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Assessment of the 'Gasaway' source of resistance to eastern filbert blight in New Jersey

Megan Muehlbauer[a], John M. Capik[a], Thomas J. Molnar[a,*], Shawn A. Mehlenbacher[b]

[a] Department of Plant Biology, Foran Hall, 59 Dudley Road, Rutgers University, New Brunswick, NJ, 08901, United States
[b] Department of Horticulture, Oregon State University, 4017 Ag and Life Sciences Bldg., Corvallis, OR, 97331, United States

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ABSTRACT

The disease eastern filbert blight (EFB), caused by *Anisogramma anomala*, severely limits hazelnut (*Corylus avellana*) production in North America. In the 1970s, 'Gasaway', a late-flowering pollenizer, was found to be resistant to EFB in the Pacific northwestern U.S., and to transmit its resistance in a predictable Mendelian pattern. Its subsequent use in breeding at Oregon State University led to the release of a number of EFB-resistant cultivars, including Jefferson, Yamhill, Dorris, Wepster, and McDonald, which are now being widely planted across the Willamette Valley of Oregon. However, some cultivars carrying the 'Gasaway' *R*-gene develop EFB in New Jersey. Thus, the utility of this resistance source for breeding plants adapted to the eastern U.S has not been fully evaluated. In this study, we examined the EFB response of seedlings from 31 different full-sib progenies expected to segregate for the 'Gasaway' *R*-gene. Trees were exposed to the disease over at least 5 years and evaluated on a scale of 0 to 5 (0 = resistant, 5 = highly susceptible). In general, we found the number of seedlings free of EFB (class 0) to be less than expected based on prior work in Oregon, but resistant individuals were identified in each progeny, indicating the presence of heritable resistance. When disease response classes 0, 1, and 2 were combined (resistant through highly tolerant) and considered as "resistant", the expected ratio of resistant to susceptible trees was recovered, signifying that the single dominant allele alone continues to provide a predictable level of at least tolerance. Modifying genes/factors appear to play a role in the final disease response of the individual seedling. It is thus hypothesized that some cultivars selected as resistant in Oregon that develop cankers in New Jersey may lack the necessary modifying genetic factors for full protection in the east. Until these modifying genes are elucidated, long-term field evaluation remains necessary to identify selections that carry the 'Gasaway' *R*-gene and express a high level of resistance to EFB in the eastern U.S.

1. Introduction

European hazelnut (*Corylus avellana*) ranks fifth in world tree nut production behind cashew (*Anacardium occidentale*), almond (*Prunus dulcis*), walnut (*Juglans regia*), and chestnut (*Castanea* sp.). Turkey produces approximately 60% of the world's hazelnut crop (736,973 t in 2014), followed by Italy (≈10%), the Republic of Georgia (≈ 5%), and the U.S. (≈ 5%), with Azerbaijan, China, Iran, and Spain making up the remaining production (Food and Agriculture Organization of the United Nations, 2017). Ninety-nine percent of U.S. production comes from the Willamette Valley of Oregon.

The lack of commercial hazelnut production in the eastern U.S. is primarily due to the disease eastern filbert blight (EFB), caused by the fungus *Anisogramma anomala* (Thompson et al., 1996). This pathogen is native to eastern North America where it is found on the wild American hazelnut, *C. americana*, on which it causes only limited damage (Capik and Molnar, 2012; Fuller, 1908; Weschcke, 1954). However, EFB is devastating to most plants of *C. avellana*, causing large, perennial stem cankers, branch die-back, and tree death several years after exposure (Johnson and Pinkerton, 2002). The pathogen was originally restricted to regions east of the Rocky Mountains, allowing commercial hazelnut production to thrive in the mild climate of the Pacific northwestern U.S. (PNW) for nearly 100 years (Thompson et al., 1996). Unfortunately, *A. anomala* was discovered in southwestern Washington in the 1960s. Soon after, the introduced pathogen caused mass orchard loss as control measures had not yet been developed and the standard cultivars were highly susceptible (Davison and Davidson, 1973; Gottwald and Cameron, 1980).

