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Hazelnut Accessions from Russia and Crimea Transmit Resistance to Eastern Filbert Blight

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Abstract

Eastern filbert blight (EFB), caused by the fungus *Anisogramma anomala*, severely restricts production of European hazelnuts (*Corylus avellana*) in North America. The planting of EFB-resistant cultivars is considered to be the most effective disease management strategy. In 2002, a seed-based germplasm collection was made in Russia and Crimea to add diversity to the U.S. hazelnut collection and search for new sources of resistance. The resulting seedlings were grown and evaluated in both Oregon and New Jersey—in Oregon, seedlings were first evaluated for horticultural traits (i.e., nut and kernel characteristics, yield) with improved selections later subjected to the EFB pathogen, whereas in New Jersey, all seedlings were first exposed to EFB with the horticultural traits of the survivors examined later. From a total of 1299 seedlings grown in Oregon, 68 Russian and 29 Crimean improved selections were identified. In this study, they were clonally propagated and evaluated for disease response after being exposed to *A. anomala* through greenhouse inoculations and/or exposure under a structure topped with diseased wood. Out of 1,285 seedlings planted in New Jersey, nearly all died from EFB; however, ~70 resistant or highly tolerant trees were identified. As part of this study, 11 improved EFB-resistant seedlings were selected and crossed with susceptible male parents to examine inheritance of resistance. Fourteen progenies represented by 1,584 seedlings were field planted in 2010 and 2011, annually exposed to high levels of *A. anomala*, and evaluated for EFB response in January 2015. A rating scale of 0 (no signs or symptoms of EFB) to 5 (all stems containing cankers) was used. Results in Oregon showed that three selections from Russia and one from Crimea remained free of disease after multiple exposures. In New Jersey, all eleven accessions transmitted resistance to a useful number (24% to 59%) of their offspring. Interestingly, all progenies showed a clear bimodal distribution of resistant (rating = 0) and highly susceptible trees (rating = 4 or 5) with few intermediate individuals, which indicates genetic control by one or a small number of major genes. The proportions of resistant trees differed among the accessions, with five parents producing progenies that segregated in a ratio of 1 resistant: 1 susceptible, four in a ratio of 1 resistant: 3 susceptible, and two producing an abundance of resistant seedlings. Additional work, including *R*-gene mapping, is needed to examine whether or not these selections represent different *R*-genes. Overall, our findings highlight and document the value of the new hazelnut germplasm from Russia and Crimea which holds substantial promise for the breeding of improved cultivars.

Introduction

Hazelnuts (*Corylus* sp.) are a major tree nut crop of the world, contributed almost entirely by the European hazelnut, *C. avellana*. They were cultivated in the Mediterranean region as early as 500 BC, and even earlier in the Black Sea region of Turkey and the Caucasus (Thompson et al., 1996). Native and cultivated forms can be found throughout much of the European continent, as well as parts of Morocco and Iran (Mehlenbacher, 1991). In North America, however, production of European hazelnut is severely limited by the disease eastern filbert blight (EFB), caused by the ascomycete fungus, *Anisogramma anomala*. The American hazelnut (*C. americana*), which is native across much of the U.S. and southern Canada (Gleason

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and Cronquist, 1998), harbors and tolerates the causal organism with no serious affect (Capik and Molnar, 2012; Fuller, 1908; Weschcke, 1954). However, in most *C. avellana* cultivars, EFB results in significant stem dieback, loss of yield, and premature death (Johnson and Pinkerton, 2002). Consequently, EFB has been the primary factor impeding commercial hazelnut production in the eastern USA (Thompson et al., 1996).

In the Pacific northwestern U.S., the hazelnut industry was thriving at the turn of the 20th century, with no apparent signs of EFB (Barss, 1930). *Corylus avellana* production flourished for decades, particularly in the moderate, Mediterranean-like climate of Oregon's Willamette Valley. *Anisogramma anomala* was first reported west of the Rocky Mountains by Davison and Davidson (1973) following its introduction to western Washington. The estimated date of introduction is around 1960 (J. Pscheidt, pers. comm.). The introduction and subsequent spread of EFB decimated orchards, especially prior to the development of effective control measures (Gottwald and Cameron, 1980; Pinkerton et al., 1992). The disease is now present in essentially all regions where hazelnuts can be grown in North America.

Today, 99% of the U.S. crop is produced in the Willamette Valley, representing ~5 % of worldwide production [858,530 t in 2013 (Food and Agricultural Organization of the United Nations, 2015)]. Due to the high cost of disease management through fungicide applications, scouting for cankers, and extensive pruning (Julian et al., 2008, 2009), developing improved, EFB-resistant cultivars has become a principal focus of hazelnut breeding programs in the United States (Mehlenbacher, 1994; Molnar and Capik, 2012a).

The obsolete pollinizer *C. avellana* 'Gasaway' was the first EFB-resistant European hazelnut identified. It was shown to carry a dominant allele at a single locus in the heterozygous state, transmitting resistance to half of its seedlings when crossed with susceptible parents (Mehlenbacher et al., 1991). Despite the notably low nut yield and poor nut quality of 'Gasaway', breeding work at Oregon State University (OSU; Corvallis, OR) over the past 25 years has moved the *R*-gene into greatly improved genotypes. This led to the recent release of several EFB-resistant, commercial-quality cultivars (Mehlenbacher et al., 2009, 2011, 2013, 2014), which have provided the basis for the expansion of Oregon's hazelnut industry by ~6,000 ha over the past 5 years (S. Mehlenbacher, personal communication, 2015).

Concerns about the long-term durability of this single gene have motivated the search for additional sources of resistance. Fortunately, over the past two decades, efforts at OSU have identified a number of promising EFB-resistant *C. avellana* accessions, the most notable being 'Crvenje' and 'Uebov' from Serbia, 'Culplà' and 'Ratoli' from Spain, and several selected seedlings and clones originating from Russia (Moscow and southern Russia), Finland, the Republic of Georgia, Turkey, and Minnesota (USA). A number of resistant accessions and interspecific hybrids with other *Corylus* species have also been identified (Chen et al., 2005, 2007; Colburn et al., 2015; Coyne et al., 1998; Lunde et al., 2000; Mehlenbacher, personal communication, 2015; Sathuvalli et al., 2009, 2010, 2011a, 2011b, 2012, 2014). Many of these resistant plants are being utilized in genetic research and breeding at OSU.

Complicating the situation, however, the Oregon isolate of *A. anomala* is believed to be from a single point introduction in southwest Washington (Pinkerton et al., 1992). This premise is supported by recent studies using simple sequence repeat (SSR) markers for *A. anomala*. The isolates sampled from Oregon (n=8) were characterized as closely related and nearly uniform (Cai et al., 2013; Muehlbauer et al., 2014a, unpublished), which fits the model of a single point introduction, while considerable genetic diversity was evident among isolates collected across North America (>200 isolates evaluated). Further, greenhouse and field studies suggest that some eastern isolates of the fungus may display pathogenic variation, especially with respect to the ‘Gasaway’ *R*-gene (Capik and Molnar, 2012; Molnar et al., 2010a, 2010b). Together these findings underscore the importance of seeking a diversity of resistance sources and using them to breed for durable resistance.

