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Interspecific Variation in Resistance to Emerald Ash Borer (Coleoptera: Buprestidae) Among North American and Asian Ash (*Fraxinus* spp.)

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ABSTRACT We conducted a 3-yr study to compare the susceptibility of selected North American ash and an Asian ash species to emerald ash borer, *Agrilus planipennis* Fairmaire, an invasive wood-boring beetle introduced to North America from Asia. Because of a coevolutionary relationship between Asian ashes and emerald ash borer, we hypothesized an Asian ash species, Manchurian ash, is more resistant to the beetle than its North American congeners. Consistent with our hypothesis, Manchurian ash experienced far less mortality and yielded far fewer adult beetles than several cultivars of North American green and white ash. Surprisingly, a black ash (North American) × Manchurian ash hybrid was highly susceptible to emerald ash borer, indicating this cultivar did not inherit emerald ash borer resistance from its Asian parent. A corollary study investigated the efficacy of soil-applied imidacloprid, a systemic, neonicotinoid insecticide, for controlling emerald ash borer in each of the five cultivars. Imidacloprid had no effect on emerald ash borer colonization of Manchurian ash, which was low in untreated and treated trees. In contrast, imidacloprid did enhance survival of the North American and hybrid cultivars and significantly reduced the number of emerald ash borer adults emerging from green and white ash cultivars. We identify a possible mechanism of resistance of Manchurian ash to emerald ash borer, which may prove useful for screening, selecting, and breeding emerald ash borer-resistant ash trees.

KEY WORDS *Agrilus planipennis*, wood borers, host plant resistance, coevolution, invasive species

Since its accidental introduction from Asia, emerald ash borer, *Agrilus planipennis* Fairmaire, has infested and killed millions of native ash (*Fraxinus* spp.) trees in managed and natural landscapes of Michigan, Indiana, Illinois, Ohio, Maryland, and Ontario, Canada (Haack et al. 2002, Cappaert et al. 2005, Poland and McCullough 2006). Emerald ash borer colonizes trees that range in size from saplings to fully mature trees, with larvae feeding under the bark on phloem and outer xylem, which girdle and kill trees within 1–4 yr of colonization (Herms et al. 2004, Cappaert et al. 2005, Poland and McCullough 2006). Despite intensive efforts to contain and eradicate emerald ash borer, it continues to spread with clear potential to decimate ash throughout North America (USDA-APHIS 2003, GAO 2006).

Congeneric wood borers endemic to North America, including bronze birch borer, *A. anxius* Gory, and twolined chestnut borer, *A. bilineatus* (Weber), colonize stressed trees (Anderson 1944, Dunn et al.

1990). However, emerald ash borer is killing healthy trees on high quality sites, which has created a wood-borer outbreak of unprecedented intensity (Herms et al. 2004, Poland and McCullough 2006). Reports indicate that emerald ash borer is rare in Asia (Bauer et al. 2005; Schaefer 2005), where Manchurian ash (*Fraxinus mandshurica* Ruprecht) and Chinese ash (*F. chinensis* Roxburgh) are primary hosts (Chinese Academy of Science 1986, Yu 1992, Haack et al. 2002). Observations also suggest that infestations may be restricted to stressed trees (Gould et al. 2005), which implies that Asian ash species may be generally resistant, with weakened trees preferentially colonized. Thus, emerald ash borer seems to behave in Asia much as its congeners do in North America.

All major eastern North American ash species are susceptible to emerald ash borer, including green (*F. pennsylvanica* Marshall), white (*F. americana* L.), black (*F. nigra* Marshall), and blue ash (*F. quadrangulata* Michaux) (Cappaert et al. 2005, Poland and McCullough 2006). Some studies suggest that emerald ash borer prefers green over white ash, with blue ash being least preferred (Anulewicz et al. 2007), although Smith (2006) found that green and white ash were killed with equal frequency in southeast Michigan forests, and black ash experienced highest mortality during initial stages of invasion.

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Table 1. Ash species and cultivars tested at Novi, MI, in 2003–2006

Production and shipping method	No. of trees treated with imidacloprid	No. of trees untreated	<i>Fraxinus</i> species	Cultivar	Symbol
Container	12	8	<i>F. pennsylvanica</i>	Patmore	FpP
	12	8	<i>F. mandshurica</i>	Mancana	FmM
	4	4	<i>F. americana</i>	Autumn Purple	FaAP
Bare root	12	13	<i>F. americana</i>	Autumn Purple	FaAP
	12	13	<i>F. pennsylvanica</i>	Marshall's Seedless	FpMS
	12	8	<i>F. nigra</i> × <i>F. mandshurica</i>	Northern Treasure	FNT

Symbols for each species/cultivar are used in figures.

