IDENTIFYING AND EVALUATING EASTERN FILBERT BLIGHT RESISTANT HAZELNUTS (*CORYLUS* SPP.) IN NEW JERSEY

By

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ABSTRACT OF THE THESIS Identifying and Evaluating Eastern Filbert Blight Resistant Hazelnuts (*Corylus* spp.) in New Jersey by JOHN MICHAEL CAPIK Thesis Director:

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Eastern filbert blight (EFB), caused by the fungus Anisogramma anomala (Peck) E. Müller, is a destructive disease of European hazelnut (*Corylus avellana*). While the wild North American hazelnut, C. americana, only experiences minor symptoms, commercially grown C. avellana is extremely susceptible. Anisogramma anomala, whose range includes much of the U.S. east of the Rocky Mountains, is considered to be the main impediment to commercial hazelnut production in the East. As such, identifying and developing resistant C. avellana germplasm is critical to establishing an industry in this region. To support this goal, several research projects were undertaken. In the first study, 193 clonal hazelnut accessions spanning multiple Corylus species and inter-specific hybrids were examined for their disease response to EFB in New Jersey. In summary, despite the fact that many of the plants were shown to be resistant in Oregon, some accessions developed EFB in New Jersey. These results support previous work that suggests different isolates of the pathogen are present in the eastern U.S., and resistance may not hold up unilaterally. A second study included searching for new sources of resistance to EFB. New hazelnut germplasm was collected from Russia, Poland, and Ukraine and exposed to EFB. After at least five years of exposure, plants were rated for

the presence of EFB. At completion, 76 trees from 24 seed lots were found to be free of EFB with several trees that also produced excellent quality kernels. The final study was predicated on evaluating known resistant plants for their flowering phenology in New Jersey. Phenological timing of flowering in hazelnuts is critical to ensure complete pollination and high crop yields. Nineteen hazelnut accessions were evaluated compared to daily temperatures over 4 years. Results showed that the accessions followed a similar progression of bloom each year (both staminate and pistillate flowers), which allowed their placement into Early, Mid-, and Late flowering groups. These findings represent the first efforts to report on flowering and bud break phenology in New Jersey, where the winter climate is colder and more variable than that of Oregon and other commercial hazelnut growing regions.

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Literature Review

The genus *Corylus* is made up of a varied group of nut-producing woody trees. *Corylus avellana*, the European hazelnut, is the most economically significant of these, although there are believed to between 9-25 different species in the genus, with current research proposing 11-13 species in four subsections (Erdogan, 1999; Erdogan and Mehlenbacher, 2000a, 2000b; Thompson et al., 1996). Almost all commercial hazelnut production occurs in areas with moderated, Mediterranean climates. The world's primary producer of hazelnut is Turkey (430,000 t in 2011), which is responsible for around 58% of total production. The next largest producers are Italy (128, 940 t), the U.S. (34, 927 t), Azerbaijan (32,922 t), and the Republic of Georgia (31,100 t). Spain, China, France, and Iran also produce notable crops (FAOStat, 2013). Despite most production occurring in moderate climates, *C. avellana* can be found as far north as Norway and the Ural Mountains, and the various other species can be found growing in temperate regions around the world (Mehlenbacher, 1991a).

Production of *C. avellana* in the eastern U.S. has been attempted since the colonial age. It has been blocked by two major impediments: the colder climate compared to European production regions, and the existence of the fungal disease eastern filbert blight (EFB) (Fuller, 1908; Halsted, 1892; Johnson and Pinkerton, 2002; Thompson et al., 1996). EFB, caused by *Anisogramma anomala* (Peck) E. Müller, an obligate, biotrophic, ascomycetous fungus, is native to the eastern U.S. and is hosted by *C. americana*, the wild American hazelnut. It is known to only infect plants of the *Corylus* genus, and has not spread beyond the borders of North America. On *C. americana*, EFB only causes minor damage. However, most plants of *C. avellana* are

extremely susceptible, and face serious, perennial cankers that girdle stems and cause branch dieback, leading to eventual death within 4-8 years of infection (Fuller, 1908; Johnson and Pinkerton, 2002; Pinkerton et al., 1993; Weschcke, 1954). Ascospores from mature EFB infections are released during extended intervals of rain, spread by wind and rain-splash, and penetrate new, actively growing shoot tips, typically in the spring. At this point, the fungus undergoes a latent period of 12-15 months, where it expresses no symptoms. After this latent period ends (following a cycle of dormancy in the host plant), cankers begin to emerge from the bark of infected stems, with tiny, black, ovular stromata seen by late summer/early fall (Johnson and Pinkerton, 2002). These stromata produce more ascopores, and the process begins anew the proceeding spring.

In an attempt to establish commercial production in the East, breeding work began in the early 1900s to develop plants adapted to the region that expressed genetic resistance to EFB. Initial efforts focused on creating hybrids between *C. avellana* and *C. americana*. These efforts were started by several breeders, notably J.F. Jones, C.A. Reed of the U.S. