

# Biology and Control of Emerald Ash Borer



Edited by Roy G. Van Driesche and Richard C. Reardon





## CHAPTER 3: HOST RANGE AND HOST RESISTANCE

Daniel A. Herms

Department of Entomology, The Ohio State University, Ohio Agricultural Research and Development Center,  
1680 Madison Ave., Wooster, Ohio 44691, herms.2@osu.edu

### INTRODUCTION

Since its discovery in North America in 2002, emerald ash borer (*Agrilus planipennis* Fairmaire) (EAB) has infested and killed many millions of ash trees (*Fraxinus* spp.) in forests, woodlots, urban forests, landscapes, and nurseries (Herms and McCullough, 2014). Ash species indigenous to eastern Asia share a coevolutionary history with EAB and are more resistant than evolutionarily naïve hosts indigenous to North America and Europe, presumably because they possess defenses targeted against EAB that have developed through natural selection (Wei et al., 2004, 2007; Liu et al., 2007; Rebek et al., 2008). By 2010, EAB had killed more than 99% of white (*F. americana* L.), green (*F. pennsylvanica* Marsh.), and black (*F. nigra* Marsh.) ash in forests in southeast Michigan near the epicenter of the invasion, and seed production and new seedling germination had ceased (Kashian and Witter, 2011; Klooster et al., 2014). In the Moscow region of Russia, EAB is causing widespread mortality of European ash (*F. excelsior* L.) (Orlova-Bienkowskaja, 2014), which also lacks a coevolutionary history with EAB. While buprestid wood-borers generally colonize only severely weakened or freshly killed trees (Evans et al. 2007), EAB is also killing healthy trees (Cappaert et al., 2005), making the invasions of North America and Russia especially devastating.

### HOST RANGE OF EMERALD ASH BORER

Ash species indigenous to east Asia reported as hosts of EAB include Manchurian ash (*F. mandshurica* Rubr.) and two species of Chinese ash (*F. chinensis* Roxb. and *F. rhyncophylla* [Hance] A.E. Murray) (Wei et al., 2004, 2007) (of which the latter is sometimes

given as a subspecies of *F. chinensis*) (Wallander, 2001). These species are presumed to share a coevolutionary history with EAB (Liu et al., 2003, 2007).

In addition to white, green, and black ash, other species indigenous to North America that have been documented as hosts of EAB include pumpkin ash (*F. profunda* [Bush] Bush) (Knight et al., 2013), and blue ash (*F. quadrangulata* Michx.) (Anulewicz et al., 2008; Tanis and McCullough, 2012). Oregon ash (*F. latifolia* Benth.), native to the west coast of North America, was found to be highly susceptible in a common garden study conducted in southeast Michigan (Table 1). Velvet ash (*F. velutina* Torr.), native to the southwest United States and Mexico, has been colonized and killed by EAB when planted as an ornamental in China (Liu et al., 2003; Wang et al., 2010), while freshly cut logs of Shamel (evergreen) ash (*F. uhdei* [Wenz.] Lingl.), which is indigenous to Mexico, were suitable for rearing emerald ash borer larvae in experimental studies (Duan et al., 2013). The susceptibility of Oregon, velvet, and Shamel ash suggests that the southwest and west coast of North America are vulnerable to EAB invasion, depending on the environmental tolerance of the insect.

Some ash species and cultivars that are indigenous to Europe also have been confirmed as hosts for EAB (i.e., supporting successful larval development and adult emergence). Following this borer's introduction to the Moscow region of Russia (Baranchikov et al., 2008), EAB caused widespread mortality of European ash (Orlova-Bienkowskaja, 2014). In a common garden study in southeast Michigan, flowering ash (*F. ornus* L.), Raywood ash (*F. angustifolia* subsp. *oxycarpa* [M. Bieb. ex Willd.] Franco & Rocha Afonso [syn. *F. oxycarpa* M. Bieb. ex Willd.] cv. 'Raywood'), and the European ash cultivar 'Aureafolia' were readily colonized by EAB (Table 1).

**CHAPTER 3: HOST RANGE AND HOST RESISTANCE**

**Table 1.** Survival and canopy condition of ash species and cultivars in 2009, 2011, and 2014 in a common garden established in southeast Michigan in 2004. Canopies of living trees were rated on a scale of 1 (severe decline) to 5 (no decline). Each taxon was replicated 20 times in a randomized complete block design.

