience flooding or standing water, and were the only sites that included white ash. Mesic sites were sites that were sometimes flooded and sometimes dry, and generally green ash was present. Hydric sites were defined as sites that often had standing water, and were the only sites that included black ash and pumpkin ash. Some sites contained admixtures of green and white ash or green and pumpkin ash. At these mixed species sites, it was generally not possible to distinguish the two species.

Beginning in 2008, purple panel traps coated with sticky adhesive (Tanglefoot®) and baited with a Manuka oil lure (Synergy Semiochemical) (Crook et al. 2008) were used to detect EAB in a subset of the stands (N = 19). Not all stands were used due to cost

and logistical constraints. Two traps per stand were used in 2008 and two to four traps per stand were used in 2009. The traps were hung in the canopies of ash trees in May, the lures were replaced and the traps were checked in late June or early July, and traps were removed and checked at the end of August or early September. The number of EAB caught on the trap was recorded. In general, in the first year of detection only one or two EAB were caught, while later in the infestation, hundreds of EAB would be caught on the traps. The traps detected EAB in 2008 or 2009 at least a year before exit holes were observed in seven of the 19 stands. In these seven stands, exit holes were generally observed 1 year after EAB was first caught on the traps. In the other 12 stands, exit holes had already been observed by 2008.

Data analysis

EAB is difficult to detect at low densities at the beginning of an infestation because infestation generally begins in the tree canopy and few visible symptoms are present (Cappaert et al. 2005). For data analysis, initial stand infestation (T = 0) was considered to be 2 years before the first EAB exit holes appeared on any tree in the stand or 1 year before the first EAB was caught on a trap in the stand, and these two metrics were generally in agreement. This is a minimum estimate of initial infestation, and it is probable that EAB was present at very low densities before that time. The timing of the beginning of the surveys in the plots relative to initial stand infestation ranged from 2 years before to 2 years after infestation (T = −2 to T = 2). The duration of infestation observed in our study plots ranged from 1 to 6 years (T = 1 to T = 6) after initial infestation.

Survival analysis with both plot-level and tree-level predictors was used to analyze the survival rate of individual trees over time. This analysis shows what factors affect how rapidly individual trees die. Survival analysis of individual trees over time was performed in SAS® (SAS version 9.2 2008) using proc PHREG, which implements the Cox proportional hazards model (Cox 1972).

$$\lambda(t; \mathbf{z}) = \exp(\mathbf{z}\beta)\lambda_0(t)$$

where, λ-lambda-hazard function, t-time, $\mathbf{z}$-a $1xp$ vector of covariates, $\boldsymbol{\beta}$-a $px1$ vector of unknown parameters, $\lambda_0(t)$-an unspecified but non-negative function.

The survival analysis only included trees ≥3 cm DBH, as EAB has been observed to attack ash saplings as small as 3 cm DBH (K.S. Knight, personal observation), and censored all trees that were dead in the first survey year, as it was not possible to know when they died, which reduced the sample size to 908 trees. An all subsets macro was written to analyze all possible models from the candidate set of predictors. The best model chosen had the lowest Aikake Information Criterion (AIC) value. The individual trees (N = 908) were repeated measures on plots (N = 98) and this dependency was accounted for with the COVSANDWICH option. This option implements a robust variance estimator without need for a specific variance structure (Allison 2010) and accounts for the repeated measures performed on trees within plots. The EXACT method was used for any ties in survival time.

Tree-level predictors used in the all subsets procedure were as follows:

CC-Crown Class (class variable: dominant, co-dominant, intermediate, suppressed)
ACE-Ash Canopy health class at first Evaluation (class variable: 1, 2, 3, 4, 5)
DBH-diameter of the tree at 1.4 m (continuous variable)
RM-Relative Median, ash canopy health class relative to the plot median class at evaluation (class variable: greater than, equal, less than)
SPP- Ash species (class variable: white ash, green ash, black ash, blue ash, pumpkin ash, white/green ash, green/pumpkin ash)

Plot-level predictors used in the all subsets procedure were as follows:

ACM-Ash Canopy health class Median, the median ash canopy health class at evaluation (class variable: 1, 2, 3, 4, 5)
Hydrology-plot hydrology (class variable: hydric, mesic, xeric)
TPHA-number of ash trees per hectare (continuous variable)
BAPHA-basal area of ash trees per hectare (continuous variable)

A validation set was created by randomly selecting 20 % of the trees, which were selected before creating the model and not used in the creation of the model. Using the best model, survival probability estimates

for these trees were estimated for the same period as was observed. Trees having survival probability estimates of <0.50 were estimated as dead, while those greater or equal to 0.50 were estimated as alive. The estimated class–alive or dead–was then compared to the observed condition for each tree and percentage of correct values was calculated for the final model.

