Eastern Filbert Blight Susceptibility of American × European Hazelnut Progenies

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Abstract. Eastern filbert blight (EFB), caused by *Anisogramma anomala*, is a devastating disease of *Corylus avellana*, the European hazelnut of commerce, and is considered the primary limiting factor of production in eastern North America. Conversely, *C. americana*, the wild American hazelnut, is generally highly tolerant of EFB, although it lacks many horticultural attributes necessary for commercial nut production. Hybrids of *C. americana* and *C. avellana* combine the EFB resistance of the wild species with the improved nut quality of the European species. However, inheritance of EFB resistance from *C. americana* remains unclear with existing hybrids derived from a very limited selection of parents. To investigate this topic, *C. americana* and advanced-generation *C. americana* × *C. avellana* hybrids were crossed with susceptible *C. avellana* and the resulting seedlings exposed to EFB through field inoculations and natural disease spread. In the winter after their fifth growing season, plants were rated for the presence of EFB using an index of 0 (no disease) through 5 (all stems containing cankers). The three progeny related to *C. americana* ‘Rush’ segregated for resistance in a ratio of one resistant to one susceptible, suggesting the presence of a single dominant *R* gene. A wide array of disease responses was observed for the other progenies with some expressing little EFB resistance or tolerance and others showing a distribution of disease phenotypes typical of control by multiple genes. Overall, the results indicate that both qualitative and quantitative resistance is present in *C. americana*. They also suggest that the choice of *C. americana* parent as well as the *C. avellana* parent will play a significant role in obtaining useful levels of EFB resistance in hybrid offspring, although the degree of disease expression in the parents may not be a useful predictor of progeny performance. Thus, more research is needed to understand inheritance of resistance, especially in advanced-generation backcrosses to susceptible *C. avellana*.

Hazelnuts (*Corylus avellana*) are a major tree nut crop ranking fifth in world production behind cashews (*Anacardium occidentale*), almonds (*Prunus dulcis*), walnuts (*Juglans regia*), and chestnuts (*Castanea* sp.). The top hazelnut-producing country in the world is Turkey, which produces ≈70% of the world’s crop (888,328 t in 2010). Turkey is followed by Italy (≈15%) and the United States (≈5%) (Food and Agriculture Organization of the United Nations, 2012), where production occurs primarily in the Willamette Valley of Oregon. Cultivated forms of *C. avellana*, of which several hundred have been described, produce the largest and highest

quality nuts of the genus. Recent taxonomic revisions suggest that *Corylus* holds 11 to 13 polymorphic species placed in four subsections (Erdogan and Mehlenbacher, 2000a, 2000b; Mehlenbacher, 1991; Thompson et al., 1996).

Although current regions of commercial hazelnut production have mild, Mediterranean-like climates, attempts have been made since colonial times to produce hazelnuts in the eastern United States with little recorded success. It was eventually understood that the fungal disease eastern filbert blight (EFB), caused by *Anisogramma anomala*, an obligate biotrophic ascomycete in the order Diaporthales, was the main limiting factor in this region (Fuller, 1908; Halsted, 1892; Johnson and Pinkerton, 2002; Thompson et al., 1996). Eastern filbert blight is found naturally occurring on the wild American hazelnut, *C. americana*, which is native to a wide swath of eastern North America, from Maine in the northeast to Minnesota and southern Manitoba in the northwest, extending south to northern Florida, and westward as far as eastern Oklahoma (Drumke, 1964; Gleason and Cronquist, 1998). Although EFB typically results in inconsequential damage to *C. americana* (Capik and Molnar, 2012; Fuller, 1908; Weschcke, 1954), in *C. avellana*,

the disease causes perennial cankers, branch dieback, and eventually death of most plants (Johnson and Pinkerton, 2002). Previously, EFB was only found east of the Rocky Mountains. Unfortunately, in the 1960s, it was inadvertently spread west and can now be found throughout the Willamette Valley, where its control measures add considerable expense to commercial-scale hazelnut production (Davison and Davidson, 1973; Johnson et al., 1996; Julian et al., 2008, 2009).

In comparison with cultivated forms of *C. avellana*, *C. americana* produces very small nuts (typically under 1.5 cm in diameter) with thick shells as well as fleshy husks (involucres) that tightly clasp the nuts. This tight involucre creates an impediment to harvesting because nuts do not fall freely to the ground at maturity. Furthermore, their extensive production of basal sprouts (suckers) is detrimental to standard orchard management in the United States, where trees are maintained with single stems. Despite these limitations, positive traits such as EFB resistance, cold-hardiness, and stress tolerance exist in the species (Capik and Molnar, 2012; Mehlenbacher, 1991; Molnar, 2011a). It is also cross-compatible with *C. avellana* in both directions (Erdogan and Mehlenbacher, 2000b), allowing it to act as a donor of these traits in a genetic improvement program. Both *C. avellana* and *C. americana* exhibit sporophytic incompatibility (Erdogan and Mehlenbacher, 2001; Mehlenbacher, 1997).