Species	Cultivar	Geographic Origin	2009		2011		2014	
			% Survival	Canopy Rating	% Survival	Canopy Rating	% Survival	Canopy Rating
<i>F. mandshurica</i>	seedling origin	Asia	85	4.6	80	4.80	80	4.20
<i>F. nigra</i> x <i>mandshurica</i>	Northern Treasure	Asia x North America hybrid	90	4.4	80	4.80	80	4.00
<i>F. excelsior</i>	Aureaefolia	Europe	25	3.8	10	5.00	5	2.00
<i>F. ornus</i>	seedling origin	Europe	20	1.5	0	NA	0	0.00
<i>F. angustifolia</i> subsp. <i>oxycarpa</i>	Raywood	Europe	35	4.8	30	3.60	0	NA
<i>F. americana</i>	Autumn Applause	North America	40	4.4	25	4.60	20	2.00
<i>F. americana</i>	Autumn Purple	North America	50	4.6	50	4.60	40	2.10
<i>F. americana</i>	seedling origin	North America	85	4.8	70	4.10	45	2.90
<i>F. americana</i>	Sparticus	North America	55	4.9	45	4.90	45	2.10
<i>F. latifolia</i>	seedling origin	North America	25	2.3	5	2.00	0	NA
<i>F. nigra</i>	Fallgold	North America	35	4.5	15	2.70	5	3.00
<i>F. nigra</i>	seedling origin	North America	10	5.0	5	5.00	0	NA
<i>F. pennsylvanica</i>	Cimmaron	North America	40	5.0	40	4.90	35	2.90
<i>F. pennsylvanica</i>	Patmore	North America	30	5.0	30	4.40	15	2.30
<i>F. pennsylvanica</i>	Summit	North America	20	20.0	15	3.30	0	NA
<i>F. quadrangulata</i>	seedling origin	North America	90	4.8	80	4.60	65	2.20

In Japan, species of *Juglans* (walnuts and butternuts), *Ulmus* (elms), and *Pterocarya* (wingnuts) have been reported as hosts for EAB (Haack et al., 2002). However, EAB has not been well studied in Japan, and host records for wood-borers can be unreliable, potentially including species from which adults were collected even when they do not colonize that species in the larval stage, or they may represent taxonomic errors or confusion (e.g. synonymy of separate species) (Muilenburg and Herms, 2012; Haack, 2013). In experimental host range studies, EAB larvae were not able to complete development on American elm (*Ulmus americana* L.), black walnut (*Juglans nigra* L.), hackberry (*Celtis occidentalis* L.), shagbark hickory (*Carya ovata* [Mill.] K. Koch), or on members of the ash family (Oleaceae) tested, including

Japanese tree lilac (*Syringa reticulata* Bl.), swamp privet (*Forestiera acuminata* [Michx.] Poir.), Chinese privet (*Ligustrum sinense* Lour.), and glossy privet (*Ligustrum lucidum* Ait.) (Anulewicz et al., 2006, 2007). Recently, white fringe tree (*Chionanthus virginicus* L.), which is also in the ash family, was confirmed as a larval host for EAB (Cipollini, 2015).

**INTERSPECIFIC PATTERNS OF ASH RESISTANCE TO EAB**

Emerald ash borer is only occasionally a damaging pest of ash species native to eastern Asia, but has caused widespread mortality of North American ash species planted in China (Wei et al., 2004, 2007). For example, EAB killed all white ash trees planted in

the city of Shenyang, as well as all trees in a 10-year-old white ash planting in the experimental forest of Northeast Forestry University in Harbin. The outbreaks occurred at the same time EAB populations were low on Manchurian ash in neighboring forests. In another study, Liu et al. (2007) observed that green ash was colonized at a higher rate than native Asian species planted at the same site. They concluded based on their field surveys that EAB does not pose a serious threat in China to indigenous ash species. However, Liu et al. (2003) and Wei et al. (2004, 2007) reported that white ash is no longer planted in China and plantings of green ash remain only in localized areas because of past EAB attack. The EAB invasion of Russia west of the Urals has made it apparent that European ash is also highly susceptible to EAB (Orlova-Bienkowskaja, 2014).

Colonization of Asian ash species by EAB has been consistently associated with stressed and dying trees (Wei et al. 2004, 2007; Liu et al. 2007), which suggests that they may be inherently resistant and that EAB has evolved as a secondary colonizer of stressed trees, as is the case with many species of Buprestidae (Evans et al. 2007). Experimental studies of EAB adult host preference and larval performance are consistent with this hypothesis. For example, EAB adults preferred to feed upon foliage from leaves from trees stressed by girdling (Chen and Poland, 2009), injured by adult feeding damage, or induced by methyl jasmonate (Rodriguez-Saona et al., 2006). In field experiments, adult-landing rates were higher on girdled trees, as were larval densities and growth rates (McCullough et al., 2009; Tluczek et al., 2011). Jennings et al. (2014) found that females preferred to oviposit on declining trees that were previously infested by EAB rather than on healthy trees.