Today, EFB has spread throughout the Willamette Valley of Oregon. Its management adds considerable expense for fungicide sprays, scouting for cankers, and yearly pruning of infected wood. Developing and utilizing EFB-resistant cultivars and pollenizers is considered to be

* Corresponding author.
E-mail address: thomas.molnar@rutgers.edu (T.J. Molnar).

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the most cost-effective means of control (Johnson et al., 1996; Julian et al., 2008, 2009; Thompson et al., 1996). While early efforts to breed for EFB resistance involved interspecific hybridization (Molnar et al., 2005), the first EFB-resistant European hazelnut identified was 'Gasaway', a late-blooming, grower-selected pollinizer from Battle Ground, WA (Cameron, 1976; Thompson et al., 1996). Mehlenbacher et al. (1991) showed that 'Gasaway' resistance is conferred by a dominant allele at a single locus, and that in crosses of susceptible with resistant selections, resistance is transmitted to the offspring in a ratio of one resistant to one susceptible. The same 1:1 ratio was observed in subsequent studies (Coyne et al., 1998; Osterbauer et al., 1997). Further, random amplified polymorphic DNA (RAPD) markers linked to resistance have been identified (Mehlenbacher et al., 2004) and mapped to linkage group 6 (Mehlenbacher et al., 2006). To date, 'Gasaway' has been widely used in the Oregon State University (OSU) hazelnut breeding program, leading to the development of the EFB-resistant cultivars Santiam (Mehlenbacher et al., 2007), Yamhill (Mehlenbacher et al., 2009), Jefferson (Mehlenbacher et al., 2011), Dorris (Mehlenbacher et al., 2013), Wepster (Mehlenbacher et al., 2014), and McDonald (Mehlenbacher et al., 2016), along with a series of pollenizers. With the planting of these cultivars carrying the Gasaway *R*-gene (mostly Jefferson), the Oregon industry has expanded ~12,000 ha over the past eight years (S. Mehlenbacher, personal communication).

Since EFB in the PNW is believed to be from a single point introduction (Pinkerton et al., 1998), it has been assumed that the isolates of the pathogen found there share a common lineage and represent limited genetic diversity compared to those found across its native range. Recent work using microsatellite markers for *A. anomala* (Cai et al., 2013; Muehlbauer, 2017) substantiates this claim. Fortunately, Oregon's strict quarantine on the movement of *Corylus* plant material from east of the Rocky Mountains has been in effect for many decades (Barss, 1930). Of biggest concern would be the introduction of new isolates that hold the ability to overcome resistance from 'Gasaway' and other sources currently being used in the OSU breeding program (Chen et al., 2005, 2007; Colburn et al., 2015; Lunde et al., 2000; Molnar and Capik, 2012; Sathuvalli et al., 2010, 2011a, 2011b). A new, more virulent introduction could have significant economic effects, especially considering that the thousands of hectares of recently-planted orchards are protected only by the 'Gasaway' *R*-gene.

The narrow diversity of isolates present in the PNW also has implications for the potential use of cultivars selected as resistant in Oregon for planting in other regions of the U.S. and Canada where they may be challenged with a wider diversity of *A. anomala* isolates. This second scenario was first evaluated by Molnar et al. (2010a), where 'Gasaway' and some of its offspring, as well as a number of other potential sources of resistance, were inoculated in the greenhouse with isolates collected from different regions across the U.S. The study showed apparent differences between the isolates, with those from Michigan and New Jersey capable of infecting plants carrying the 'Gasaway' gene. The isolate from Michigan stood out as it was able to infect more individual trees from other sources of resistance than the other isolates, further suggesting that differences in virulence exist among isolates.

