Journal of Economic Entomology, 112(1), 2019, 201–212
doi: 10.1093/jee/toy282
Advance Access Publication Date: 25 September 2018
Research

Forest Entomology

Emerald Ash Borer (Coleoptera: Buprestidae) Densities Over a 6-yr Period on Untreated Trees and Trees Treated With Systemic Insecticides at 1-, 2-, and 3-yr Intervals in a Central Michigan Forest

Deborah G. McCullough,[1,2,7] Therese M. Poland,[3] Andrew R. Tluczek,[1] Andrea Anulewicz,[1,4] James Wieferich,[1,5] and Nathan W. Siegert[1,6]

[1]Department of Entomology, Michigan State University, East Lansing, MI 48824, [2]Department of Forestry, Michigan State University, East Lansing, MI 48824, [3]USDA Forest Service, Northern Research Station, 3101 Technology Boulevard, Suite F, Lansing, MI 48910, [4]Current address: USDA Animal Plant Health Inspection Service, 5936 Ford Court, Brighton, MI 48116, [5]Current address: Michigan Department of Natural Resources, Forest Resource Division, 525 Allegan Street, Lansing, MI 48929, [6]Current address: USDA Forest Service, Northeastern Area State and Private Forestry, Forest Health Protection, 271 Mast Road, Durham, NH 03824, and [7]Corresponding author, e-mail: mccullo6@msu.edu

Disclaimer: Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

Subject Editor: Brian Sullivan

Received 31 May 2018; Editorial decision 31 August 2018

Abstract

We assessed density of emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) larvae over a 6-yr period by felling and sampling a total of 315 green ash (*Fraxinus pennsylvanica* Marsh.) trees that were left untreated or treated with imidacloprid, dinotefuran, or emamectin benzoate products at 1-yr, 2-yr, or 3-yr intervals. Our study, conducted across a 32-ha forested area, began soon after emerald ash borer became established and continued through the peak and eventual decline of the emerald ash borer population. Less than half of the 96 trees in the pretreatment sample were infested and larval densities were very low. Densities of emerald ash borer remained low for 3 yr, then increased exponentially, eventually resulting in mortality of most untreated overstory ash. Trees treated with either low or moderate rates of emamectin benzoate applied via trunk injection had few or no emerald ash borer galleries, even 3 yr post-treatment. Basal trunk sprays of dinotefuran applied annually were also effective at preventing larval densities from reaching damaging levels. Average larval densities on trees treated with a trunk injection of imidacloprid were lower but did not differ from untreated trees, regardless of treatment frequency. Larval parasitism was rare, while woodpecker predation was common and accounted for nearly all natural larval mortality, even on trees with very low densities of larvae.

Key words: invasive forest pest, emamectin benzoate, woodpecker predation, dinotefuran, imidacloprid

Emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), threatens more than eight billion ash (*Fraxinus* spp.) trees in U.S. forests plus millions of ash in residential and urban landscapes (Herms and McCullough 2014, Poland and McCullough 2006). This phloem-feeding pest, a native of Asia, has killed hundreds of millions of ash trees since it was discovered near Detroit, Michigan in 2002 (Cappaert et al. 2005) and is now considered the most destructive and costly invasive forest insect in North America (Aukema et al. 2011, Herms and McCullough 2014). The range of emerald ash borer continues to expand and to date, emerald ash borer infestations have been confirmed in 35 states and four Canadian provinces (EAB.info 2018).

Green ash and white ash (*F. americana*) are especially abundant and widely distributed in eastern U.S. forests (Kennedy 1990, Schlesinger 1990, Gucker 2005) and cultivars of both species are common landscape trees in all 48 continental states (MacFarlane and Meyer 2005, Poland and McCullough 2006). An estimated 38 million landscape ash trees grow in urban areas in the eastern United States, and if suburbs of those areas are included, the number of ash trees doubles (Kovacs et al. 2010, 2011). Popularity of ash for landscapes and street trees reflects several appealing traits, including an upright and attractive form, the ability to tolerate poor or stressful growing conditions, and prior to the emerald ash borer invasion, a lack of major pests (Poland and McCullough 2006). In many municipalities, ash trees comprise 20–30% of the urban forest canopy and in some cities, ash accounts for more than 50% of the landscape and street trees (Ball et al. 2007; Kovacs et al. 2010, 2011; McCullough and Mercader 2012; Sydnor et al. 2011; Sadof et al. 2017). Without effective insecticide protection, these trees can be expected to succumb to emerald ash borer, usually within 6–8 yr of infestation (Mercader et al. 2011, McCullough and Mercader 2012, Knight et al. 2013, Sadof et al. 2017).

When emerald ash borer was first identified as the cause of widespread ash mortality in 2002, only a few systemic insecticides were available and efficacy was inconsistent (McCullough et al. 2004, 2007; Herms 2011). Advances in our understanding of emerald ash borer biology, along with development of new systemic insecticide compounds, formulations, and application methods, have substantially improved the ability of arborists to protect valuable ash trees in landscapes (McCullough et al. 2011, Herms et al. 2014, Bick et al. 2018).

Registration of a systemic insecticide with emamectin benzoate as the active ingredient (AI) in 2010 markedly increased interest in protecting ash trees from emerald ash borer. An extensive field study encompassing 175 trees demonstrated that a trunk injection of this product, sold as TREE-äge, provided nearly 100% protection from emerald ash borer for 2 yr (McCullough et al. 2011). Other field trials similarly documented the remarkable efficacy and persistence of this product for emerald ash borer control (Smitley et al. 2010, Herms 2011, Flower et al. 2015). Further, an extensive 4-yr project encompassing 390 km^2 showed that treating even a very small proportion of ash trees with the emamectin benzoate product significantly slowed emerald ash borer population growth and the rate of ash decline across the project area (McCullough et al. 2015, Mercader et al. 2015).

Most trials to evaluate systemic insecticides for emerald ash borer control, including imidacloprid, dinotefuran, and emamectin benzoate, assessed larval densities either on very small trees in plantations or on one to two branches of landscape trees, or relied on visual estimates of canopy condition (McKenzie et al. 2010; Smitley et al. 2010, 2015; Herms 2011; Flower et al. 2015). More intensive evaluations of treatment efficacy have involved felling entire trees to quantify larval densities (McCullough et al. 2011, Lewis and Turcotte 2015). Although felling and destructively sampling trees is labor intensive and not practical in many settings, such data are the most accurate means to assess efficacy of insecticide products. This intensive form of sampling also prevents confounding emerald ash borer–related canopy decline with stress related to weather, growing conditions, or other factors. Persistence of emerald ash borer control has been monitored in past studies for 2–3 yr post-treatment (McKenzie et al. 2010, Herms 2011, McCullough et al. 2011, Flower et al. 2015, Smitley et al. 2015), but few trials have extended beyond 4 yr (Bick et al. 2018).

Here, we report results from a large-scale field study designed to evaluate changes in emerald ash borer larval density and efficacy of imidacloprid, dinotefuran, and emamectin benzoate products applied annually, or at 2-yr or 3-yr intervals over a 6-yr period. Our study, which was conducted across a 32-ha forest, began shortly after emerald ash borer invaded the area and continued through the peak and eventual decline of the local emerald ash borer population. In total 315 ash trees were intensively sampled over the course of the 6-yr study. Our results document changes in emerald ash borer larval density over time, differences in insecticide efficacy and persistence, and the extent of larval mortality caused by natural enemies.

Materials and Methods

Study Area

We established this study in fall 2007 in a 32.4-ha (80 acres) area of forested land in the Au Sable State Forest in Jasper Township, Midland County, in central lower Michigan, United States. This area is accessible only by foot and consists of mixed forest types varying in size and stocking density, intermixed with swamps, and open fields. Green ash (*Fraxinus pennsylvanica* Marsh.) was relatively abundant across the area, along with scattered black ash (*F. nigra* Marsh.) trees. Other common overstory species included aspen (*Populus tremuloides* Michx), maples (*Acer* spp.), and oaks (*Quercus* spp.). Alder (*Alnus* spp.) thickets were common in wet areas. We suspected emerald ash borer could be in or near this area, but we observed no signs or symptoms associated with emerald ash borer infestation on any ash trees in the study area or in adjacent stands at the outset of the study.

Pretreatment Ash Inventory and Emerald Ash Borer Sampling

A systematic grid consisting of 50 × 50 m cells (total of 128 grid cells) was overlaid on a map of the area. Geo-referenced coordinates for each grid cell corner were identified and marked in the field with handheld GPS units (Garmin ETrex; Garmin, Inc., Olathe, KS). During the 2007–2008 winter, we tallied all ash trees >2.5 cm DBH by DBH class in each grid cell. Small trees, i.e., 2.5–10 cm DBH, were included in our inventory because emerald ash borer can colonize and kill trees down to 2.5 cm DBH (Cappaert et al. 2005, Poland and McCullough 2006). Ash phloem area was estimated by DBH class following methods of McCullough and Siegert (2007).

To systematically assess emerald ash borer presence and quantify initial emerald ash borer larval densities, we felled one or two ash trees in each grid cell where ash occurred between December 2007 and March 2008. In total 96 felled trees (Table 1) were limbed, then sampled by sectioning the trunk and branches into 1 m long bolts from the base to the point where the leader or branches were approximately 8 cm in diameter. Alternate bolts beginning at 1 m above ground were examined and distinctive D-shaped exit holes made by adult emerald ash borer beetles upon emergence and larger holes left by woodpeckers preying on emerald ash borer larvae were recorded (Cappaert et al. 2005). Bolts were carefully debarked with drawknives to expose emerald ash borer larval galleries and measured (bolt length and diameter at both ends). Larvae were tallied by condition (live, dead, predated, parasitized) and life stage as early (first or second instar), third instars, fourth instars, prepupae, or emerged adults (Cappaert et al. 2005). Counts were summed and standardized by the exposed surface area for each tree.