All North American ash species encountered to date by EAB have proven susceptible to varying degrees (Herms and McCullough, 2014). Black, green, and white ash are highly susceptible (Klooster et al., 2014), although white ash is somewhat less preferred, possibly because its smoother bark (at least in younger trees) may be a less preferred oviposition substrate (Anulewicz et al., 2008). In forests, trees with rougher bark were reported to be killed at a slightly faster rate than smoother barked

trees (Marshall et al., 2013). However, at the stand level, black, white, and green ash declined at similar rates, with populations of all three species ultimately reaching greater than 99% mortality at about the same time (Smith, 2006; Smith et al., 2015; Klooster et al., 2014). Blue ash (*F. quadrangulata*) appears to be the least vulnerable North American ash species encountered by EAB to date. Tanis and McCullough (2012) observed that more than 60% of blue ash in wooded areas in southeastern Michigan appeared healthy, while white ash with trunks greater than 10 cm in diameter were all killed.

Patterns of ash decline and mortality in an ongoing common garden study established at Michigan State University's Tollgate Education Center in Novi, Michigan in 2004 are largely consistent with the hypothesis that coevolved species indigenous to Asia are more resistant than evolutionary naïve hosts native to North America and Europe (Table 1). The resident EAB population was low when the plot was established as most trees in the region had been killed. As EAB populations began to resurge and susceptible trees in the plot began to be killed, Manchurian ash had the highest rate of survival and little canopy decline. Mortality of Manchurian ash that did occur was concentrated in the first few years after planting, perhaps due to transplant stress. The only tree killed after 2009 had its trunk badly injured by a deer rub. The high EAB resistance of this Manchurian ash population of seedling origin is consistent with that observed by Rebek et al. (2008) for the clonal Manchurian ash cultivar 'Mancana,' suggesting that EAB resistance is a species-level trait.

*Fraxinus* x 'Northern Treasure' ash, which is a Manchurian (Asian) x black ash (North American) hybrid (Davidson, 1999) had similarly high survival and low canopy decline, suggesting introgression of Manchurian ash resistance genes into the hybrid (Table 1). However, this pattern contrasts sharply with that observed by Rebek et al. (2008), who found 'Northern Treasure' ash to be highly susceptible to EAB. This suggests there is taxonomic confusion in the nursery industry surrounding this cultivar that has yet to be resolved.

Most North American species and cultivars in the common garden study experienced substantial

mortality, with green ash cultivars, black ash, and Oregon ash declining more rapidly than white ash cultivars (Table 1). Blue ash has survived at a higher rate than other North American species, but by 2014 had lower survival and greater canopy decline than Manchurian ash. Furthermore, decline and mortality of blue ash increased over time, suggesting that surviving trees may continue to succumb to EAB as other hosts are eliminated. The European species and cultivars evaluated in the common garden also experienced high decline and mortality, including *F. ornus*, *F. excelsior* 'Aureaefolia', and *F. angustifolia* subsp. *oxycarpa* 'Raywood' (Table 1).

The high level of resistance of Asian ash relative to North American and European species has been attributed to a coevolutionary history that has stabilized the interaction between EAB and its indigenous hosts in Asia (Liu et al., 2003, 2007; Rebek et al., 2008). Conversely, the widespread mortality of Nearctic and European ash species in invaded regions has been attributed to very high susceptibility of evolutionarily naïve host plants, which has facilitated the spread and population growth of EAB in defense-free space (Gandhi and Herms, 2010; Raupp et al., 2010). A similar pattern has been observed for birch (*Betula* spp.) resistance to congeneric bronze birch borer (*Agrilus anxius* Gory), which is endemic to North America. North American birch (*Betula*) species share a coevolutionary history with bronze birch borer and are much more resistant than evolutionarily naïve Eurasian birch species (Nielsen et al., 2011).

