Eastern Filbert Blight Resistance in American and Interspecific Hybrid Hazelnuts

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ABSTRACT. Eastern filbert blight (EFB), caused by the fungus *Anisogramma anomala*, is a primary limitation to European hazelnut (*Corylus avellana*) cultivation in eastern North America. American hazelnut (*Corylus americana*) is the endemic host of *A. anomala* and, despite its tiny, thick-shelled nuts, is a potentially valuable source of EFB resistance and climatic adaptation. Interspecific hybrids (*Corylus americana* × *C. avellana*) have been explored for nearly a century as a means to combine EFB resistance with wider adaptability and larger nuts. Although significant progress was made in the past, the genetic diversity of the starting material was limited and additional improvements are needed for expansion of hazelnut (*Corylus* sp.) production outside of Oregon, where 99% of the U.S. crop is currently produced. Our objective was to determine if *C. americana* can be a donor of EFB resistance. We crossed 29 diverse EFB-resistant *C. americana* accessions to EFB-susceptible *C. avellana* selections (31 total progenies) to produce 2031 F₁ plants. In addition, new *C. americana* germplasm was procured from across the native range of the species. The new collection of 1335 plants from 122 seed lots represents 72 counties and 22 states. The interspecific hybrid progenies and a subset of the American collection (616 trees from 62 seed lots) were field planted and evaluated for EFB response following field inoculations and natural disease spread over seven growing seasons. EFB was rated on a scale of 0 (no EFB) to 5 (all stems containing cankers). Results showed that progeny means of the interspecific hybrids ranged from 0.96 to 4.72. Fourteen of the 31 progenies were composed of at least one-third EFB-free or highly tolerant offspring (i.e., ratings 0–2), transmitting a significant level of resistance/tolerance. Several corresponding *C. americana* accessions that imparted a greater degree of resistance to their hybrid offspring were also identified. In addition, results showed that 587 (95.3%) of the 616 *C. americana* plants evaluated remained completely free of EFB. These findings confirm reports that the species rarely expresses signs or symptoms of the disease and should be robustly studied and exploited in breeding.

Hazelnut (*Corylus* sp.) includes 13 polymorphic deciduous shrub and tree species that bear edible nuts (Bassil et al., 2013; Erdogan and Mehlenbacher, 2000a). The genus demonstrates wide morphological diversity and adaptability, with species inhabiting forests throughout the northern hemisphere (Mehlenbacher, 1991; Molnar, 2011). Current cultivation depends almost entirely on European hazelnut (*C. avellana*) and is restricted to Mediterranean-like climates that allow consistent yields. The scale of global hazelnut production closely mirrors that of pistachio (*Pistacia vera*) at ≈1 million tonnes of annual in-shell production (Food and Agriculture Organization of the United Nations, 2017), and its market is experiencing steady growth (Technavio, 2017). Production in the United States occurs pri-

marily in the Willamette Valley of Oregon [U.S. Department of Agriculture (USDA), 2018], which produces ≈5% of the global supply. There is considerable interest in expanding cultivation to other regions in the United States and Canada (Fischbach, 2017; Molnar and Capik, 2012a).

Climatic suitability and the broad presence of EFB limit the cultivation of European hazelnut in the eastern and midwestern United States (Thompson et al., 1996). The causal organism of EFB is *Anisogramma anomala*, an obligate biotrophic ascomycete that is endemic to eastern North America (Johnson and Pinkerton, 2002). In nature, *A. anomala* coexists with American hazelnut (*C. americana*), occasionally producing minor, inconsequential stem cankers (Capik and Molnar, 2012; Fuller, 1908; Weschcke, 1953). Conversely, infection of *C. avellana* results in severe, perennial stem cankers that lead to branch dieback, yield decline, and in many cases plant death (Johnson and Pinkerton, 2002). *C. americana* is native to much of North America east of the Rocky Mountains, extending from Maine to

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northern Florida in the east, over to its western boundary that extends from eastern Oklahoma to North Dakota and southern Manitoba (Drumke, 1964; Gleason and Cronquist, 1963). This extensive geography suggests that *C. americana* may represent a diverse source of resistance and tolerance to EFB, and moreover, a source of adaptation to a spectrum of soil types and climatic zones that nearly span the latitudinal range of the United States.

Thus, if systematically exploited for breeding interspecific hybrids, *C. americana* may enable the expansion of commercial hybrid hazelnut production to a wide portion of the eastern and midwestern United States (Molnar, 2011; Molnar et al., 2005). Unfortunately, the plant architecture and nuts of *C. americana* are not well-suited for commercial production and existing markets. The shrubby architecture and aggressive production of basal sprouts by *C. americana* also present challenges for maintaining the desired single-stemmed form found in modern European hazelnut orchards. Compared with those of *C. avellana* cultivars, the nuts of *C. americana* are very small and enclosed in thick, clasping involucre, which complicates harvest. Further, the shells tend to be very thick. Nevertheless, *C. americana* and *C. avellana* can be crossed in either direction, and the resulting hybrids are viable and fertile (Erdogan and Mehlenbacher, 2000b). Past breeders have noted the potential for continued improvement, with the recovery of most *C. avellana* traits in selected individuals of the first or second backcross generation following interspecific hybridization (Molnar, 2011; Molnar et al., 2018).

Attempts have been made to develop interspecific hybrids since the early 20th century (reviewed in Molnar, 2011; Molnar and Capik, 2012b). In 1919, J.F. Jones of Lancaster, PA, made the first reported *C. americana* × *C. avellana* F₁ hybrids using the wild selection ‘Rush’ as the *C. americana* parent crossed with a number of *C. avellana* cultivars. Compared with other *C. americana*, ‘Rush’ appeared to be better adapted and produced higher yields of larger nuts, and continued to be used as parent by C.A. Reed of the Bureau of Plant Industry, USDA in Beltsville, MD, and G.H. Slate of the New York State Agricultural Experiment Station in Geneva, NY. From 1928 to 1930, Reed and Slate each produced ≈2000 F₁ hybrids from crosses of ‘Rush’ as the female parent with pollen of several *C. avellana* cultivars, and then oversaw their long-term evaluation.

S.H. Graham of Ithaca, NY, also built on Jones’ work, evaluating seedlings derived from open-pollinated ‘Rush’ F₁ hybrids. In addition, Graham made controlled crosses with a wild *C. americana* selection from Iowa called ‘Winkler’. Unfortunately, much of Graham’s materials were eventually lost to EFB.