The life history of emerald ash borer (Cappaert et al. 2005) is strikingly similar to that of bronze birch borer (Barter 1957) and twolined chestnut borer (Haack and Benjamin 1982). In southeast Michigan, adult beetles emerge from host trees in late May through early September (Brown-Rytlewski and Wilson 2005). Eggs are deposited singly in crevices and furrows on the outer bark of host trees. On eclosion, first instars immediately tunnel through the bark and larvae feed on phloem and outer xylem as they create serpentine, frass-packed galleries that impede translocation of water, nutrients, and photosynthate. Most individuals complete their life cycle in 1 yr; however, a proportion of the population requires 2 yr to complete development (Cappaert et al. 2005).

In this study, we compare susceptibility of selected green and white ash cultivars to Manchurian ash, and a North American × Asian hybrid. Theory of biogeography predicts that variation in plant resistance to herbivores corresponds with geographic patterns of natural selection exerted by key herbivores (Bryant et al. 1994). Our a priori hypothesis was that Manchurian ash and the Asian × North American hybrid are more resistant to emerald ash borer than North American ashes because Asian species possess targeted defenses by virtue of a coevolutionary history with emerald ash borer that North American ashes lack. We also present data from a concurrent study showing the effect of soil drenches of imidacloprid on resistant versus susceptible ash cultivars.

Materials and Methods

Experimental Design. We established a 0.2-ha plantation of ash trees in May 2003 at Michigan State University's Tollgate Education Center in Novi, MI, an area of southeast Michigan harboring large populations of emerald ash borer. Five cultivars of North American and Asian ash were compared for their susceptibility to emerald ash borer (Table 1). These included two cultivars of native green ash, Patmore and Marshall's Seedless; one cultivar of native white ash, Autumn Purple; a cultivar of the Asian species, *F. mandshurica* variety Mancana (hereafter referred to as Manchurian ash); and a hybrid of native black ash and Manchurian ash, *F. nigra* × *F. mandshurica* variety Northern Treasure. This cultivar is an F₁ hybrid cross between its North American (female) and Asian (male) parents (Davidson 1999). We acquired all

trees from Bailey Nurseries (St. Paul, MN); all trees had been grafted on green ash root stock and were produced as bare root or containerized nursery stock (Table 1). At planting, trees were 4 yr old and ranged in size from 2.3 to 3.8 cm diameter breast height (DBH). Ash trees of this size are large enough to be colonized but small enough to facilitate shipping and successful transplanting. Trees were planted in a completely randomized design in five rows on 2-m centers. A double row of electric fence was placed around the perimeter of the ash plantation to impede deer browsing. Trees were trickle-irrigated to reduce transplanting stress and facilitate establishment.

The plantation was inoculated with emerald ash borer during spring 2003 by placing ash logs infested with emerald ash borer within each row at an approximate interval of every seven trees. Experimental trees were colonized in summer 2003 by the progeny of beetles that emerged from the infested logs, as well as from trees in the surrounding area. Because local beetle populations were sufficiently dense in 2004–2005, it was no longer deemed necessary to inoculate the plots.

In another experiment, imidacloprid (Merit 75 WP; Bayer CropScience, Research Triangle Park, NC) was applied as a soil drench to a subset of trees of each cultivar from fall 2003 through summer 2005 (Table 1). We conducted this experiment to determine how applications of imidacloprid at different times of year affect emerald ash borer control in resistant and susceptible cultivars. Treatments consisted of fall, spring, and early summer drenches and were compared with untreated trees from each cultivar (Smitley et al. 2006).

Sampling. After leaf expansion in early summer 2004–2006, we recorded percent canopy dieback for each tree by averaging visual estimates of two independent observers. Trees were also recorded as live or dead, with dead trees having 100% canopy dieback. In fall 2004 and 2005, we monitored emerald ash borer attacks by surveying the trunks of each tree for the presence of characteristic D-shaped exit holes in the outer bark, which are formed when adult beetles emerge from their host trees. We used the cumulative number of exit holes per tree from 2004 to 2005 to assess the overall impact of emerald ash borer on each ash cultivar because the host impact of larval feeding is cumulative from 1 yr to the next and because it was not possible to determine what proportion of the pop-

Table 2. ANOVA and χ^2 statistics for ash cultivar comparisons of square root (x) transformed exit hole density (2004–2005) and percent survival (2004–2006)

