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The relationship between the emerald ash borer (*Agrilus planipennis*) and ash (*Fraxinus* spp.) tree decline: Using visual canopy condition assessments and leaf isotope measurements to assess pest damage

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ABSTRACT

Ash trees (*Fraxinus* spp.) in North America are being severely impacted by the invasive emerald ash borer (*Agrilus planipennis* Fairmaire) which was inadvertently introduced to the US in the 1990s from Asia. The emerald ash borer (EAB) is a phloem boring beetle which relies exclusively on ash trees to complete its life cycle. Larvae feed in the cambial tissue forming serpentine galleries that may girdle the tree, causing mortality in as little as two years. Although larval feeding is thought to be the cause of rapid tree mortality, the relationship between tree-level water stress and EAB larval activity has never been quantified. Identifying symptoms of an emerald ash borer outbreak at an early stage can facilitate informed management decisions. Although a user-friendly system of ash canopy condition rating has been used extensively to study EAB impacts, the mechanistic relationship between canopy ratings and EAB larval activity has not been quantified.

The objective of this research was to use the stable carbon isotopic composition of canopy leaf tissue (foliar $\delta^{13}C$, a proxy of tree level water stress) to quantify the mechanism by which EAB causes tree mortality and to relate this mechanism to the ash canopy condition rating system. We found that as the canopy condition was rated as less healthy, EAB density and gallery cover increased, and foliar $\delta^{13}C$ became more enriched as well. The rating system was able to identify trees in early stages of EAB infestation with relatively low levels of EAB (<20% gallery cover or < 40 EAB/m^2). We also found that foliar $\delta^{13}C$ and EAB larval gallery cover exhibited a significant positive correlation. These results suggest that as EAB larval feeding occurs, the tree canopy exhibits thinning, and as feeding continues the tree experiences chronic water stress and canopy dieback occurs. This study highlights the usefulness of the ash canopy condition rating system as a proxy of emerald ash borer densities at the tree level.

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1. Introduction

The emerald ash borer (*Agrilus planipennis* Fairmaire, EAB) was inadvertently introduced to North America from Asia in the 1990s and was first discovered in Detroit, Michigan, USA in 2002 (Haack et al., 2002; Cappaert et al., 2005; Siegert et al., 2007). The EAB has been radiating from southeastern Michigan resulting in the widespread death of ash trees (*Fraxinus* spp. (Oleaceae)) across 18 states and portions of Canada (McCullough and Katovich, 2004; Pugh et al., 2011; Flower et al., 2013; USDA Animal Plant Health Inspection Service). In North America, all native ash species within the current range of EAB (and tested in common garden studies) are highly susceptible to EAB attack (Cappaert et al., 2005; Poland and McCullough, 2006). EAB feeds exclusively on ash trees killing both healthy and stressed trees. Ash trees are geographically distributed across the lower 48 states and achieve their highest density and abundance in the Great Lakes region (Burns and Honkala, 1990; MacFarlane and Meyer, 2005; Flower et al., 2013). Validating methods for identifying EAB symptoms will allow land owners and managers to rely on visual classification schemes to guide informed decision making regarding forest management.

The life cycle of the EAB begins with egg deposition on the bark surface and inside bark cracks during the summer by adults. The larvae hatch from the eggs approximately 2 weeks later and tunnel into and feed in the cambial region of ash stems (>3 cm in diameter) (Lyons et al., 2004). Larvae overwinter in the trunk, pupate and typically emerge through the bark, producing distinctive D-shaped exit holes the following April and May at latitudes of 39–42°

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(Lyons et al., 2004; Cappaert et al., 2005). Depending on climatic conditions and tree health, EAB may exhibit 1–2 generations per year (Wei et al., 2007). The foraging behavior of EAB larvae which create serpentine galleries is thought to be largely responsible for their negative impact on ash trees (Flower et al., 2010). Although it is difficult to determine the time of first infestation, EAB has been observed killing mature ash trees within 3 to 5 years of infestation (McCullough and Katovich, 2004).