Systemic Insecticides and Treatment Regimes

In spring 2008, we divided the study area into eight quadrants, each 4.05 ha (10 acres) and comprised of 16 (i.e., 4 × 4) grid cells. We selected a block of 28 similarly sized green ash trees within each quadrant. All trees appeared healthy with full canopies and we observed no external evidence of emerald ash borer infestation on any ash trees.

We randomly assigned five trees in each of the eight blocks to be treated with one of four systemic insecticide products/rates (20 trees total). For each insecticide product/rate, three trees per block were treated annually until felled, one tree per block was treated at 2-yr intervals (2008 and 2010) and one tree per block was treated at 3-yr intervals (2008 and 2011) (Table 1). Systemic insecticides included a basal trunk spray of dinotefuran (Safari), trunk-injected emamectin benzoate (TREE-äge) applied at a low rate (EB-Low) or at a moderate to high rate (EB-High), and trunk-injected imidacloprid (Imicide) (Table 2). Systemic insecticides were applied when leaf expansion was nearly complete in early- to mid-June each year. The remaining eight trees in each block were left untreated to serve as controls (Table 1).

Basal trunk sprays of dinotefuran (Safari) (formulated with distilled water) were applied with a 7.6-liter garden sprayer at a rate of 95 ml of formulated product per 2.5 cm DBH (Table 2) using a conical spray nozzle and low pressure to avoid splash-back or overspray. We added 89 ml (3 oz) of a nontoxic surfactant (Pentra Bark) to each 3.8 liters (1 gallon) of formulated product. Previous observations had suggested Pentra Bark could potentially enhance dinotefuran penetration of outer bark (McCullough et al. 2007). Spray was applied evenly to the outer bark around the circumference of the tree from approximately 4 to 1.6 m aboveground.

Trunk injections of emamectin benzoate and imidacloprid (Table 1) were evenly spaced around the base of the tree, avoiding areas with previous wounds, cankers, or dead tissue. We applied emamectin benzoate (TREE-äge) using #4 Arborplugs. Trees treated at the lowest label rate (2.5 ml per 2.5 cm DBH) were injected with the QUIK jet device (one injection site per 5 cm DBH). Trees assigned to the moderate-high rate of emamectin benzoate (5 ml per 2.5 cm DBH) were injected with TREE-äge combined with an equal amount of distilled water using the ArborJet TREE IV system with four or eight delivery lines, depending on tree size, following label directions. When needed, containers were re-pressurized or valves were moved to other injection sites to ensure complete uptake. Imidacloprid (Imicide 10%) was applied using Mauget micro-injection capsules (one 3 ml capsule per 5 cm DBH). After an hour, capsules were checked and re-pressurized if any product remained in the capsules.

Post-treatment Sampling

Subsets of trees were felled and sampled between January and early April each year from 2009 to 2014, as indicated in the treatment and sampling schedule summarized in Table 1. In 2009, we felled one tree that had been treated with each insecticide product/rate in the preceding summer (June 2008) and one control tree per block. In 2010 and again in 2011, we felled one control tree per block. In 2012, we felled one of the trees treated annually, the tree treated biennially (2 yr intervals) with each insecticide product/rate, and two control trees per block. In 2013, two control trees per block were felled. In 2014, one of the trees treated annually, the tree treated triennally (3 yr intervals) with each insecticide product/rate, and one control tree per block were felled. One dinotefuran tree designated for annual treatment fell in a 2011 windstorm and was not sampled in 2012. In 2013, two control trees per block were felled and sampled. In 2014, one of the trees treated annually, the tree treated triennually (3 yr intervals) with each insecticide product/rate, and one control tree per block were felled and sampled. Three of the original 72 trees could not be sampled in 2014 because they blew down during 2009 or 2011 windstorms. An additional tree treated annually

Table 1. Number of green ash (*F. pennsylvanica*) trees felled and sampled in the 2007–2008 winter before treatments were applied, number of trees per treatment treated annually in early June with one of four systemic insecticide products/rates for 1, 2, or 6 yr, or treated at 2-yr or 3-yr intervals, and number of trees felled and sampled the following winter.

	No. of trees per treatment treated with each insecticide (June) and no. of trees felled and sampled (Jan.–April) by year												
	2007/2008	2008–2009		2009–2010		2010–2011		2011–2012		2012–2013		2013–2014	
Treatment regime	Felled	Treated	Felled	Treated	Felled	Treated	Felled	Treated	Felled	Treated	Felled	Treated	Felled
Annual		—											
1 yr		8	8										
4 yr		8		8		8		8	8[a]				
6 yr		8		8		8		8		8		8	8[b]
Multi-year		—											
2-yr intervals		8				8			8				
3-yr intervals		8						8					8[b]
Not treated	96		8		8		8		14		16		8
Total trees	96	160	40	64	8	96	8	96	77[a]	32	16	32	68[b]

[a]One tree treated annually with dinotefuran fell during a 2011 windstorm and was not sampled in 2012.

[b]Four trees were not sampled in 2014 because they blew down during 2009 or 2011 windstorms or could not be safely felled, including one tree treated triennial with the high emamectin benzoate rate, one tree treated annually with the low emamectin benzoate rate and two trees treated triennially with imidacloprid.

Table 2. Systemic insecticide products and distributors, application rates (grams of AI per 2.5 cm DBH), and application methods used to treat green ash (*F. pennsylvanica*) trees in early June, either annually or at 2-yr or 3-yr intervals from 2008 to 2013

AI	Product	Distributor	Rate (AI)	Application method
Dinotefuran + Pentra Bark[a]	Safari 20 SG	Valent USA Corp., Walnut Creek, CA	1.70 g	Basal trunk spray (3.2 fl oz per 2.5 cm DBH)
Emamectin benzoate—low	TREE-äge 4% ME	Arborjet, Inc., Woburn, MA	0.10 g	Trunk macro-injection; Quik jet (2.5 ml per 2.5 cm DBH)
Emamectin benzoate—high	TREE-äge 4% ME	Arborjet, Inc., Woburn, MA	0.20 g	Trunk macro-injection; TREE I.V. (5.0 ml per 2.5 cm DBH)
Imidacloprid	Imicide HP 10%	JJ Mauget Co., Arcadia, CA	0.07 g	Trunk micro-injection; (3 ml capsule per 5.1 cm DBH)

[a]Pentra-Bark is an agricultural organosilicone surfactant (Quest Products, Lindwood, KS). We added 89 ml per 3.8 liters of formulated dinotefuran.

with imidacloprid became entangled with the canopy of a very large adjacent tree and could not be safely felled for sampling (Table 1).

Felled trees were sectioned, debarked, measured, and examined as described above. We recorded D-shaped emerald ash borer adult exit holes and larger woodpecker holes, along with the number of old galleries (from previous larval cohorts). Current-year larvae/galleries were tallied by condition (live, dead, predated, parasitized) and life stage. Larvae parasitized by native *Atanycolus* spp. (Braconidae) or the introduced *Tetrastichus planipennisi* Yang (Eulophidae) were identified by cocoons or gregarious larvae, respectively, and recorded. In total 1,755 adult *T. planipennisi* (75% female) were released for emerald ash borer biocontrol in 2009, approximately 800 m from the nearest border of our study area (D.G.M., unpublished data). Counts of emerald ash borer exit holes, holes left by woodpeckers, emerald ash borer larvae, galleries, and parasitized larvae were summed for each tree and standardized by the exposed surface area (density per m^2).

Ash Condition in 2015

Although we were not able to repeat the complete inventory of ash trees across the project area at the conclusion of the study, we established a variable radius plot (5 baf prism) in the center of each of the original 50 × 50 m grid cells in August 2015. We counted and recorded DBH of live and dead ash trees (>10 cm DBH) and visually estimated canopy dieback on live ash trees in 10% increments.

Statistical Analysis

Normality was tested for all variables using the PROC Univariate procedure and residual plots. Pretreatment density of larvae in untreated trees (felled during the 2007–2008 winter and density of larvae in untreated control trees felled each winter from 2009 to 2014) were compared among years by a general linear mixed model (PROC GLIMMIX) with year felled as a fixed effect and block as a random effect in the model, followed by the Tukey–Kramer least significant means test. Using the gamma distribution and log link allowed assumptions of residual analysis to be met. The variance matrix was blocked by study block, the estimator technique was set as residual PL, and denominator degrees of freedom were determined using the Kenward–Rogers method.

Each year when treated trees were felled (i.e., 2009, 2012, and 2014), we similarly compared densities of current-year larval galleries in trees among treatments with a general linear mixed model (PROC GLIMMIX), using treatment as a fixed effect and block as a random effect, followed by the Tukey–Kramer least significant means test. As above, the response distribution was set as gamma with the log link function. The variance matrix was blocked by study block, the estimator technique was set as residual PL, and degrees of freedom were determined using the Kenward–Rogers method. Other response variables, including density of live larvae, dead larvae, old galleries, woodpecker attacks, and total galleries, were also analyzed with a similar general linear mixed model (PROC GLIMMIX). Response distributions and link functions were altered as necessary for assumptions of residual analyses to be met and were set to lognormal distribution with identity link function for density of dead larvae in 2014 and density of live larvae in 2012.

Differences in ash tree DBH among blocks were compared using a general linear model (PROC GLM) followed by the Tukey means comparison test. Linear relationships between tree DBH and density of current-year galleries in untreated control trees and between densities of woodpecker attacks and current-year galleries in untreated control and insecticide-treated trees were assessed with regression analysis (PROC REG). All analyses were conducted at the $P < 0.05$ level of significance using SAS 9.4 statistical software (SAS Institute 2012).