To help meet this need and bolster genetic diversity available to breeders, seed-based germplasm collections have been made in the past 15 years across a wide area of the native range of *C. avellana* in Europe and the Caucasus by researchers at Rutgers University and OSU. Seed collection origins include Estonia, Latvia, Lithuania, Poland, Moldova, Ukraine, Russia, Georgia, Azerbaijan, Armenia, and Turkey (Capik et al., 2013; Leadbetter et al., 2015; Mehlenbacher, unpublished; Molnar et al., 2007, unpublished; Muehlbauer et al., 2014b). A large subset of the trees grown from these collections (totaling over 5000) have been planted in the field in New Jersey and exposed to high EFB pressure over multiple years. Additional trees were planted in the field at OSU where EFB pressure is lower and evaluated first for early nut production (precocity), nut characteristics, nut yield, and the presence of nut and kernel defects, and later for EFB response. Nuts collected in Russia and Crimea were shared and seedlings from the same seed lots were planted at Rutgers and OSU. While most trees from these collections were highly susceptible to EFB (>95%), a small percentage remained resistant (no cankers) or highly tolerant (only small numbers of inconsequential cankers). Unfortunately, however, nearly all of the new resistant plants are deficient in at least one horticultural trait necessary for commercial production, and most selections from Turkey, Georgia, and southern Russia have long, clasping husks that make them poorly suited to mechanical harvest. Thus, breeding is required to make use of these potentially valuable sources of resistance. However, very little is known about the level at which they transmit resistance to their offspring.

The focus of this study is to characterize plants originating from Russia and Crimea, where ~70 new resistant or highly tolerant trees were identified out of 1,285 trees originating from 32 seed lots grown in New Jersey (Capik et al., 2013; Molnar et al., 2007). From these, 11 resistant trees were chosen from a diversity of seed lots spanning multiple geographic origins. They were crossed with susceptible male parents and the response of their progeny to EFB was examined after at least 5 years in the field. Additional trees from the same seed lots were planted in the field at OSU and selections with improved horticultural traits were later tested for their EFB response. The results from OSU are presented alongside the progeny evaluations in New Jersey to document outcomes and value of the collaborative germplasm collection expedition.

Materials and Methods

Hazelnuts are wind pollinated and self incompatible. European hazelnut germplasm in the form of nuts resulting from open pollination was collected by the authors in southern Russia and the Crimean Peninsula in 2002. Approximately 30 different seed lots were collected from research institutes as well as local markets, bazaars, and roadside stands representing a significant diversity of hazelnut plant material. The seed was brought back to the United States and equally divided between OSU and Rutgers University for subsequent germination and evaluation. The subset of material evaluated at Rutgers University (a total of 1285 seedlings) was examined for its response to EFB and previously described in Molnar et al. (2007) and Capik et al. (2013). The subset grown at OSU (a total of 1299 seedlings) was first evaluated for horticultural traits (nut and kernel characteristics, kernel yield, etc.) (Mehlenbacher, unpublished). Improved selections were then clonally propagated and exposed to the EFB pathogen as described subsequently.

Evaluation of disease response at OSU.

Two methods, greenhouse inoculation and structure exposure, were used to identify EFB-resistant selections. Russian and Crimean selections that showed improved horticultural traits (data not shown) were inoculated in the greenhouse in 2008 and 2010. Scions were collected in Dec. or early Jan. and three trees per selection were grafted the following spring. Additional diverse selections from the OSU breeding program were included, giving a total of 139 and 286 in the 2008 and 2010 inoculations, respectively. ‘Ennis’ (highly susceptible) and 'Tonda di Giffoni' (quantitative resistance) were included as controls in both tests (Table 1). Greenhouse inoculations of these grafted trees were conducted as described by Sathuvalli et al. (2010).

Table 1. Results of greenhouse inoculation of grafted trees of Crimean and Russian hazelnut selections with *Anisogramma anomala*.

Year	Selection	Exposed	Infected	Parentage	Origin
2008	1169.021	2	1	AluSim #1Lg	Crimea
2008	1169.032	2	1	AluSim #1Lg	Crimea
2008	1169.034	3	2	AluSim #1Lg	Crimea
2008	1169.035	3	2	AluSim #1Lg	Crimea
2010	1185.033	3	3	AluSim #1Lg	Crimea
2010	1185.034	3	3	AluSim #1Lg	Crimea
2010	1185.041	3	3	AluSim #1Lg	Crimea
2010	1169.052	3	2	AluSim #1Sm	Crimea
2008	1169.072	3	3	AluSim #2Sm	Crimea
2008	1169.077	2	0	AluSim #2Sm	Crimea
2010	1169.077	3	0	AluSim #2Sm	Crimea
2008	1185.069	1	1	AluSim #2Sm	Crimea
2008	1185.077	3	2	AluSim #2Sm	Crimea
2008	1185.083	3	1	AluSim #2Sm	Crimea
2008	1185.091	3	3	AluSim #2Sm	Crimea
2008	1185.092	2	1	AluSim #2Sm	Crimea
2010	1185.092	3	1,0,0*	AluSim #2Sm	Crimea
2010	1169.103	3	3	AluSim #4	Crimea
2010	1169.122	3	3	AluSim #4	Crimea
2010	1185.107	3	3	AluSim #4	Crimea
2008	1170.002	3	2	AluSim #5	Crimea
2008	1170.006	3	2	AluSim #5	Crimea
2008	1170.017	3	2	AluSim #5	Crimea
2008	1185.126	2	0	AluSim #5	Crimea
2010	1185.126	3	0	AluSim #5	Crimea
2008	1186.002	2	2	AluSim #5	Crimea
2008	1186.003	3	3	AluSim #5	Crimea
2008	1186.007	3	3	AluSim #5	Crimea
2008	1186.012	3	3	AluSim #5	Crimea
2010	1170.021	3	3	Hall's Giant x Furfulak o.p.	Crimea
2010	1186.031	3	3	Hall's Giant x Furfulak o.p.	Crimea
2010	1186.046	3	3	Hall's Giant x Furfulak o.p.	Crimea
2010	1169.131	3	3	Adygejsk Roadside	Russia
2010	1185.014	3	3	Dzhubga	Russia
2008	1166.083	2	2	Holmskij #1	Russia
2008	1166.087	3	3	Holmskij #1	Russia
2008	1166.093	3	3	Holmskij #1	Russia
2008	1166.097	3	3	Holmskij #1	Russia
2008	1166.102	3	3	Holmskij #2	Russia