Throughout the 1930s and 1940s, Carl Weschcke of River Falls, WI, also used ‘Winkler’ to develop many interspecific hybrids. Over time, fatal EFB infections spread throughout most of Weschcke’s progenies and no cultivars were released, although there were some survivors (Weschcke, 1953, 1963). Later, seeds from select, EFB-resistant individuals that remained in Weschcke’s infected plantings were collected by Philip Rutter of Canton, MN, to begin a mass selection program. Rutter subsequently supplemented his population with other wild selections and improved hybrid germplasm, including plants derived from ‘Rush’. From this work, populations were developed that expressed EFB resistance, cold hardiness, and improved nut traits (Rutter, 1987). Seedlings

from this population have been disseminated widely throughout the upper midwest, where ≈130 growers have more than 30,000 shrubs in production (Demchik et al., 2011). The Arbor Day Foundation (ADF, Nebraska City, NE) established 5000 seedlings purchased from Rutter in 1996, and from this planting several consistently high-yielding, EFB-resistant selections have been identified (Capik and Molnar, 2012; Hammond, 2006). Additional clonal selections are under replicated evaluation across Wisconsin and Minnesota by the Upper Midwest Hazelnut Development Initiative (Braun et al., 2018).

Each of the aforementioned efforts identified EFB-resistant hybrids with improved commercial traits, and Oregon State University (OSU) and the USDA-Agriculture Research Service (ARS)-National Clonal Germplasm Repository (NCGR) in Corvallis, OR, have conserved a number of these selections for future use. However, although thousands of seedlings and several clonal selections have been sold and distributed by nurseries, none from this early work has supported commercial-scale planting to date. In addition, these interspecific hybrids were developed from a small number of parents and represent a relatively narrow genetic base. Sathuvalli and Mehlenbacher (2012) characterized 67 *C. americana* × *C. avellana* hybrids jointly held by the NCGR, OSU, and the ADF using microsatellite markers in comparison with a collection of 87 pure *C. americana*, and found nearly all of the hybrid accessions clustered with either ‘Rush’ or ‘Winkler’ and the Weschcke hybrid group. Although levels of diversity were similarly high in these interspecific hybrid groups and wild *C. americana*, the interspecific hybrids had fewer alleles at the microsatellite marker loci (Sathuvalli and Mehlenbacher, 2012). Moreover, these early reports presented few data on the inheritance of EFB resistance, but their records mention instances in which large seedling populations were almost entirely lost to EFB (Rutter, 1991; Slate, 1969). The absence of systematic studies and a poor understanding of the inheritance of EFB resistance from *C. americana* is a challenge for reaching breeding objectives, which expand beyond disease resistance and include kernel traits, yield, and climatic adaptation.

Several recent studies have begun to shed light on the inheritance of EFB resistance from *C. americana*. Molnar and Capik (2012b) reported that three ‘Rush’-related progenies segregated in a ratio of 1 resistant:1 susceptible, indicating a dominant allele at a single locus. Bhattarai et al. (2017a) confirmed this mode of inheritance from ‘Rush’ and the closely related hybrid ‘Yoder #5’, and placed the resistance locus on linkage group 7. Molnar and Capik (2012b) reported segregation data from biparental crosses between eight *C. americana* × *C. avellana* hybrids of Rutter origin and susceptible *C. avellana*. Little to no resistance or tolerance was recovered in seven of these progenies, which was surprising, as five of the hybrid parents had been completely resistant to EFB at the experimental site. In the eighth progeny, however, ≈50% of the seedlings were rated tolerant and 15% were free of disease. A similar response pattern was observed in three of the six progenies derived from wild *C. americana* crossed to susceptible *C. avellana*, whereas seedlings in the other three showed little tolerance (Molnar and Capik, 2012b). These studies and the results of past breeding efforts demonstrate that EFB resistance from *C. americana* can be accessed through interspecific hybridization. However, the species transmits resistance to its interspecific offspring variably, with both major and minor genes for resistance and tolerance likely

present in the germplasm pool. Furthermore, the disease response of the *C. americana* parent may not indicate its ability to transmit resistance or tolerance to its progeny.

The current collections of the USD-ARS-NCGR and OSU contain a total of ≈ 80 *C. americana* accessions. These accessions were derived primarily from wild seed procured by S.A. Mehlenbacher in the late 1980s with help from members of the Northern Nut Growers Association (NNGA). From among several hundred seedlings, selections were made based on geographic origin, nut characteristics, and a reduced tendency to biennial bearing. Based on genetic characterization of the collection using microsatellite markers, Sathuvalli and Mehlenbacher (2012) described these accessions as highly diverse and valuable as initial germplasm for breeding. However, given the extensive native range of *C. americana*, this collection does not represent the full extent of the genetic and trait diversity present within the species, and further collection is warranted.

The lack of understanding regarding the transmission of EFB resistance combined with poor nut quality and other negative production traits of *C. americana* complicates the process of developing hybrid cultivars that are competitive with *C. avellana* with respect to nut quality. Fortunately, intraspecific hybridization became a viable strategy for developing disease-resistant cultivars following the identification of EFB-resistant *C. avellana* ‘Gasaway’ in the 1970s, which was found to be heterozygous for a dominant allele at a single resistance locus (Mehlenbacher et al., 1991). Although ‘Gasaway’, an obsolete late-shedding pollenizer, has many horticultural deficiencies, it was subsequently used to develop several EFB-resistant cultivars (Santiam, Yamhill, Jefferson, Dorris, Wepster, and McDonald) (Mehlenbacher, 2018; Mehlenbacher et al., 2007, 2009, 2011, 2013, 2014, 2016). These cultivars have supported a landmark expansion of the Oregon hazelnut industry, which grew from 11,700 ha to greater than 31,000 ha from 2009 to 2018 (N.G. Wiman, personal communication).

Concerns over the long-term durability of a single source of resistance as well as potential pathogen diversity led breeders to concurrently assemble and screen vast germplasm collections for EFB response. Initial screens of collected germplasm identified additional sources of resistance (Chen et al., 2007; Coyne et al., 1998; Lunde et al., 2000), and linkage mapping confirmed monogenic resistance from multiple sources [e.g., ‘Ratoli’ and ‘Culplà’ from Spain, OSU 759.010 from Georgia, OSU 495.027 from Russia, OSU 408.040 from Minnesota, ‘Crvenje’ and ‘Uebov’ from Serbia (Bhattarai et al., 2017b; Chen et al., 2005; Colburn et al., 2015; Sathuvalli et al., 2011a, 2011b)]. Resistance was mapped to three different linkage groups (LGs), although most sources map to a cluster on LG 6 in the region near the ‘Gasaway’ *R* gene (Sathuvalli et al., 2014). These selections are now being used by OSU and Rutgers University in further breeding and gene pyramiding schemes in an attempt to improve the durability of resistance (Molnar et al., 2018; Sathuvalli et al., 2014).

Continued screening efforts by both OSU and Rutgers University have identified EFB-resistant *C. avellana* from Estonia, Latvia, Lithuania, Poland, Russia, Crimea, Georgia, Moldova, and Turkey (Capik and Molnar, 2012; Capik et al., 2013; Leadbetter et al., 2016; Molnar et al., 2007, 2018; Muehlbauer et al., 2014). The continued discovery of EFB resistance in *C. americana* is additive to the work previously completed for *C. avellana* and may expand, through interspecific hybridization, potential for enhanced climatic adaptability to the more severe summer and winter conditions of the midwest United States.

