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.

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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 (1991), and clones or seedlings from these.

The relationship of ‘Yoder #5’ and OSU 533.029 with C. americana was evaluated previously by Weschcke (1970). It was reported that Weschcke (1970) and Hammond. 1966 (Hammond et al. (2007)). 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 EBF became an additional objective of the OSU program. The early identification of C. avellana ‘Gasaway’, a cultivar transmitting a dominant gene for EBF resistance (Mehlenbacher et al., 1991), has supported the use of intraspecific hybridization as a breeding option, leading to the recent release of improved, EBF-resistant C. avellana cultivars (Mehlenbacher et al., 2007, 2009, 2011). Furthermore, a number of other additional C. avellana sources of EBF 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. | Pedigree no. | Progeny | Pedigree no. |
|--------------------------|-------------|--------|-------------|
| Rutgers 01-Adel-2 | WBT-11 = C. avellana ‘Syrena’ (PI 617237, CCOR 669.001) | WBT-11 = Open-pollinated (OP) Badgersett C. americana × C. avellana seedling | WBT-11 = C. avellana ‘Hall’s Giant’ (PI 557027, CCOR 16.001) |
| Rutgers 03006 | WBT-06 = C. avellana ‘Hall’s Giant’ (PI 557027, CCOR 16.001) | WBT-06 = OP Badgersett C. americana × C. avellana seedling | WBT-06 = OP Badgersett C. americana × C. avellana seedling |
| Rutgers 03007 | WBT-05 = C. avellana ‘Rote Zeller’ (PI 271280, CCOR 13.001) | WBT-05 = OP Badgersett C. americana × C. avellana seedling | WBT-05 = OP Badgersett C. americana × C. avellana seedling |
| Rutgers 03008 | WBT-13 = C. avellana ‘Rote Zeller’ | WBT-13 = OP Badgersett C. americana × C. avellana seedling | WBT-13 = OP Badgersett C. americana × C. avellana seedling |
| Rutgers 03009 | WBT-12 = C. avellana ‘Rote Zeller’ | WBT-12 = OP Badgersett C. americana × C. avellana seedling | WBT-12 = OP Badgersett C. americana × C. avellana seedling |
| Rutgers 03010 | WBT-11 = C. avellana ‘Rote Zeller’ | WBT-11 = OP Badgersett C. americana × C. avellana seedling | WBT-11 = OP Badgersett C. americana × C. avellana seedling |
| Rutgers 05011 | OSU 05064 = OSU 401.016 (PI 557082, CCOR 192.001) | OSU 05064 = ‘Syrena’ (from Geneva, NY) × NY 485 | OSU 05064 = ‘C. americana’ ‘Rush’ (PI 557022, CCOR 386.001) × C. avellana ‘DuChilly’ (PI 557099, CCOR 232.001) |
| Rutgers 05013 | OSU 05065 = OSU 401.016 (PI 557082, CCOR 192.001) | OSU 05065 = ‘Rote Zeller’ (PI 271280, CCOR 13.001) | OSU 05065 = ‘C. americana’ ‘Rush’ (PI 557022, CCOR 386.001) × C. avellana ‘DuChilly’ (PI 557099, CCOR 232.001) |

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

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

WBT numbered accessions correspond to EBF-resistant seedling selection made at Rutgers University originating from open-pollinated hybrid hazelnut seedlings purchased from Badgerset Research Corporation in 1996.

For 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.

*P*rogenies Rutgers 01-Adel-1 and OSU-0061 were previously discussed in Molnar et al. (2009).

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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 family location at the Rutgers University Adelphia Research and Extension Farm, Adelphia, NJ) were chosen based on their importance to the 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.

Materials and Methods

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

| Progeny identification no. | Yr planted | Total no. of plants | Disease rating a,b | Progeny mean c,d | 0 | 1 | 2 | 3 | 4 | 5 |
|----------------------------|------------|---------------------|-------------------|-----------------|---|---|---|---|---|---|
| Corylus americana × C. avellana F1; 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 | 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 | 2002 | 118 | 2.7 c | 17 | 3 | 13 | 58 | 22 | 5 |
| Rutgers 03006 | 2004 | 48 | 4.7 ab | 0 | 0 | 0 | 2 | 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 | 3 | 18 | 0 |
| Rutgers 05013 | 2006 | 74 | 4.5 ab | 0 | 2 | 2 | 6 | 14 | 50 |
| C. americana ‘Rush’-related progeny | | | | | | | | | | |
| OSU 00061 | 2002 | 50 | 2.5 c | 24 | 0 | 0 | 4 | 0 | 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 |

a-Badgersett 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.

b-Evaluations were made in the dormant season five years after planting.

c-Responses 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.

d-Progeny 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).