While the symptoms of EAB infestation (e.g. canopy decline, D-shaped exit holes, and epicormic sprouting) have long been recognized, the underlying mechanism of EAB-induced tree mortality has not been quantified. Anulewicz et al. (2007) and Smitley et al. (2008) quantified the relationship between EAB densities and ash canopy decline, yet they did not quantify living EAB larvae and they largely overlooked the likely mechanism of mortality, i.e. water stress caused by EAB larval galleries. The active tunneling behavior of EAB larvae is thought to sever the tree's phloem tissue, thereby rendering the tree incapable of transporting water and essential nutrients (Flower et al., 2010). A user-friendly visual canopy condition rating system has been developed for ash trees (Smith, 2006; Flash et al., in press) and has been extensively used in ecological studies in multiple states (Knight et al., 2008; Royo and Knight, 2012; Klooster, 2012; Flower, 2013). This system appears to uniquely fit the typical progression of EAB-infested ash tree decline where tree canopies may exhibit thinning before undergoing dieback. However, the relationships between this rating system, EAB densities gallery cover, and the mechanism of water stress have never been tested. Providing a more mechanistic understanding of the physiological underpinnings behind the decline rating system is informative and may permit a better understanding of ecophysiological responses.

The objective of this study was to quantify the mechanism by which EAB causes tree mortality and to relate that mechanism to the ash canopy rating system. To quantify the underlying mechanism by which EAB results in tree mortality we destructively harvested mature ash trees in an early successional forest and quantified EAB populations, gallery cover, and the stable carbon isotopic composition of canopy leaf tissue (foliar $\delta^{13}C$). Stable isotopes represent non-biased integrators of chemical and physical processes at a variety of spatiotemporal scales and can be used to study interactions between plants and the surrounding biotic and abiotic environment (in this case ash trees and EAB) (Dawson et al., 2002). Carbon naturally exists in the two stable isotopes ^{12}C and ^{13}C. The lighter naturally more abundant atmospheric isotope (^{12}C) is preferred in plant biochemical reactions such as photosynthesis (Farquhar et al., 1982, 1989). Previous studies have suggested that foliar $\delta^{13}C$ reflects an integrated measure of intrinsic water use efficiency (Saurer et al., 2004). During times of stress, such as those induced by phloem-damaging EAB or unfavorable weather conditions, stomatal closure may cause the plant to incorporate more of the heavier isotope. Hence, we hypothesized that foliar $\delta^{13}C$ would be positively correlated with the percentage of EAB gallery cover. Additionally, we tested the canopy condition rating system as a visual proxy for assessing tree-level EAB densities and tree water stress.

2. Methods

2.1. Site description

This study was conducted from 2008 to 2010 in a ~15 ha secondary successional forest located in Delaware, Ohio on the grounds of the Dempsey Middle School (40°18.47′N, 83°05.11′W). This forest is dominated by ash (*Fraxinus americana* L. and *Fraxinus pennsylvanica* Marshall). Other canopy species include American elm (*Ulmus americana* L.), cottonwood (*Populus deltoides* Bartram ex Marshall), black cherry (*Prunus serotina* Ehrh.), sycamore (*Platanus occidentalis* L.), pin oak (*Quercus palustris* Münchh.), and black walnut (*Juglans nigra* L.). The understory consists of boxelder (*Acer negundo* L.), Amur honeysuckle (*Lonicera maackii* (Rupr.) Maxim.), multiflora rose (*Rosa multiflora* Thunb.), and seedlings of the canopy species.

