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Caterina Villari

Justin G.A. Whitehill

Don Cipollini

Wright State University - Main Campus, don.cipollini@wright.edu

Daniel A. Herms

Pierluigi Bonello

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## MECHANISMS OF ASH RESISTANCE TO EMERALD ASH BORER: PROGRESS AND GAPS

**Caterina Villari<sup>1</sup>, Justin G.A. Whitehill<sup>1,2</sup>, Don F. Cipollini<sup>3</sup>, Daniel A. Herms<sup>4</sup>  
and Pierluigi Bonello<sup>1</sup>**

<sup>1</sup>Department of Plant Pathology, The Ohio State University, 2021 Coffey Road,  
Columbus, OH 43210, USA villari.2@osu.edu

<sup>2</sup>Michael Smith Laboratories, The University of British Columbia, 301-2185 East Mall,  
Vancouver, BC V6T 1Z4, Canada

<sup>3</sup>Department of Biological Sciences and Environmental Sciences, Wright State University,  
3640 Colonel Glenn Highway, Dayton, OH 45435, USA

<sup>4</sup>Department of Entomology, The Ohio State University, Ohio Agricultural Research and Development  
Center, 1680 Madison Ave., Wooster, Ohio 44691, USA

### ABSTRACT

The emerald ash borer (EAB) invasion of North America has caused widespread mortality of native ash, and is threatening the native ash resources. As a consequence of its devastating impact, EAB has caught the attention of the scientific community, and several studies have focused on different aspects of the biology and behavior of this pest, including its interaction with host defenses. Here we present a review of the published literature on mechanisms of ash resistance to EAB, the understanding of which, despite starting from a *tabula rasa*, has achieved significant progress in the last few years.

The native North American species white, green and black ash, which did not coevolve with *Agrilus planipennis*, are highly susceptible to the beetle. In contrast, Asian ash species, such as Manchurian ash, which share a coevolutionary history with EAB, are more resistant, and appear to be susceptible only when stressed.

Recently it has been shown that resistant Manchurian ash is less preferred as a host for oviposition compared to susceptible North American species, which confirms the importance of antixenosis mechanisms in interspecific variation of ash resistance to EAB. Decreased performance of EAB larvae on Manchurian ash compared to black ash confirms that antibiosis mechanisms are also important, and studies published to date suggest that its constitutive bark defense system plays a major role, including higher constitutive levels of lignans, a faster browning reaction, higher expression of four putative defensive proteins, and higher levels of the amino acid proline and the monoamine tyramine. Larval feeding induces the accumulation of the lignan pinosresinol A, which suggests that induced responses may also be involved. However, no biochemical responses of Manchurian ash to exogenous application of methyl jasmonate (MeJA) (a key defense phytohormone) were detected in a recent study. Drought stress increases susceptibility of Manchurian ash to EAB, but has no effect on its bark phenolic content. This suggests that phenolics are perhaps not as significant in the intraspecific variation of resistance resulting from stress as previously hypothesized, although this could also depend on how quickly and strongly phenolic compounds of healthy Manchurian ash re-

spond to browning reactions and enzymes relative to those of drought stress trees.

In contrast, white and green ash, which have no evolutionary history with EAB, have been shown to become more resistant after induction with MeJA. This phenotypic variation has been mainly associated with increased concentrations of verbascoside, which was confirmed to have a detrimental impact on EAB larvae *in vitro*. Accumulation of lignin and higher trypsin inhibitor activity were associated with this phenotype as well, and proxies of these traits were also found to have a detrimental impact on EAB larvae *in vitro*. This suggests that white and green ash possess the genetic potential for inducible resistance. However, both species experience very high mortality in the field, suggesting that they are ultimately unable to mount an effective resistance response against EAB. Timing of induction might perhaps be a crucial factor in the phenotypic outcome.

Black ash, despite being phylogenetically closely related to resistant Manchurian ash, is highly susceptible to EAB. Its phenolic profile is highly similar to that of Manchurian ash, but its browning reaction is not as strong, suggesting that phenolics may not be as strongly oxidized when consumed. Application of MeJA also induced increased resistance of black ash to EAB, and this response was associated with higher activity of trypsin inhibitors.

Lastly, blue ash, which is more phylogenetically distantly related to the other North American species tested, as well as to Manchurian ash, had a distinct bark phenolic profile that was particularly rich in the hydroxycoumarin esculin, which might in part explain the higher EAB resistance of this species relative to other North American ash species evaluated to date.