In this study, a diverse collection of 29 *C. americana* accessions were evaluated as donor parents of EFB resistance in interspecific hybridization with EFB-susceptible *C. avellana*. In addition, an extensive new *C. americana* germplasm collection was assembled to expand the genetic base of the material available for breeding. The F_1 hybrids and new *C. americana* plant materials were established in the field in New Jersey, exposed to high EFB pressure, and assessed for their response to disease after seven growing seasons.

Materials and Methods

Plant materials and culture

***C. AMERICANA* $\times$ *C. AVELLANA* F_1 PROGENIES.** Twenty-nine *C. americana* accessions were crossed with EFB-susceptible *C. avellana* to examine transmission of resistance to their F_1 offspring (Table 1). Crosses were made in 2009 to 2011 following methods described in Mehlenbacher (1994). Twelve interspecific crosses were made at Rutgers University and the remainder at OSU. A total of 2031 plants representing 31 different progenies were evaluated in the field. The *C. americana* parents originated from the seed collection made by S.A. Mehlenbacher (described earlier) and are held in the collections at OSU and the USDA-ARS-NCGR, with a subset of grafted trees held at Rutgers University. Twenty-two of the 29 *C. americana* parents were evaluated and rated free of disease in New Jersey [as noted in Table 1 (Capik and Molnar, 2012)], with the remaining parents only tested in Oregon, where they have shown no signs or symptoms of EFB (S.A. Mehlenbacher, unpublished data). The *C. avellana* parents were selected based on their known susceptibility to EFB and improved nut and kernel characteristics with the aim of producing F_1 offspring that would segregate for disease response as well as improved production traits. One *C. avellana* $\times$ *C. avellana* cross was included as a control (OSU 11041) and was expected to segregate for quantitative resistance/tolerance.

The resulting hybrid seeds were collected in mid-August of each year and kept in cold storage until October when they were placed in moist peatmoss and stratified at 4 °C until March of the following year. Seeds were germinated in the greenhouse (24/18 °C day/night with 16-h daylength) in wooden planting boxes (61 $\times$ 91 $\times$ 15 cm) containing a peat-based medium. The seedlings were transplanted after 6 weeks into 2.8-L containers using the same media and top-dressed with 5 g of 15N–3.9P–10K slow-release fertilizer with micronutrients [5 to 6 months (Osmocote Plus; ICL Specialty Fertilizers, Summerville, SC)]. Plants were moved outdoors in late May for acclimation under shade cloth (40% shade) until field planting in October of the same year. Tree spacing was ≈ 1.0 m within the row by ≈ 3.5 m between rows. Plants from each progeny were planted consecutively in rows at the Rutgers University Horticultural Farm 1 in New Brunswick, NJ, and the Cream Ridge Fruit Research and Extension Station, Cream Ridge, NJ. Weed control, irrigation, and fertilizer were provided as needed, but no chemical control of pests or diseases was applied. The seedling bushes were not pruned.

***C. AMERICANA* GERMPLASM.** A total of 1335 *C. americana* seedlings from 122 seed lots representing 22 states and 72 counties was procured. The collection effort was initiated and assembled through the help of partners, colleagues, and the interested public, especially members of NNGA and ADF (Molnar et al., 2018). Open-pollinated seed was obtained from many locations across the native range of the species and sent to Rutgers for germination and subsequent field planting. The

Table 1. Parentage of *Corylus americana* × *Corylus avellana* progeny rated for eastern filbert blight (EFB) disease in New Jersey.

Progeny no. ^z	Parentage ^{y,x}
OSU 09041	OSU 403.028 (<i>C. americana</i> Nebraska, PI 87145) × OSU Mix A 2009 ^w
OSU 09042	OSU 531.016 ^v (<i>C. americana</i> Michigan) × OSU Mix B 2009 ^w
OSU 09044	OSU 533.069 ^v (<i>C. americana</i> Pennsylvania) × OSU Mix B 2009
OSU 09045	OSU 557.075 ^v (<i>C. americana</i> Pennsylvania) × OSU Mix B 2009
OSU 09046	OSU 557.102 (<i>C. americana</i> Wisconsin) × OSU Mix B 2009
OSU 09047	OSU 557.125 ^v (<i>C. americana</i> Wisconsin) × OSU Mix A 2009
OSU 10052	OSU 405.038 ^v (<i>C. americana</i> New Jersey) × OSU Mix 2010 ^v
OSU 10058	<i>C. avellana</i> ‘Clark’ × OSU 400.033 ^v (<i>C. americana</i> Indiana) (CCOR 684.001, PI 617251)
OSU 10059	<i>C. avellana</i> ‘Clark’ × OSU 405.006 (<i>C. americana</i> Pennsylvania)
OSU 11041 ^u	OSU 1197.113 (<i>C. avellana</i>) × OSU 1155.009 (<i>C. avellana</i>)
OSU 11050	OSU 405.043 ^v (<i>C. americana</i> New Jersey) × OSU Mix 2011
OSU 11051	OSU 532.082 (<i>C. americana</i> Michigan) × OSU Mix 2011
OSU 11052	OSU 588.044 ^v (<i>C. americana</i> Illinois) × OSU Mix 2011
OSU 11053	CCOR 857 (<i>C. americana</i> Illinois) × OSU Mix 2011
OSU 11055	<i>C. avellana</i> ‘Clark’ × OSU 400.042 (<i>C. americana</i> Wisconsin)
OSU 11058	<i>C. avellana</i> ‘Clark’ × OSU 531.037 ^v (<i>C. americana</i> Wisconsin) (CCOR 676.001, PI 617243)
OSU 11059	<i>C. avellana</i> ‘Clark’ × OSU 531.043 ^v (<i>C. americana</i> North Dakota) (CCOR 677.001, PI 617244)
OSU 11060	<i>C. avellana</i> ‘Clark’ × OSU 532.048 (<i>C. americana</i> Kentucky) (CCOR 680.001, PI 617248)
OSU 11061	<i>C. avellana</i> ‘Clark’ × CCOR 59.001 ^v (<i>C. americana</i> Mississippi) (PI 433984)
OSU 11062	<i>C. avellana</i> ‘Clark’ × CCOR 847 (<i>C. americana</i> Illinois) (PI 641150)
Rutgers 11525	OSU 403.040 ^v (<i>C. americana</i> Nebraska) × <i>C. avellana</i> ‘Tonda di Giffoni’
Rutgers 11529	OSU 557.125 ^v (<i>C. americana</i> Wisconsin) × <i>C. avellana</i> ‘Tonda di Giffoni’
Rutgers 11530	OSU 533.069 ^v (<i>C. americana</i> Pennsylvania) × <i>C. avellana</i> ‘Tonda di Giffoni’
Rutgers 11533	OSU 366.060 ^v (<i>C. americana</i> Mississippi) (CCOR 59.002, PI 433984) × <i>C. avellana</i> ‘Tonda Gentile delle Langhe’ (PI 557035, CCOR 31.001)
Rutgers 11534	OSU 557.026 ^v (<i>C. americana</i> Virginia) × <i>C. avellana</i> ‘Tonda Gentile delle Langhe’
Rutgers 11535	OSU 531.027 ^v (<i>C. americana</i> Indiana) × <i>C. avellana</i> ‘Tonda Romana’
Rutgers 11540	OSU 557.122 ^v (<i>C. americana</i> Wisconsin) (CCOR 710.001, PI 617273) × <i>C. avellana</i> ‘Tonda di Giffoni’
Rutgers 11541	OSU 531.043 ^v (<i>C. americana</i> North Dakota) (CCOR 677.001, PI 617244) × <i>C. avellana</i> ‘Tonda di Giffoni’
Rutgers 11543	OSU 557.153 ^v (<i>C. americana</i> Wisconsin) (CCOR 713.001, PI 617276) × <i>C. avellana</i> ‘Tonda di Giffoni’
Rutgers 11545	CCOR 507.001 ^v (<i>C. americana</i> Minnesota) (PI 557023) × <i>C. avellana</i> ‘Tonda di Giffoni’
Rutgers 11547	OSU 532.076 ^v (<i>C. americana</i> Michigan) (CCOR 682.001, PI 617249) × <i>C. avellana</i> ‘Tonda di Giffoni’
Rutgers 11550	OSU 405.047 ^v (<i>C. americana</i> Minnesota) (CCOR 694.001, PI 617261) × <i>C. avellana</i> ‘Tonda di Giffoni’