2.2. Tree selection, ash tree canopy condition rating, and tree harvest

In this study 42 *F. americana* and 4 *F. pennsylvanica* (29 trees in 2008 and 17 trees in 2009) were selected from dominant or co-dominant canopy positions and to represent a range of canopy decline symptoms). Trees ranged from 8 to 25.1 cm in diameter at breast height (DBH, 1.37 m from ground), and there were no significant differences in the tree diameters across the canopy condition classes (data not presented). The ash canopy condition rating method used in this study is a visual assessment of canopy health graded on a 1–5 categorical scale (Smith, 2006). The canopy condition rating we used is a modification of a canopy decline scale developed to assess birch (*Betula* spp.) dieback caused by a native *Agrilus* species, the bronze birch borer (*Agrilus anxius* Gory) (Ball and Simmons, 1980). A canopy condition 1 represents a healthy tree canopy with no defoliation, a canopy condition 2 represents a tree canopy with a slight reduction in leaf density (thinning), yet all top branches exposed to sunlight have leaves, a canopy condition 3 represents a canopy that is thinning and some of the top branches exposed to sunlight are defoliated (<50% dieback), a canopy condition 4 represents a canopy with greater than 50% defoliation/dieback, and a canopy condition 5 represents a dead/defoliated tree with no leaves remaining in the canopy portion of the tree (epicormic sprouting is excluded) (Flash et al., in press). Although this canopy condition rating system is correlated with FIA measures such as canopy dieback and canopy density (Royo et al., 2012), this system appears to uniquely fit the typical progression of EAB-infested ash tree decline where tree canopies may exhibit thinning before undergoing progressive dieback. In addition, the classification used is easy and fast, facilitating adoption and use by resource managers.

In the summer prior to each dormant-season tree harvest, each tree's canopy condition was rated; and foliar tissue was randomly selected and excised from the upper sun-exposed canopy using a pole pruner. Foliar tissue was dried and subsequently analyzed for its C isotopic composition ($\delta^{13}C$) using isotope ratio mass spectrometry. Trees were felled during the dormant season each year (December 2008 and February 2010) and limbs were removed using a chainsaw. Each tree bole was labeled and cut into 1-m subsections to simplify handling and transportation of the logs. Trees harvested ranged from 8.4 to 25.1 cm DBH in 2008 and from 8.0 to 15.9 cm DBH in 2009.

2.3. Tree-level emerald ash borer quantification

On each 1-m tree subsection, EAB emergence holes and woodpecker attack holes were counted then filled with washable non toxic tempera paint so that it would seep into the hole and mark the underlying wood tissue. When filling holes with paint, if necessary, a paint brush was used to ensure that the paint permeated the hole enough to allow further identification. After the woodpecker attack holes and EAB emergence holes were painted (each with a defined unique color), the bark was removed using a draw knife. Care was taken not to cut too deep into the cambial tissue to remove EAB galleries. De-barking the tree segments revealed EAB galleries, live/dead EAB larvae, painted adult EAB exit holes, and woodpecker attack holes. If EAB exit holes and woodpecker attack holes could be traced back to an EAB serpentine gallery, they were counted as an EAB. If EAB larvae were found inside serpentine galleries during the bark peeling process, they were also counted. This process quantified all EAB larvae remaining inside the tree, all adult EAB that emerged, and all EAB that were attacked by woodpeckers. The number of EAB at the tree level was weighted by the surface area of tree to allow for inter-tree comparison.

2.4. Percent EAB gallery cover

Following debarking, the percent of EAB gallery cover (% EAB gallery cover) was measured on the north and south side of each 1-m peeled tree segment at the bottom, middle and top using a 10 × 10cm, 25-cell grid, printed on an overhead transparency sheet. The number of grid cells containing a gallery was counted at each of these six locations and averaged. To allow for inter-tree comparison, we normalized % EAB gallery cover of each log segment relative to the surface area of a tree resulting in a surface area weighted % EAB gallery cover for a given tree.