Contrasts between the several levels of each class variable were performed using a Bonferroni correction for multiple comparisons. We performed 15 pairwise comparisons, so the Bonferroni correction yields a p value of $0.05/15 = 0.00333$. For class variables, levels within a class are examined using the hazard ratio, which is the hazard rate of the first class divided by the hazard rate of the second. For continuous variables, the hazard ratio is the ratio resulting from comparing the selected value of the variable to a one unit increase in the value of the variable. Allison (2010) suggests using the formula of 100(hazard ratio-1) to examine the hazard ratio resulting from comparing unit changes in continuous variables. This is the estimated percent change in the hazard rate.

Results

The stands experienced dramatic ash mortality over the 6 years time period after EAB infestation. Approximately one quarter of the trees were dead by year three, half of the trees were dead by year four, three quarters were dead by year five, and more than 99 % were dead by year six (data not shown). The survival analysis showed that both tree-level and plot-level factors were important in predicting the survival rate of ash trees (how rapidly the ash trees died).

Ash species and hydrology were closely correlated and models with both of these predictors would not converge, so the model was run with only one or the other. The best model and validation test results were identical with these two runs, except that one model included ash species and the other model included hydrology. Only the hydrology model is presented here.

The best model, selected from the all subsets analysis, included all significant terms CC ($p < 0.001$), hydrology ($p < 0.001$), ACE ($p < 0.001$), and TPHA ($p = 0.009$) (Table 1). This model had the lowest AIC of 3,950. This model correctly predicted 73 % of the validation data. There was a dependency introduced by the repeated sampling of trees on plots, $p < 0.0001$. This

Table 1 Significance tests for model main effects

Effect	df	Wald χ^2	p
Crown class	3	43.40	<0.0001
ACE	3	30.82	<0.0001
Hydrology	2	25.22	<0.0001
TPHA	1	11.07	0.0009

was accounted for in the proc PHREG analysis by keeping the COVSANDWICH option enabled.

Dominant and codominant trees have greater survival rates (i.e., slower mortality) than intermediate and suppressed trees (Fig. 3). Multiple comparisons tests for CC indicate that the dominant and codominant classes individually differ from each of the intermediate and suppressed classes (Table 2). Each of these significant pairwise comparisons has an approximate 0.40 hazard ratio. For example, the hazard of a dominant tree dying is about 41 % of the hazard of an intermediate tree dying. The confidence intervals for CC hazard ratios varied in width from 0.23 to 0.60 for codominant versus intermediate crown class to 0.18–0.92 for dominant versus codominant crown class.

Initially healthier trees had greater survival rates (i.e., slower mortality) than initially less healthy trees (Fig. 4). Pairwise comparisons for ACE are not as readily split into groups as the CC results. Pairwise comparisons for ACE have one dissimilar class and several overlapping classes (Table 2). ACE class 1 is different from all other classes, suggesting that even trees with mild canopy thinning (ACE = 2) are predisposed to die more rapidly than trees with full, healthy canopies. The hazard ratios range from 0.69 (1 vs. 2) to 0.19 (1 vs. 4) (Table 2). The single other pairwise difference is ACE class 2 versus 4 and the hazard ratio is 0.27, which shows that trees with canopy thinning survive longer than trees with >50 % canopy dieback.

Trees at hydric and xeric sites had greater survival rates than trees at mesic sites (Fig. 5). Tests for pairings of the levels of hydrology indicate that mesic sites differ from both hydric and xeric sites (Table 2). Hydric sites have an estimated 0.50 hazard ratio versus mesic sites, and xeric sites have an estimated 0.35 hazard ratio versus mesic sites (Table 2).