### MECHANISMS OF RESISTANCE OF ASH TO EAB

Host plant resistance to insects is considered a continuous trait ranging from complete immunity at one end of the spectrum to extreme susceptibility at the other (Painter, 1958; Beck, 1965). Mechanisms of resistance have been broadly classified as antibiosis (plant traits that lower herbivore performance, including fecundity, growth, and survival), antixenosis (plant traits that reduce behavioral preferences for feeding or oviposition), and tolerance (traits that allow a plant to grow or repair injury to

a greater degree than another host experiencing the same amount of herbivory) (Painter, 1958; Beck, 1965; Wiseman, 1985). Biogeographically, resistance has been classified as coevolved (host defenses resulting from natural selection) or allopatric (herbivore lacks the pre-adaptations needed to perform well on a novel host) (Harris, 1975).

Because the devastating impact of EAB on its host is due to larval feeding, research on mechanisms of resistance have focused on factors affecting larval density and survival, including traits affecting female fecundity and oviposition preferences, as well as stem defenses and nutritional quality that influence larval establishment, growth, and survival. However, the relative importance of antibiosis and antixenosis in inter- or intraspecific variation in resistance of ash to EAB has yet to be fully delineated, and the role of tolerance has not been investigated.

EAB adults have demonstrated variation in host preference for maturation feeding and oviposition. Pureswaran and Poland (2009) found that adults preferred to feed on green, black, and white ash relative to Manchurian, blue, and European ash. This pattern corresponds largely with patterns of resistance and vulnerability observed in the field, with the most susceptible species also being preferred (with the exception of European ash, which is highly susceptible), and suggests that there might be general correspondence between adult feeding preferences and female oviposition preferences. Consistent with this hypothesis, Rigsby et al. (2014) observed in two common garden experiments that females oviposited much more extensively on white and green ash than on Manchurian ash, and Anulewicz et al. (2008) found that females preferred to oviposit on green and white ash relative to blue ash. These findings also suggest that oviposition preference is an important determinant of interspecific variation in ash mortality and decline observed in field studies.

Mechanisms of tree resistance to wood-borer larval feeding are not well understood but have been postulated to result from integrated constitutive and induced physical and chemical defenses of the phloem and outer xylem (Matson and Hain, 1985; Dunn et al., 1990; Muilenburg and Herms, 2012). Studies to elucidate the mechanism of resistance of Manchurian



ash to EAB have focused on comparing its induced and constitutive phloem chemistry to that of susceptible species. Eyles et al. (2007) compared the constitutive phloem phenolic chemistry of dormant stems of Manchurian, white, and green ash and identified compounds present in the Manchurian ash cultivar 'Mancana' that were not present in the more susceptible species, including several hydroxycoumarins and two phenylethanoids (calceolariosides A and B) and suggested they might represent potential EAB resistance mechanisms. In a similar analysis conducted during the growing season, Cipollini et al. (2011) also found the constitutive phenolic profile of Manchurian to be distinctly different from that of green and white ash, observing patterns of qualitative variation similar to those reported by Eyles et al. (2007).

In more phylogenetically controlled comparisons, however, Whitehill et al. (2012) detected these putative resistance compounds in concentrations comparable to or higher in highly susceptible black and European ash, which are much more closely related to Manchurian ash than are green and white ash. This strongly suggests that hydroxycoumarins and calceolariosides A and B are, in fact, not responsible for the high resistance of Manchurian ash. Pinoresinol dihexoside and a tentatively identified coumarin derivative were the only phenolic compounds detected that were unique to Manchurian ash, which suggests that the other 25 phenolic compounds detected are unlikely to play a role in resistance unless they synergize other classes of compounds that are unique to Manchurian ash (Whitehill et al., 2012). They did speculate that that two unique lignans may serve as markers for, or contribute directly to, the higher EAB resistance of Manchurian ash (Whitehill et al., 2012). They also proposed that the very distinct phenolic profile of blue ash may contribute to its higher level of resistance to EAB relative to green and white ash.

The constitutive protein chemistry of ash phloem also has been examined. Manchurian ash had higher soluble protein concentration and a higher rate of browning (oxidation) reaction than did green or white ash, although trypsin inhibitor activity, peroxidase activity, and total soluble phenolic concentrations of Manchurian ash were lower than in at least one of the more susceptible species (Cipollini et al.,

2011). Whitehill et al. (2011) compared the phloem proteomes of Manchurian, black, green, and white ash, and they identified several proteins implicated as defenses in other species that were constitutively over-expressed in Manchurian ash relative to the other species and might contribute to resistance. These include a PR-10 protein, phenylcoumarin benzylic ether reductase, an aspartic protease, and ascorbate peroxidase.