2008	1166.108	3	2	Holmskij #2	Russia
2008	1166.118	3	3	Holmskij #2	Russia
2008	1166.119	3	0	Holmskij #2	Russia
2010	1166.119	3	2	Holmskij #2	Russia
2008	1166.120	3	3	Holmskij #2	Russia
2008	1187.095	3	3	Holmskij #2	Russia
2008	1187.099	3	3	Holmskij #2	Russia
2008	1187.101	3	0	Holmskij #2	Russia
2008	1187.109	3	3	Holmskij #2	Russia
2008	1168.122	3	3	Holmskij #3	Russia
2008	1168.125	3	3	Holmskij #3	Russia
2008	1168.130	3	4	Holmskij #3	Russia
2008	1168.003	3	2	Holmskij #4	Russia
2008	1168.009	3	3	Holmskij #4	Russia
2008	1168.010	3	2	Holmskij #4	Russia
2008	1168.013	2	0	Holmskij #4	Russia
2010	1168.013	3	0	Holmskij #4	Russia
2008	1187.111	3	3	Holmskij #4	Russia
2008	1187.112	3	3	Holmskij #4	Russia
2008	1187.125	2	2	Holmskij #4	Russia
2008	1187.127	3	3	Holmskij #4	Russia
2010	1187.003	3	3	Krasnodar #1	Russia
2010	1187.008	3	3	Krasnodar #1	Russia
2010	1187.010	3	2	Krasnodar #1	Russia
2010	1187.020	1	0	Krasnodar #3	Russia
2010	1187.029	3	2	Krasnodar #3	Russia
2010	1166.066	3	3	Krasnodar #4	Russia
2010	1187.056	3	3	Krasnodar #4	Russia
2010	1187.058	3	3	Krasnodar #4	Russia
2010	1187.062	3	3	Krasnodar #4	Russia
2010	1187.065	3	3	Krasnodar #4	Russia
2010	1187.070	3	3	Krasnodar #4	Russia
2010	1165.098	3	3	Maikop	Russia
2010	1181.081	3	3	Maikop	Russia
2010	1181.051	3	1	Moscow (Momonov)	Russia
2010	1165.044	3	3	Sochi Institute	Russia
2010	1165.052	3	3	Sochi Institute	Russia
2010	1165.066	3	3	Sochi Institute	Russia
2010	1165.069	3	3	Sochi Institute	Russia
2010	1166.123	4	0	Sochi Institute Redleaf	Russia
2010	1171.106	3	3	Sochi Institute	Russia
2010	1181.131	3	3	Sochi Institute	Russia
2010	1189.015	3	3	Sochi Institute	Russia
2010	1184.001	3	3	Sochi Market #1	Russia
2010	1168.047	3	1	Sochi Market #2	Russia
2010	1184.033	3	3	Sochi Market #2	Russia
2010	1184.050	3	3	Sochi Market #2	Russia
2010	1168.065	3	2	Sochi Market #3	Russia
2010	1168.069	3	3	Sochi Market #3	Russia
2010	1168.073	3	3	Sochi Market #3	Russia
2010	1168.074	3	3	Sochi Market #3	Russia
2010	1184.067	3	3	Sochi Market #3	Russia
2010	1168.098	3	0	Sochi Market #4	Russia

2010	1184.096	3	1	Sochi Market #4	Russia
2010	1184.098	3	3	Sochi Market #4	Russia
2010	1168.105	3	2	Sochi Market #5	Russia
2010	1168.115	3	2	Sochi Market #5	Russia
2010	1169.009	3	3	Sochi Market #6	Russia
2010	1185.005	3	3	Sochi Market #6	Russia
2010	1185.011	3	3	Sochi Market #6	Russia
2008	Barcelona	5	5	Susceptible control	Spain
2008	Ennis	3	3	Susceptible control	Oregon
2010	Ennis	14	14	Susceptible control	Oregon
2010	Eta	3	0	Resistant control	Oregon
2010	Gasaway	3	0	Resistant control	Washington
2008	Tonda di Giffoni	2	1	Tolerant control	Italy
2010	Tonda di Giffoni	13	7	Tolerant control	Italy
2010	Theta	3	0	Resistant control	Oregon

A second method, structure exposure of potted trees, was used in 2013 and 2014 to quantify the relative susceptibility of selections from the OSU breeding program, as well as the selections from Russia and Crimea. The method is based on that of Pinkerton et al. (1992) and was used to document the quantitative resistance of ‘Sacajawea’ (Mehlenbacher et al., 2008). Approximately ten potted trees per selection were placed in randomized blocks under a wooden structures topped with EFB-diseased wood. The method is also useful for identifying and confirming highly resistant selections, for which fewer trees are needed. The 2013 and 2014 tests exposed 168 and 139 selections, respectively, with 'Ennis' and 'Tonda di Giffoni' again as control cultivars (Table 2). The resulting EFB cankers were counted and measured in early Jan., approximately 20 months after exposure. Canker lengths were summed for each tree, a square root transformation was used to remove the association between mean and variance, and mean total canker length on a square root scale was used to provide a ranking of relative susceptibility of genotypes.

Plant material, controlled crosses, and culture at Rutgers University. Eleven EFB-resistant or highly tolerant seedling selections were chosen at Rutgers to represent a diversity of origins and seed lots from a germplasm collection made in Russia and Crimea (Table 3; Capik et al., 2013; Molnar et al., 2007). The 11 trees were chosen based on their phenotype (round kernels, large nut/kernel size, nut yields, and overall tree health and vigor) and origin, and were included in a diversity study of 323 unique accessions using 17 SSR markers (Muehlbauer et al., 2014b). The study resolved 11 distinct groups, and placed the resistant selections in four of them. Four selections (H3R04P23, H3R04P28, H3R04P30, and H3R7P25) were placed in the “Black Sea Group 1”. Another four (H3R10P88, H3R13P40, H3R14P26, and CRXR16P57) were placed in the “Black Sea Group 2”, while H3R12P58 and H3R12P62 were placed in the “Wild *C. avellana* Group”; and CRXR13P91 was placed in the “Moscow Group” (Table 3). Interestingly, as a further indication of their diverse backgrounds, they were placed in genetic groups that were different from most previously identified sources of EFB resistance, including ‘Gasaway’, ‘Ratoli’, OSU 408.040, and OSU 759.010 (from the Republic of Georgia), as well as several known EFB-resistant interspecific hybrids.

The 11 plants were crossed with various pollen mixtures from known EFB-susceptible *C. avellana* accessions in the OSU breeding program (Table 4; Supplemental Table 1). Each mixture contained approximately equal amounts of pollen from three parents with non-overlapping incompatibility (S) al-

Table 2. Results of 2013 and 2014 exposures of potted hazelnut trees to eastern filbert blight under a structure topped with diseased wood. Selections from Russia and Crimea and control cultivars (Ennis = highly susceptible, Barcelona = susceptible, Tonda di Giffoni = tolerant, and Lewis = tolerant) are ranked from most to least susceptible based on square root of total canker length per tree. Selections with no disease were excluded for the calculation of LSD.

Selection	No. Trees Exposed	Infected	Canker Length (cm)	SRCL[z]	No. Cankers	Origin/Parentage
2013 exposure						
Ennis	12	12	118.6	10.61	4.7	Oregon
1185.107	9	9	92.4	9.32	3.7	Crimea AluSim #4
1189.015	13	13	75.7	8.31	3.7	RUS Sochi Inst.
1187.070	13	12	73.7	8.15	3.6	RUS Holmskij #2
1187.112	13	13	63.8	7.57	3.4	RUS Holmskij #4
Lewis	13	12	50.8	6.58	3.0	Oregon, USA
1185.014	12	11	45.0	6.20	2.6	RUS Dzhubga Mkt.
1187.062	13	11	42.1	5.72	2.3	RUS Krasnodar #4
1184.050	10	8	46.3	5.64	2.6	RUS Sochi Mkt #2
T. di Giffoni	10	9	34.5	5.02	2.0	southern Italy
Barcelona	11	9	36.1	4.98	1.9	Oregon, USA
1185.092	8	5	7.4	2.14	0.8	Crimea AluSim #2
1184.096	12	4	9.8	1.77	0.4	RUS Sochi Mkt #4
1181.051	5	2	6.5	1.54	0.6	RUS Moscow
1185.126	13	0	0.0	0.00	0.0	CRIMEA AluSim #5
1187.101	3	0	0.0	0.00	0.0	RUS Holmskij #2
Mean (168 selections)[y]	9.0	5.6	35.9	18.55	2.6	
LSD (0.05)			28.5	2.42	1.4	
2014 exposure						
1168.074	6	6	183.5	13.41	7.63	RUS Sochi Market #3
1165.098	13	13	177.6	13.20	6.38	RUS Maikop
1171.106	12	12	166.5	12.76	5.17	RUS Sochi Inst.
1166.083	13	13	165.3	12.72	8.13	RUS Holmskij #1
1166.066	13	13	158.1	12.47	5.79	RUS Krasnodar #4
1171.085	12	12	136.6	11.45	6.02	RUS Maikop
Ennis	12	12	136.9	11.43	5.63	Oregon, USA
1169.131	8	8	133.0	11.42	4.13	RUS Adygejsk
1165.066	13	13	123.6	11.01	3.69	RUS Sochi Inst.
1170.021	11	11	132.3	10.85	5.33	Crimea NBS
1169.072	13	13	118.5	10.81	5.27	Crimea AluSim #2
1169.122	8	8	122.8	10.62	4.63	Crimea AluSim #4
1168.009	11	11	90.1	8.96	5.58	RUS Holmskij #4
1166.093	13	12	76.8	8.24	4.08	RUS Holmskij #2
1165.044	5	5	64.5	7.88	3.63	RUS Sochi Inst.
1168.130	13	12	57.1	7.18	2.33	RUS Holmskij #3
1181.051	12	11	29.6	5.04	3.08	RUS Moscow
T.di Giffoni	12	10	25.6	4.23	1.77	southern Italy
1169.077	13	8	18.8	3.29	1.67	Crimea AluSim #2
1166.108	13	5	8.2	1.91	0.56	RUS Holmskij #2
1166.123	4	0	0.0	0.00	0.0	RUS Sochi Inst. RL
1168.013	6	0	0.0	0.00	0.0	RUS Holmski #4
Mean (139 selections)[y]	10.3	9.3	89.4	8.48	3.70	
LSD (0.05)			35.3	2.15	1.43	