Ash tree density had a positive relationship with survival rates (Fig. 6). For TPHA, a one unit increase (i.e., one tree) has a small effect so increases of 10 and 100 units were examined. Since the parameter estimates are exponentiated the hazard ratios change in
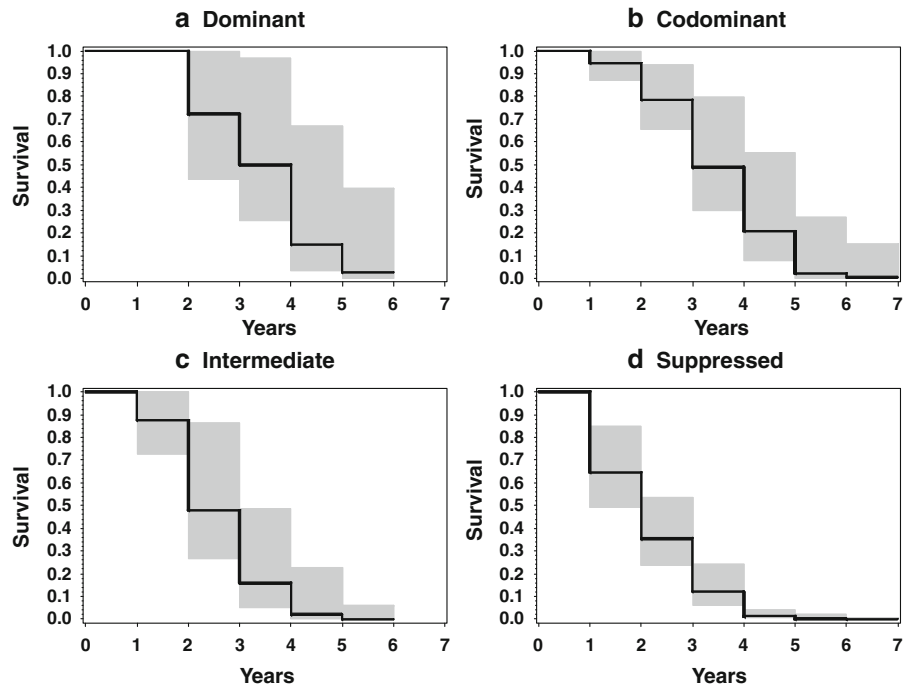
Fig. 3 Model estimates of survival rates of ash trees for the four levels of CC (crown class) over the 6 years time period following infestation by emerald ash borer. The graphs from the model estimates are useful for understanding differences among the four CC's, not for interpreting absolute levels of survival within infested stands. Dominant and co-dominant trees survived longer than intermediate or suppressed trees. Default levels for other predictors were trees with >50 % dieback (ACE = 4) in mesic stands (hydrology = mesic) (categories with the lowest survival rates) with 747 ash trees per ha (TPHA = 747, the mean TPHA for the default class levels). Confidence intervals (*grey shaded area*) are at the 95 % level

non-linear fashion. Using Allison's (2010) formula, a change of ten trees per hectare has a 0.9 % decrease in the hazard rate and an increase of one hundred trees per hectare has an 8.9 % decrease in the hazard rate.

Discussion

Overall, the results suggest a pattern of almost complete mortality of ash trees within 6 years according to our definition of initial infestation. This means that 5 years after EAB is caught on traps or 4 years after EAB exit holes appear, >99 % mortality of ash in a stand is probable. Some trees died much earlier: half of the trees were dead by year four, only 2 years after EAB exit holes were first observed at the site. Both site-level (hydrology and ash density) and tree-level (initial health and crown class) factors were important in determining how quickly the ash trees died.

We found that ash trees in low density stands died faster. This effect on the host population contradicts the resource concentration hypothesis through its logical extension to host populations (Carson et al. 2004). Although pest biomass was not measured, the slower mortality in high host density sites contradicts the resource concentration hypothesis theory that greater host density leads to greater pest biomass per host (Root 1973) which would logically lead to greater and more rapid host mortality (Carson et al. 2004), and instead suggests support for the resource dilution hypothesis that greater herbivore loads occur in areas of lower host density (Otway et al. 2005). Our analysis focuses on the speed of mortality rather than the ultimate proportion of dead trees, yet is the first time the resource dilution hypothesis has been supported for an insect pest of forest trees.