^zOregon State University (OSU), Corvallis, OR; Rutgers University, New Brunswick, NJ; Controlled crosses were made in the year indicated by the first two digits of the progeny identification number.

^y(*C. americana* State) denotes the U.S. state in which seeds of the *C. americana* parent were collected.

^xThe OSU selection ID number (i.e., OSU 403.028) represents the location (row, tree) at the OSU Smith Horticulture Research Farm, Corvallis, OR; PI is the Plant Inventory number of the accession in the USDA-Agriculture Research Service-National Clonal Germplasm Repository (USDA-ARS-NCGR) collection; CCOR is local inventory number of the accession in the USDA-ARS-NCGR collection.

^w*C. avellana* pollen mixtures were composed of three OSU EFB-susceptible breeding selections to ensure compatibility with the *C. americana* accessions that at the time carried unknown (S) alleles. The 2009A pollen mixture consisted of one-third each of the following selections (S alleles are listed with the dominant allele underlined): ‘Sacajawea’ (1 22), OSU 786.091 (2 4), and OSU 806.051 (8 19). The 2009B pollen mixture consisted of one-third each of the following selections: OSU 1039.010 (15 21), OSU 1051.038 (2 14), and OSU 1033.068 (4 8). The 2010 pollen mixture consisted of one-third each of the following selections: OSU 995.042 (2 3), OSU 1156.105 (8 10) and OSU 1158.109 (22 25). The 2011 pollen mixture consisted of one-third each of the following selections: OSU 1156.105 (8 10), OSU 1213.038 (1 2), and OSU 1224.065 (12 22).

^v*C. americana* parents were rated as free of EFB in New Jersey (Capik and Molnar 2012). Other selections have not been tested in New Jersey but remain free of EFB in Oregon.

^uA pure *C. avellana* × *C. avellana* control segregating for quantitative resistance. OSU 1197.113 has quantitative resistance. OSU 1155.009 is susceptible.

collection locations closely reflect the native range of the species (Fig. 1). A subset of the *C. americana* collection that included 616 bushes from 62 seed lots was evaluated in this study. This subset included all bushes of the collection that had been under long-term disease pressure for 6 years or more and thus clearly expressed mature disease phenotypes. These were trees from seeds obtained before 2011, which were planted at the Cream Ridge Fruit Research and Extension Station in 2012 under conditions similar to those described previously for the

interspecific hybrid seedlings in rows adjacent to most of them, thus providing a direct basis for comparison.

Exposure to EFB

All interspecific hybrid seedlings and the subset of *C. americana* germplasm were exposed to EFB through field inoculations. Hazelnut stems harboring EFB stromata were tied into the canopy of every fifth tree in April at the time of leaf budbreak for the first 3 years following planting (Molnar et al., 2007). The hazelnut stems

Fig. 1. A geographic information systems map depicting the native distribution of *Corylus americana* and the distribution of the existing university and U.S. Department of Agriculture (USDA)–Agriculture Research Service–National Clonal Germplasm Repository collections. Herbarium records compiled from the USDA are shown in light green. Collection sites of the Upper Midwest Hazelnut Development Initiative (Demchik et al., 2018) are shown in yellow, from Oregon State University, and USDA (Sathuvalli and Mehlenbacher, 2012) are shown in green, and the Rutgers University collection is shown in red. The map demonstrates the additive nature of the new germplasm reported here.

used as inoculum were collected from infected trees growing in Rutgers University field plots. Disease pressure was also provided by natural spread from adjacent breeding nurseries and experimental plots harboring hundreds of infected plants. In addition, the susceptible seedlings within this planting added to the amount of inoculum as the study progressed.

Evaluation of disease response

Disease ratings followed the six-point rating index developed by Pinkerton et al. (1992): 0 = no visible EFB; 1 = a single canker; 2 = multiple cankers on a single branch; 3 = a tree with several cankered branches; 4 = greater than 50% of the tree's branches have cankers; and 5 = all branches contain cankers, except for the basal sprouts. Disease ratings were collected in Jan. 2017 and again in 2018 following the plants' sixth, seventh, or eighth growing season. Previous studies have demonstrated that under field inoculations, five growing seasons provide sufficient time to observe plant phenotypes while minimizing escapes (Capik and Molnar, 2012; Leadbetter et al., 2016; Molnar et al., 2007, 2009).

To contextualize the EFB ratings, rating 0 is considered complete resistance, and ratings 1 and 2 are considered highly

tolerant, as the canker growth does not typically cause abnormal tree growth or reduced nut production. Rating 3 is considered tolerant, with branch dieback and yield reduction over time. Ratings 4 and 5 are for susceptible individuals in which yield reduction occurs soon after cankering, and perennial spread of cankers leads to plant death in 5 to 7 years.

Disease response ratings were assigned to each seedling, and the means tabulated for each progeny (Table 1). The statistical significance of differences among progeny means were ascertained through a one-way analysis of variance using the AOV function in R 3.3.2 (R Core Team, 2014). A post hoc multiple mean comparison was then conducted using the Tukey-Kramer test and the HSD.test function. The disease class scores were presented in histograms indicating percentages of the total for each progeny to aid visualization and comparisons.