[z] Square root transformation of mean total canker length

[y] The data presented is a subset of a larger population of breeding selections originating from the Oregon State University breeding program. Only the Russian and Crimean selections and control plants are shown but the mean data reflects the larger population of plants.

Table 3. Origin and incompatibility (S) alleles of the eastern filbert blight resistant accessions from Russia and Crimea included in this study.

Selection	Seed lot[z]	S-alleles[y]	Collection origin	Genetic group[x]
CRXR13P91	RUS 02	unknown	Sochi, Russia (parent tree originally from Moscow)	Moscow
H3R13P40	RUS 09	1 2	Holmskij, Russia	Black Sea 2
H3R07P25	RUS 12	2 10	Holmskij, Russia	Black Sea 1
H3R04P23	RUS 13	16 24	Holmskij, Russia	Black Sea 1
H3R04P28	RUS 13	4 19	Holmskij, Russia	Black Sea 1
H3R04P30	RUS 13	17 24	Holmskij, Russia	Black Sea 1
H3R14P26	RUS 22	2 2	Simferopol, Crimea	Black Sea 2
H3R12P58	RUS 23	20 24	Simferopol, Crimea	wild *C. avellana*
H3R12P62	RUS 23	20 24	Simferopol, Crimea	wild *C. avellana*
CRXR16P57	RUS 28	unknown	Yalta, Crimea	Black Sea 2
H3R10P88	RUS 28	2 10	Yalta, Crimea	Black Sea 2
OSU 1166.123[w]	02112	4 6	Sochi, Russia	--[v]
OSU 1168.013	02108	unknown	Holmskij, Russia	--
OSU 1187.101	02106	24 26	Holmskij, Russia	--
OSU 1185.126	02126	2 6	Simferopol, Crimea	--

[z] Seed lot RUS 02 through RUS 28 corresponds to collections described in Molnar et al. (2007) and Capik et al. (2013) and 5-digit code corresponds to breeding records held at Oregon State University.

[y] Incompatibility (S) alleles were identified by fluorescence microscopy. Dominant alleles are underlined.

[x] Genetic group of the 11 resolved by Muehlbauer et al. (2014b).

[w] Eastern filbert blight hazelnut selections identified at Oregon State University (OSU) from same seed collection. Note, these were not included in the controlled crosses but are included to represent addition sources of resistance identified from the collection expedition.

[v] Dashed line represents data not available

leles to increase the likelihood of compatible pollination (Table 5). At the time of crossing, the S-alleles (Table 3) of the Russian/Crimean selections were unknown. Fourteen controlled hybridizations were made at Rutgers University following protocols described by Mehlenbacher (1994): one in 2008 (progeny designated Rutgers 08529), 11 in 2009 (Rutgers 09511, 09512, 09588, 09589, 09590, 09592, 09597, 09601, 09602, 09603, and 09605), and two in 2010 (Rutgers 10506 and 10507). At maturity, seeds were harvested, stored, germinated, and grown according to protocols described by Molnar and Capik (2012b). Plants were removed from the greenhouse in July for acclimation outdoors under shade cloth (40% shade) until field planting in Oct. Tree spacing was ~1.0 m in-row by ~3.5 m between rows. The progenies were planted in blocks at the Rutgers University Horticultural Farms 1 and 3 in New Brunswick, NJ. Weed control using herbicides, irrigation, and annual applications of fertilizer were all provided as needed with no use of insecticides or fungicides.

Disease exposure in the field (Rutgers). Trees were field-inoculated prior to budbreak each year to keep disease pressure high and reduce the possibility of susceptible plants escaping infection. Branches containing mature *A. anomala* stromata were collected in winter from nearby trees at the Rutgers University research farms and stored at -20°C in polyethylene bags until needed. Starting in 2011, 10- to 15-cm pieces of these infected branches were tied into the canopy of each tree around the time of budbreak (Molnar et al., 2007). In addition, nearby infected trees in the breeding plots contributed a steady influx of EFB inoculum.

Evaluation of disease response in the field (Rutgers). All of the trees were evaluated in Dec. 2012 and Dec. 2013 for signs of EFB, which was recorded for each as the presence

Table 4. Disease response following exposure to *Anisogramma anomala* in hazelnut progenies segregating for resistance from new accessions from Russia and Crimea. Rating scale corresponds to 0 = no detectable eastern filbert blight; 1 = single canker with fully formed stromata; 2 = multiple cankers on a single branch; 3 = multiple branches with cankers; 4 = greater than 50% of branches contain cankers; 5 = all branches contain cankers, except basal sprouts.

Resistant parent		Pollen Mix	Progeny code	Number of trees	Expected ratio	Observed		Chi squared		Disease ratings (0-5)					
						Resistant	Susceptible	Value	*P*	0	1	2	3	4	5
CRXR13P91	×	OSU #5	09511	112	1 : 1	54	58	0.14	0.706	54	2	6	7	16	27
H3R13P40	×	OSU #6	09603	191	1 : 3	52	139	0.50	0.478	52	7	8	1	3	120
H3R07P25	×	OSU #6	09592	109	1 : 3	33	76	1.62	0.203	33	3	2	6	27	38
H3R07P25	×	OSU #7	10506	35	1 : 3	11	24	0.77	0.380	11	0	0	1	15	8
H3R07P25	×	OSU #8	10507	61	1 : 3	21	40	2.89	0.089	21	3	1	1	19	16
H3R04P23	×	OSU #1	08529	89	1 : 1	45	44	0.01	0.916	45	2	4	2	7	29
H3R04P23	×	OSU #5	09588	168	1 : 1	76	92	1.52	0.217	76	3	4	11	28	46
H3R04P28	×	OSU #6	09589	163	1 : 3	39	124	0.10	0.752	39	2	20	13	10	79
H3R04P30	×	OSU #6	09590	77	1 : 3	28	49	5.30	0.021	28	1	2	2	7	37
H3R14P26	×	OSU #5	09605	153	1 : 1	83	70	1.11	0.293	83	3	0	3	1	63
H3R12P58	×	OSU #5	09601	71	1 : 1	40	31	1.14	0.286	40	0	0	0	0	31
H3R12P62	×	OSU #6	09602	130	1 : 1	64	66	0.03	0.861	64	0	0	2	10	54
CRXR16P57	×	OSU #5	09512	131	1 : 1	77	54	4.04	0.045	77	3	6	8	5	32
H3R10P88	×	OSU #6	09597	94	1 : 3	25	69	0.13	0.721	25	2	4	1	0	62

Table 5. Oregon State University (OSU) selections in pollen mixtures used in controlled crosses and their incompatibility (S) alleles. Dominant alleles are underlined. All pollen parents in this table are susceptible to eastern filbert blight. Pedigrees can be found in Supplemental Table 1.