We propose that some insects may cause greater or more rapid mortality in areas of lesser host density because the insects are concentrated onto a smaller number of host plants. The negative density dependence of mortality observed in our study may be due to the particular biology of EAB and ash. EAB adults have been shown to detect olfactory cues from ash

Table 2 Multiple comparisons tests using a Bonferroni corrected alpha of 0.00333 for class variables in the best survival model for ash trees in stands infested by emerald ash borer in Ohio 2005–2009

Contrast	Hazard ratio			Wald χ^2	df	p
	Lower CL	Estimate	Upper CL			
Crown class						
Dominant versus codominant	0.59	1.09	2.00	0.16	1	0.6895
Dominant versus intermediate	0.18	0.41	0.92	10.43	1	**0.0012**
Dominant versus suppressed	0.20	0.43	0.93	10.36	1	**0.0013**
Codominant versus intermediate	0.23	0.37	0.60	37.83	1	**<0.0001**
Codominant versus suppressed	0.21	0.40	0.77	17.06	1	**<0.0001**
Intermediate versus suppressed	0.48	0.94	1.85	0.07	1	0.7908
Ash canopy health at evaluation[a]						
1 versus 2	0.48	0.69	0.99	8.97	1	**0.0027**
1 versus 3	0.20	0.41	0.83	13.81	1	**0.0002**
1 versus 4	0.07	0.19	0.53	22.48	1	**<0.0001**
2 versus 3	0.32	0.59	1.10	6.09	1	0.0136
2 versus 4	0.11	0.27	0.70	16.27	1	**0.0001**
3 versus 4	0.69	2.16	6.74	3.94	1	0.0472
Hydrology						
Hydric versus mesic	0.26	0.50	0.94	10.54	1	**0.0012**
Hydric versus xeric	0.62	1.42	3.23	1.55	1	0.2130
Xeric versus mesic	0.18	0.35	0.70	19.93	1	**<0.0001**

The hazard ratio is the hazard rate of the first class divided by the hazard rate of the second (e.g., the hazard rate of a dominant tree dying is about 41 % of the rate of an intermediate tree)

[a] Canopy health rating of 1 is healthy and 2–4 are stages of decline (Smith 2006)

Bold values indicate statistical significance at the Bonferroni corrected α-level of 0.00333

trees (Rodriguez-Saona et al. 2006). Mated female EAB also have the ability to fly long distances (Taylor et al. 2007), which may enable them to find individual ash trees even in stands where ash trees are rare and scattered. In stands with a low density of ash, the EAB female adults may be "concentrated" onto the few ash trees in the stand to lay their eggs, causing rapid decline of these trees. In contrast, in stands with a high density of ash, the EAB female adults may be "diluted" among the stressed ash trees in a stand, slowing the decline of these trees. We expect the resource dilution hypothesis would primarily apply to smaller spatial scales within the dispersal distance of the insect, and may break down at larger regional scales. Another possible explanation, similar to observations of lodgepole pine and mountain pine beetle (Waring and Pitman 1985), is that in high density ash stands, as the initially stressed trees are killed by EAB, the stand is "thinned", increasing the vigor of the remaining trees and increasing their survival. In low density ash stands, where the majority

of the trees are non-ash, the mortality of one infested ash tree will not necessarily positively impact the vigor of remaining ash trees. Research that examines the relationship between EAB population dynamics and the decline and mortality of ash trees is needed to understand the possible mechanisms leading to the observed relationship.