2.5. Isotopic analysis

Foliage tissue was dried in a forced-air convection oven at 60 °C for 48 h or until no change in mass was detected and ground to a fine powder using a Spexmill mixer/mill 8000 (SPEX SamplePrep, NJ). Subsequently ~1 mg of tissue was measured into a silver foil capsule for analysis. Stable isotope analyses of C were conducted at the University of Illinois at Chicago Stable Isotope Laboratory using a Costech Elemental Analyzer (Valencia, CA, USA) in line with an Finnigan Deltaplus XL IRMS (isotope ratio mass spectrometer) (Bremen, Germany) operated in continuous flow mode and calibrated to the ^{13}C Vienna PeeDee Belemnite (vPDB) scale using USGS 40 with a precision of 0.05‰. International and secondary isotope standards were used for instrument calibration and sample conversion to δ values. Carbon isotope values are reported in δ_{VPDB} notation relative to the standard Vienna Pee Dee Belemnite ($\delta_{sample} = 1000 \ [(R_{sample}/R_{standard}) - 1]$, $R = {}^{13}C/{}^{12}C$) (Farquhar et al., 1989).

2.6. Statistical analyses

The relationship between the carbon isotopic composition of ash leaf tissue (foliar $\delta^{13}C$) and the percent EAB larval gallery cover (% EAB gallery cover) was assessed using a least squares linear regression model ($P < 0.05$). A general linear model (GLM) was used to assess the effect of canopy condition classes on foliar $\delta^{13}C$. Assumptions of normality were tested using a Shapiro–Wilk test ($P > 0.05$) and homogeneity of variance tested using a Levene's test ($P > 0.05$), and a single outlier was removed prior to analysis (Sokal and Rohlf, 2003; Burdenski, 2000). Additionally, a GLM was used to assess the effect of canopy condition classes on % EAB gallery cover, and EAB (adult and larval) density. Gallery cover and EAB density data were rank order transformed prior to analyses to address violations in the variance structure, again a single outlier was removed prior to analysis. Differences among canopy condition classes for each of the tested variables were compared using Tukey's HSD, $\alpha = 0.05$. In all analyses canopy condition was treated as a categorical variable. Due to the low numbers of green ash ($n = 4$) relative to white ash ($n = 42$), and their uneven distribution across the canopy condition classes, differences between species were not tested (although not presented herein, removal of the green ash trees from the analyses did not affect the overall trends). All statistical analyses were conducted using SYSTAT (2007) statistical software (v. 12, SPSS, Chicago IL, USA).

3. Results

Foliar $\delta^{13}C$ exhibited a significant positive relationship with % EAB gallery cover at the tree-level (Fig. 1; Adj. $r^2 = 0.704$, $P < 0.001$). Foliar $\delta^{13}C$ became more enriched (less negative) as the canopy condition class increased from 1 to 4 (GLM; $F_{3,41} = 17.21$; $P < 0.001$; Fig. 2). Ash foliar $\delta^{13}C$ tissue was most depleted (more negative) in trees with healthy canopies, canopy condition 1 (−27.11 ± 0.30SE), relative to declining canopies, canopy condition 3 (−25.08 ± 0.35SE) and 4 (−24.14 ± 0.24SE; Fig. 2). Ash foliar $\delta^{13}C$ did not differ between canopy condition 1 and canopy condition 2.

The presence of EAB insects and gallery cover in trees of every canopy condition class indicates that EAB may impact both healthy trees and those in decline. The EAB density (insects per m^2) and percent EAB gallery cover increased as the tree canopy health declined (GLM; $F_{3,41} = 30.41$; $P < 0.001$ and $F_{3,41} = 42.43$; $P < 0.001$ respectively, Fig. 3A and B). Fewer EAB (larvae and adults) and significantly lower percentages of EAB gallery cover were found in trees with an healthy canopies (canopy condition 1) relative to the other canopy condition classes (Fig. 3).