Results

Pre-treatment Ash Inventory and Emerald Ash Borer Sampling

During our initial inventory in winter 2007–2008, we tallied 12,315 ash trees (>2.5 cm DBH) representing 850 m^2 of basal area across the 32.4 ha area. Most ash trees (79.5%) were small, ranging from 2.5 to 12.5 cm in DBH, while 15.1% and 5.2% of the trees fell into the 12.6–25.1 cm and 25.2–45.0 cm DBH classes, respectively. There were 64 trees (0.5%) with a DBH > 45 cm. Despite the prevalence of small trees, larger trees in the 25.2–45 cm DBH class accounted for approximately 40% of the ash phloem. Given that an average of 89 emerald ash borer adults can potentially emerge per m^2 of ash phloem (McCullough and Siegert 2007), we estimated the ash trees in this area could potentially have produced more than 3.3 million adult emerald ash borer beetles.

Baseline emerald ash borer larval densities across the project area were determined between January and March 2008, before any insecticide treatments began, by sampling the 96 felled ash trees, which averaged 21.6 ± 1.0 cm and ranged from 7.0 to 43.2 cm DBH. In total 113.5 m^2 of ash phloem and an average of 1.2 ± 0.3 m^2 of phloem per tree was debarked and examined. We found 12 exit holes left by emerged emerald ash borer adults on six trees. We tallied 681 emerald ash borer larval galleries on the 45 trees that were infested and nearly all (97.5%) were from current-year larvae. Density of galleries from previous and current-year larvae on infested trees averaged 0.4 ± 0.17 and 6.7 ± 1.48 per m^2 of exposed area, respectively. Only 33% of current-year galleries had live, apparently healthy emerald ash borer larvae, while 62% were galleries of late stage larvae that had been predated by woodpeckers. Dead larval cadavers were found in 4.7% of the current-year galleries.

Post-treatment Sampling

Size of trees included in our insecticide study varied significantly among blocks ($F = 5.91$; df = 7, 305; $P < 0.0001$) and ranged from an average of 20.7 ± 1.5 cm DBH (block 5) to 30.8 ± 1.5 cm DBH (block 6) (Table 3). There was no significant correlation between tree DBH and total density of emerald ash borer larvae in control trees in any year ($r^2 = -0.08$, $P = 0.47$ in 2007/8; $r^2 = 0.07$, $P = 0.87$ in 2009; $r^2 = -0.008$, $P = 0.98$ in 2010; $r^2 = 0.28$, $P = 0.49$ in 2011; $r^2 = -0.51$, $P = 0.06$ in 2012; $r^2 = -0.16$, $P = 0.53$ in 2013; $r^2 = -0.43$, $P = 0.29$ in 2014). Therefore, differences in tree size among blocks were not a confounding factor in comparing emerald ash borer densities among different insecticide treatments. Nevertheless, study block was included as a fixed effect or blocking factor in all analyses to control for any other site-related variation among blocks. Most trees in our study were relatively tall. Height of the tallest 1 m long bolt sampled on individual trees ranged from 6 to 25 m aboveground and 70 to 85% of the trees sampled annually from 2009 to 2014 were at least 15 m tall.

Untreated Control Trees

We felled and sampled one control tree per block in late winter each year from 2009 to 2011. These trees averaged (±SE) 31.5 ± 2.76 cm, 26.0 ± 1.06 cm and 22.0 ± 1.61 cm in DBH and we exposed an average of 7.4 ± 0.86 m^2, 5.0 ± 0.54 m^2, and 3.0 ± 0.34 m^2 of phloem surface area per tree, respectively, in 2009–2011. In 2012 and

Table 3. Mean (±SE) diameter at breast height (DBH) of ash trees by block (N = 28 trees per block).

Block	Mean ± SE DBH (cm)
1	27.0 ± 1.0ab
2	25.6 ± 1.3abc
3	23.2 ± 1.1bc
4	23.4 ± 1.1bc
5	20.7 ± 1.5c
6	30.8 ± 1.5a
7	24.9 ± 1.2bc
8	28.1 ± 1.4ab
F = 5.91; df = 7,305; P < 0.0001	

Means followed by different letters are significantly different, Tukey HSD test, P < 0.05.

2013, we felled and sampled two control trees per block, averaging 29.2 ± 1.51 cm and 20.2 ± 1.06 cm DBH, respectively. We exposed an average of 6.5 ± 0.65 and 3.1 ± 0.29 m² of phloem area per tree in 2012 and 2013, respectively. In 2014, we felled one control tree per block (eight trees) averaging 26.8 ± 2.47 cm DBH, and exposed an average of 5.6 ± 0.86 m² of phloem area per tree.

During the first 4 yr of the study, from 2007/8 through 2011, emerald ash borer larval densities on the control trees remained very low (Fig. 1). Density of current-year larval galleries averaged 8.0 ± 3.62 and 7.4 ± 2.68 per m² in 2010 and 2011, respectively (Fig. 1B). Total gallery density, which included current-year larval galleries plus old galleries from previous years of larval feeding, averaged 10.4 ± 4.39 and 9.9 ± 3.22 in 2010 and 2011, respectively (Fig. 1A). Current-year gallery density nearly doubled from 2011 to 2012, averaging 16.8 ± 4.10 larvae per m² while total (i.e., cumulative) gallery density averaged 25.1 ± 5.97 larvae per m² in 2012. The increase in current-year gallery densities between 2012 and 2013 was even more striking (Fig. 1B). Densities of current-year and total galleries averaged 43.8 ± 5.26 and 62.0 ± 5.23 per m², respectively, in 2013. By 2014, total gallery densities averaged 72.4 ± 11.42 per m². In contrast, current-year larval density decreased, averaging 35.9 ± 14.2 galleries per m² in 2014 (Fig. 1A), largely because much of the ash phloem was either dead or had been previously consumed. Three of the eight control trees sampled in 2014 had no current-year galleries, but galleries from previous years were abundant. Total gallery densities were significantly higher in 2012–2014 than in 2007/2008 and 2009, while total densities in 2010 and 2011 were intermediate (Fig. 1A). Current-year gallery density was significantly higher in 2013 and 2014 than it was until 2011, and was intermediate in 2012 (Fig. 1B).

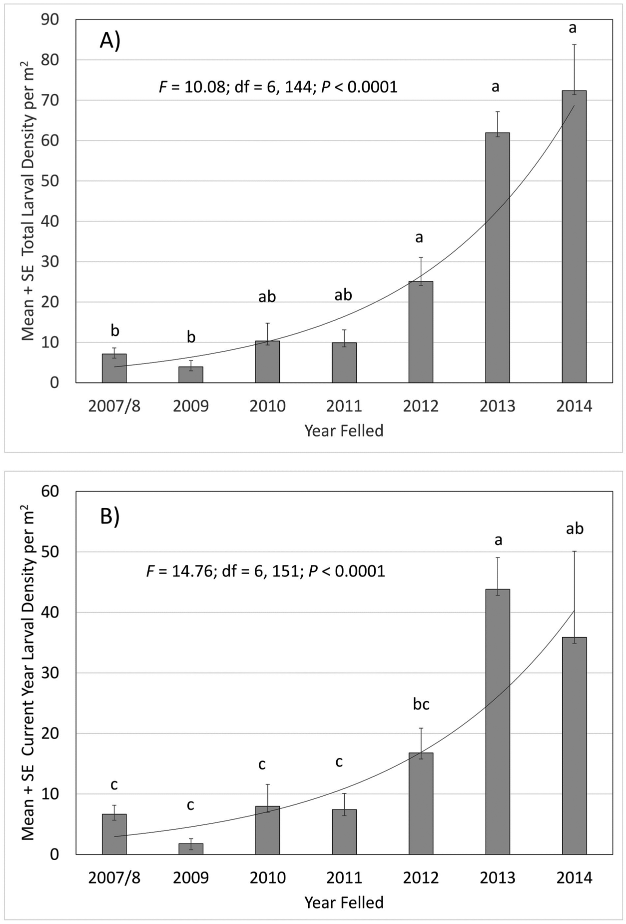

Fig. 1. Mean (+SE) density of (A) total and (B) current-year emerald ash borer larval galleries in untreated control trees felled and sampled each winter (between January and early April) from 2008 through 2014 in the Au Sable State Forest in Midland Co., Michigan. Bars topped with the same letters are not significantly different (Tukey HSD test; P < 0.05). (N = 96 in 2007/8; N = 14 in 2012; N = 16 in 2013; N = 8 in 2009, 2010, 2011, and 2014.)

Insecticide Treatment Evaluation

Between January and March 2009, we felled and sampled 40 trees, including one untreated control tree and one tree that was treated with each of the insecticide products/rates within each of the eight blocks in June 2008. Sampled trees averaged 28.8 ± 1.25 cm DBH and an average of 5.9 ± 0.4 m of phloem per tree was exposed. On untreated trees, average density of current-year larval galleries was less than 2.0 per m² and total gallery density was less than 4.0 per m² (Table 4). We identified a total of 12 emerald ash borer adult exit holes on bolts from 10 trees; average density of exits was only 0.3 ± 0.1 per m². Although densities of current-year emerald ash borer galleries were very low in all trees, they were significantly higher in control trees and trees treated with imidacloprid than in trees treated with the low dose of emamectin benzoate, which had no larval galleries (Fig. 2). Density of current-year galleries in trees treated with the dinotefuran trunk sprays or the high dose of emamectin benzoate were intermediate, but still averaged less than 0.1 gallery per m² (Fig. 2). Only one of the 16 trees treated with emamectin benzoate and two of the eight trees treated with dinotefuran had any live larvae, whereas live larvae were present on seven of the eight imidacloprid trees and seven of eight control trees (Table 4).