Table 2. Results of hybrid Corylus progenies exposed to Anisogramma anomala, the causal agent of eastern filbert blight (EFB), in New Jersey.
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* F$_1$ 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 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. Mehlhenbacher 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 (Minnesotan), 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
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 H312R05P51 (rated 2) and H312R05P05 (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
to understand and best use EFB resistance from C. americana.

**Literature Cited**

Braun, L.C., J.H. Gillman, E.E. Hoover, and M.P. Russelle. 2011. Nitrogen fertilization for new plantings of hybrid hazelnuts in the upper midwest of the United States of America. Can. J. Plant Sci. 91:773–782.

Braun, L.C., J.H. Gillman, and M.P. Russelle. 2009. Fertilizer nitrogen timing and uptake efficiency of hybrid hazelnuts in the upper midwest, USA. HortScience 44:1688–1693.

Capik, J.M. and T.J. Molnar. 2012. Assessment of host (Corylus sp.) resistance to eastern filbert blight in New Jersey. J. Amer. Soc. Hort. Sci. 137:157–172.

Chen, H., S.A. Mehlenbacher, and D.C. Smith. 2005. AFLP markers linked to eastern filbert blight resistance from OSU 408.040 hazelnut. J. Amer. Soc. Hort. Sci. 130:412–417.

Chen, H., S.A. Mehlenbacher, and D.C. Smith. 2007. Hazelnut accessions provide new sources of resistance to eastern filbert blight. HortScience 42:466–469.

Coyne, C.J., S.A. Mehlenbacher, and D.C. Smith. 1998. Sources of resistance to eastern filbert blight. J. Amer. Soc. Hort. Sci. 124:253–257.

Crane, H.L., C.A. Reed, and M.N. Wood. 1937. Nut breeding, p. 835–844. In: Hambidge, G. and E.S. Bressman (eds.). 1937 Yearbook of agriculture U.S. Govt. Printing Office, Washington, DC.

Davison, A.D. and R.M. Davidson. 1973. *Apioporthe* and *Monchecia* canker reported in western Washington. Plant Dis. Rptr. 57:522–523.

Drumke, J.S. 1964. A systematic survey of *Corylus* in North America. PhD diss., Univ. of Tenn., Knoxville, TN.

Erdogan, V. and S.A. Mehlenbacher. 2000a. Interspecific hybridization in hazelnut (*Corylus*). J. Amer. Soc. Hort. Sci. 125:489–497.

Erdogan, V. and S.A. Mehlenbacher. 2000b. Phylogenetic relationships of *Corylus* species (Betulaceae) based on nuclear ribosomal DNA ITS region and chloroplast *matK* gene sequences. Syst. Bot. 25:727–737.

Erdogan, V. and S.A. Mehlenbacher. 2001. Incompatibility in wild *Corylus* species. Acta Hort. 556:163–169.

Food and Agriculture Organization of the United Nations. 2012. Agricultural production, crops primary. FAO, Geneva, Switzerland. 20 Feb. 2012. <http://faostat.fao.org/site/567/default.aspx#ancor>.

Fuller, A.S. 1908. The nut culturist. Orange Judd, New York, NY.

Gleason, H.A. and A. Cronquist. 1998. Manual of vascular plants of Northeastern United States and adjacent Canada. The New York Botanical Gardens, Bronx, NY.

Graham, S.H. 1936. Notes on an experimental planting in central New York. Annu. Rpt. Northern Nut Growers Assn. 27:64–67.

Halsted, B.D. 1892. A serious filbert disease. New Jersey Agr. Expt. Sta. Annu. Rpt. 13:287–288.

Hobson, E. 2006. Identifying superior hybrid hazelnut plants in southeast Nebraska. MS thesis, Univ. Nebraska–Lincoln, Lincoln, NE.

Hybrid Hazelnut Consortium. 2012. Hybrid hazelnut consortium overview. 31 May 2012. <http://www.arborday.org/programs/hazelnuts/consortium/overview.cfm>.

Johnson, K.B. and J.N. Pinkerton. 2002. Eastern filbert blight, p. 44–46. In: Tevildate, B.L., T.J. Michailides, and J.W. Pscheidt (eds.).

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**Table 3. Segregation for resistance to eastern filbert blight (EFB) in progenies related to *C. americana***

| Progeny no. | Parents             | Disease response (no. of trees) | \( \chi^2 \) | \( P \) |
|-------------|---------------------|---------------------------------|-------------|-------|
| OSU 00601   | Yoder #5 × OSU 612.015 | 24                              | 0.080       | 0.773 |
| OSU 04027   | OSU 527.070 × OSU 786.091 | 60                              | 0.077       | 0.782 |
| OSU 06060   | OSU 753.054 × OSU 533.029 | 22                              | 2.571       | 0.109 |
| Pooled data |                     | 106                            | 0.543       | 0.461 |