Results and Discussion

***C. AMERICANA* × *C. AVELLANA* F₁ PROGENIES.** Useful resistance and tolerance was transmitted to seedlings in most of the 31 progenies. Across the entire study, 24% of the offspring were

Twenty-seven progenies retained some level of resistance and/or tolerance, whereas four progenies were effectively lost to EFB (Table 2). Ratings of 0 and 3 were the most prevalent in these progenies, representing 26% and 33% of the seedlings, respectively, and a continuum of ratings from 0 to 5 was recorded in most progenies. On closer inspection, we noted

The first pattern is a continuous distribution, where a major intermediate peak was observed at a single rating within a more or less continuous distribution across the classes. The distribution reflected the “bell-shaped curve” typically observed for segregation of quantitative traits. Thirteen of the progenies exhibited a major peak at rating 3 or across ratings 3 and 4, suggesting that the respective *C. americana* parents carry quantitative (multigenic) resistance. The trait is partially recovered in the F₁ progeny in the form of tolerance (rating 3), which manifests itself as a high frequency of plants with intermediate phenotypes between the completely resistant *C. americana* and susceptible *C. avellana* parents. This pattern fits the previous descriptions of EFB on *C. americana* as an occasional occurrence of small cankers and general ability to abate perennial canker spread following infection (Capik and Molnar, 2012; Fuller, 1908; Weschcke, 1953). The disease class with the highest frequency varied in the progenies with continuous distributions. For eight progenies, the peak occurred exclusively at rating 3, whereas the remaining five progenies of this distribution type held similarly high frequencies of progeny

Interestingly, the choice of susceptible *C. avellana* parent appears to also influence the degree to which resistance is recovered, as previously observed by Molnar and Capik (2012b) and Muehlbauer et al. (2018). Here, the influence can be seen by comparing progenies OSU 09044 and Rutgers 11530 (Fig. 2), which both used the *C. americana* Pennsylvania OSU 533.069 as the pistillate parent. The male parents of OSU 09044, which displayed a major peak across ratings 3 and 4, come from a *C. avellana* pollen mix (Table 2). The male parent of Rutgers 11530, with a peak at rating 3, is *C. avellana* Tonda di Giffoni, a cultivar shown to be somewhat tolerant to EFB in prior studies in Oregon (i.e., equivalent to rating 3) and New Jersey (i.e., equivalent to rating 4) (Capik and Molnar, 2012; Mehlenbacher et al., 2000, 2001, 2008; Pinkerton

Table 2. Eastern filbert blight (EFB) disease ratings in *Corylus americana* × *Corylus avellana* progenies exposed to *Anisogramma anomala* in New Jersey. Individual shrubs were rated on a scale of 0 (no disease) to 5 (disease on all branches). Differences among progeny means were compared using a one-way analysis of variance followed by a post hoc multiple mean comparison using the Tukey-Kramer test.

Progeny no. ^z	Total plants (no.)	Progeny mean (0–5 scale)	Seedlings for each disease rating (no.) ^y					
			0	1	2	3	4	5
<i>Continuous distribution</i>								
OSU 09045	31	2.29 de ^x	3	7	4	13	3	1
Rutgers 11540 ^w	198	2.38 de	34	12	34	90	19	9
OSU 11059	50	2.58 def	8	5	10	12	7	8
Rutgers 11530 ^w	211	2.71 def	36	12	15	93	24	31
OSU 09046	61	2.84 defg	8	4	4	24	16	5
OSU 11051	47	3.00 efgh	4	2	1	24	15	1
Rutgers 11545 ^w	37	3.03 efgh	3	1	4	17	8	4
OSU 09044	41	3.05 efgh	3	1	7	13	14	3
OSU 11053	37	3.14 efgh	4	1	4	8	17	3
OSU 11062	34	3.21 fgh	4	0	1	10	18	1
Rutgers 11535	91	3.23 fgh	3	0	2	56	28	2
OSU 11055	42	3.26 fghi	6	1	2	5	23	5
OSU 11050	43	3.60 ghij	1	0	2	15	19	6
<i>Bimodal distribution</i>								
Rutgers 11547 ^w	26	0.96 a	16	1	3	6	0	0
Rutgers 11529 ^w	147	1.01 a	84	16	16	25	4	2
Rutgers 11541 ^w	121	1.04 a	69	8	16	27	0	1
OSU 09041	60	1.25 ab	32	5	3	16	4	0
Rutgers 11543 ^w	54	1.28 abc	29	3	6	12	2	2
Rutgers 11550 ^w	25	1.64 abcd	11	0	3	9	2	0
Rutgers 11525	124	2.04 bcd	34	12	22	37	9	10
Rutgers 11534 ^w	64	2.20 cde	19	0	5	31	7	2
OSU 10059	58	2.34 de	12	6	9	13	17	1
OSU 09047	57	2.37 de	13	4	7	19	10	4
OSU 11058	50	2.54 def	13	1	2	15	18	1
OSU 10058	56	2.63 def	16	1	4	9	19	7
OSU 09042	25	2.76 defg	6	1	0	8	6	4
OSU 10052	58	2.79 defg	14	1	3	9	27	4
<i>Low transmission of resistance</i>								
OSU 11052	49	3.90 hijk	0	0	0	13	28	8
OSU 11060	37	4.59 jk	0	0	0	0	15	22
Rutgers 11533	47	4.60 jk	0	0	0	2	15	30
OSU 11061	50	4.72 k	0	0	0	1	12	37
Pooled progeny	2,031	2.68	485	105	189	632	406	214
Pooled (%)			0.24	0.05	0.09	0.31	0.20	0.11
<i>C. avellana</i> × <i>C. avellana</i>								
OSU 11041 ^v	51	4.69 k	0	0	0	1	14	36

^zOregon State University (OSU), Corvallis, OR; Rutgers University (Rutgers), New Brunswick, NJ; Control crosses were made in the year indicated by the first two digits of the progeny identification number. Continuous refers to a distribution in which a major peak at a single intermediate disease class was most prominent within a more or less continuous distribution among the other classes. Bimodal refers to a distribution that exhibited both a high frequency of EFB-free and tolerant individuals with major peaks occurring at ratings 0 and 3.

^yDisease was rated in 2018 during the dormant season 6 to 8 years after field establishment and correspond to phenotypes as follows: 0 = no visible EFB, 1 = a single canker, 2 = multiple cankers on a single branch, 3 = multiple branches with cankers, 4 = more than 50% of branches have cankers, and 5 = all branches have cankers or the plant has died from EFB.

^xThe same letter following the progeny means indicates a lack of significant difference ($P < 0.05$).

^wProgenies with ‘Tonda di Giffoni’ as the pollen parent.

^vOSU 11041 is a control cross (OSU 1197.113 × OSU 1155.009) made in Oregon and expected to segregate for quantitative resistance from *C. avellana* based on its parentage.

et al., 1993). This comparison indicates that the *C. avellana* parent can contribute to the quantitative resistance and disease response of interspecific hybrids.