4. Discussion

The positive relationship between foliar $\delta^{13}C$ and % EAB gallery cover suggests that the mechanism by which EAB results in tree mortality is via the feeding of EAB larvae which create serpentine galleries that inhibit the mass flow of nutrients and water between the canopy and roots (Fig. 1). This reduced acropetal water transport causes the carbon isotopic enrichment of ash foliar tissue. This enriched $\delta^{13}C$ signal in the foliar tissue of trees with declining canopies manifests from the reduced discrimination against the heavy isotope following closure of the stomata in response to EAB induced drought stress (Farquhar et al., 1989). Furthermore, the relationship between canopy condition and foliar $\delta^{13}C$ lend support to the long held notion that carbon isotopes can be used to reveal the physiological status of a tree (Fig. 2). The carbon isotopic enrichment of foliar tissue observed in this study is similar to trends summarized by Arndt and Wanek (2002) who observed enriched carbon during periods of water stress. Hartman and Danin (2010) also found that plant $\delta^{13}C$ was related to mean annual rainfall in the Mediterranean.

Our study highlights the negative impacts of the invasive EAB on ash tree health. The results indicate that EAB (larvae and exit holes) can be present in trees that appear to be healthy and not

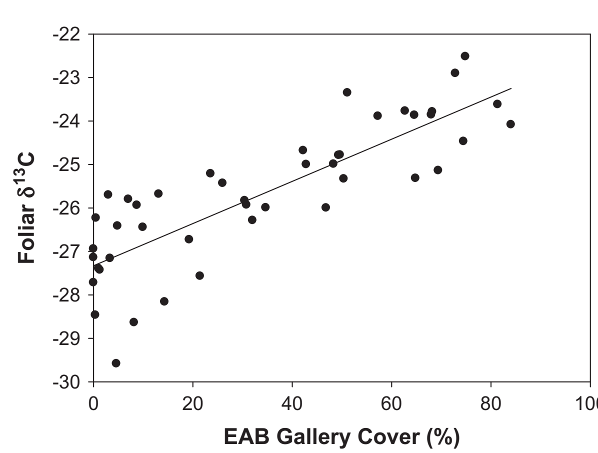

Fig. 1. Linear regression between the carbon isotopic composition of leaf tissue (leaf $\delta^{13}C$) and tree level percent EAB gallery cover (Adj. $r^2 = .704$).

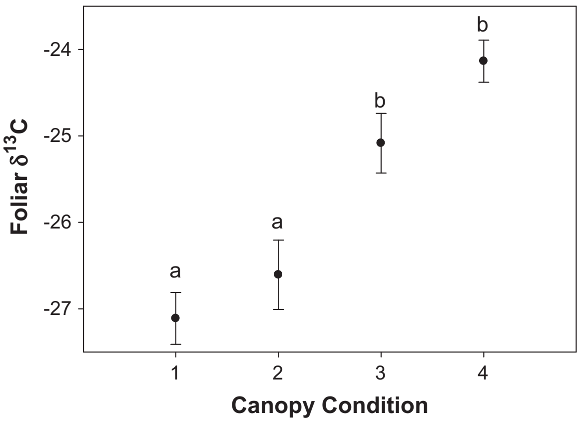

Fig. 2. The relationship between the ash canopy condition class and the carbon isotopic composition of foliar tissue (foliar $\delta^{13}C$) (GLM; $P < 0.001$). Letters represent significance levels determined by Post Hoc Tukey's HSD pairwise comparisons ($P < 0.05$), error bars denote ± 1SE.