Starting in the early 1900s, efforts were made to hybridize *C. americana* and *C. avellana* to develop better-adapted, EFB-resistant plants. The pioneer was J.F. Jones of Lancaster, PA, who in 1919 crossed the local Pennsylvania *C. americana* selection ‘Rush’ with several *C. avellana* cultivars including Barcelona, Cosford, Daviana, Italian Red, and DuChilly. His work was continued by C.A. Reed of the U.S. Department of Agriculture (USDA) at Beltsville, MD, and G.H. Slate of the New York Agricultural Experiment Station in Geneva, NY, both of whom used ‘Rush’ in their hybrid breeding programs (Crane et al., 1937; Reed, 1936; Slate, 1961). Additional hybrid breeding work was performed by S.A. Graham of Ithaca, NY, using seedlings of the ‘Rush’ hybrids. Graham also used *C. americana* ‘Winkler’ (from Iowa) in crosses with *C. avellana* in his breeding program (Graham, 1936; Slate, 1961, 1969).

Further breeding using ‘Winkler’ was conducted by Weschcke (1954) in River Falls, WI. ‘Winkler’, along with several wild selections from the surrounding area, was crossed with cold-hardy selections of *C. avellana*, although detailed parental records are not available. Germplasm from Weschcke’s program was later used at Badgersett Research Corporation, Canton, MN, which also included plant material related to ‘Rush’ and other wild *C. americana* and *C. cornuta* (beaked hazelnut) accessions (Rutter, 1987, 1991). Seedlings from Badgersett have been planted across many states in the upper Midwest region of the United States. Plants were purchased from Badgersett by the

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National Arbor Day Foundation (NADF), Nebraska City, NE, to establish their 9-acre orchard, from which many thousands of subsequent seedlings, also derived from open pollination, have been further distributed around the United States and Canada (Hammond, 2006; Molnar, 2011b).

Eastern filbert blight-resistant hybrids were successfully developed from this body of early work, as discussed in Capik and Molnar (2012), Chen et al. (2007), Coyne et al. (1998), Lunde et al. (2000), and Rutter (1991), and clones or seedlings from these early efforts are still available today. However, despite the development of these resistant plants, little has been documented on the inheritance and expression of EFB resistance in seedlings from interspecific cross of *C. americana* and *C. avellana*. In fact, it was reported that Weschcke (1970) and Graham (Slate, 1961, 1969) eventually lost much of their breeding material to EFB, which provides some insight into the complex nature of the system. Current efforts are complicated by the lack of genetic diversity used in past breeding. Sathuvalli and Mehlenbacher (2011) used simple sequence repeat marker analysis to characterize 67 *C. americana* × *C. avellana* hybrid hazelnut accessions held in the USDA Agricultural Research Service National Clonal Germplasm Repository, Oregon State University (OSU) (both in Corvallis, OR), and NADF collections. They discovered that nearly all of them grouped with plants related to ‘Rush’ or the ‘Winkler’/Weschcke hybrids. Furthermore, of the 23 hybrid accessions examined for response to EFB in New Jersey, only 13 remained free of signs or symptoms of EFB, and all of these traced back to the ‘Rush’ or ‘Winkler’/Weschcke hybrids (Capik and Molnar, 2012). Thus, the inheritance of EFB resistance in seedlings from crosses of *C. americana* and *C. avellana* remains unclear.

Besides the early hybrid breeding work described above, hazelnut breeding efforts to date have been focused primarily on improving nut and kernel characteristics and increasing yield of *Corylus avellana* grown in existing production regions (Thompson et al., 1996). The world’s largest hazelnut breeding program has been ongoing at OSU since the late 1960s (Mehlenbacher, 1994). With the introduction of *A. anomala* in the Willamette Valley, breeding for resistance to EFB became an additional objective of the OSU program. The early identification of *C. avellana* ‘Gasaway’, a cultivar transmitting a dominant gene for EFB resistance (Mehlenbacher et al., 1991), has supported the use of intraspecific hybridization as a breeding option, leading to the recent release of improved, EFB-resistant *C. avellana* cultivars (Mehlenbacher et al., 2007, 2009, 2011). Furthermore, a number of other additional *C. avellana* sources of EFB resistance have also been identified at OSU (Chen et al., 2005, 2007; Coyne et al., 1998; Lunde et al., 2000) that are being incorporated into intraspecific breeding efforts (S.A. Mehlenbacher, personal communication).