Nutritional quality of plants also contributes to variation in their resistance to herbivores, and Hill et al. (2012) quantified phloem compounds in Manchurian, green, and white ash that are thought to be of nutritional significance to EAB larvae, including nitrogen, total protein, free amino acids, total soluble sugars, and macro- and micro-nutrients. They found few differences, although concentrations of the amino acid proline, as well as the amino acid derivatives tyramine and tyrosol were higher in Manchurian ash. Chen et al. (2011) reported that larval growth was reduced on artificial diets in which protein or amino acids were limiting, and that the downward orientation of feeding as larvae formed their galleries allowed them to consume phloem with higher water and essential amino acid concentrations.

Chakraborty et al. (2014) examined induced responses of Manchurian and black ash phloem to larval feeding, which has received far less attention than constitutive patterns. They found that EAB larval biomass was lower on Manchurian ash, which provides evidence that antibiosis as well as ovipositional non-preference contributes to high resistance of Manchurian ash, as does the observation of Duan et al. (2012) that host plant factors caused higher mortality of larvae feeding on Asian species of ash than on North American green ash. EAB larval feeding induced higher concentrations of pinoresinol A in Manchurian than black ash, which Chakraborty et al. (2014) speculated might contribute to resistance. Drought stress increased larval performance on both species, which is consistent with the hypothesis that stress increases host quality.

Counter adaptations of EAB larvae to ash defenses have also been examined. Transcriptomic studies of EAB have focused on larval enzymes that function in detoxification of host defenses (Rajarapu et al., 2011;

Rajarapu and Mittapalli, 2013). Chen et al. (2012) found that phenolic concentrations were lower in EAB frass than in phloem tissue and inferred that larvae may excrete phenolics and/or convert them to non-phenolic compounds before excretion.

### BREEDING FOR RESISTANCE TO EAB

Because of their inherent resistance to EAB, Asian ash species are a likely source of resistance genes that might be introgressed into North American species (Whitehill et al., 2011), and efforts to breed EAB-resistant ash are ongoing (Koch et al., 2012). Extensive surveys of ash stands in Michigan and Ohio have revealed a very small proportion of ash that remain healthy where EAB-ash induced mortality exceeds 99%, and thus may provide a potential source of allopatric resistance genes in native ash populations (Knight et al., 2012). However, it remains to be documented whether these genotypes are truly resistant or just lucky. Genomic sequencing of Asian and North American ash species have also been conducted to provide a molecular foundation for targeted breeding (Bai et al., 2011; Rivera-Vega et al., 2012) that ultimately may lead to restoration of ash to urban and natural forests of North America.

### ACKNOWLEDGEMENTS

David Smitley (Department of Entomology, Michigan State University) and Bert Cregg (Department of Horticulture, Michigan State University) and their laboratory groups helped with establishment of the ash common garden study at the Michigan State University Tollgate Education Center in Novi, Michigan. Roy Prentiss, Farm Manager at the Tollgate Education Center, provided excellent support in the establishment and maintenance of the plantation. This work was funded by USDA APHIS and USDA Forest Service Northern Research Station, as well as by state and federal funds appropriated to The Ohio State University and the Ohio Agricultural Research and Development Center.

### REFERENCES

- Anulewicz, A. C., D. G. McCullough, and D. L. Miller. 2006. Oviposition and development of emerald ash borer (*Agrilus planipennis*) (Coleoptera: Buprestidae) on hosts and potential hosts in no-choice bioassays. *Great Lakes Entomologist* 39: 99–112.
- 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. *Arboriculture and Urban Forestry* 33: 338–349.
- Anulewicz, A. C., D. G. McCullough, D. L. Cappaert, and T. M. Poland. 2008. Host range of the emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) in North America: results of multiple-choice field experiments. *Environmental Entomology* 37: 230–241.
- Bai, X., L. Rivera-Vega, P. Mamidala, P. Bonello, D. A. Herms, and O. Mittapalli. 2011. Transcriptomic signatures of ash (*Fraxinus* spp.) phloem. *PLoS ONE* 6(1): 1–12
- Baranchikov, Y., E. Mozolevskaya, G. Yurchenko, and M. Kenis. 2008. Occurrence of the emerald ash borer, *Agrilus planipennis*, in Russia and its potential impact on European forestry. *EPPO Bulletin* 38: 233–238.
- Beck, S. D. 1965. Resistance of plants to insects. *Annual Review of Entomology* 10: 207–232.
- Cappaert, D., D. G. McCullough, T. M. Poland, and N. W. Siegert. 2005. Emerald ash borer in North America: a research and regulatory challenge. *American Entomologist* 51: 152–163.
- Chakraborty, S., J. G. A. Whitehill, A. L. Hill, S. O. Opiyo, D. Cipollini, D. A. Herms, and P. Bonello. 2014. Effects of water availability on emerald ash borer larval performance and phloem phenolics of Manchurian and black ash. *Plant, Cell and Environment* 37: 1009–1021.
- Chen, Y. and T. M. Poland. 2009. Biotic and abiotic factors affect green ash volatile production and emerald ash borer feeding preference. *Environmental Entomology* 38: 1756–1764.