Whatever the cause may be, our finding that mortality is more rapid in lower-density ash stands has direct implications for the management of ash forests threatened by emerald ash borer. Our results suggest that lowering the density of ash in a stand will not protect the stand from EAB; rather, the remaining ash trees will die, perhaps even at a slightly faster rate. As invasive insect pests become a more widespread problem due to accidental introductions and climate change, it is important to appreciate that the biology of both the insect and the host may determine the direction of the relationship between host density and host mortality, and that recommendations to reduce the host density may not prevent the remaining
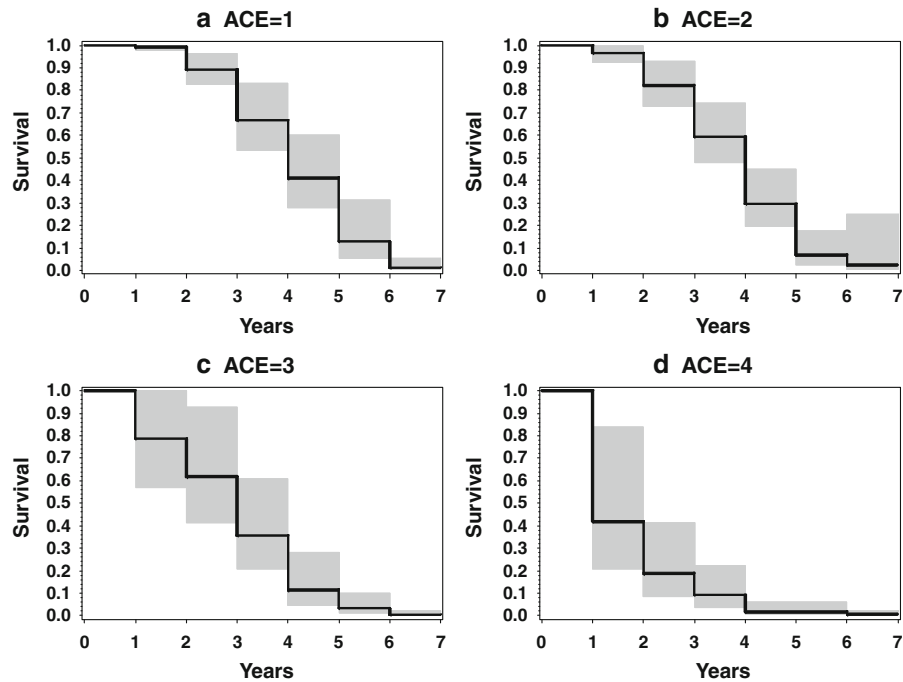
Fig. 4 Model estimates of survival rates for ash trees with four levels of ACE (ash canopy health at evaluation) over the 6 years time period following infestation by emerald ash borer. The graphs from the model estimates are useful for understanding differences among the four ACE's, not for interpreting absolute levels of survival within infested stands. Trees that were initially healthier survived longer. Default levels for other predictors were suppressed trees (CC = 4) in mesic stands (hydrology = mesic) (categories with the lowest survival rates) with 747 ash trees per ha (TPHA = 747, the mean TPHA for the default class levels). Confidence intervals (*grey shaded area*) are at the 95 % level

host trees from succumbing to the pest in all cases. Nonetheless, reductions in host density may be worthwhile as a part of a management strategy to diversify ash-dominated forest stands to mitigate EAB impacts on forest ecosystem function, ecological services, and economic or cultural values (D'Amato 2010).

Another site-level factor, hydrology, also influenced the mortality rate of ash trees. We found that trees in mesic stands exhibited more rapid mortality than those in xeric or hydric stands. It is unclear what the mechanism responsible for this finding might be. Trees that inhabit more stressful environments may allocate greater resources to defense (Herms and Mattson 1992), so it is possible that the ash trees inhabiting xeric or hydric sites may be better defended than those in mesic sites. Ash species were closely correlated with hydrology due to differing flooding tolerance of different ash species, so differences in mortality rates may be due to species differences. Other site characteristics that covary with hydrology may also be to blame, including stand density, climate,

site index, landscape characteristics, and ecological region, which other studies have found to be correlated with tree mortality due to pests and pathogens (He and Alfaro 2000, Jules et al. 2002, Robertson et al. 2008).