Table 1. Breeding histories of progeny examined for their response to eastern filbert blight (EFB) caused by *Anisogramma anomala* in New Jersey.

Progeny identification no. ^{z,y}	Pedigree ^{x,w,v}
Rutgers 01-Adel-1 ^u	WBT-11 × <i>C. avellana</i> ‘Syrena’ (PI 617237, CCOR 669.001) WBT-11 = Open-pollinated (OP) Badgersett <i>C. americana</i> × <i>C. avellana</i> seedling
Rutgers 03006	WBT-06 × <i>C. avellana</i> ‘Hall’s Giant’ (PI 557027, CCOR 16.001) WBT-06 = OP Badgersett <i>C. americana</i> × <i>C. avellana</i> seedling
Rutgers 03007	WBT-05 × <i>C. avellana</i> ‘Rote Zeller’ (PI 271280, CCOR 13.001) WBT-05 = OP Badgersett <i>C. americana</i> × <i>C. avellana</i> seedling
Rutgers 03008	WBT-13 × <i>C. avellana</i> ‘Rote Zeller’ WBT-13 = OP Badgersett <i>C. americana</i> × <i>C. avellana</i> seedling
Rutgers 03009	WBT-12 × <i>C. avellana</i> ‘Rote Zeller’ WBT-12 = OP Badgersett <i>C. americana</i> × <i>C. avellana</i> seedling
Rutgers 03010	WBT-11 × <i>C. avellana</i> ‘Rote Zeller’ WBT-11 = OP Badgersett <i>C. americana</i> × <i>C. avellana</i> seedling
Rutgers 05011	H3I2R05P05 × <i>C. avellana</i> ‘Contorta’ (PI 557049, CCOR 50.001) H3I2R05P05 = WBT-11 × <i>C. avellana</i> ‘Syrena’
Rutgers 05013	H3I2R05P52 × <i>C. avellana</i> ‘Contorta’ H3I2R05P52 = WBT-11 × <i>C. avellana</i> ‘Syrena’
OSU 00061 ^u	Yoder #5 [†] (PI 641155, CCOR 853.001) × <i>C. avellana</i> OSU 612.015 Yoder #5 = <i>C. avellana</i> × <i>C. americana</i> hybrid from R. Yoder, Smithville, OH OSU 612.015 = OSU 336.036 × OSU 313.078 OSU 336.036 = ‘Tombul Ghiaghli’ (PI 304634, CCOR 55.001) × ‘Willamette’ (PI 557234, CCOR 500.001) OSU 313.078 = OSU 23.017 × ‘Tonda Gentile delle Langhe’ (PI 557035, CCOR 31.001) OSU 23.017 = ‘Barcelona’ (PI 557037, CCOR 36.001) × ‘Extra Ghiaghli’
OSU 04027	OSU 527.070 × <i>C. avellana</i> OSU 786.091 OSU 527.070 = NYF-45 (PI 557339, CCOR 102.001) × OSU <i>C. avellana</i> mix 1989 NYF-45 = <i>C. americana</i> ‘Snyder’ (from Geneva, NY) × NY 485 (PI 557082, CCOR 192.001) NY 485 = <i>C. americana</i> ‘Rush’ (PI 557022, CCOR 386.001) × <i>C. avellana</i> ‘DuChilly’ (PI 557099, CCOR 232.001) OSU 786.091 = OSU 256.005 × OSU 439.063 OSU 256.005 = OSU 54.046 (Giresun, Turkey) × OSU 17.083 OSU 17.083 = ‘Barcelona’ × ‘Camponica’ (PI 296204, CCOR 40.001) OSU 439.063 = ‘Ribet’ (PI 557055, CCOR 82.001) × ‘Willamette’
OSU 05063	OSU 401.006 (PI 617253, CCOR 686.001) (<i>C. americana</i> PA) × <i>C. avellana</i> pollen mix 2005 [†]
OSU 05064	OSU 405.047 (<i>C. americana</i> MN) × <i>C. avellana</i> pollen mix 2005
OSU 06048	OSU 401.016 (<i>C. americana</i> PA) × <i>C. avellana</i> pollen mix 2006 [†]
OSU 06051	OSU 405.088 (<i>C. americana</i> PA) × <i>C. avellana</i> pollen mix 2006
OSU 06052	OSU 531.027 (<i>C. americana</i> IA) × <i>C. avellana</i> pollen mix 2006
OSU 06053	OSU 532.025 (PI 617246, CCOR 679.001) (<i>C. americana</i> WV) × <i>C. avellana</i> pollen mix 2006
OSU 06060	<i>C. avellana</i> OSU 753.054 × OSU 533.029 [†] OSU 533.029 = <i>C. americana</i> hybrid seedling selection from C. Farris, Lansing, MI OSU 753.054 = ‘Iannusa Ricinante’ (PI 557183, CCOR 368.001) × OSU 384.014 OSU 384.014 = ‘Casina’ (PI 557033, CCOR 28.001) × OSU 55.129 OSU 55.129 = ‘Tonda Gentile delle Langhe’ × ‘Extra Ghiaghli’

[†]Rutgers University, New Brunswick, NJ; Oregon State University (OSU), Corvallis, OR; Badgersett Research Corporation, Canton, MN.