- Chen, Y., T. Ciaramitaro, and T. M. Poland. 2011. Moisture content and nutrition as selection forces for emerald ash borer larval feeding behavior. *Ecological Entomology* 36: 344–354.
- Chen, Y., M. D. Ulyshen, and T. M. Poland. 2012. Differential utilization of ash phloem by emerald ash borer larvae: ash species and larval stage effects. *Agricultural and Forest Entomology* 14: 324–330.
- Cipollini, D. F., Q. Wang, J. G. A. Whitehill, J. R. Powell, P. Bonello, and D. A. Herms. 2011. Distinguishing defensive characteristics in the phloem of ash species resistant and susceptible to emerald ash borer. *Journal of Chemical Ecology* 37: 450–459.
- Cipollini, D. 2015. White fringetree, *Chionanthus virginicus* L., as a novel larval host for emerald ash borer. *Journal of Economic Entomology*. (In press)
- Davidson, C. G. 1999. 'Northern Treasure' and 'Northern Gem' hybrid ash. *HortScience* 34: 151–152.
- Duan, J. J., G. Yurchenko, and R. Fuester. 2012. Occurrence of emerald ash borer (Coleoptera: Buprestidae) and biotic factors affecting its immature states in the Russian Far East. *Environmental Entomology* 41: 245–254.
- Duan, J. J., K. Larson, T. Watt, J. Gould, and J. P. Lelito. 2013. Effects of host plant and larval density on intraspecific competition in larvae of the emerald ash borer (Coleoptera: Buprestidae). *Environmental Entomology* 42: 1193–1200.
- Dunn, J. P., D. A. Potter, and T. W. Kimmerer. 1990. Carbohydrate reserves, radial growth, and mechanisms of resistance of oak trees to phloem-boring insects. *Oecologia* 83: 458–468.
- Evans, H. F., L. G. Moraal, and J. A. Pajares. 2007. Biology, ecology and economic importance of Buprestidae and Cerambycidae, pp. 447–474. In: Lieutier, F., K. R. Day, A. Battisti, J. C. Grégoire, and H. F. Evans (eds.). *Bark and Wood-boring Insects in Living Trees in Europe, a Synthesis*. Springer, Dordrecht, The Netherlands.
- Eyles, A., W. Jones, K. Riedl, D. Cipollini, S. Schwartz, K. Chan, D. A. Herms, and P. Bonello. 2007. Comparative phloem chemistry of Manchurian (*Fraxinus mandshurica*) and two North American Ash species (*F. americana* and *F. pennsylvanica*). *Journal of Chemical Ecology* 33: 1430–1448.
- Gandhi, J. K. J. and D. A. Herms. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biological Invasions* 12: 389–405.
- Haack, R. A. 2013. The host range of the emerald ash borer: a matter of international concern. *Newsletter of the Michigan Entomological Society* 58(3–4): 35.
- Haack, R. A., E. Jendek, H. Liu, K. R. Marchant, T. R. Petrice, T. M. Poland, and H. Ye. 2002. The emerald ash borer: a new exotic pest in North America. *Newsletter of the Michigan Entomological Society* 47(3–4): 1–5.
- Harris, M. K. 1975. Allopatric resistance: searching for sources of insect resistance for use in agriculture. *Environmental Entomology* 4: 661–669.
- Herms, D. A. and D. G. McCullough. 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annual Review of Entomology* 59: 13–30.
- Hill, A. L., J. G. A. Whitehill, S. O. Opiyo, P. L. Phelan, and P. Bonello. 2012. Nutritional attributes of ash (*Fraxinus* spp.) outer bark and phloem and their relationship to resistance against the emerald ash borer. *Tree Physiology* 32: 1522–1532.
- Jennings, D. E., P. B. Taylor, and J. J. Duan. 2014. The mating and oviposition behavior of the invasive emerald ash borer (*Agrilus planipennis*), with reference to the influence of host tree condition. *Journal of Pest Science* 87: 71–78.
- Kashian, D. M. and J. A. Witter. 2011. Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. *Forest Ecology and Management* 261: 480–488.
- Klooster, W. S., D. A. Herms, K. S. Knight, C. P. Herms, D. G. McCullough, A. S. Smith, K. J. K. Gandhi, and J. Cardina. 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). *Biological*