Variables	Exit hole density			Percent survival		
	df	F	P	df	χ^2	P
Taxon	4,104	7.39	<0.0001	4	32.60	<0.0001
Treatment	1,104	3.37	0.0693	1	6.97	0.0083
Taxon \times treatment	4,104	1.60	0.1807	4	4.78	0.3104

ulation completed their life cycle in 1 versus 2 yr (Cappaert et al. 2005). We estimated beetle density for each tree by dividing the number of exit holes recorded from the trunk by the total surface area sampled (number/m²). We approximated bark surface area (A) using the following equation:

$$A = [(C_m \times (H/2)) + [(C_m + C_t/2) \times (H/2)]] \quad [1]$$

where C_m and C_t are the circumference of the trunk at the midpoint and top, respectively, and H is the height of the tree.

Statistical Analysis. Four trees (two Manchurian ash, one ‘Autumn Purple’ white ash, and one ‘Patmore’ green ash) failed to establish or died by factors unrelated to emerald ash borer (e.g., deer browsing) within the first year and were removed from all analyses. We used Spearman rank correlation (PROC CORR, SAS v. 9.1; SAS Institute 1999) to compare the relationship between density of exit holes and percent canopy dieback in 2004–2005. Correlations were based on a larger number of replicates in 2004 ($N = 114$) than 2005 ($N = 30$) for two reasons: (1) imidacloprid applied in fall 2003 and spring and summer 2004 would not have impacted larvae that colonized trees in summer 2003, whereas imidacloprid treatments would have reduced densities of the 2004 generation; and (2) trees that died in 2004 were not included in the 2005 analysis.

We used logistic analysis (PROC GENMOD, SAS v. 9.1; SAS Institute 1999) to analyze main effects of ash taxon and imidacloprid treatment, as well as the taxon \times imidacloprid interaction, on percent tree survival from 2004 to 2006. Differences in percent survival

among taxa were tested using χ^2 analysis ($P \leq 0.05$). We used two-way analysis of variance (ANOVA; PROC GLM, SAS v. 9.1; SAS Institute 1999) for a completely randomized design to test the effects of taxon, imidacloprid treatment, and taxon \times imidacloprid interaction on density of exit holes, which were square root (x) transformed to meet assumptions of homogeneity of variance and normality. Means were separated using a protected least significant difference (LSD) test for unbalanced data ($P \leq 0.05$; PDIF statement, SAS v. 9.1; SAS Institute 1999).

Results and Discussion

Tree mortality data and emergence hole data from 2004 to 2006 clearly support our a priori hypothesis that Manchurian ash is more resistant to emerald ash borer than North American taxa. During the 3-yr study, survival of Manchurian ash (FmM) was much higher than any of the other taxa (Table 2; Figs. 1 and 2). Low-level mortality occurred only during the first year of the study when trees may have experienced stress associated with transplanting. In contrast, all North American ash taxa experienced high levels of mortality caused by emerald ash borer from 2004 to 2006 (Figs. 1 and 2). All ‘Patmore’ green ash (FpP) trees that were not treated with imidacloprid died by summer 2005 (Fig. 1), whereas 54% of untreated ‘Marshall’s Seedless’ green ash (FpMS) and 63% of untreated ‘Autumn Purple’ white ash (FaAP) died during the same period (Fig. 1). Hence, ‘Patmore’ green ash seems to be more susceptible to emerald ash borer than ‘Autumn Purple’ white ash and the conspecific cultivar, ‘Marshall’s Seedless’. Ultimately, 75 and 92%

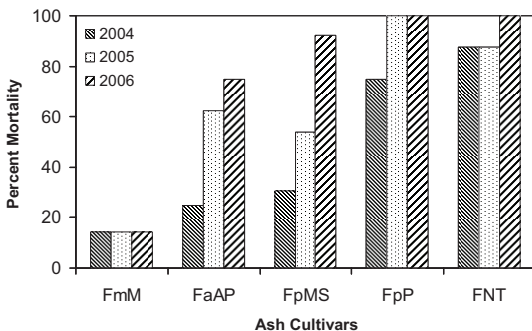


Fig. 1. Percent mortality from 2004 to 2006 for ash taxa that were not treated with imidacloprid. See Table 1 for list of cultivar abbreviations.