Pollen Mix	Tree #1	S-alleles	Tree #2	S-alleles	Tree #3	S-alleles
OSU #1	OSU 684.104	2, 22	OSU 713.068	3, 10	OSU 978.064	1, 17
OSU #5	'Sacajawea'	1, 22	OSU 786.091	2, 4	OSU 806.051	8, 19
OSU #6	OSU 1039.010	15, 21	OSU 1051.038	2, 14	OSU 1033.068	4, 8
OSU #7	OSU 1158.109	22, 25	OSU 1156.105	8, 10	OSU 1051.0.38	2, 14
OSU #8	OSU 896.082	1, 17	OSU 1088.083	3, 25	OSU 1031.035	2, 4

or absence of *A. anomala* stem cankers. In Jan. 2015, final disease ratings were recorded using a scale of 0 to 5, according to an index adapted from Pinkterton et al. (1992): 0 = no detectable EFB (includes "sunken lesion" phenotypes where a few small, inconsequential sunken cankers are present that lack stromata); 1 = single canker (with fully formed stromata); 2 = multiple cankers on a single branch; 3 = multiple branches with cankers; 4 = greater than 50% of branches contain cankers; 5 = all branches contain cankers, except basal sprouts. Trees that had previously died from EFB were given a score of 5. The ratings were tabulated for each progeny, a mean disease response was calculated, and histograms were developed to visualize distribution of disease response (Table 4; Fig. 1, Fig. 2). Although plants rated from 1 to 3 can sometimes exhibit sufficient field tolerance for survival and nut production, in this analysis plants rated 0 were considered "resistant," and plants with all other scores designated as "susceptible." The results for each progeny were then subjected to a Chi-square test to examine fit to models of simple Mendelian inheritance.

Results and Discussion

A total of 29 Crimean and 68 Russian selections were inoculated in the greenhouse at OSU (Table 1). Nearly all trees developed EFB; however, three showed no signs or symptoms of EFB and two appeared highly tolerant. The Crimean selections OSU 1169.077 and OSU 1185.126 were inoculated in both years and all trees remained free of EFB. Further, the Crimean selection OSU 1185.092 appears to express high quantitative resistance, as only one of two trees developed a canker from the 2008 inoculation, and one of three trees developed a sunken canker but no stromata from the 2010 inoculation. The Russian selections OSU 1168.013 and OSU 1166.119 were also inoculated in both years. While all trees of OSU 1168.013 remained free of disease across both years, OSU 1166.119 showed some signs of EFB. All three trees remained free of disease following the 2008 inoculation, but two of three trees developed cankers following the 2010 test, suggesting that a moderate level of quantitative resistance may be expressed by the selection.

In addition, a total of 29 Crimean and 65 Russian selections were exposed to EFB by structure inoculation at OSU (Table 2). The disease response of the selections ranged from highly susceptible (similar to 'Ennis') to no disease. After the 2013 exposure, Crimean selection OSU 1185.126 and Russian selection OSU 1187.101 remained free of EFB, while Crimean selection OSU 1185.092 and Russian selections OSU 1184.096 and OSU 1181.051 had less disease than 'Tonda di Giffoni'. After the 2014 exposure, Russian selections OSU 1166.123 and OSU 1168.013 remained free of EFB, while Russian selection OSU 1166.108 showed less disease than 'Tonda di Giffoni'. The structure exposure confirmed the high resistance seen in greenhouse inoculations of Crimean selection OSU 1185.126 and Russian selection OSU 1168.013. Overall, these four new EFB-resistant plants add to the germplasm base from Russia and Crimea available for further study and breeding.

Eleven of the EFB-resistant selections identified at Rutgers were used as parents in crosses with susceptible parents to yield 14 progeny. While signs of EFB became visible in the plots as early as 2012 and 2013 (data not shown), additional time was provided for the infections to proliferate throughout the

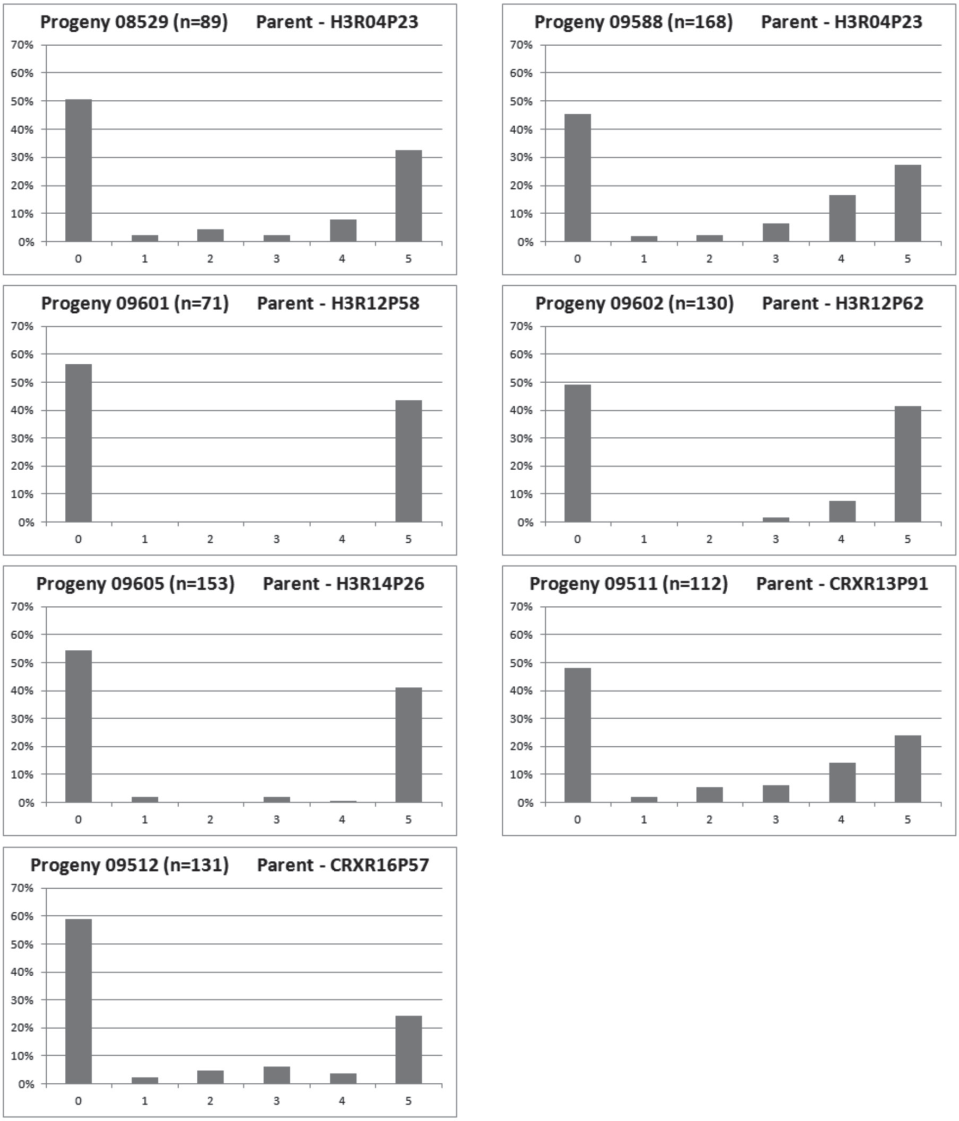

Figure 1. Normalized histograms of progenies fitting a 1 resistant: 1 susceptible ratio. The proportion of plants (out of 100%) in each category is shown, where 0 = no detectable eastern filbert blight; 1 = single canker with fully formed stromata; 2 = multiple cankers on a single branch; 3 = multiple branches with cankers; 4 = greater than 50% of branches contain cankers; and 5 = all branches contain cankers, except basal sprouts.