A bimodal distribution type was observed in 14 progenies, which exhibited both a high frequency of EFB-free (rating 0) and tolerant individuals with a major peak at rating 3. Compiled

histograms of these progenies are displayed (Fig. 4). Tolerance (ratings 1–3) was obtained at frequencies similar to the previously described progenies exhibiting continuous distributions (Table 2). However, the frequency of plants exhibiting resistance in these progenies was much higher and resulted in a defined peak at rating 0, which is unlike what would be

Fig. 3. Histograms illustrating the three distribution types observed in the *Corylus americana* × *Corylus avellana* F₁ progenies, showing the proportion of offspring for each eastern filbert blight disease rating. Disease ratings ranged from 0 (no disease) to 5 (much disease). Plants with ratings of 1 to 3 were considered tolerant of eastern filbert blight, whereas ratings 4 and 5 were susceptible phenotypes. The continuous distribution of Rutgers 11545 (left) was observed in 13 progenies in which the largest peak occurred at either rating 3 or across ratings 3 and 4. The bimodal distribution of Rutgers 11534 (center) was observed in 14 progenies, with peaks occurring at ratings 0 and 3 or ratings 0 and 3/4. Very little transmission, as in OSU 11061 (right), occurred in four progenies. Together, these histograms show that the genetic control of EFB resistance in *C. americana* varies, with sources segregating for minor loci, both major and minor loci, or not at all.

expected if disease response was under strict multigenic control. The frequency of resistant offspring was higher than expected. This distribution type is generally to be expected if a dominant allele (or two) was segregating in a background of quantitative resistance. *C. americana* and *A. anomala* share an extended coevolutionary history, in which long-term disease pressure often gives rise to a complex pathosystem with a variety of *R* genes and corresponding pathogen effectors (Petit-Houdenot and Fudal, 2017). In such systems, the cosegregation of two or more *R* genes (e.g., two-gene epistatic model) is common, and both alleles must be recovered to obtain a rating of 0. Two progenies with a similar bimodal distribution were previously observed by Molnar and Capik (2012b). However, although the regularity of this pattern of transmission had not yet been observed from a broad collection of *C. americana*, a single dominant gene for resistance has recently been mapped to LG 7 in *C. americana* ‘Rush’ (Bhattarai et al., 2017a). The frequent observation of this bimodal pattern suggests a promising outlook for the use of *C. americana* in systematic crossing by showing that amenable resistance is available within a geographically diverse collection of *C. americana* accessions.

These bimodal segregation patterns highlight parental genotypes that may be preferential for future breeding. The corresponding *C. americana* parents return a greater number of EFB-free and tolerant offspring and thus increase the opportunity to identify rare recombinant individuals during backcross generations. These accessions represent seedlings from nine different states, stretching the geographic range from North Dakota to New Jersey. Three accessions [OSU 532.076, OSU 557.125, and OSU 531.043 (Table 1)] appear the most promising as donor parents, as their disease rating means are significantly lower than most of the other bimodal progenies (Table 2).

In four progenies, plus the *C. avellana* × *C. avellana* control progeny (OSU 11041), resistance and tolerance were recovered in few seedlings. The distribution of disease ratings for these pro-

genies (Fig. 2) shows peaks at rating 4 or across ratings 4 and 5 (average progeny mean of 4.45). This segregation pattern suggests that quantitative resistance in these *C. americana* accessions is highly polygenic. Although this pattern characterizes only a small group of the tested progenies, it highlights the extent to which the recovery of the quantitative resistance of *C. americana* can vary and emphasizes the need for testcrosses before substantial investment in their use as breeding parents.

Across our study, nine progenies used the pollen parent ‘Tonda di Giffoni’ (Table 1), allowing separation of the *C. americana* female parents’ contribution to the disease phenotypes of the half-sib progenies. For example, Rutgers 11545 exhibits a continuous distribution with a progeny mean of 3.03, whereas Rutgers 11547 exhibits a bimodal pattern with a progeny mean of 0.96. Disease incidence in the remaining seven *C. americana* ×

‘Tonda di Giffoni’ varies between *C. americana* parents, distinguishing the various contributions from the *C. americana* parents. Significantly lower progeny means were observed for some (but not all) of the *C. americana* × ‘Tonda di Giffoni’ crosses compared with other progenies in their respective distribution classes. The contribution of ‘Tonda di Giffoni’ to resistance and tolerance becomes clearer when comparing the progeny means of pooled disease ratings across all *C. americana* × ‘Tonda di Giffoni’ progenies to that of the other progenies. For continuous distributions, pooled progenies of ‘Tonda di Giffoni’ have a mean rating of 2.59 compared with a mean of 3.04 for the pooled ratings of all other progenies. The lower mean of ‘Tonda di Giffoni’ progenies is primarily due to a 12% increase in tolerant offspring (ratings 1–3) and a 20% reduction in susceptible offspring. For the bimodal distributions, pooled means of ‘Tonda di Giffoni’ progenies were again lower (1.26) than those of other progenies (2.26). Quite interestingly, this difference is due to a 23% increase in EFB-free progeny in the ‘Tonda di Giffoni’ crosses and a corresponding decrease in the quantity of susceptible progeny; an equal amount of tolerant progeny (42%) was obtained in both groups. Taken together, the ‘Tonda di Giffoni’ progenies are additional evidence that the *C. avellana* parent can contribute to the transmission of resistance and tolerance from *C. americana* to hybrid offspring, and furthermore, these bimodal progenies provide evidence for the hypothesis of interplay between qualitative and quantitative pathways contributed by both *C. americana* and *C. avellana*. This also indicates value in selecting *C. avellana* genotypes known to express a high level of tolerance, such as ‘Sacajawea’ (Mehlenbacher et al., 2008), for use in future interspecific hybrid crosses.

There are several underlying mechanisms of resistance that could allow for such high levels of complete resistance without clear goodness-of-fit to Mendelian segregation patterns. The combination of multiple quantitative trait loci can give an additive, strong quantitative defense response to confer

Fig. 4. Consolidated histograms of the *Corylus americana* × *Corylus avellana* F₁ progenies with bimodal distributions. A wide range of percentages of seedlings with complete resistance (rating 0) to eastern filbert blight was observed but without consensus for the segregation of monogenic resistance. Plants with ratings of 1 to 3 were considered tolerant of eastern filbert blight, whereas ratings 4 and 5 were susceptible phenotypes. These distributions represent families segregating for both major and minor resistance loci, which interestingly respond to the disease along a continuum and suggest genetic variation.

complete resistance (Niks et al., 2015), which was observed with *Xanthomonas campestris* in tomato [*Solanum lycopersicum* (Stall et al., 2009)]. In some cases, highly effective basal resistance can also yield complete resistance (Dangl and Jones, 2001; Niks et al., 2015). Pattern recognition receptor (e.g., receptor-like kinases) signaling of pathogen-associated molecular pattern triggered immunity with segregating downstream pathways is another possible explanation for this distribution pattern (Corwin and Kliebenstein, 2017; Poland et al., 2009). It is also possible that *R* genes of the *Anisogramma-Corylus* pathosystem behave outside of the traditional gene-for-gene model that incites effector triggered immunity in which complete resistance is the consequence of a rapid hypersensitive response (i.e., localized cell death) following the recognition of a pathogen effector by a single *R* gene (i.e., a pattern recognition receptor) (Coll et al., 2011; Jones and Dangl, 2006; Zhou et al., 2017).