- Invasions* 16: 859–873. DOI: 10.1007/s10530-013-0543-7.
- Knight, K. S., D. A. Herms, R. Plumb, E. Sawyer, D. Spalink, E. Pisarczyk, B. Wiggin, R. Kappler, E. Ziegler, and K. Menard. 2012. Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*), pp.143–152. *In*: Snieszko, R. A., A. D. Yanchuk, J. T. Kliejunas, K. M. Palmieri, J. M. Alexander, and S. J. Frankel (tech. coords.). *Proceedings of the 4<sup>th</sup> International Workshop on Genetics of Host-Parasite Interactions in Forestry*. General Technical Report PSW-GTR-240. Pacific Southwest Research Station, Forest Service, USDA. Albany, California. 372 pp.
- 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*). *Biological Invasions* 15: 371–383.
- Koch, J. L., D. W. Carey, K. S. Knight, T. Poland, D. A. Herms, and M. E. Mason. 2012. Breeding strategies for the development of emerald ash borer-resistant North American ash, pp. 235–239. *In*: Snieszko, R. A., A. D. Yanchuk, J. T. Kliejunas, K. M. Palmieri, J. M. Alexander, and S. J. Frankel (tech. coords.). *Proceedings of the 4<sup>th</sup> International Workshop on Genetics of Host-Parasite Interactions in Forestry*. General Technical Report PSW-GTR-240. Pacific Southwest Research Station, Forest Service, USDA. Albany, California. 372 pp.
- Liu, H. P., L. S. Bauer, R. T. Gao, T. H. Zhao, T. R. Petrice, and R. A. Haack. 2003. Exploratory survey for the emerald ash borer, *Agrilus planipennis* (Coleoptera : Buprestidae), and its natural enemies in China. *Great Lakes Entomologist* 36: 191–204.
- Liu, H., L. S. Bauer, D. L. Miller, T. Zhao, R. Gao, L. Song, Q. Luan, R. Jin, and C. Gao. 2007. Seasonal abundance of *Agrilus planipennis* (Coleoptera: Buprestidae) and its natural enemies *Oobius agrili* (Hymenoptera: Encyrtidae) and *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) in China. *Biological Control* 42: 61–71.
- Marshall, J. M., E. L. Smith, and R. Mech. 2013. Estimates of *Agrilus planipennis* infestation rates and potential survival of ash. *American Midland Naturalist* 169: 179–193.
- Matson, P. A. and F. P. Hain. 1985. Host conifer defense strategies: a hypothesis, pp. 33–42. *In*: Safranyik, L. (ed.). *The Role of the Host in the Population Dynamics of Forest Insects*. Proceedings of the IUFRO Conference, 4-7 Sept, 1983, Banff, Alberta, Canada. Canadian Forest Service. & USDA Forest Service.
- McCullough, D. G., T. M. Poland, A. C. Anulewicz, and D. Cappaert. 2009. Emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) attraction to stressed or baited ash trees. *Environmental Entomology* 38: 1668–1679.
- Muilenburg, V. L. and D. A. Herms. 2012. A review of bronze birch borer (*Agrilus anxius*, Coleoptera: Buprestidae) life history, ecology, and management. *Environmental Entomology* 41: 1372–1385.
- Nielsen, D. G., V. L. Muilenburg, and D. A. Herms. 2011. Interspecific variation in resistance of Asian, European, and North American birches (*Betula* spp.) to bronze birch borer (Coleoptera: Buprestidae). *Environmental Entomology* 40: 648–653.
- Orlova-Bienkowskaja, M. J. 2014. Ashes in Europe are in danger: the invasive range of *Agrilus planipennis* in European Russia is expanding. *Biological Invasions* 16: 1345–1349.
- Painter, R. H. 1958. Resistance of plants to insects. *Annual Review of Entomology* 3: 267–290.
- Pureswaran, D. S. and T. M. Poland. 2009. Host selection and feeding preferences of *Agrilus planipennis* (Coleoptera: Buprestidae) on ash (*Fraxinus* spp.). *Environmental Entomology* 39: 757–765.
- Rajarapu, S. P. and O. Mittapalli. 2013. Glutathione-S-transferase profiles in the emerald ash borer, *Agrilus planipennis*. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 165: 66–72.
- Rajarapu, S. P., P. Mamidala, D. A. Herms, P. Bonello, and O. Mittapalli. 2011. Antioxidant genes of the emerald ash borer (*Agrilus planipennis*): gene characterization and expression profiles. *Journal of Insect Physiology* 57: 819–824.
- Raupp, M. J., P. M. Shrewsbury, and D. A. Herms. 2010. Ecology of herbivorous arthropods in urban