plots. The final Jan. 2015 ratings showed that all 14 progenies from the 11 EFB-resistant accessions segregated for disease response, with the proportion of resistant (rating = 0) seedlings across the progenies ranging from 24 to 59 percent (Table 4). This transmission of resistance confirms our earlier classification of the 11 accessions as resistant (Capik et al., 2013; Molnar et al., 2007) and supports their use in a resistance breeding program.

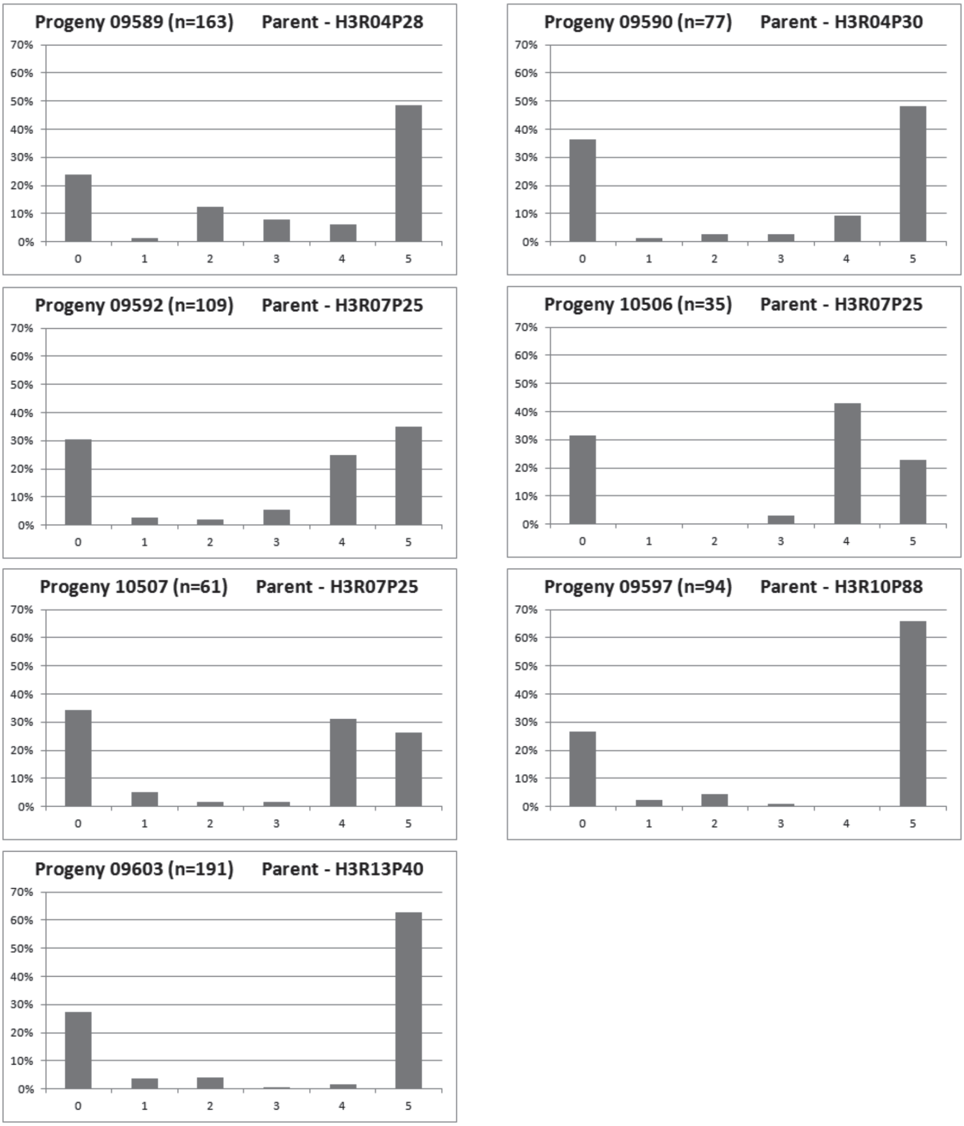

Figure 2. Normalized histograms of progenies fitting a 1 resistant: 3 susceptible ratio. The proportion of plants (out of 100%) in each category is shown, where 0 = no detectable eastern filbert blight; 1 = single canker with fully formed stromata; 2 = multiple cankers on a single branch; 3 = multiple branches with cankers; 4 = greater than 50% of branches contain cankers; and 5 = all branches contain cankers, except basal sprouts.

Interestingly, each progeny across all parents showed a clear bimodal distribution with resistant and highly susceptible trees (Rating = 4 or 5) making up a majority of each, but with few intermediate (rating 1 to 3) individuals present (Fig. 1, Fig. 2). To further clarify the disease rating scale, trees rating 0 are considered "resistant" to EFB showing no signs or symptoms of infection, while ratings of 1 or 2 are regarded as "highly tolerant" of EFB; our experiences show trees placed in these two categories typically do not develop cankers severe enough to impede normal long-term growth or nut production. Plants rated 3 are considered "moderately tolerant". At this infection level it is unlikely that EFB will kill the plant, although regular branch dieback will lead to reduction in long-term nut yields. Trees rated as 4 or 5 are designated "susceptible". They show significantly reduced growth within two years post infection and generally die within five to seven years. Most plants rated as 4 progress to 5 over time, unlike those rating 1-3, which typically remain at that level of infection.

Our results, in general, indicate control of resistance across the progenies by one or a small number of major genes (qualitative inheritance), which is in contrast to multigenic (quantitative) inheritance where a greater proportion of intermediate individuals would have been expected, as was shown in some progenies discussed in Molnar and Capik (2012b). However, the proportions of trees in each of the two categories (resistant vs. highly susceptible) differed among the parents, with most fitting either a resistant: susceptible model of 1:1 or 1:3 (Fig. 1, Fig. 2; Table 4).

Progenies of H3R04P23, H3R12P58, H3R12P62, H3R14P26, and CRXR13P91 segregated in a 1 resistant: 1 susceptible ratio (Table 2; Fig.1), which suggests control at a single locus by a dominant allele in the heterozygous state. It should be noted that the parent CRXR16P57 yielded progeny with a slight increase of resistant plants over the 1 resistant: 1 susceptible model (59% resistant), not fitting the Chi-square test but still suggestive of single locus control. Overall, these results are similar to previous reports on inheritance of EFB resistance in Oregon from 'Gasaway' (Mehlenbacher et al., 1991), 'Ratoli' (Sathuvalli et al., 2011a), OSU 408.040 (Chen et al., 2005; Sathuvalli et al., 2012), and some progenies of 'Culplà' and OSU 495.072 (Colburn et al., 2015), including an abundance of resistant plants found in some progenies where mapping indicated controlled of resistance by a single locus.