^zThe first two numbers of the progeny identification number designate the year the controlled cross was made.

^yIn all progenies, the female parent is a *C. americana* or advanced-generation *C. americana* × *C. avellana* hybrid and the male parent is an EFB-susceptible *C. avellana*, except for OSU 06060 in which the male parent is the hybrid accession. Of the *C. americana* (or hybrid) parents, all were found to be EFB-resistant in New Jersey or Oregon except for OSU 532.025, which was found to be susceptible in Capik and Molnar (2012). The EFB responses of OSU 401.016 and OSU 405.088 are unknown.

^wWBT numbered accessions correspond to EFB-resistant seedling selection made at Rutgers University originating from open-pollinated hybrid hazelnut seedlings purchased from Badgersett Research Corporation in 1996.

^vFor the OSU breeding selections (i.e., OSU 401.006), the three digits preceding the decimal represent the row number and the three digits after the decimal represent the plant number within the row, planted at the OSU Smith Horticultural Research Farm, Corvallis, OR.

^uProgenies Rutgers 01-Adel-1 and OSU 00061 were previously discussed in Molnar et al. (2009).

^tTo ensure compatibility in the crosses without knowing the incompatibility (S) alleles of the *C. americana* accessions, the *C. avellana* pollen mixtures used were comprised of three OSU EFB-susceptible breeding selections, each with different allele combinations. The pollen mixture for 2005 consisted of one-third each of the following breeding selections (S alleles are listed with the dominant allele underlined): OSU 540.130-1 22, OSU 675.028-2 8, and OSU 810.083-5 19.

^sOSU *C. avellana* pollen mix for 2006 consisted of one-third each of OSU 713.068-3 10, OSU 743.109-4 23, and 856.064-1 2.

^rThe relationship of ‘Yoder #5’ and OSU 533.029 with *C. americana* ‘Rush’ was resolved using simple sequence repeat markers in Sathuvalli and Mehlenbacher (2011).

Today, interest in developing hazelnuts as a commercial crop for regions outside of Oregon is rising (Braun et al., 2009, 2011; Hybrid Hazelnut Consortium, 2012; Molnar, 2011b; Olsen, 2011; Upper Midwest Hazelnut Development Initiative, 2012). In these regions, especially the Midwest and Upper Midwest, hybrid hazelnuts will be important not only for their resistance to EFB, but also their ability to tolerate cold temperatures. Hybrid plants adapted to these regions have been identified that are both EFB-resistant and high-yielding (Capik and Molnar, 2012; Hammond, 2006; Rutter, 1987). However, their nut size and kernel characteristics are generally poor compared with cultivars of *C. avellana* (Molnar, unpublished data; Xu and Hanna, 2010). Consequently, further breeding work is necessary to combine the cold-hardiness and EFB resistance from *C. americana* with the excellent nut and kernel quality of *C. avellana*. The lack of knowledge of inheritance of EFB resistance in crosses of *C. americana* with susceptible *C. avellana* makes reaching this breeding goal very challenging.

To gain a better understanding of the inheritance of EFB resistance from *C. americana*, 17 controlled crosses were made using pollen of susceptible *C. avellana* with resistant *C. americana* and advanced-generation hybrids. The seedlings were planted in the field in New Jersey. The plants were evaluated for their response to the disease after five years.

Materials and Methods

Plant material and culture. The seedling progenies were derived from controlled hybridizations made at Rutgers University, New Brunswick, NJ, and OSU in 2001 through 2006 following the protocol described by Mehlenbacher (1994). Pedigrees of the progenies are shown in Table 1. In general, each progeny resulted from crossing a *C. americana* or EFB-resistant advanced-generation *C. americana* × *C. avellana* hybrid accession with a known EFB-susceptible *C. avellana*. We place the progenies into three groups based on the origin of the resistant parent. The first group (*Corylus americana* × *C. avellana* F₁ progeny) consists of six crosses using *C. americana* accessions held in the OSU germplasm collection. These plants were selected by S.A. Mehlenbacher from a much larger population of wild hazelnuts collected from around the United States and southern Canada as a result of their improved nut characteristics and more consistent yields (Sathuvalli and Mehlenbacher, 2011; S.A. Mehlenbacher, personal communication). They were crossed (two in 2005 and four in 2006) with a pollen mixture collected from three EFB-susceptible *C. avellana* accessions (a different mixture each year), each having different incompatibility (S) alleles to ensure that the mixtures included at least one compatible pollen in all crosses (S alleles of the *C. americana* parents are not known). Identification of the S alleles of