The bimodal distributions may, or may not, reflect the presence of major *R* genes. Segregation distortion for both phenotypic resistance and corresponding resistance-linked markers have been observed in many crosses between susceptible genotypes and those carrying a single dominant resistance

locus (Bhattarai et al., 2017b; Mehlenbacher, 2018). The percentage of resistant offspring recovered in these progenies ranged from 20% to 75% (Bhattarai et al., 2017b; Colburn et al., 2015; Lunde et al., 2006; Sathuvalli et al., 2011b). Although the cause of distortion is not clear, it is hypothesized that reciprocal translocations are involved. Reciprocal translocations occur commonly in prevalent cultivars (Salesses and Bonnet, 1988; Torello Marinoni et al., 2018) and could lead to chromosomal rearrangements in gametic cells that distort segregation in either direction. Other researchers suggest this deviation is caused by “modifying” or transcription factors that must be coinherited with the major gene, and when absent, minor EFB infections (i.e., ratings 1 and 2) can occur despite the presence of an *R* gene (Muehlbauer et al., 2018). Similar segregation distortion has been observed with apple scab [*Venturia inaequalis* (Crosby et al., 1990; Gessler and Pertot, 2012)] as well as other pathosystems involving biotrophic ascomycete pathogens like *Zymoseptoria tritici* (Chartrain et al., 2005; Saintenac et al., 2018), *Leptosphaeria maculans* (Parlange et al., 2009), and *Verticillium dahliae* (Castroverde et al., 2017; Hayes et al., 2011). Such distortions can complicate the interpretation of bimodal inheritance from new *Corylus* germplasms based on

phenotyping and present an added challenge in readily identifying new *R* genes, although DNA markers have been very useful to deconvolute segregation (Torello Marinoni et al., 2018). Nevertheless, the patterns provide a basis for interplay between qualitative and quantitative pathways and insight as to the possible models for resistance.

C. AMERICANA GERMPLASM COLLECTION. The collection of 1335 bushes representing 122 seed lots originates from 72 counties and 22 states (Supplemental Table 1), and its distribution is depicted by the geographic information systems map (Fig. 1). Previously collected germplasm preserved in the USDA-ARS-NCGR and university holdings, in addition to herbarium records of wild *C. americana*, are indicated to show the extent to which this new collection complements them. A subset of 616 bushes underwent long-term evaluation for EFB response, and disease ratings are reported by seed lot (Supplemental Table 2). At the final evaluation, 587 (95%) of these trees remained free of disease symptoms (i.e., rating 0). The remaining 29 trees were represented by ratings 1 through 5, where 20 individuals were tolerant (ratings 1–3) and the remaining 9 susceptible (ratings 4–5). Disease-free trees were present in all 62 seed lots. The evaluated plots of *C. americana* were directly adjacent to most of the hybrid seedlings discussed subsequently (those planted in 2012) and provide a stark contrast of disease infection under similar conditions. The multiple years of exposure reduce the likelihood that trees free of EFB simply escaped infection.

Given that the collection was derived from open-pollinated seeds from a broad geographic range, the results validate that *C. americana* populations carry a high level of innate resistance to EFB. These results also corroborate prior evaluation of clonal *C. americana* in New Jersey, where 51 accessions from the OSU and USDA-ARS-NCGR collections were exposed to EFB and 49 remained free of disease at the conclusion of the study (Capik and Molnar, 2012). Some of the 49 clones that remained free of EFB were used to develop the interspecific hybrid progenies evaluated in this current study. Further, the collection reported here is a robust expansion of available *C. americana* germplasm (Fig. 1). *Corylus americana* is a highly heterozygous, obligate outcrossing species that is wind-pollinated and sporophytically self-incompatible (Demchik et al., 2018; Sathuvalli and Mehlenbacher, 2012). As a result, seeds of a wild plant are typically derived from a multitude of pollen parents. The reproductive biology of *C. americana*, coupled with the wide geographic range represented in this collection and the high genetic variation in the pathogen (Muehlbauer et al., 2018), indicate that this collection holds plants representing diverse sources of genetic resistance to EFB.

Conclusions

Our study confirms *C. americana* as an abundant source of EFB resistance and tolerance, which is recoverable in interspecific F_1 offspring from a wide diversity of parents. Although EFB-free individuals were common in the studied germplasm collection, as well as the parents used to make the crosses, the transmission of resistance to interspecific progeny was variable and at times absent. Thus, transmission from specific *C. americana* parents was not predictable based on its phenotype, and some form of test crossing is required to identify the most promising genotypes for use in breeding. Due to the long maturity times of hazelnut where test crosses are not always

feasible, a practical approach may be to make many crosses using a diversity of parents, select the best offspring, and move forward expecting that a portion of the offspring or entire progenies (in some cases) will not be useful. However, now that the recovery of resistance from *C. americana* has been demonstrated using a diversity of parents, resources can be dedicated to developing a greater number of large progenies with more confidence. This study represents a significant step toward better informed utilization of *C. americana* in hybrid hazelnut breeding and points to a need for additional research to elucidate the genetic control and mechanisms of resistance. The results of the F_1 progenies demonstrate that a wider collection of wild *C. americana* accessions should be tested as donor parents, which can now be pursued further using the collection reported here. In addition, a greater diversity of *C. avellana* parents with known phenotypes should be systematically incorporated into such studies to better ascertain the species' effect on inheritance.

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Supplemental Table 1. *Corylus americana* germplasm at the Rutgers University Research and Extension Center in Cream Ridge, NJ, by state and county of origin.

U.S. state	County	Total plants (no.)	Seed lot no. ^z
Arkansas		1	
	Saline	1	12556
Iowa		45	
	Clarke	21	11607
	Jones	23	12508
	Union	1	11594
Illinois		34	
	Cook	11	12533
	Menard	20	11567
	Pike	1	10543
	Rock Island	2	11612
Indiana		40	
	Steuben	32	14553, 15563
	Tippecanoe	8	12560
Kentucky		30	
	Casey	30	11568
Massachusetts		22	
	Nantucket	22	10532, 11605, 11606
Maine		2	
	Lincoln	2	10520
Michigan		116	
	Calhoun	7	11602
	Ingham	4	14542, 14543, 16518–16522
	Jackson	43	14537, 14539, 14540
	Kalamazoo	7	14538
	Montmorency	16	14544
	Ontonagon	16	11588, 12540, 16518–16522
	Washtenaw	23	11587
Minnesota		199	
	Aiken	49	11563, 11571
	Anoka	2	12553
	Chisago	34	11579
	Crow Wing	3	11608
	Fillmore	9	11599
	Isanti	64	14551, 15568, 15569
	Mississippi River	29	11565, 15566
	Sherburne	7	11601
	Washington	2	12509
Missouri		33	
	Jackson	29	11613
	Macon	4	11583
North Carolina		10	
	Madison	10	12561
North Dakota		56	
	Burleigh	40	12547, 15564
	Barnes	16	15567
Nebraska		119	
	Lancaster	1	11600
	Richardson	118	10556–10579, 12507
New Jersey		43	
	Mercer	27	11570
	Middlesex	6	11554
	Morris	10	11578A
Ohio		207	
	Belmont	23	11569
	Butler	48	15571–15577
	Carroll	128	15572–15576

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Supplemental Table 1. Continued.