Tree-level factors also affected the mortality of ash trees in stands infested by EAB. Dominant and co-dominant ash trees survived longer than intermediate and suppressed trees. This may be due to the dominant and co-dominant trees having greater light exposure, possibly leading to greater carbohydrate reserves. Large trees also have a larger phloem area, which may take longer for EAB larvae to girdle. This finding is in agreement with other studies that have found both the absolute and relative size of trees to affect survival rates. Small, suppressed trees were found to have greater probability of mortality in several tree species attacked by insects, including trees attacked by gypsy moth (*Lymantria dispar*) (Campbell and Sloan 1977), oaks (*Quercus* spp.) attacked by red oak borer (*Enaphalodes rufulus*) (Haavic and Stephen 2010), jack pine (*Pinus banksiana*) attacked by jack pine budworm (*Choristoneura pinus*) (Volney 1998),
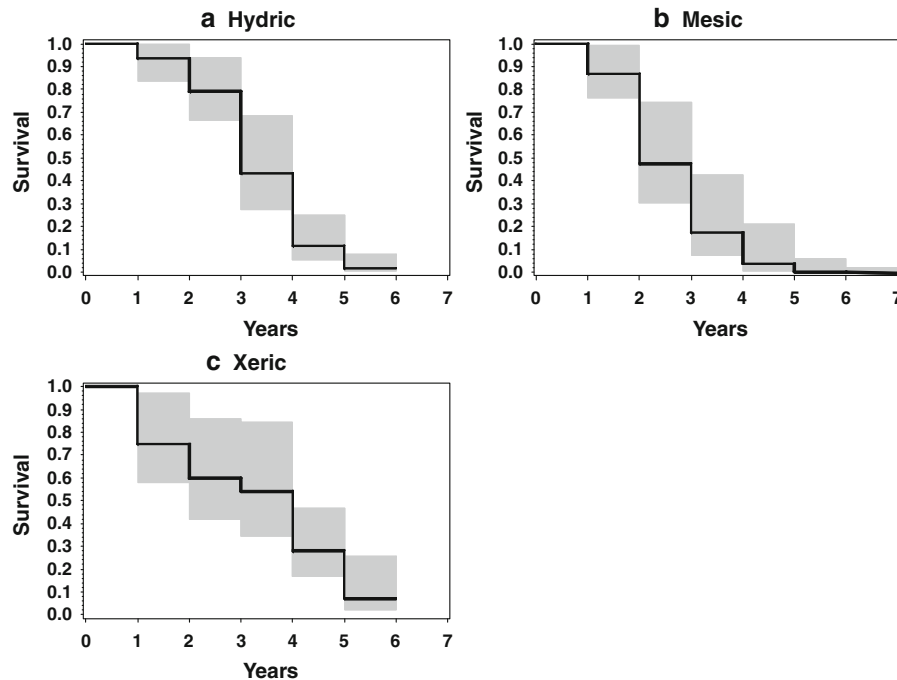
Fig. 5 Model estimates of survival rates for ash trees in forests with three hydrology types over the 6 years time period following infestation by emerald ash borer. The graphs from the model estimates are useful for understanding differences among the three hydrology types, not for interpreting absolute levels of survival within infested stands. Trees in xeric and hydric sites survived longer than trees in mesic sites. Default levels for other predictors were suppressed trees (CC = 4) with >50 % dieback (ACE = 4) (categories with the lowest survival rates) in stands with 747 ash trees per ha (TPHA = 747, the mean TPHA for the default class levels). Confidence intervals (*grey shaded area*) are at the 95 % level

and white spruce (*Picea glauca*) attacked by the white pine weevil (*Pissodes strobi*) (He and Alfaro 2000). Analysis of FIA data for insect-damaged trees in Minnesota (Woodall et al. 2005a) and for oak species in Missouri (Woodall et al. 2005b) showed that both slow-growing small trees and slow-growing large trees had increased mortality rates. These findings are helpful to managers who must prioritize the removal of ash hazard trees due to yearly budget or personnel constraints. Our results suggest that removing the intermediate and suppressed ash trees first, followed by the dominant and co-dominant trees in later years, would be a reasonable strategy. Managers of sites where concerns about hazard trees or long-term effects of high-grading are minimal may choose to harvest the largest, healthiest trees first to get the maximum value for the timber.

Trees initially rated as healthy survived longer than trees that were initially exhibiting decline. This may be due to the healthy trees having greater reserves that could allow them to survive longer during attack. Alternatively, attraction of EAB to volatiles emitted by stressed ash trees (Rodriguez-Saona et al. 2006) may result in the observed EAB preference for stressed trees (McCullough et al. 2009a, b). EAB females may select stressed trees for oviposition because EAB larvae develop slower in healthy trees (2 year development in healthy trees versus 1 year development in stressed trees), possibly due to tree defenses against larval feeding which may be greater in healthy trees (Siegert et al. 2007b; Tluczek et al. 2008).