selected hybrids will allow determination of the *C. avellana* parent. It should be noted that the EFB responses of the *C. americana* selections used were not known at the time the crosses were made. Since then, four of the six were assessed by Capik and Molnar (2012) and only OSU 532.025 from West Virginia was found to be susceptible (average proportion of diseased wood was 0.42, equivalent to rating between 3 and 4). Three showed no signs or symptoms of EFB, whereas the EFB responses of OSU 401.016 and OSU 405.088 are not yet known.

In the second group (Badgersett-related progeny), the EFB-resistant parents were selected at Rutgers University from a population of seedlings purchased from Badgersett Research Corporation in 1996. The hybrid accessions used as female parents (designated WBT based on field location at the Rutgers University Adelphia Research and Extension Farm, Adelphia, NJ) were chosen based on their complete resistance to EFB in New Jersey and their apparent high nut yields under low-maintenance conditions. Although the plants are considered to be of interspecific origin (advanced-generation *C. americana* × *C. avellana* hybrids) (Rutter, 1987), they originated from open-pollinated seed and the exact contribution of each species is not known. Based on their morphological characteristics (growth habit, leaf shape, husk type, and nut size and shape), the plants appear very similar to *C. americana*.

The third group (*C. americana* ‘Rush’-related progeny) consists of EFB-resistant

hybrid accessions selected at OSU and believed to be descendants of *C. americana* ‘Rush’ based on their pedigrees or microsatellite marker data (Sathuvalli and Mehlenbacher, 2011).

Hybrid seeds resulting from the crosses were harvested in August of each year and placed in cold storage until undergoing moist-chilling at 4 °C from October to March. Seedlings were germinated in wooden flats (61 × 91 × 15 cm) containing a peat-based planting medium (Promix BX; Premier Horticulture, Rivière-du-Loup, Quebec, Canada) in a greenhouse maintained at 24/18 °C (day/night) with 16-h daylengths. After 4 to 6 weeks, seedlings were transplanted into 3.7-L containers using the same planting medium. Each seedling was top-dressed with 5 g of slow-release fertilizer (Osmocote Plus 15N-3.9P-10K with micronutrients, five to six months; The Scotts Co., Marysville, OH) and watered as needed. Plants remained in the greenhouse until they were moved outside in July under 40% shade cloth. Trees were field-planted in October of the year of germination at either the Rutgers Fruit Research and Extension Center, Cream Ridge, NJ, or the Rutgers Vegetable Research and Extension Farm, North Brunswick, NJ. Trees were planted in blocks by progeny with the progenies organized in a completely randomized design at a spacing of ≈1.0 m in the row by 3.5 m between the rows. Irrigation, chemical weed control, and fertilizer were applied as needed, but there were no applications of fungicides or pesticides.

Table 2. Results of hybrid *Corylus* progenies exposed to *Anisogramma anomala*, the causal agent of eastern filbert blight (EFB), in New Jersey.

Progeny ^z identification no.	Yr planted	Total no. of plants	Disease rating ^{y,x}						
			Progeny mean ^w	0	1	2	3	4	5
<i>Corylus americana</i> × <i>C. avellana</i> F ₁ progeny									
OSU 05063 (PA)	2006	14	1.9 c	4	1	4	2	3	0
OSU 05064 (MN)	2006	21	4.3 ab	0	1	1	3	2	14
OSU 06048 (PA)	2007	19	2.5 c	4	1	3	5	4	2
OSU 06051 (PA)	2007	49	3.7 b	3	0	6	10	10	20
OSU 06052 (IA)	2007	38	4.6 ab	0	0	0	3	11	24
OSU 06053 (WV)	2007	48	3.9 ab	0	2	5	7	16	18
Badgersett-related progeny									
Rutgers 01-Adel-1 ^v	2002	118	2.7 c	17	3	13	58	22	5
Rutgers 03006	2004	48	4.7 ab	0	0	0	0	15	33
Rutgers 03007	2004	82	4.8 a	1	0	1	0	7	73
Rutgers 03008	2004	50	4.8 a	0	0	0	2	5	43
Rutgers 03009	2004	49	5.0 a	0	0	0	0	1	48
Rutgers 03010	2004	49	4.1 ab	1	0	4	7	13	24
Rutgers 05011	2006	21	4.9 a	0	0	0	0	3	18
Rutgers 05013	2006	74	4.5 ab	0	2	2	6	14	50
<i>C. americana</i> ‘Rush’-related progeny									
OSU 00061 ^v	2002	50	2.5 c	24	0	0	0	4	22
OSU 04027	2005	117	1.9 c	60	0	8	12	14	23
OSU 06060	2007	56	2.6 c	22	0	4	7	1	22

^zBadgersett Research Corporation, Canton, MN; Rutgers University, New Brunswick, NJ; Oregon State University (OSU), Corvallis, OR; The first two numbers of the progeny identification number designate the year the controlled cross was made.