In spring 2012, we felled and sampled one tree treated annually and the tree treated biennially with each insecticide product/rate, along with two untreated control trees in each of the eight blocks. Density of current-year emerald ash borer galleries was significantly higher in untreated control trees than in trees treated annually or biennially with either the high or the low dose of emamectin benzoate, while trees treated annually or biennially with either dinotefuran or imidacloprid had intermediate densities (Fig. 3). Live, current-year larvae were found on all 16 controls, the eight trees treated biennially with imidacloprid and seven of eight trees treated annually with imidacloprid. Five trees treated annually and seven trees treated biennially with dinotefuran had live, current-year larvae, although densities were very low on the trees treated annually (Table 4). Three of the 16 trees treated with the high emamectin benzoate rate and

Table 4. Mean (±SE) densities per m^2 of total and current-year emerald ash borer galleries, old emerald ash borer galleries, live and dead current-year emerald ash borer larvae, and woodpecker attacks in untreated control trees and trees treated in June with dinotefuran (Dino; Safari basal trunk spray), emamectin benzoate (EmBen; TREE-äge trunk injection) at a high or low dose, or with imidacloprid (Imi; Imicide; Mauget microinjection capsules) in 2008 then felled and sampled in between January and early April in 2009, or treated annually or biennially from 2008 to 2011 and felled in 2012, or treated annually or triennially from 2008 to 2013 and felled in 2014 (*N* = 8 trees per insecticide product/rate per year)

Year felled/ treatment	Current-year galleries	Live larvae	Dead larvae	Woodpecker attacks	Old galleries	Total galleries
2009						
Control	1.78 ± 0.84a	1.77 ± 0.84a	0.01 ± 0.01a	0.40 ± 0.19a	2.16 ± 0.97a	3.95 ± 1.54a
Dino—annual	0.09 ± 0.05ab	0.07 ± 0.05b	0.02 ± 0.02a	0.05 ± 0.05ab	0.02 ± 0.02b	0.11 ± 0.07c
Em Ben high—annual	0.05 ± 0.04ab	0 ± 0c	0.05 ± 0.04a	0 ± 0b	0.84 ± 0.40a	0.89 ± 0.41ab
Em Ben low—annual	0 ± 0b	0 ± 0c	0 ± 0a	0 ± 0b	0.62 ± 0.50a	0.62 ± 0.50bc
Imi—annual	1.27 ± 0 49a	1.25 ± 0.49a	0.03 ± 0.03a	0.18 ± 0.06ab	1.06 ± 0.49a	2.34 ± 0.92a
F; df; *P*	4.44; 4,30; 0.006	72.21; 4,28; <0.0001	0.60; 4,30; 0.66	3.49; 4,28; 0.02	16.96; 4,28; <0.0001	10.91; 4,28; <0.001
2012						
Control	16.78 ± 4.12a	16.35 ± 4.11a	0.43 ± 0.27a	6.74 ± 1.96a	8.32 ± 2.76a	25.10 ± 5.97a
Dino—biennial	3.72 ± 0.87ab	3.68 ± 0.86b	0.04 ± 0.03a	1.69 ± 0.58ab	4.53 ± 2.15a	8.25 ± 2.69ab
Dino—annual	1.27 ± 0.71ab	0.91 ± 0.42b	0.36 ± 0.33a	0.16 ± 0.09bc	5.50 ± 2.10a	6.77 ± 2.74ab
Em Ben high—biennial	0.64 ± 0.35bc	0.62 ± 0.33b	0.03 ± 0.03a	0.38 ± 0.26bc	2.04 ± 1.35a	2.68 ± 1.58bc
Em Ben high—annual	0.04 ± 0.04c	0.04 ± 0.04b	0 ± 0a	0.04 ± 0.04c	0.89 ± 0.63b	0.93 ± 0.66c
Em Ben low—biennial	0.57 ± 0.51bc	0.57 ± 0.51b	0 ± 0a	0.55 ± 0.50abc	2.00 ± 0.69a	2.57 ± 0.98bc
Em Ben low—annual	0.05 ± 0.05c	0.05 ± 0.05b	0 ± 0a	0.05 ± 0.05c	1.95 ± 0.78a	2.00 ± 0.83c
Imi—biennial	7.38 ± 3.38ab	7.27 ± 3.32ab	0.11 ± 0.09a	2.55 ± 1.32ab	6.00 ± 4.50a	13.39 ± 7.12ab
Imi—annual	4.82 ± 2.35ab	4.62 ± 2.22b	0.20 ± 0.13a	0.68 ± 0.29abc	6.00 ± 1.82a	10.82 ± 3.48ab
F; df; *P*	12.39; 8,8; <0.0001	5.87; 8,61; <0.0001	2.10; 8,22; 0.08	8.11; 8,68; <0.0001	3.27; 8,61; 0.004	8.02; 8,61; <0.0001
2014						
Control	35.88 ± 14.23a	34.19 ± 13.84a	1.68 ± 0.65a	6.93 ± 2.75ab	36.51 ± 6.78a	72.39 ± 11.42a
Dino—triennial	36.74 ± 8.33a	36.11 ± 8.27a	0.64 ± 0.27ab	11.22 ± 4.13a	21.90 ± 6.01a	58.65 ± 10.92a
Dino—annual	1.02 ± .034b	0.4 ± 0.18b	0.57 ± 0.22ab	0.11 ± 0.07d	5.86 ± 3.68ab	6.89 ± 3.82bc
Em Ben high—triennial	0 ± 0d	0 ± 0d	0 ± 0d	0 ± 0e	1.31 ± 0.85bc	1.31 ± 0.85cd
Em Ben high—annual	0 ± 0d	0 ± 0d	0 ± 0d	0 ± 0e	1.23 ± 0.84bc	1.23 ± 0.84cd
Em Ben low—triennial	0.11 ± 0.09c	0.02 ± 0.02c	0.09 ± 0.09c	0 ± 0e	0.45 ± 0.29c	0.57 ± 0.29d
Em Ben low—annual	0.10 ± 0.07c	0 ± 0d	0.10 ± 0.07bc	0 ± 0e	0.35 ± 0.27c	0.45 ± 0.25d
Imi—triennial	13.25 ± 1.49a	12.22 ± 1.36a	1.03 ± 0.43a	1.17 ± 0.52bc	8.44 ± 2.87ab	21.69 ± 3.95ab
Imi—annual	9.15 ± 2.41a	7.55 ± 2.34a	1.56 ± 0.40a	1.05 ± 0.56c	10.14 ± 2.84a	19.29 ± 4.03ab
F; df; *P*	105.7; 8,53; <0.0001	122.8; 8,54; <0.0001	34.05; 8,53; <0.0001	112.18; 8,53; <0.0001	12.71; 8,52; <0.0001	16.94; 8,52; <0.0001

Means within the same year and column followed by different letters are significantly different; Tukey HSD test, $P < 0.05$.

four of the 16 trees treated with the low rate (either annually or biennially) had live larvae.

Between January and early April 2014, we felled and sampled one tree treated annually and the tree treated triennially with each insecticide product/rate, plus one control tree in each of the eight blocks. Density of current-year emerald ash borer galleries was significantly higher in untreated control trees, trees treated annually or triennially with imidacloprid, and trees treated triennially with dinotefuran than in trees treated annually with dinotefuran or annually or triennially with either dose of emamectin benzoate (Fig. 4). No live larvae were recorded on the 16 trees treated annually or triennially with the high rate of emamectin benzoate, while one of the 16 trees treated triennially with the low rate of emamectin benzoate had a total of two live larvae (Table 4). Three trees treated annually with dinotefuran had live larvae but the density was very low, averaging ≤1.0 current-year gallery per m^2 (Table 4). In comparison, densities of current-year galleries on untreated controls and the trees treated with dinotefuran triennially (2008, 2011) varied, but averaged over 35 galleries per m^2 (Fig. 4). Average densities of current-year larvae on trees treated with imidacloprid, either annually or triennially, did not differ statistically from those on control trees (Table 4). Although average densities of emerald ash borer galleries on all the imidacloprid trees were consistently lower than on controls in 2014 (Table 4; Fig. 4), variation among trees was substantial. For example, total and current-year larval densities on trees treated annually with imidacloprid ranged from 1.5 to 81.0 and from 0 to 43.7 galleries per m^2, respectively. Live larvae were present on five of the eight control trees, all eight trees

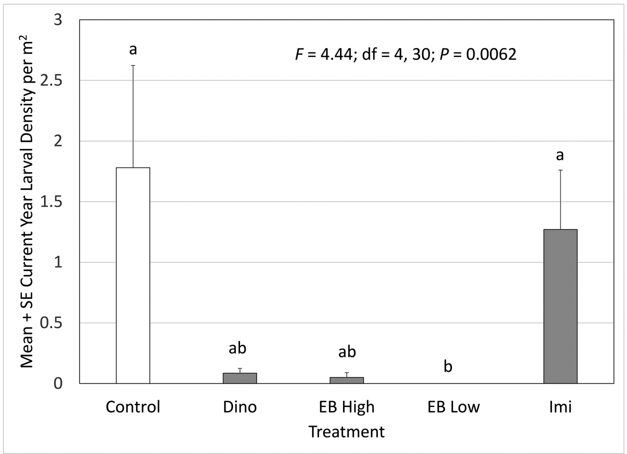

Fig. 2. Mean (+SE) density of current-year emerald ash borer larvae in trees treated with systemic insecticides in mid-June 2008 then felled and dissected between January and March 2009. Insecticide treatments included dinotefuran (Dino; Safari basal trunk spray), emamectin benzoate (EB; TREE-äge trunk injection) at a high or low dose, or imidacloprid (Imi; Imicide Mauget microinjection capsules). Bars topped with the same letters are not significantly different, Tukey HSD test, $P < 0.05$. ($N = 8$.)