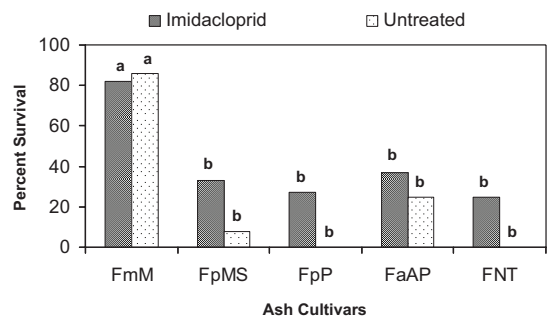


Fig. 2. Percent survival of ash taxa, with and without being treated with imidacloprid, after 3 yr of attack from emerald ash borer. Bars with different letters are significantly different (χ^2 , $P \leq 0.05$). See Table 1 for list of cultivar abbreviations.

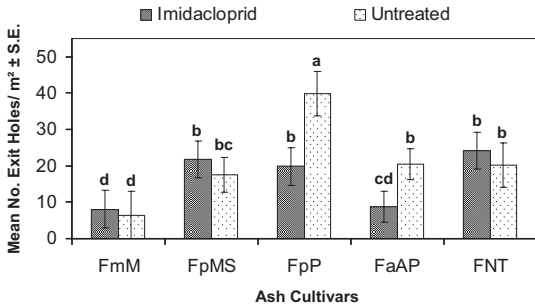


Fig. 3. Mean density of emerald ash borer exit holes (\pm SE) for each ash taxon, with and without being treated with imidacloprid. Data were pooled from 2004 and 2005 and square root (x) transformed for statistical comparison. Means with different letters are significantly different (LSD for unbalanced data, $P \leq 0.05$). See Table 1 for list of cultivar abbreviations.

of the untreated 'Autumn Purple' and 'Marshall's Seedless' ash cultivars, respectively, were killed within 3 yr (Fig. 1), suggesting that any variation in resistance among these white and green ash cultivars may be of little practical significance (Fig. 2). Surprisingly, we observed 100 and 75% mortality of the untreated and treated, respectively, North American \times Asian hybrid 'Northern Treasure' (FNT) ash (Fig. 2). This suggests that this cultivar more closely aligns genetically with its susceptible North American parent relative to emerald ash borer resistance traits.

The imidacloprid treatment significantly increased tree survival and decreased density of exit holes (Table 2; Figs. 2 and 3). The taxon \times imidacloprid interaction terms were not significant for either variable (Table 2). However, there were clearly differential responses of the ash taxa to the imidacloprid treatment (Fig. 2). Imidacloprid had no effect on survival of Manchurian ash, which was high for untreated as well as treated trees, exceeding 80% for both (Fig. 2). Thus, the significant main effect of imidacloprid on survival (Table 2) must be attributed to the higher percent survival of the three North American taxa and the 'Northern Treasure' hybrid when treated with imidacloprid (Fig. 2). Although survival was low for treated trees, most mortality resulted from infestation during the first year before application of the imidacloprid treatment. We will focus on the efficacy of soil-applied imidacloprid against emerald ash borer in a separate paper.

Treatment effects on density of exit holes (Table 2; Fig. 3) closely mirrored those on survival, confirming that emerald ash borer was the cause of tree mortality. Exit hole density was also positively correlated with percent canopy dieback in 2004 ($N = 114$, $r = 0.70$, $P < 0.0001$) and 2005 ($N = 30$, $r = 0.71$, $P < 0.0001$), suggesting a positive relationship between internal feeding injury and external symptoms of tree stress. Regardless of insecticide treatment, Manchurian ash had the lowest density of exit holes among all cultivars tested (Fig. 3), providing further evidence of its higher level of resistance.

In contrast to bark beetle/conifer interactions, interactions between wood-boring insects and angiosperm trees have been examined in only a few cases (Dunn et al. 1990; Hanks et al. 1991, 1999; Paine 2002). Consequently, little is known about mechanisms of resistance of deciduous trees to wood-borers. The high rate of survival of Manchurian ash relative to that of the North American and hybrid taxa suggest that Manchurian ash has evolved targeted defenses to emerald ash borer over the course of their coevolutionary history. Eyles et al. (2007) have identified quantitative and qualitative variation in the constitutive secondary chemistry of Manchurian ash phloem relative to that of green and white ash that may contribute to this resistance.

Although host plant resistance has been recognized as an ideal management strategy for insect pests of trees for many years (Hanover 1975), little progress has been made in deployment of insect resistance in natural or urban forests (Herms 2002). This study marks a start toward efforts to identify emerald ash borer-resistant germplasm needed to facilitate screening, selection, and/or breeding of trees that are resistant to this devastating pest.

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