^yEvaluations were made in the dormant season five years after planting.

^xResponses were recorded as follows: 0 = no detectable EFB, 1 = single canker, 2 = multiple cankers on single branch, 3 = multiple branches with cankers, 4 = greater than 50% of the branches with cankers, and 5 = all branches containing cankers, excluding basal sprouts. The total number of plants observed in each disease category (0 through 5) for each progeny is listed in each column below the disease rating category.

^wProgeny means followed by a different letter in the column are considered significantly different ($P < 0.05$) based on a Tukey-Kramer test using the TUKEY option of PROC GLM in SAS (Version 9.2; SAS Institute, Cary, NC).

^vResults of progeny were previously reported in Molnar et al. (2009).

Exposure to eastern filbert blight. Plants were exposed to EFB through natural spread from adjacent breeding nurseries holding hundreds of infected hazelnut plants, as well as through annual field inoculations, which consisted of tying infected hazelnut stems into the canopies of each tree in early April at budbreak (Molnar et al., 2007). The infected stems were collected from the Rutgers Fruit Research and Extension Center and the Rutgers Vegetable Research and Extension Farm. Disease pressure increased as the study progressed and EFB spread among the susceptible plants in the trials.

Evaluation of disease response. Trees were assessed according to an index developed by Pinkerton et al. (1992): 0 = no detectable EFB, 1 = single canker, 2 = multiple cankers on a single branch, 3 = multiple branches with cankers, 4 = greater than 50% of branches have cankers, and 5 = all branches containing cankers, except for basal sprouts. For a more accurate comparison of disease responses between progenies planted in different years, ratings in the winter after the fifth growing season were used. At that time, three previous seasons of canker development could be visualized. In the author's experience (Capik and Molnar, 2012; Molnar et al., 2007, 2009), this length of time is sufficient to both assess a plant's longer-term response to the disease and to ensure that escapes are minimized.

The number of seedlings in each disease category for each progeny was tabulated (Table 2). The ratings of the individual trees were used to calculate mean disease ratings for each progeny, which were then separated with the Tukey-Kramer test using the TUKEY option of PROC GLM in SAS (Version 9.2; SAS Institute, Cary, NC). To improve visualization and compare disease responses among progenies within each group, the disease ratings for each progeny were normalized to show the proportion of plants (of the total number) that fell into each of the six disease categories (0 to 5) (Figs. 1 to 3).

Results and Discussion

Disease ratings of the progeny, including progeny means, are presented (Table 2) and discussed for the three groups described in the "Materials and Methods." As a point of reference, we consider trees rating 0 to be resistant and those rating 1 or 2 to be highly tolerant. In our experience, trees rating 1 or 2 do not develop large enough infections over the long term to impede normal growth or cropping. Trees rating 3 are regarded as tolerant, where it is unlikely tree death would occur, although some branches will die leading to a reduction in yield over time. Plants rating 4 or 5 are regarded as susceptible. They typically have reduced yields within two years of exposure and completely die from EFB within five to seven years.

Corylus americana × C. avellana F₁ progeny. Results showed a spectrum of disease responses for the group of *C. americana* × *C. avellana* progeny with some being mostly susceptible and others showing a range of

Fig. 1. Normalized histograms of *C. americana* × *C. avellana* F₁ progeny showing the proportion of plants out of the total (100%) in each disease category (0 through 5). Responses were recorded as follows: 0 = no detectable eastern filbert blight, 1 = single canker, 2 = multiple cankers on single branch, 3 = multiple branches with cankers, 4 = greater than 50% of the branches with cankers, and 5 = all branches containing cankers, excluding basal sprouts.

useful resistance and tolerance. The different *C. americana* parents of progeny OSU 05063, OSU 06048, and OSU 06051 are derived from a wild seed collection made in Pennsylvania by G. Evans and selected by S.A. Mehlenbacher at OSU. These progeny stand out, because they were the only ones of this group holding any plants rating 0, and their mean disease responses were lower than the other three in the group, although only OSU 05063 and OSU 06048 were shown to be significantly different from the other three progenies in the group ($P < 0.05$) (Table 2; Fig. 1). Both of these progeny, in particular, showed a continuum of EFB responses with several trees rating 2 or 3. The other three progeny [OSU 05064 (Minnesota), OSU 06052 (Iowa), and OSU 06053 (West Virginia)] each held only a small proportion of tolerant plants with the majority of the seedlings being quite susceptible.