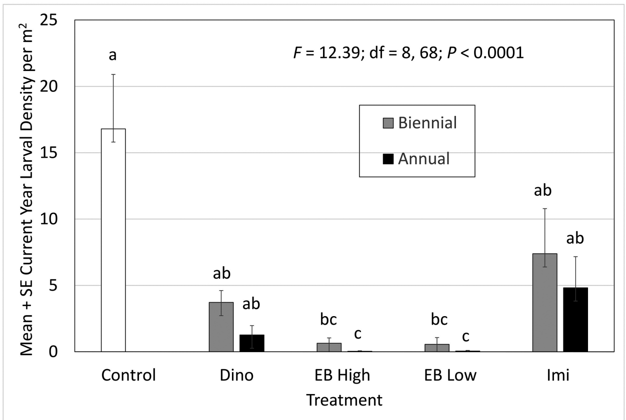

Fig. 3. Mean (+SE) density of current-year emerald ash borer larvae in trees treated with systemic insecticides annually or biennially (every 2 yr) in mid-June from 2008 to 2011 then felled and dissected between January and March 2012. Insecticide treatments included dinotefuran (Dino; Safari basal trunk spray), emamectin benzoate (EB; TREEäge trunk injection) at a high or low dose, or imidacloprid (Imi; Imicide Mauget microinjection capsules). Bars topped with the same letters are not significantly different (Tukey HSD test, $P < 0.05$). ($N = 8$.)

treated triennially with dinotefuran, and all 16 trees treated with imidacloprid, either annually or triennially.

Overall, density of live larvae was similar to density of current-year emerald ash borer galleries, which included larvae killed by natural enemies (Table 4). Differences in densities of live larvae among treatments were similar to those for densities of current-year emerald ash borer galleries (Table 4). Larval cadavers were rare and the density of dead larvae was extremely low overall. No dead larvae were found in trees with extremely low emerald ash borer attack densities (i.e., trees treated with emamectin benzoate or annually with dinotefuran) and only a few were present in trees with higher emerald ash borer attack densities (Table 4). Larval cadavers were typically desiccated and cause of death was uncertain.

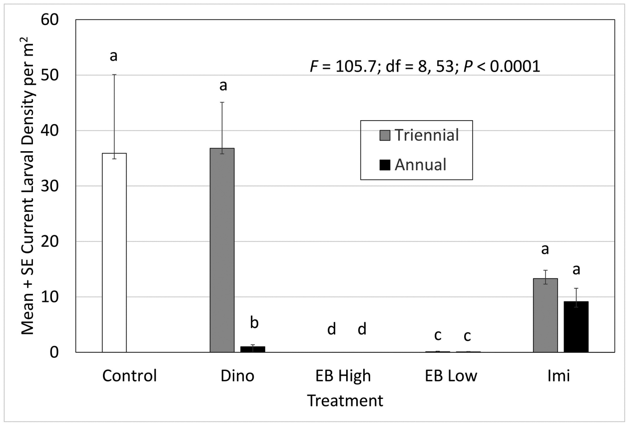

Fig. 4. Mean (+SE) density of current-year emerald ash borer larvae in trees treated with systemic insecticides annually or triennially (every 3 yr) in mid-June from 2008 to 2013 then felled and dissected in winter 2013–2014. Trees were treated with dinotefuran (Dino; Safari basal trunk spray), emamectin benzoate (EB; TREE-äge trunk injection) at a high or low dose, or imidacloprid (Imi; Imicide Mauget microinjection capsules). Bars topped with the same letters are not significantly different (Tukey HSD test, $P < 0.05$). ($N = 8$.)

There was little difference in density of old galleries among treatments in either 2009 or 2012, when most old galleries would have originated from attacks prior to insecticide treatments. In 2014, we encountered old galleries that had originated during years following initiation of the insecticide treatments (i.e., between 2008 and 2013) and there were significant differences in density of old galleries among treatments. In 2014, density of old galleries was significantly higher on untreated control trees than on trees treated annually or triennially with either dose of emamectin benzoate, while trees treated annually or triennially with dinotefuran or imidacloprid had intermediate densities of old galleries (Table 4). For total gallery density, which included all current-year and old galleries, differences among treatments were similar to differences for current-year gallery densities (Table 4).

Woodpecker predation of late instar emerald ash borer larvae was common and in some trees, killed more than half of the emerald ash borer that would otherwise have emerged as adults. Even in the pretreatment survey in 2007/8 when emerald ash borer densities were extremely low, woodpecker predation was observed on 37.5% of the sampled trees and woodpeckers killed more than 60% of the current-year larvae. Over the 6-yr period of the study, woodpecker predation was recorded on 70 of the 111 trees that had relatively low current-year emerald ash borer densities, ranging from 0.3 to 10.0 galleries per m^2. Of those 70 trees, woodpeckers killed at least 20% of the larvae on 60 trees and 50–100% of the larvae on 35 of the trees. In 2010, 2011, and 2013, when we sampled only control trees, woodpeckers predated larvae on 75–100% of the trees, whereas when we sampled control and insecticide-treated trees in 2009, 2012, and 2014, woodpecker predation was recorded on 27–37% of trees. Woodpecker holes in the outer bark were consistently associated with removal of the corresponding fourth instar or prepupal larva below the hole. Overall, for all years and treatments combined, density of current-year emerald ash borer galleries significantly predicted density of woodpecker attacks ($y = 0.4491x - 0.1596$; $R_2 = 0.7472$; $P < 0.0001$) (Fig. 5).

In contrast, larval parasitism was rare. We found no evidence of parasitized larvae until 2012 when a few larvae parasitized by *Atanycolus* spp. were recovered from three trees. Density of larvae parasitized by *Atanycolus* spp. averaged 0.3 ± 0.02 per m^2 in a

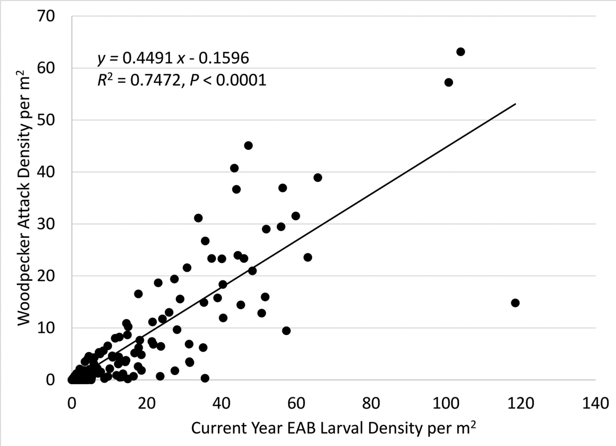

Fig. 5. Relationship between densities of woodpecker attacks and current-year emerald ash borer larval galleries per m^2 recorded from 2008 through early 2014 in untreated control trees and trees treated with systemic insecticides. (N = 315 trees.)

control tree, which had 103.1 current-year emerald ash borer larvae per m^2. Densities of larvae parasitized by *Atanycolus* spp. in two trees treated biennially with imidacloprid were 2.8 and 0.1 larvae per m^2, while current-year emerald ash borer densities in these trees were 43.7 and 7.8 larvae per m^2, respectively. No parasitism was observed in any other control or treated tree in 2012. In 2014, parasitism was slightly more common, but 11 of the 12 trees with *Atanycolus* spp. parasitism were heavily attacked by emerald ash borer. On average, current-year emerald ash borer gallery density averaged 78.6 ± 18.61, while density of larvae parasitized by *Atanycolus* spp. averaged 0.8 ± 0.24 per m^2 in three untreated control trees, 0.6 ± 0.24 in five trees treated triennially and one tree treated annually with dinotefuran, and 0.6 ± 0.35 in three trees treated triennially or annually with imidacloprid. No parasitized larvae were found in any trees treated with either dose of emamectin benzoate. In one tree treated triennially with dinotefuran, a few larvae were parasitized by *T. planipennisi*, but the density was extremely low, averaging 0.02 ± 0.02 parasitized larvae per m^2.

Ash Condition in 2015

In total 208 standing ash trees (>10 cm DBH) were tallied in the variable radius plots surveyed in August 2015. Only 32 of the ash trees were alive and 15–60% of the canopy on 11 of those trees was dead. Nearly all the dead ash trees remained standing in 2015; few trees had fallen or broken off near the base.

Discussion

Ongoing expansion of the geographic range of emerald ash borer threatens an ever increasing number of ash trees in urban, rural, and forested settings in North America, compelling arborists, foresters, and property owners within infested areas to determine how ash on their land will be managed. Systemic insecticides provide options for protecting ash trees in landscapes and, on a larger scale, for slowing emerald ash borer population growth across a given area (McCullough et al. 2011, 2015; Herms et al. 2014; Mercader et al. 2015; Sadof et al. 2017; Bick et al. 2018). Results from our study encompassed a 6-yr period when the emerald ash borer population increased from nearly undetectable levels to densities associated with widespread ash mortality (McCullough and Siegert 2007, Mercader et al. 2011). In addition to documenting changes in emerald ash borer density over time, our data provide a long-term evaluation of the efficacy and persistence of three commonly used systemic insecticide products, and quantify effects of woodpeckers and other natural enemies of emerald ash borer.

Our 2007/2008 pretreatment sampling began soon after emerald ash borer invaded the project area; less than 10% of the 96 trees had a single emerald ash borer exit hole and less than 50% of those trees had any larval galleries. Although total and current-year larval densities on all trees remained extremely low in 2009, differences among insecticide treatments and between treated and control trees were beginning to emerge. In 2009, live larvae were recorded on seven of the eight controls and the eight imidacloprid-treated trees, while 15 of the 16 emamectin benzoate trees (low and high rates) and six of the eight dinotefuran trees had no live larvae. In a previous study, external signs of emerald ash borer infestation, including canopy decline and bark cracks over larval galleries, corresponded to densities of 25–30 larval galleries per m^2 in green ash and white ash landscape trees (Anulewicz et al. 2007). By 2012, average cumulative (total) gallery densities on control trees in our study were approaching these levels.