The progeny of four of the five remaining parents (H3R04P28, H3R7P25, H3R10P88, and H3R13P40) segregated in a pattern of 1 resistant: 3 susceptible, with progeny of the final parent (H3R04P30) showing a slight abundance of resistant trees (36%) above this ratio (Table 4; Fig. 2). This 1 resistant: 3 susceptible segregation ratio could potentially be explained by a two gene, dominant epistasis model. For example, crossing AaBb resistant × aabb susceptible yields 1 AaBb (resistant): 1 Aabb (susceptible): 1 aaBb (susceptible): 1 aabb (susceptible). Additional progeny evaluations including examination of F_2 and backcross generations are needed.

An alternative explanation is control by a single gene with segregation distortion, possibly caused by chromosomal abnormalities. This phenomenon was previously observed with progenies of 'Zimmerman', which SSR markers indicate is a hybrid of 'Barcelona' × 'Gasaway' (Gökirmak et al., 2009). When 'Zimmerman' (or EFB-resistant 'Zimmerman' offspring) was crossed with susceptible parents the progenies yielded an abundance of resistant seedlings over the expected model, with seedlings generally segregating in a 3 resistant: 1 susceptible ratio (Lunde et al., 2006). This pattern was consistently observed despite resistance known to be provided by the 'Gasaway' *R*-gene, which is a dominant allele in the heterozygous state mapped to a single locus on linkage group (LG) 6 (Mehlenbacher et al., 1991, 2004, 2006). Reciprocal translocations were discussed as a likely mechanism for the unex-

Supplement Table 1. Pedigrees of Oregon State University (OSU) hazelnut pollen parents used in controlled crosses.

Pollen Mix	Pollen Parent	Pedigree
OSU #1	OSU 684.104	Birkemeier 5-39 × 'Mortarella'
		Birkemeier 5-39 = 14.084 × 'Negret' (OSU seedling grown at Rich Birkemeier's farm)
	OSU 713.068	OSU 384.023 × OSU 244.001
		OSU 384.023 = 'Casina' × 55.129
		55.129 = 'Tonda Gentile delle Langhe' × 'Tombul' (syn. 'Extra Ghiaghli')[z]
		OSU 244.001 is a full sib of 'Lewis'
	OSU 978.064	OSU 556.019 × 'Sacajawea'
		OSU 556.019 was selected seeds purchased in the market in Istanbul, Turkey
OSU #5	'Sacajawea'	OSU 43.091 × 'Sant Pere'
		OSU 43.091 = 'Montebello' seedling
	OSU 786.091	OSU 256.005 × OSU 439.063
		OSU 256.005 = OSU 54.056 (Giresun, Turkey)[y] × OSU 17.083
		OSU 17.083 = 'Barcelona' × 'Camponica'
		OSU 439.063 = 'Ribet' × 'Willamette'
	OSU 806.051	'Lewis' × OSU 452.019
		OSU 452.019 = 'Fusco Rubra' × OSU 55.129
		OSU 55.129 = 'Tonda Gentile delle Langhe' × 'Tombul' (syn. 'Extra Ghiaghli')
OSU #6	OSU 1039.010	OSU 381.147 × OSU 556.011
		OSU 381.147 = 'Casina' × OSU 55.129
		OSU 55.129 = 'Tonda Gentile delle Langhe' × 'Tombul' (syn. 'Extra Ghiaghli')
		OSU 556.011 was selected from nuts purchased in the market in Istanbul, Turkey
	OSU 1051.038	OSU 681.043 (Turkish)[x] × OSU 616.018
		OSU 616.018 = 'Tonda di Giffoni' × OSU 252.146
		OSU 252.146 = OSU 41.083 × OSU 17.028
		OSU 41.083 = 'Montebello' × 'Compton'
		OSU 17.028 = 'Barcelona' × 'Tombul Ghiaghli'
	OSU 1033.068	OSU 689.078 × OSU 599.042
		OSU 689.078 = 'Sant Jaume' × OSU 350.089
		OSU 350.089 = 'Tombul Ghiaghli' × 'Tonda Romana'
		OSU 599.042 = OSU 312.068 × OSU 226.122
		OSU 312.068 = OSU 23.017 × 'Tonda Gentile delle Langhe'
		OSU 23.017 = 'Barcelona' × 'Tombul' (syn. 'Extra Ghiaghli')
		OSU 226.122 = 'Tonda Gentile delle Langhe' × OSU 67.026
		OSU 67.026 = OSU 14.019 × OSU 17.068
		OSU 14.019 = 'Barcelona' × 'Butler'
		OSU 17.068 = 'Barcelona' × 'Tombul Ghiaghli'
OSU #7	OSU 1158.109	'Sacajawea' × 693.109 (Turkish)
	OSU 1156.105	OSU 474.084 × OSU 490.072
		OSU 474.084 = 'Lewis' × 'Tonda di Giffoni '
		OSU 490.072 = OSU 55.129 × OSU 175.123
		OSU 175.123 = 'Creswell' × OSU 44.134
		OSU 44.134 = 'Montebello' × 'Compton'
	OSU 1051.038	OSU 681.043 (Turkish) × OSU 616.018
		OSU 616.018 = 'Tonda di Giffoni' × OSU 252.146
		OSU 252.146 = OSU 41.083 × OSU 17.028
		OSU 41.083 = 'Montebello' × 'Compton'
		OSU 17.028 = 'Barcelona' × 'Tombul Ghiaghli'
OSU #8	OSU 896.082	'Nocchiolino Sangrato' × OSU 443.107
		OSU 443.107 = OSU 183.060 × OSU 54.056 (Turkish)
		OSU 183.060 = 'Montebello'× OSU 14.084
	OSU 1088.083	OSU 686.058 (Turkish) × OSU 654.017
		OSU 654.017 = OSU 244.001 × OSU 309.074
		OSU 244.001 = OSU 17.028 × 'Willamette'
		OSU 17.028 = 'Barcelona' × 'Tombul Ghiaghli'
		OSU 309.074 = 'Tonda Gentile delle Langhe' × OSU 23.017
		OSU 23.017 = 'Barcelona' × 'Extra Ghiaghli'
	OSU 1031.035	OSU 702.041 (Turkish) × OSU 620.032
		OSU 620.032 = OSU 332.097 × OSU 313.078
		OSU 332.097 = 'Montebello' × OSU 74.037
		OSU 74.037 = OSU 14.084 × OSU 17.068
		OSU 14.084 = 'Barcelona' × 'Daviana'
		OSU 17.068 = 'Barcelona' × 'Tombul Ghiaghli'
		OSU 313.078 = OSU 23.017 × 'Tonda Gentile delle Langhe'
		OSU 23.017 = 'Barcelona' × 'Extra Ghiaghli'

[z] Note that 'Extra Ghiaghli' is a clone of 'Tombul'. 'Tombul Ghiaghli' is not the same as 'Extra Ghiaghli'; it is similar to (or the same as) Mincane.

[y] Turkish selections designed with a 54 (row 54 at OSU Smith Horticulture Research Farm) are selections derived from seed collected by Maxine Thompson in Turkey in the 1970's.