An interesting development becomes apparent when comparing the mean disease rating of progeny OSU 06053 (3.9) with that of OSU 05064 (4.3) and OSU 06052 (4.6). What makes these ratings significant is the fact that the parent of OSU 06053 (OSU 532.025) was found to be highly susceptible to EFB in New Jersey, whereas the other two parents were shown to be resistant (Capik and

Molnar, 2012). This finding indicates that the disease phenotype of the *C. americana* parent may not be a good predictor of progeny performance, which could add an additional challenge to developing an understanding of the inheritance of EFB resistance in hybrid hazelnuts.

Badgersett-related progeny. The Badgersett-related progenies, besides Rutgers 01-Adel-1, expressed a very low level of tolerance with most seedlings rating 4 or 5 (Table 2; Fig. 2). This poor level of tolerance in the progeny was surprising, because the female parents remain resistant to EFB in our trials in New Jersey under high disease pressure. The complex nature of inheritance of EFB resistance in this hybrid cross is apparent when comparing the results of progeny Rutgers 03010 and Rutgers 01-Adel-1. Both share the same female parent (WBT-11) but were crossed with *C. avellana* 'Rote Zeller' and 'Syrena', respectively. However, although 'Syrena' and 'Rote Zeller' were both previously found to be very susceptible to EFB in New Jersey (data not shown), their progenies differed considerably in their disease responses. Although the different planting dates may add a confounding effect, the substantial differences observed between the two progenies suggest that the choice of

Fig. 2. Normalized histograms of Badgersett-related progeny showing the proportion of plants out of the total (100%) in each disease category (0 through 5). Responses were recorded as follows: 0 = no detectable eastern filbert blight, 1 = single canker, 2 = multiple cankers on single branch, 3 = multiple branches with cankers, 4 = greater than 50% of the branches with cankers, and 5 = all branches containing cankers, excluding basal sprouts.

susceptible *C. avellana* parent also plays a role in disease response of the progeny in this interspecific cross. It should be mentioned that, although Rutgers 03010 held a higher frequency of resistant and tolerant plants, the means were not significantly different compared with the other Badgersett progenies from 2003.

Further challenges in using *C. americana* in breeding for EFB resistance were uncovered in the progenies Rutgers 05011 and Rutgers 05013. The female parents in these crosses were H3I2R05P51 (rated 2) and

H3I2R05P05 (rated 0), respectively, and the male parent for both was *C. avellana* 'Contorta' (also known as 'Harry Lauder's Walking Stick'). 'Contorta' is highly susceptible to EFB. The female plants were superior seedling selections from the progeny Rutgers 01-Adel-1 and used with the expectation of finding some resistant or tolerant offspring. Surprisingly, mean disease responses in progenies 05011 (4.9) and 05013 (4.5) were much higher than in Rutgers 01-Adel-1.

Corylus americana 'Rush'-related progeny. The three progeny believed to derive from

C. americana 'Rush' segregated for resistance in a ratio of one resistant to one susceptible seedling, which was supported by chi-squared analysis (Table 3). These results strongly suggest that resistance is controlled by a single locus, that resistance is dominant, and that the resistant parent is heterozygous. A similar finding for seedlings related to *C. americana* 'Rush' has been recently determined at OSU (S.A. Mehlenbacher, personal communication), further supporting this premise. Interestingly, at the initiation of this study, we were only certain that OSU 04027 was related to 'Rush' based on NYF-45 in its pedigree (Table 1). The EFB-resistant parents of progenies OSU 00061 and OSU 06060 were thought to be unrelated, although little was known of their origin. The EFB-resistant parent of OSU 00061 is 'Yoder #5', which is an interspecific hybrid seedling selection with unknown parentage from R. Yoder of Smithville, OH, obtained by S.A. Mehlenbacher in the late 1980s (S.A. Mehlenbacher, personal communication). Lunde et al. (2000) subjected 'Yoder #5' to inoculation with *A. anomala* at OSU and all trees proved completely resistant to EFB. No connection with 'Rush' was known at that time. Furthermore, the EFB-resistant parent of progeny OSU 06060 is OSU 533.029, which is an apparent hybrid seedling selection made by S.A. Mehlenbacher from seeds obtained from C. Farris in Lansing, MI.