By 2014, the local emerald ash borer population was at or near peak density. Previous research showed an average of 89 emerald ash borer adults could potentially develop per m^2 of ash phloem area and individual emerald ash borer larvae required approximately 10 cm^2 of phloem to complete development (McCullough and Siegert 2007, Mercader et al. 2011). In 2014, total larval galleries on untreated control trees averaged 72 ± 11.4 per m^2, slightly lower than densities typically associated with ash mortality (McCullough and Siegert 2007). All the control trees we felled and sampled in spring 2014, however, were still alive and could have provided phloem for development of at least some additional larvae in 2014 and perhaps subsequent years. Additionally, many trees in our study were more than 25 m tall. We observed that larval galleries sometimes girdled the trunk of these trees >3 m aboveground, killing the tree before phloem in the lower, thick-barked portion of the trunk was fully colonized, which reduced the overall larval density estimates. Divergence between average densities of current-year galleries, which decreased from 2012 to 2014, and total larval galleries, which increased every year, however, represents the diminishing availability of live phloem in the control trees. When we re-inventoried ash in the project area in 2015, most overstory ash trees had been killed by emerald ash borer and many of the live trees had declining canopies.

The scale, sampling intensity and duration of our study demonstrate substantial differences in the level and persistence of emerald ash borer control between the emamectin benzoate insecticide and the two neonicotinoid compounds. Given the extremely low emerald ash borer densities at the outset of our project, virtually all trees were presumably able to translocate insecticides to the canopy for at least the first 3–4 yr of the study. Extending the study over the 6-yr time frame enabled us to assess insecticide efficacy as the emerald ash borer population approached peak densities and trees experienced very high levels of emerald ash borer pressure (Knight et al. 2013, Burr and McCullough 2014, Sadof et al. 2017).

Very few emerald ash borer galleries were present on any of the trees treated with emamectin benzoate in any year, regardless of whether the trees were injected annually, biennially, or triennially with either the low or the high rate of insecticide. Of the 32 emamectin benzoate trees sampled in 2014, 13 trees (41%) had no larval galleries, 16 trees (50%) had 0.1–3.0 total galleries per m^2 and three trees (9%) had 3.2–6.8 galleries per m^2, still well below densities likely to affect tree health. In previous studies, foliar residues of emamectin benzoate (also applied as trunk-injected-TREE-age), declined exponentially from the first to the second year (McCullough et al. 2011, Lewis and Turcotte 2015). Nevertheless, biennial trunk injections of emamectin benzoate provided nearly complete emerald ash borer control and protected ash canopies for at least 2 yr in numerous studies (Smitley et al. 2010, McCullough et al. 2011, Flower et al. 2015, Bick et al. 2018). Evidence from bioassays with emerald ash borer adults and diet studies with emerald ash borer larvae have indicated relatively low levels of emamectin benzoate are notably toxic to this species (McCullough et al. 2011, Poland et al. 2015). While emerald ash borer adults can be killed by feeding on foliage of treated trees (McCullough et al. 2011, Herms et al. 2014), mechanisms by which emerald ash borer larvae encounter emamectin benzoate, or other systemic insecticides, are not as clear. Trunk-injected systemic insecticides are translocated to the canopy in xylem tissue (Mota-Sanchez et al. 2009, Tanis et al. 2012), whereas emerald ash borer larvae feed on phloem and cambium. After debarking hundreds of infested trees in this and other studies, we have noted that early stage emerald ash borer larvae frequently fed through the phloem and into the cambium region, then began excavating a characteristic serpentine gallery that scored the outer xylem as well as the phloem. Given that ash are ring porous trees, even young larvae may encounter lethal doses of insecticide in the outer xylem. Additionally, insecticide may move from xylem into phloem through horizontal ray parenchyma cells (Pfautsch et al. 2015).

The consistently high level of emerald ash borer control observed in this and other multi-year studies indicate the interval between emamectin benzoate injections can be extended to at least 3 yr. Ash trees are highly sectorial, effectively compartmentalize xylem wounds (Santamour 1986), and with the exception of small trees (e.g., <10 cm DBH), are unlikely to be seriously injured by a low density of emerald ash borer larvae (Anulewicz et al. 2007, Mercader et al. 2011). Moreover, our data indicate the lowest application rate on the product label (2.5 ml TREE-äge per 2.54 cm DBH) was as effective as the higher rate we tested (5.0 ml per 2.54 cm DBH). Reducing the insecticide application rate and extending the interval between treatments from 2 to 3 yr would yield substantial cost savings. Additionally, in a recent study, stumps and the basal portion of the trunk on trees treated annually, biennially, or triennially with emamectin benzoate applied with either the ArborJet QuikJet or Tree IV macroinjection systems were examined to assess injury, decay, or other problems (Tanis and McCullough 2016). Despite an abundance of injection sites, particularly on trees treated annually with the QuikJet, injury associated with the injections was minimal. Nevertheless, decreasing the frequency of treatments would reduce the number of injection sites and provide treated trees with additional time to produce new xylem around and over previous injections (Tanis and McCullough 2016). Since our study was conducted, additional emamectin benzoate products have become available. Whether these products, which may differ in terms of formulation, application rates, or methods, provide similar levels of emerald ash borer control over time will require further study.

Annual applications of dinotefuran, applied as a basal trunk spray, effectively protected trees from emerald ash borer–caused injury, although the level of control was somewhat lower than that recorded on the emamectin benzoate trees. Foliar residue data have shown dinotefuran, which is highly water soluble, moves through the outer bark and is readily translocated to foliage in the canopy (McCullough et al. 2011, Faulkenberry et al. 2012, Nix et al. 2013). In 2014, seven of the eight trees treated annually with dinotefuran had less than 10 total galleries per m^2, a level that should adequately protect all but very small trees from significant emerald ash borer–related injury. Current-year emerald ash borer larval density was more than twice as high on dinotefuran trees treated biennially compared with trees treated annually, although differences were not significant. Applying dinotefuran at 3-yr intervals provided no emerald ash borer control; current-year larval densities on trees treated triennially were as high as those on control trees. Basal trunk sprays are commonly applied with a backpack or garden sprayer and can be a simple and fairly rapid method for treating trees in landscapes or along roads. In our study, water for the basal trunk sprays had to be carried approximately 1.5 km from the vehicle to the project area, a laborious activity that limited efficiency of this application method. In areas with trees that are readily accessible, this would not be a problem.

Mean densities of current-year and total larval galleries on trees treated with imidacloprid (applied via micro-injection with Mauget capsules) were consistently lower than densities on untreated controls, but differences were not significant in any year of sampling, even when trees were injected annually. By 2014, total gallery densities averaged approximately 20 larvae per m^2 on annual and triennially treated imidacloprid trees. Whether continued injections, even if applied annually, would have ultimately protected the trees from emerald ash borer is difficult to determine. Because galleries score the outer xylem, increasing larval densities can disrupt translocation of insecticides to the canopy and stress from larval feeding can alter volatile profiles of infested trees, potentially increasing their attraction to emerald ash borer adults, including ovipositing females (Rodriguez-Saona et al. 2006; McCullough et al. 2009, 2016; Mercader et al. 2013). Injecting imidacloprid with the Mauget capsules was relatively efficient, although some capsules had to be re-pressurized during the day to ensure uptake. A related study showed the low pressure, micro-injection system caused little injury, even when trees were treated annually (Tanis and McCullough 2016). The low level of emerald ash borer control relative to annual dinotefuran bark sprays and all emamectin benzoate treatments may reflect the low dose of imidacloprid applied with the capsules. Other studies have reported imidacloprid applied annually at higher rates via macro-injection or as a soil drench can effectively protect trees emerald ash borer–related canopy decline (Smitley et al. 2015, Bick et al. 2018).

Numerous simulations have compared economic costs of protecting landscape ash trees with a highly effective systemic insecticide, typically emamectin benzoate applied in alternate years via trunk injection, versus removing the same trees, either proactively or as trees decline and die. Results consistently show total and annualized costs of systemic insecticide treatments in alternate years are substantially lower than costs of tree removal, plus annual labor needs are stabilized (Kovacs et al. 2011, 2014; McCullough and Mercader 2012; McKenney et al. 2012; Vannatta et al. 2012; Hauer and Peterson 2017). Value of ecological services, such as stormwater uptake, pollutant capture, shade, and aesthetics (Vannatta et al. 2012, Wolf et al. 2015), and social or cultural benefits provided by mature ash (Poland and McCullough 2006, Donovan et al. 2013, McCullough 2013, Nowak et al. 2016, Donovan 2017, Jones 2017) were not quantified in these simulations, but would further increase the benefit:cost ratio of protecting trees. Extending the period between insecticide applications would reduce annualized treatment costs even further.

Whether our sampling and insecticide treatments had an effect on emerald ash borer population growth in the project area is difficult to ascertain. Results from simulations showed effects of emamectin benzoate on emerald ash borer population growth were more pronounced when treated trees were distributed systematically across a project area than when insecticide treatment was focused on only large trees or trees within a specific area (Mercader et al. 2011, 2015; McCullough and Mercader 2012; McCullough et al. 2015). In our study, blocks of trees, including those assigned to highly effective insecticide treatments, were distributed across the project area, presumably increasing the likelihood that emerald ash borer adults would encounter toxic foliage. Additionally, over the 6-yr period, we felled and debarked more than 300 trees, which represented approximately 2.5% of the ash stems tallied in our pretreatment inventory. Larvae developing in the sampled trees would have been killed, plus the felled trees were eliminated as potential emerald ash borer hosts in subsequent years. Moreover, while trees assigned to triennial imidacloprid or dinotefuran treatments probably became suitable emerald ash borer hosts 1–2 yr post-treatment, 32 trees injected with either low or high rates of emamectin benzoate were toxic for the entire 6-yr study. Adult emerald ash borer females that emerged from other trees and fed on foliage of an emamectin benzoate tree or other trees with lethal insecticide levels in the leaves (e.g., trees annually treated with dinotefuran) would have been killed. Reduced emerald ash borer population growth resulting from the tree felling and insecticide treatments, however, was likely offset by immigrating beetles from adjacent forest land, especially near the end of our study when most ash in adjacent forests had been killed. Results from our 2015 assessment using variable radius plots indicated that more than 90% of the original ash phloem in the study area was dead.