A similar finding was made using field grown trees in New Jersey, where after 8 years of natural exposure, trees of 'Gasaway' and its offspring VR20-11 developed EFB (Molnar et al., 2010b). This work was later expanded to include a wider range of cultivars, selections, and species (Capik and Molnar, 2012), which showed clear differences in EFB responses between Oregon and New Jersey, especially with respect to the 'Gasaway' *R*-gene. However, cultivars with 'Gasaway' resistance showed a range of responses, with some ('Zimmerman' and 'Santiam'), displaying no cankers after nearly 10 years of exposure, whereas others (VR20-11 and 'Jefferson') developed a considerable amount of EFB. The number of cankers per tree (proportion of diseased wood) and average size of the cankers also differed. It should be noted, however, that the infected trees with 'Gasaway' resistance, in general, remained much more tolerant to EFB (had a lower proportion of disease wood) than the susceptible control 'Barcelona' and tolerant control 'Tonda di Giffoni' (Capik and Molnar, 2012).

Based on these results, it was clear that further work was needed to examine the utility of 'Gasaway' resistance for regions outside of the PNW. The objective of this study is to assess the wider utility of the 'Gasaway' source of resistance in New Jersey by evaluating the disease response of seedlings representing dozens of full-sib families segregating for the *R*-gene under high disease pressure.

2. Materials and methods

2.1. Background of plant materials evaluated

A total of 1319 plants representing 31 full-sib progenies was evaluated. Thirty were the result of controlled hybridizations made at OSU from 2004 to 2009, and one was from a cross made at Rutgers University. The number of seedlings in each progeny ranged from 10 to 93 (mean 43). Of the 31 progenies, 24 were from crosses of a susceptible selection with a breeding selection or cultivar known to carry the Gasaway *R*-gene in a heterozygous state. The remaining seven progenies were from crosses in which both parents were resistant (in the heterozygous state). Based on previous work in Oregon, it was expected that seedlings in the 24 progenies would segregate in a ratio of one resistant to one susceptible (Mehlenbacher et al., 1991, 2004; Osterbauer et al., 1997), and that the other 7 progenies were expected to segregate in a ratio of three resistant to one susceptible. Condensed pedigrees of each progeny are shown (Tables 1 and 2) and full breeding histories are found in Supplemental Table 1. Eight of the progenies were previously discussed by Molnar et al. (2014).

2.2. Preparation of plant materials

Seeds derived from the controlled crosses described in Section 2.1 were collected in mid-to-late August of each year and kept in cold storage until October. They were then stratified in moist peat moss at 4 °C in polyethylene bags until early March of the following year. Stratified seeds were brought to the greenhouse (24 °C day/18 °C night with 16-h daylength) and planted in wooden planting boxes (61 × 91 × 15 cm) holding a peat-based medium (ProMix BX; Premier Horticulture, Quebec, Canada). The resulting seedlings were transplanted after 4–6 weeks into 3.7 L pots (Rootmaker, Huntsville, AL), filled with ProMix BX, top-dressed with 5 g of slow-release fertilizer (Osmocote Plus 15N-3.9P-10K with micronutrients, 5 to 6 months; The Scotts Co., Marysville, Ohio), and watered regularly. Plants were removed from the greenhouse in early July for outdoor acclimation under shade cloth (40% shade) until field planting in late September or October. Typical tree spacing was ~1.0 m in-row by ~3.5 m between rows. Individual progenies were planted in blocks at the Rutgers University Horticultural Farm 1 and Horticultural Farm 3 in New Brunswick, NJ. Herbicidal weed control, irrigation, and annual applications of fertilizer were provided as needed, but no fungicides were applied. The seedling trees were allowed to grow naturally with multiple stems.

2.3. Disease exposure, evaluations, and statistical analysis

The seedling trees were exposed to EFB through natural spread from nearby, heavily infected hazelnut breeding plots. Direct field inoculations were also conducted, where stems from local hazelnut plants infected with EFB were gathered, cut into 10–15 cm pieces, and stored in polyethylene bags at −20 °C until used. In the spring (typically early April), the infected stems were tied into the upper canopy of each seedling (Molnar et al., 2007). Trees were annually rated using a 0–5 scale developed by Pinkerton et al. (1992), where 0 = no visible EFB, 1 = only a single canker, 2 = multiple cankers on the same branch, 3 = multiple branches with cankers, 4 = over 50% of stems have