- landscapes. *Annual Review of Entomology* 55: 19–38.
- Rebek, E. J., D. A. Herms, and D. R. Smitley. 2008. Interspecific variation in resistance to emerald ash borer (Coleoptera: Buprestidae) among North American and Asian ash (*Fraxinus* spp.). *Environmental Entomology* 37: 242–246.
- Rigsby, C. M., V. Muilenburg, T. Tarpey, D. A. Herms, and D. Cipollini. 2014. Oviposition preferences of *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) for different ash species support the Mother Knows Best Hypothesis. *Annals of the Entomological Society of America* 107: 773–781.
- Rivera-Vega, L., P. Mamidala, J. L. Koch, M. E. Mason, and O. Mittapalli. 2012. Evaluation of reference genes for expression studies in ash (*Fraxinus* spp.). *Plant Molecular Biology Reports* 30: 242–245.
- Rodriguez-Saona, C., T. M. Poland, J. R. Miller, L. L. Stelinski, G. G. Grant, P. de Groot, L. Buchan, and L. MacDonald. 2006. Behavioral and electrophysiological responses of the emerald ash borer, *Agrilus planipennis*, to induced volatiles of Manchurian ash, *Fraxinus mandshurica*. *Chemoecology* 16: 75–86.
- Smith, A. 2006. Effects of community structure on forest susceptibility and response to the emerald ash borer invasion of the Huron River Watershed in southeastern Michigan. M.S. Thesis, Ohio State University, Columbus, Ohio, USA.
- Smith, A., D. A. Herms, R. P. Long, and K. J. K. Gandhi. 2015. Community composition and structure had no effect on forest susceptibility to invasion by emerald ash borer (*Agrilus planipennis*). *Canadian Entomologist*. (In press)
- Tanis, S. R. and D. G. McCullough. 2012. Differential persistence of blue ash and white ash following emerald ash borer invasion. *Canadian Journal of Forest Research* 42: 1542–1550.
- Tluczek, A. R., D. G. McCullough, and T. M. Poland. 2011. Influence of host stress on emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) adult density, development, and distribution in *Fraxinus pennsylvanica* trees. *Environmental Entomology* 40: 357–366.
- Wallander, E. 2001. Evolution of wind-pollination in *Fraxinus* (Oleaceae) – an ecophylogenetic approach. Ph.D. Dissertation. Göteborg University, Göteborg, Sweden.
- Wang, X. Y., Z. Q. Yang, J. R. Gould, Y. N. Zhang, G. J. Liu, and E. S. Liu. 2010. The biology and ecology of the emerald ash borer, *Agrilus planipennis*, in China. *Journal of Insect Science* 10: 128: doi: 10.1673/031.010.12801.
- Wei, X., R. Reardon, Y. Wu, and J.-H. Sun. 2004. Emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), in China: a review and distribution survey. *Acta Entomologica Sinica* 47: 679–685.
- Wei, X., Y. Wu, R. Reardon, T. H. Sun, M. Lu, and J.-H. Sun. 2007. Biology and damage traits of emerald ash borer (*Agrilus planipennis* Fairmaire) in China. *Insect Science* 14: 367–373.
- Whitehill, J. G. A., A. Popova-Butler, K. B. Green-Church, J. L. Koch, D. A. Herms, and P. Bonello. 2011. Interspecific proteomic comparisons reveal ash phloem genes potentially involved in constitutive resistance to the emerald ash borer. *PLoS ONE* 6(9): e24863 doi: 10.1371/journal.pone.0024863.
- Whitehill, J. G. A., S. O. Opiyo, J. L. Koch, D. A. Herms, D. F. Cipollini, and P. Bonello. 2012. Interspecific comparison of constitutive ash phloem phenolic chemistry reveals compounds unique to Manchurian ash, a species resistant to emerald ash borer. *Journal of Chemical Ecology* 38: 499–511.
- Wiseman, B. R. 1985. Types and mechanisms of host plant resistance to insect attack. *Insect Science and Application* 6: 239–242.