[x] Turkish selections designed with 686 to 702 (rows 686 to 702) are from seed collected by Shawn Mehlenbacher in Turkey in 1993.

pected segregation pattern of 'Zimmerman' offspring, supported by the fact that they have been previously reported in 'Barcelona' (the parent of 'Zimmerman') and 'Tonda Gentile delle Langhe', as indicated by the presence of quadrivalents or trivalents at meiosis (Lunde et al., 2006; Salesses, 1973; Salesses and Bonnet, 1988). Colburn et al. (2015) also discussed this phenomenon for hazelnut in reference to the unexpected segregation ratios observed for progenies of 'Culplà', 'Crvenje', and OSU 495.072 when crossed with susceptible parents, despite each mapping to a single locus on LG 6 (Mehlenbacher et al., 2006). Both 'Barcelona' and 'Tonda Gentile delle Langhe' are common ancestors of the plants used by Colburn et al. (2015), and also happen to be common ancestors in the pedigrees of most of the pollen parents used in our study (Supplemental Table 1). Similarly, Sathuvalli et al. (2011b) investigated resistance from Georgian selection OSU 759.010 and reported segregation ratios (resistant: susceptible) of 3:1 in one progeny and 1:1 in a second progeny. Mapping the *R*-genes in segregating progenies of these Russian and Crimean selections would be a logical next step to clarify genetic control, and is currently in progress.

To date, resistance to EFB has been mapped in progenies derived from a number of *C. avellana* sources of resistance. Resistance from 'Gasaway', as mentioned previously, was mapped to LG 6 (Mehlenbacher et al., 2006). Resistance from 'Culplà' (Spain), 'Crvenje' (Serbia), and selection OSU 495.072 (southern Russia) (Colburn et al. 2015) and OSU 408.040 (Minnesota) (Sathuvalli et al., 2012) also map to the same region on LG 6. They may represent the same locus or, more likely, components of a gene cluster. This was unexpected given the wide geographic origin of these resistant accessions (Gökirmak et al., 2009). Thus, we may find that resistance in many of our Russian and Crimean parents also maps to LG 6. However, the *R*-gene from 'Ratoli' from Spain (Sathuvalli et al., 2011a) and OSU 759.010 from Republic of Georgia (Sathuvalli et al., 2011b) map to LG 7 and LG 2, respectively. This finding increases the likelihood of different EFB resistance genes (or loci or gene clusters) being present across the hazelnut genome, and supports the potential for finding additional loci when screening a broader diversity of plants, such as our collection from Russia and Crimea. Having access to a broader array of *R*-genes located on different linkage groups will give breeders the opportunity for gene pyramiding to potentially enhance the durability of resistance. Efforts are currently underway at Rutgers and OSU to investigate the feasibility of *R*-gene pyramiding. As a further point of discussion, irrespective of *R*-gene location, adding to the overall genetic diversity of the breeding population can be extremely important when working with a highly heterozygous, clonal crop. One benefit of this is demonstrated by the presence of several rare S-alleles in the 11 parent trees and other selections from this collection expedition (Table 3), which allows for the development of a diversity of pollenizers and compatible nut-producing cultivars complementary to those already available, many of which tend to share common alleles (Mehlenbacher, 2014).

From an applied breeding perspective, those progenies yielding ≥50% resistant offspring in a predictable manner may represent priority targets for improvement efforts. This becomes important when considering the long life cycle of *A. anomala* and the years of evaluation needed to identify resistant segregates, combined with the associated expenses of growing large populations of trees in the field to maturity for nut evaluations. It is also important to consider the horticultural qualities of a number of these new potential parents. The earliest breeding with *C. avellana* sources of EFB resistance involved 'Gasaway'. This was somewhat unfortunate from a horticultural perspective as 'Gasaway', besides its dominant *R*-gene, produces low yields of tiny (< 0.5 grams per kernel), oblong, late-maturing nuts. A modified backcross approach was adopted at OSU, leading to the release of 'Yamhill' from the BC_1 generation and 'Jefferson', 'Dorris', 'Wepster' and 'McDonald' from the BC_2 generation (Mehlenbacher et al., 2009, 2001, 2013, 2014).

We expect fewer generations to be needed to develop commercial-quality cultivars from these new sources of resistance. Of the 11 resistant accessions examined in this study, all but H3R12P62 and CRXR13P19 have round or nearly round kernels and most have kernels weighing close to 1.0 g, with H3R14P26 and H3R13P40 having 1.1 g and 1.3 g kernels, respectively, which puts them in the category of appropriate size for the confectionary kernel market (Mehlenbacher et al., 2009). As a point of reference, an acceptable cultivar for the hazelnut kernel market should have round-shaped kernels between 12-14 mm in diameter that are free of defects and weighing a minimum of 1.0 g with a kernel to shell ratio (kernel weight/total nut weight × 100) close to 50% . Further, H3R14P26, H3R13P40, and H3R10P88 have very good pellicle removal when roasted (Capik et al., 2013; data not shown), which is another important trait for the processing industry.

Nut and kernel traits of hazelnut have been shown to be under strong genetic control (Thompson, 1977; Yao and Mehlenbacher, 2000), and our nut evaluations support this claim. In 2014 and 2015, we evaluated nut and kernel characteristics of most of the resistant and tolerant trees from each progeny. While the use of pollen mixtures from plants grown in Oregon precluded a heritability analysis (EFB susceptible trees generally do not grow to maturity in New Jersey), our data shows that significant improvements were realized in this F_1 generation. Parent H3R14P26 has an average single kernel weight of 1.11 g and a ratio of kernel to shell of 39.7% (Capik et al., 2013). Based on nut samples from 66 trees of progeny 09605 (H3R14P26 x OSU #5) collected in 2015, the top 90th percentile for kernel size (7 individuals), when averaged, was 1.25 g (max 1.68 g) and the average kernel to shell ratio of the top 90% percentile for this trait was 49.7% (max 53.0%) (data not shown). These results demonstrate sizeable increases in these two important traits in just one generation (when crossed with superior susceptible male parents). As a further example, H3R10P88 has a very round, somewhat small kernel with a nearly acceptable average kernel size of 0.9 grams and a good kernel to shell ratio (50.3%). In evaluating 30 resistant/tolerant trees of progeny 09597 (H3R10P88 x OSU #6), 14 produced round kernels of 1.0 g or larger and seven have a kernel to shell ratio >50% with a maximum of 54.2%. Thus, nearly 50% of the resistant trees from this cross met or exceeded minimal quality requirements for these important nut traits, which ultimately provides a larger body of plants to select from to identify the rare individuals holding cultivar potential. Similar improvements were realized in most of the other progeny (data not shown), supporting their substantial value as diverse breeding parents beyond their sources of potential new *R*-genes and assorted S-alleles.

Conclusions

The progeny of 11 new EFB-resistant European hazelnut accessions were evaluated for response to disease under high pressure over multiple years, and results showed each conveyed resistance to their offspring. Segregation patterns suggest control by only one or two major genes, as most progenies closely fit either a resistant: susceptible ratio of 1:1 or 1:3. The divergent origins of the plants, supported by the SSR fingerprinting data (Muehlbauer et al., 2014b), show that the 11 accessions are diverse. This fact, combined with the different segregation patterns observed in the study, indicate that there may be multiple sources (genes) for resistance present among the parents. Four additional EFB-selections from the same seed collection expedition were identified at OSU that further increase the pool of plants available for breeding. Overall, these findings highlight and document the substantial value of the new hazelnut germplasm from Russia and Crimea and signify that this material merits further study, including *R*-gene mapping as well as use in developing improved EFB-resistant cultivars.

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