Woodpecker predation was by far the most important natural mortality factor affecting the emerald ash borer population across our project area, accounting for nearly all larval mortality we observed over the 6-yr period. Consistent with other reports, woodpeckers preyed on fourth instars or prepupae (Lindell et al. 2007, Tluczek 2009, Duan et al. 2014, Flower et al. 2014) and there was a strong positive relationship between densities of current-year emerald ash borer larvae and woodpecker attacks (Fig. 5), a pattern also noted in previous studies (Jennings et al. 2013, Flower et al. 2014). Some authors have speculated that prevalence of woodpecker predation increases with the age of the emerald ash borer infestation because dead trees with cavities for woodpecker nesting sites are more abundant (Lindell et al. 2007, Jennings et al. 2013, MacQuarrie and Scharback 2015). However, we observed woodpecker predation at the very onset of the invasion when the emerald ash borer population was newly established and at an extremely low density. Given the extensive forest where our study occurred, availability of cavities for nesting was probably not a limiting factor for the woodpeckers. While woodpeckers can use acoustic signals (vibration) to identify subcortical prey, much of their foraging behavior is not well understood. Flowers et al. (2014) noted average woodpecker predation rates in trees with declining canopies were twice as high as those in trees with healthy canopies and suggested woodpeckers selected ash trees for foraging based on their visual observations of canopy condition. This seems improbable, however, given that woodpecker predation mainly occurs between late fall and spring (Jennings et al. 2016, Tluczek 2009), when large, late stage larvae and prepupae are most likely to be available, but visual cues of canopy condition, e.g., foliage, are largely absent. Recent evidence indicated birds that prey on Lepidopteran larvae use host volatiles induced by severe defoliation to locate their prey (Amo et al. 2013), but whether volatiles of ash trees stressed by emerald ash borer larval feeding can similarly attract woodpeckers has not been confirmed.

While woodpecker predation was common and sometimes accounted for a high proportion of emerald ash borer larvae on individual trees, neither woodpeckers nor the combination of woodpecker predation and larval parasitoids prevented the emerald ash borer population from building to densities that resulted in the mortality of most overstory ash by the end of our 6-yr project. Extremely low densities of native *Atanycolus* spp. parasitoids were observed in 2012 and 2014 on a total of 15 trees, 13 of which were heavily attacked by emerald ash borer and likely would have died within a year. A few current-year emerald ash borer larvae on a single tree sampled in 2014 were parasitized by *T. planipennisi*, indicating this introduced species had become established and dispersed following the 2009 release of 1,755 adult *T. planipennisi*, roughly 800 m away.

Whether natural enemies will adequately protect ash regeneration once the emerald ash borer invasion wave has peaked and emerald ash borer population densities have dropped remains to be seen. McCullough et al. (2015) noted that systemic insecticides should not interfere with woodpecker predation nor parasitism because woodpeckers and larval parasitoids attack only live larvae and neither egg nor larval parasitoids will encounter systemic insecticides. Combining highly effective systemic insecticide treatments with biological control may actually enhance the efficacy of natural enemies by reducing overall emerald ash borer densities and focusing woodpeckers and parasitoids on untreated infested trees. Long-term studies to evaluate post-invasion ash dynamics in areas where integrated emerald ash borer management strategies are employed would be valuable.

Acknowledgments

Many students and technicians worked on this project over the years. We especially thank Jacob Baker, Jacob Bournay, David Cappaert, Nick Gooch and Emily Pastula, all of MSU, and Tina Ciamarato, of the US Department of Agriculture, Forest Service, for their assistance. We also thank Joe Doccola of ArborJet, Jason Fausey of Valent USA, Jim Rollins of the JJ Mauget Co., and Bill Stringfellow of Agric-Chem, who provided insecticide products. We appreciate the cooperation of personnel at the Gladwin District office of the Michigan Department of Natural Resources. We thank John Stanovick, US Department of Agriculture, Forest Service, for directing the statistical analyses. Funding for this work was provided by grants from the USDA Forest Service, Northeastern Area, State and Private Forestry and USDA APHIS PPQ.

References Cited

Amo, L. J. J., Jansen, N. M. van Dam, M. Dicke, and M. E. Visser. 2013. Birds exploit herbivore-induced plant volatiles to locate herbivorous prey. Ecol. Lett. 16: 1348–1355.

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

Aukema, J. E., B. Leung, K. Kovacs, C. Chivers, K. O. Britton, J. Englin, S. J. Frankel, R. G. Haight, T. P. Holmes, A. M. Liebhold, et al. 2011. Economic impacts of non-native forest insects in the continental United States. PLoS One 6: e24587.

Ball, J., S. Mason, A. Kiesz, D. McCormick and C. Brown. 2007. Assessing the hazard of emerald ash borer and other exotic stressors to community forests. Arboric. Urban For. 33: 350–359.

Bick, E., N. Forbes, C. Haugen, G. Jones, S. Bernick, and F. Miller. 2018. Evaluation of insecticide tools for seven year management of the emerald ash borer (*Agrilus planipennis*) in green ash (*Fraxinus pennsylvanica*) trees. J. Econ. Entomol. 11: 732–740.

Burr, S. J., and D. G. McCullough. 2014. Condition of green ash (*Fraxinus pennsylvanica*) overstory and regeneration at three stages of the emerald ash borer invasion wave. Can. J. For. Res. 44: 768–776.

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

Donovan, G. H. 2017. Including public-health benefits of trees in urban-forestry decision making. Urban For. Urban Green. 22: 120–123.

Donovan, G. H., D. T. Butry, Y. L. Michael, J. P. Prestemon, A. M. Liebhold, D. Gatziolis, and M. Y. Mao. 2013. The relationship between trees and human health: evidence from the spread of the emerald ash borer. Am. J. Prev. Med. 44: 139–145.

Duan, J. J., K. J. Abell, L. S. Bauer, J. R. Gould, and R. Van Driesche. 2014. Natural enemies implicated in the regulation of an invasive pest: a life table analysis of the population dynamics of the emerald ash borer. Agric. For. Entomol. 16: 406–416.

(EAB.info) Emerald Ash Borer Information. 2018. (http://www.emeraldashborer.info/index.cfm). (Accessed September 2018).

Faulkenberry, M. S., J. D. Culin, S. N. Jeffers, M. B. Riley, and W. C. Bridges. 2012. Efficacy of imidacloprid and dinotefuran applied as soil drenches or trunk sprays for managing *Adelges tsugae* (Hemiptera: Adelgidae) on mature hemlock trees in a forest. J. Entomol. Sci. 47: 369–374.

Flower, C. E., C. L. Long, K. S. Knight, J. Rebbeck, J. S. Brown, M. A. Gonzalez-Meler, and C. J. Whelan. 2014. Native bark-foraging birds preferentially forage in infected ash (*Fraxinus* spp.) and prove effective predators of the invasive emerald ash borer (*Agrilus planipennis* Fairmaire). For. Ecol. Manage. 313: 300–306.

Flower, C. E., J. E. Dalton, K. S. Knight, M. Brikha, and M. A. Gonzalez-Meler. 2015. To treat or not to treat: diminishing effectiveness of emamectin benzoate tree injections in ash trees heavily infested by emerald ash borer. Urban For. Urban Green. 14: 790–795.

Gucker, C. L. 2005. *Fraxinus pennsylvanica*. Fire effects information systems. USDA Forest Service, Rocky Mountain Research Station, Fire Science Lab, Fort Collins, Colorado. (http://www.fs.fed.us/database/feis/plants/tree/frapen/all.html). (Accessed April 2016).

Hauer, R. J., and W. D. Peterson. 2017. Effects of emerald ash borer on municipal forestry budgets. Landscape Urban Plan. 157: 98–105.

Herms, D. A. 2011. Multiyear evaluation of efficacy of soil and trunk applied systemic insecticides for ash canopy conservation. pp. 26–27, In G. Parra, D. Lance, V. Mastro, R. Reardon and C. Benedict (eds.), Emerald Ash Borer National Research and Technology Development Meeting, 12–13 October 2011, Wooster, Ohio. USDA Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV. FHTET-2011-06.

Herms, D. A. and D. G. McCullough. 2014. The emerald ash borer invasion of North America: history, biology, ecology, impacts and management. Ann. Rev. Entomol. 59: 13–30.

Herms, D. A., D. G. McCullough, D. R. Smitley, C. S. Sadof and W. Cranshaw. 2014. Insecticide options for protecting ash trees from emerald ash borer, 2nd ed. North Central IPM Center, University of Illinois, Urbana-Champaign. 16 p. Available at www.emeraldashborer.info (Accessed January 2018).

Jennings, D. E., J. J. Duan, L. S. Bauer, J. M. Schmude, M. T. Wetherington and P. M. Shrewsbury. 2016. Temporal dynamics of woodpecker predation on emerald ash borer (*Agrilus planipennis*) in the northeastern U.S.A. Agric. For. Entomol. 18: 174–181

Jennings, D. E., J. R. Gould, J. D. Vandenberg, J. J. Duan, and P. M. Shrewsbury. 2013. Quantifying the impact of woodpecker predation on population dynamics of the emerald ash borer (*Agrilus planipennis*). PLoS One 8: e83491.

Jones, B. A. 2017. Invasive species impacts on human well-being using the life satisfaction index. Ecol. Econ. 134: 250–257.