U.S. state	County	Total plants (no.)	Seed lot no. ^z
Pennsylvania	Richland	5	11610
	Warren	0	13552–13555
	Wayne	3	12552
		134	
	Adams	1	13564, 13565
	Beaver	19	14555, 15570
	Butler	11	11564, 11593
	Center	17	10525–10529
	Crawford	21	11575
	Franklin	25	10537
South Dakota	Lancaster	4	12550
	Lycoming	31	11574
Tennessee	Westmore	5	12557
		2	
Virginia	Lawrence	2	11611
		11	
Wisconsin	Putnam	11	<i>C. americana</i> TN
		8	
West Virginia	Gloucester	3	12548
	Nelson	5	13561
		166	
	Adams	23	10542
	Burnett	14	10530
	Dane	20	11591
	Jefferson	3	12543
	Langlade	8	12538
	Marathon	1	12546
	Marinette	27	12510, 12539, 12541, 12551
	Oneida	13	11585, 12535, 12536
	Price	24	11577
	Sheboygan	9	12534
	Trempealeau	2	11581
	Wood	22	11580, 11603
		14	
	Mason	5	11614
	Putnam	9	11584

^zSeed lots received from cooperators were assigned numbers by the Rutgers University breeding program.

Supplemental Table 2. Disease ratings for the subset of the *Corylus americana* germplasm collection rated in Winter 2018 after seven seasons of growth under high disease pressure from *Anisogramma anomala*.

Seed lot no. ^z	County ^y	U.S. state ^x	Total plants (no.) ^w	Seedlings for each disease rating (no.) ^{w,v}						
				Avg	0	1	2	3	4	5
10520	Jefferson	ME	2	0	2	0	0	0	0	0
10530	Grantsburg	WI	15	0	15	0	0	0	0	0
10532	Nantucket	CT	16	0	16	0	0	0	0	0
10537	Willow Hill	PA	25	1.60	14	0	0	5	5	1
10542	Adams	WI	23	0	23	0	0	0	0	0
10543	Pike	IL	1	0	1	0	0	0	0	0
10556	Richardson	NE	5	0	5	0	0	0	0	0
10557	Richardson	NE	5	0	5	0	0	0	0	0
10559	Richardson	NE	4	0	4	0	0	0	0	0
10560	Richardson	NE	5	0	5	0	0	0	0	0
10561	Richardson	NE	4	0	4	0	0	0	0	0
10562	Richardson	NE	3	0	3	0	0	0	0	0
10563	Richardson	NE	5	0	5	0	0	0	0	0
10564	Richardson	NE	3	0	3	0	0	0	0	0
10565	Richardson	NE	4	0	4	0	0	0	0	0
10566	Richardson	NE	4	0	4	0	0	0	0	0
10567	Richardson	NE	2	0	2	0	0	0	0	0
10568	Richardson	NE	3	0	3	0	0	0	0	0
10569	Richardson	NE	4	0	4	0	0	0	0	0
10570	Richardson	NE	3	0	3	0	0	0	0	0
10571	Richardson	NE	5	0	5	0	0	0	0	0
10572	Richardson	NE	5	0	5	0	0	0	0	0
10573	Richardson	NE	4	0	4	0	0	0	0	0
10574	Richardson	NE	5	0	5	0	0	0	0	0
10575	Richardson	NE	1	0	1	0	0	0	0	0
10576	Richardson	NE	3	0	3	0	0	0	0	0
10577	Richardson	NE	2	0	2	0	0	0	0	0
10578	Richardson	NE	4	1.00	3	0	0	0	1	0
10579	Richardson	NE	4	0	4	0	0	0	0	0
10581	Center	PA	9	0	9	0	0	0	0	0
11554	Cream Ridge	NJ	6	1.83	2	1	1	0	2	0
11563	Aiken	MN	22	0	22	0	0	0	0	0
11564	Butler	PA	3	0	3	0	0	0	0	0
11565	Mississippi River	MN	21	0	21	0	0	0	0	0
11567	Menard	IL	25	0.04	23	0	1	1	0	0
11568	Casey	KY	23	0.04	22	1	0	0	0	0
11569	Belmont	OH	24	0	24	0	0	0	0	0
11570	Mercer	NJ	24	0.04	23	1	0	0	0	0
11571	Aiken	MN	22	0	22	0	0	0	0	0
11574	Hughesville	PA	20	0	20	0	0	0	0	0
11575	Titusville	PA	15	0.13	14	0	1	0	0	0
11577	Prentice	WI	24	0	24	0	0	0	0	0
11578A	Morris	NJ	10	0.30	9	0	0	1	0	0
11579	Stacy	MN	24	0	24	0	0	0	0	0
11583	Ethel	MO	7	0	7	0	0	0	0	0
11585	Oneida	WI	1	0	1	0	0	0	0	0
11587	Pittsfield	MI	14	0.08	13	1	0	0	0	0
11591	Madison	WI	23	0	23	0	0	0	0	0
11593	West Subury	PA	8	0	8	0	0	0	0	0
11594	Union	IA	1	1	0	1	0	0	0	0
11601	Livonia	MN	10	0	10	0	0	0	0	0
11602	Calhoun	MI	7	0	7	0	0	0	0	0
11603	Arpin	WI	24	0.04	23	1	0	0	0	0
11604	Venturini	VA	7	0	7	0	0	0	0	0
11605	Nantucket	CT	3	0	3	0	0	0	0	0
11606	Nantucket	CT	9	0	9	0	0	0	0	0

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Supplemental Table 2. Continued.

Seed lot no. ^z	County ^y	U.S. state ^x	Total plants (no.) ^w	Seedlings for each disease rating (no.) ^{w,v}						
				Avg	0	1	2	3	4	5
11607	Clarke	IA	21	0	21	0	0	0	0	0
11608	Crosslake	MN	3	0	3	0	0	0	0	0
11610	Mansfield	OH	4	1.75	1	0	2	1	0	0
11612	East Moline	IL	4	0	4	0	0	0	0	0
11613	Kansas City	MO	24	0.08	23	0	1	0	0	0
11614	Pt. Pleasant	WV	5	0	5	0	0	0	0	0
Total			616		587	6	6	8	8	1

^zSeed lots received by cooperators were assigned numbers by the Rutgers University breeding program.

^yThe county in which the *C. americana* seeds were collected.

^xThe state in which the *C. americana* seeds were collected.

^wNumber of living seedlings at the Rutgers University Research and Extension Center in Cream Ridge, NJ.

^vDisease ratings correspond to phenotypes: 0 = no visible eastern filbert blight (EFB), 1 = a single canker, 2 = multiple cankers on a single branch, 3 = multiple branches with cankers, 4 = more than 50% of branches have cankers, and 5 = all branches have cankers or the plant has died from EFB.