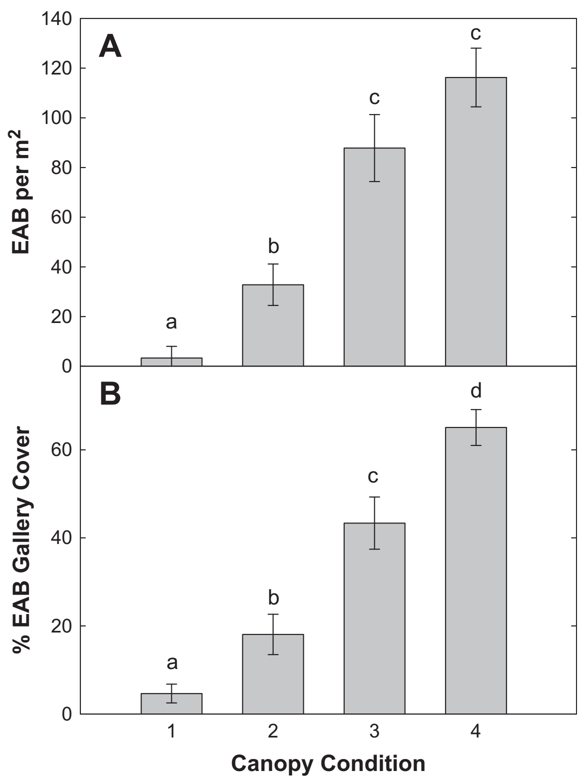

Fig. 3. (A) Relationship between ash canopy condition class and EAB m^2 (GLM; $P < 0.001$). (B) Relationship between ash canopy condition class and % EAB gallery cover at the tree level (GLM; $P < 0.001$). Lower case letters represent significance levels determined by posthoc Tukey's HSD pairwise comparisons ($P \leqslant 0.05$), error bars denote ± 1SE.

infested by EAB. The results of this study show that the canopy condition classes adapted for ash trees by Smith (2006) are closely related to tree-level EAB densities, % EAB gallery cover (Fig. 3), and water stress. These relationships indicate that visual canopy condition ratings can be deployed as a useful and effective technique for classifying canopy decline in ash trees as a result of EAB infestation. The rating system was able to distinguish trees in early stages of EAB infestation with relatively low levels of EAB: <20% gallery cover or <40 EAB/m^2 in canopy condition 2 trees. These trees had thinning canopies but did not yet exhibit water stress (Fig. 2) or dieback. Trees with canopy conditions of 3 and 4, with 50% or >50% dieback, respectively, had increasing levels of EAB gallery cover. Even with the severely decreased amount of foliage in the canopy of these trees, the remaining foliage was not receiving adequate water as evidenced by the foliar $\delta^{13}C$.

It should be noted that the ash canopy condition ratings used here may only be applicable in places without ash decline, ash yellows (a mycoplasma-like infectious organism), or any other biotic or abiotic agent having a significant impact on ash health (Sinclair and Griffiths, 1994; Sinclair and Lyon, 2005). In these areas the presence/absence of characteristic D shaped exit holes will be a valuable indicator.

Categorical rating systems, similar to the ash canopy condition class system utilized in this study, have long been used to simplify biologically relevant continuous variables into easily definable classes (Ball and Simmons, 1980; Fajvan and Wood, 1996; Gottschalk and MacFarlane, 1993; Millers et al., 1991). This user-friendly classification scheme, used in conjunction with other detection techniques (such as trapping or the direct observation of EAB holes) can help managers identify EAB symptoms at an early stage of invasion (Ryall et al., 2013). Recognizing early EAB induced tree decline can help managers determine the time course at which trees will die thus permitting the development of appropriate responses strategies (i.e. removal, treatment, or replacement).

5. Conclusion

The EAB induced ash tree decline studied herein highlights the negative consequences of a non-native insect on tree physiology. This study puts forth that the mechanism by which EAB result in ash tree mortality is via the feeding behavior of EAB larvae, which form serpentine galleries in the cambial tissue and reduce the acropetal supply of water. The relationship between percent EAB gallery cover and foliar $\delta^{13}C$ validates the underlying physiological basis of the EAB induced canopy decline. Our results also indicate that visual canopy decline characteristics are an appropriate and effective proxy for assessing EAB (adult and larval) density and larval activity at the tree level in areas where EAB is present and is the only major cause of ash tree decline. To confirm that EAB is causing tree decline, the canopy condition classes used herein should be used with other EAB identification techniques (e.g., EAB exit holes and lured purple panel traps). This will help managers and landowners identify EAB infestations at the tree or forest level. Early detection of EAB populations will help facilitate management actions.

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