Recently, the microsatellite marker study of Sathuvalli and Mehlenbacher (2011) placed 'Yoder #5' and OSU 533.029 in the same group as 'Rush' and selected hybrid offspring of 'Rush'. This finding is not surprising, because both R. Yoder and C. Farris were active members of the Northern Nut Growers Association, a group that shares seeds and scion wood on a regular basis. Based on our results here and the findings of Sathuvalli and Mehlenbacher (2011), and supported by the rarity of major genes for EFB resistance previously found in *Corylus* (Capik and Molnar, 2012), there is a high likelihood that progenies OSU 00061 and OSU 06060 segregated for a dominant *R* gene from 'Rush'.

Conclusions

Our results, which are among the first reported on this topic, indicate that both quantitative and qualitative resistance to EFB is present in *C. americana*. However, the results from each progeny varied considerably with a surprisingly low level of resistance transmitted in a number of cases. It was also observed that the phenotype of the wild (or interspecific hybrid) parent could not be used to accurately predict the performance of its progeny. The progeny of the *C. americana* accessions from Pennsylvania, especially OSU 06053, expressed a significant level of EFB resistance and tolerance, whereas those from the other states were found to exhibit very little. Similarly, only one (WBT-11) of five EFB-resistant Badgersett-derived hybrids transmitted a

Fig. 3. Normalized histograms of 'Rush'-related progeny showing the proportion of plants out of the total (100%) in each disease category (0 through 5). Responses were recorded as follows: 0 = no detectable eastern filbert blight, 1 = single canker, 2 = multiple cankers on single branch, 3 = multiple branches with cankers, 4 = greater than 50% of the branches with cankers, and 5 = all branches containing cankers, excluding basal.

Table 3. Segregation for resistance to eastern filbert blight (EFB) in progenies related to *C. americana* 'Rush' and goodness of fit to 1:1 ratio of resistant to susceptible seedlings.

Progeny no.	Parents	Disease response (no. of trees)		χ^2	P
		Resistant ^a	Susceptible ^b		
OSU 00061	Yoder #5 × OSU 612.015	24	26	0.080	0.773
OSU 04027	OSU 527.070 × OSU 786.091	60	57	0.077	0.782
OSU 06060	OSU 753.054 × OSU 533.029	22	34	2.571	0.109
Pooled data		106	117	0.543	0.461

^aPlants considered resistant showed no signs or symptoms of EFB.

^bPlants considered susceptible ranged from multiple cankers on single branch to all branches containing cankers, excluding basal sprouts.

useful level of resistance. Disease ratings were also affected by the *C. avellana* parent of the cross. Further confounding our understanding of the system, resistant seedlings of WBT-11 were backcrossed to susceptible *C. avellana*, but almost no resistance or tolerance was found in the resulting progeny.

On a more positive note, results showed that the three progeny related to *C. americana* 'Rush' segregated for resistance in a ratio of one resistant to one susceptible, supporting the presence of a single dominant *R* gene. This simply inherited *R* gene may prove to be quite valuable for breeding, because plants related to 'Rush' have been observed growing in the East for decades and have remained free of cankers. No cankers have been observed after greenhouse inoculations using multiple isolates of *A. anomala* and long-term field studies at Rutgers University (Capik and Molnar, 2012; Molnar et al., 2010).

It is clear that more research is needed to elucidate the inheritance of EFB resistance in crosses of *C. americana* and *C. avellana*. Unfortunately, this need for more research presents an exigent scenario as a result of the difficulties of working with a perennial crop with a generation time of five to six years combined with a fungus with a long latent period, where the necessary test crosses and other genetic studies are typically not economically feasible. Deciphering the underlying mechanisms of resistance will require the screening of

a much wider diversity of *C. americana* for use as parents, including test crosses using a spectrum of *C. avellana* parents with well-characterized disease phenotypes. Work will also include the development of *F*₂ generations to assess the likelihood of recessive *R* genes. Developing *F*₂ generations is a challenge because a large number of the *F*₁ progeny die from EFB before reaching reproductive maturity in regions where *A. anomala* is endemic, although this can be overcome through the use of a fungicide spray schedule. Furthermore, the sporophytic self-incompatibility system of *Corylus* (Mehlenbacher, 1997) reduces our efficiency in developing *F*₂ generations because a significant proportion of the full-sib progenies will be incompatible and the compatible partners can only be resolved after the plants reach flowering age. Regardless, our results, although only based on a limited number of *C. americana* parents and limited number of seedlings, are some of the first documented, systematic assessments of this interspecific cross outside of the use of *C. americana* 'Rush' and 'Winkler', which themselves have only been reported on a superficial level. The demonstration of a wide variation in disease responses across the progenies, with clear and significant differences between some of the parents, along with the fact that disease phenotype of the parent was not a good predictor of progeny performance in the *F*₁ and backcross generations, provides insight into how to design future experiments

to understand and best use EFB resistance from *C. americana*.

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