Kennedy, H. E. 1990. *Fraxinus pennsylvanica* Marsh. *In* R. M. Burns and B. H. Honkala (eds.), Silvics of North America: hardwoods. Agriculture handbook 654, vol. 2. US Dept. Agriculture, Forest Service, Washington, DC.

Knight, K. S., J. P. Brown, and R. P. Long. 2013. Factors affecting the survival of ash (*Fraxinus spp.*) trees infested by emerald ash borer (*Agrilus planipennis*). Biol. Invasions 15: 371–383.

Kovacs, K. F., R. G. Haight, D. G. McCullough, R. J. Mercader, N. W. Siegert, and A. M. Liebhold. 2010. Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. Ecol. Econ. 69: 569–578.

Kovacs, K., R. J. Mercader, R. Haight, N. Siegert. D. G. McCullough, and A. Liebhold. 2011. The influence of satellite populations of emerald ash borer on projected economic damage in U.S. communities, 2010–2020. Environ. Manage. 92: 2170–2181.

Kovacs, K. F., R. G. Haight, R. J. Mercader, and D. G. McCullough. 2014. A bioeconomic analysis of an emerald ash borer invasion of an urban forest with multiple jurisdictions. Resour. Energy Econ. 36: 270–289.

Lewis, P. A., and R. M. Turcotte. 2015. Use of chemical protection and host tree reduction to control an emerald ash borer infestation in West Virginia. J. Biodivers. Manage. For. 4: 1–5.

Lindell, C., D. G. McCullough, D. Cappaert, N. M. Apostolou, and M. B. Roth. 2007. Factors influencing woodpecker predation on emerald ash borer. Am. Midl. Nat. 159: 434–444.

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

MacQuarrie, D. J. K., and R. Scharback. 2015. Influence of mortality factors and host resistance on the population dynamics of emerald ash borer (Coleoptera: Buprestidae). Can. Entomol. 44: 160–173.

McCullough, D. G. 2013. Will we kiss our ash goodbye? American Forests. 118: 16–23.

McCullough, D. G., and R. J. Mercader. 2012. SLAM in an urban forest: evaluation of potential strategies to slow ash mortality caused by emerald ash borer (*Agrilus planipennis*). Int. J. Pest. Manage. 58: 9–23.

McCullough, D. G., and N. W. Siegert. 2007. Estimating potential emerald ash borer (*Agrilus planipennis* Fairmaire) populations using ash inventory data. J. Econ. Entomol. 100: 1577–1586.

McCullough, D., T. Poland, D. Cappaert, P. Lewis, and J. Molongowski. 2004. Evaluation of trunk injections for control of emerald ash borer, pp. 38–39. *In* V. Mastro and R. Reardon (comps.), Proceedings, the Emerald Ash Borer Research and Technology Development Meeting, 5Ð6 October 2004, Romulus, MI. FHTET-2004–15. USDA Forest Service, Forest Health Technology Enterprise Team, Fort Collins, CO.

McCullough, D. G., D. Cappaert, T. M. Poland, P. Lewis, and J. Molongoski. 2007. Evaluation of neo-nicotinoid insecticides applied as trunk sprays, pp. 52–54. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra (comps.), Proceedings, the Emerald Ash Borer and Asian Longhorned Beetle Research and Technology Development Meeting, 29 October to 2 November 2006, Cincinnati, OH. USDA Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV. FHTET-2007-04.

McCullough, D. G., T. M. Poland, D. Cappaert, and A. C. Anulewicz. 2009. Emerald ash borer (*Agrilus planipennis*) attraction to ash trees stressed by girdling, herbicide and wounding. Can. J. For. Res. 39: 1331–1345.

McCullough, D. G., T. M. Poland, A. C. Anulewicz, P. Lewis, and D. Cappaert. 2011. Evaluation of *Agrilus planipennis* control provided by emamectin benzoate and two neonicotinoid insecticides, one & two seasons after treatment. J. Econ. Entomol. 104: 1599–1612.

McCullough, D. G., R. J. Mercader, and N. W. Siegert. 2015. Developing and integrating tactics to slow ash mortality caused by emerald ash borer. Can. Entomol. 147: 349–358.

McCullough, D. G., T. M. Poland, and P. Lewis. 2016. Lethal trap trees: a potential option for emerald ash borer management. Pest Manage. Sci. 72: 1023–1030.

McKenney, D. W., J. H. Pedlar, D. Yemshanov, D. Barry Lyons, K. L. Campbell, and K. Lawrence. 2012. Estimates of the potential cost of emerald ash borer (*Agrilus planipennis* Fairmaire) in Canadian municipalities. Arboric Urban For. 38: 81–91.

McKenzie, N., B. Helson, D. Thompson, C. Otis, J. McFarlane, T. Buscarini, and J. Meating. 2010. Azadirachtin: an effective systemic insecticide for control of *Agrilus planipennis* (Coleoptera: Buprestidae). J. Econ. Entomol. 103: 708–717.

Mercader, R. J., N. W. Siegert, A. M. Liebhold, and D. G. McCullough. 2011. Estimating the effectiveness of three potential management options to slow the spread of emerald ash borer populations in localized outlier sites. Can. J. For. Res. 41: 254–264.

Mercader, R. J., D. G. McCullough, and J. M. Bedford. 2013. A comparison of girdled ash detection trees and baited artificial traps for emerald ash borer (*Agrilus planipennis* Fairmaire) detection. Environ. Entomol. 42: 1027–1039.

Mercader, R. J., D. G. McCullough, A. J. Storer, J. Bedford, T. M. Poland, and S. Katovich. 2015. Evaluation of the potential use of a systemic insecticide and girdled trees in area wide management of the emerald ash borer. For. Ecol. Manag. 350: 70–80.

Mota-Sanchez, D., B. M. Cregg, D. G. McCullough, T. M. Poland, and R. M. Hollingworth. 2009. Distribution of trunk-injected 14C imidacloprid in ash trees and effects on emerald ash borer (Coleoptera: Buprestidae) adults. Crop Prot. 28: 655–661.

Nix, K., P. Lambdin, J. Grant, C. Coots, and P. Merten. 2013. Concentration levels of imidacloprid and dinotefuran in five tissue types of black walnut, *Juglans nigra*. Forests. 4: 887–897.

Nowak, D. J., R. E. Hoehn, A. R. Bodine, E. J. Greenfield, and J. O'Neil-Dunne. 2016. Urban forest structure, ecosystem services and change in Syracuse, NY. Urban Ecosyst. 19: 1455–1477.

Pfautsch, S., J. Renard, M. G. Tjoelker, and A. Salih. 2015. Phloem as capacitor: radial transfer of water into xylem of tree stems occurs via symplastic transport in ray parenchyma. Plant Physiol. 167: 963–971.

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

Poland, T. M., T. M. Ciaramitaro, and D. G. McCullough. 2015. Laboratory evaluation of the toxicity of systemic insecticides to emerald ash borer larvae. J. Econ. Entomol. 99: 81–93.

Rodriguez-Saona, C., T. M. Poland, J. R. Miller, L. L. Stelinski, G. G. Grant, and P. De Groot. 2006. Behavioral and electrophysiological responses of the emerald ash borer, *Agrilus planipennis*, to induced volatiles of Manchurian ash, *Fraxinus mandshurica*. Chemoecol. 16: 75–86.

Sadof, C. S., G. P. Hughes, A. R. Witte, D. J. Peterson, and M. D. Ginzel. 2017. Tools for staging and managing emerald ash borer in the urban forest. Arboric. Urban For. 43: 15–26.

Santamour, F. S. 1986. Wound compartmentalization in tree cultivars: addendum. J. Arboric. 12: 227–232.

SAS Institute. 2012. PROC User's Manual, version 12.1. SAS Institute, Cary, NC.

Schlesinger, R. C. 1990. *Fraxinus americana* L. white ash, pp. 333–338. *In* Silvics of North American hardwoods, R. M. Burns and B. H. Honkala, Technical Coordinators, USDA Forest Service, Agric. Handbook 654. Washington DC.

Smitley, D. R., J. J. Doccola, and D. L. Cox. 2010. Multiple-year protection of ash trees from emerald ash borer with a single trunk injection of emamectin benzoate and single-year protection with an imidacloprid basal drench. Arbor. Urban For. 36: 2016–211.

Smitley, D. R., D. A. Herms, and T. W. Davis. 2015. Efficacy of soil-applied neonicotinoid insecticides for long-term protection against emerald ash borer (Coleoptera: Buprestidae). J. Econ. Entomol. 108: 2344–2353.

Sydnor, T. D., M. Bumgardner, and S. Subburayalu. 2011. Community ash densities and economic impact potential of emerald ash borer (*Agrilus planipennis*) in four Midwestern states. Arboric. Urban For. 37: 84–89.

Tanis, S. R., and D. G. McCullough. 2016. Evaluation of xylem discoloration in ash trees associated with macro-injections of a systemic insecticide. Arbor. Urban For. 42: 389–398.

Tanis, S. R., B. M. Cregg, D. Mota-Sanchez, D. G. McCullough, and T. M. Poland. 2012. Spatial and temporal distribution of trunk-injected ^{14}C-imidacloprid in *Fraxinus* trees. Pest Manage. Sci. 68: 529–536.

Tluczek, A. R. 2009. Influence of host vigor on larval distribution, development and mortality of *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in North America. M.S. thesis, Department of Entomology, Michigan State University, East Lansing, MI. 120 p.

Vannatta, A. R., R. H. Hauer, and N. M. Schuettpelz. 2012. Economic analysis of emerald ash borer (Coleoptera: Buprestidae) management options. J. Econ. Entomol. 105: 196–206.

Wolf, K. L., M. K. Measells, S. C. Grado, and A. S. T. Robbins. 2015. Economic values of metro nature health benefits: a life course approach. Urban For. Urban Green. 14: 694–701.