We expect that EAB will initially infest, and then continue to re-infest, trees that are stressed until these trees die, and then move on to healthier trees. This effect of initial tree vigor on tree survival rates is in agreement with other studies. Trees initially exhibiting symptoms of stress or low vigor, including canopy decline, canopy dieback, previous defoliation, low crown ratio, and low crown density often have a greater probability of mortality once exposed to the additional stress of insect pests. Examples include trees attacked by gypsy moth (Campbell and Sloan 1977), pine trees (*Pinus* spp.) infested by pine needle gall midge
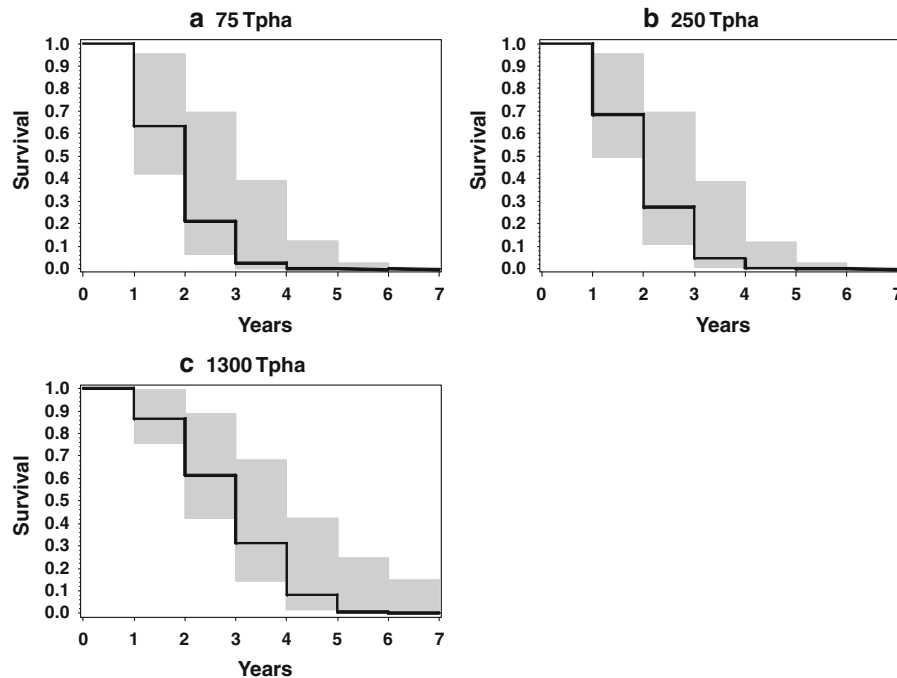
Fig. 6 TPHA (trees per ha) was modeled as a continuous variable. For illustration purposes, this figure shows model estimates of survival rates for ash trees in forests with three values of TPHA, which are roughly the fifth, fiftieth, and ninety-fifth percentiles of recorded TPHA. The graphs from the model estimates are useful for understanding differences among forests with different ash densities, not for interpreting absolute levels of survival within infested stands. Trees in sites with greater ash density survived longer than trees in low-density sites. Default levels for other predictors were suppressed trees (CC = 4) with >50 % dieback (ACE = 4) in mesic stands (hydrology = mesic) (categories with the lowest survival rates). Confidence intervals (*grey shaded area*) are at the 95 % level

(*Thecodiplosis japonensis*) (Park and Chung 2006), jack pine attacked by jack pine budworm (Volney 1998), and sugar maple (*Acer saccharum*) attacked by forest tent caterpillar (*Malacosoma distria*) (Hartmann and Messier 2008). The management implications of our study are again applicable for managers who must prioritize removal of ash hazard trees. Our results suggest that prioritizing removal of trees that are initially exhibiting dieback, and then removing the other trees in later years, is a reasonable strategy.

Conclusions

Survival analysis of yearly surveys of ash trees in EAB-infested stands showed that nearly complete stand mortality can occur within 6 years. Shaded trees and trees initially exhibiting dieback had the most rapid mortality. Trees in hydric and xeric sites survived longer than trees in mesic sites. Trees in sites with a low density of ash trees died more rapidly than trees in high-density ash sites, suggesting that rapid host mortality may result from concentration of insects onto few trees in areas with low host density.

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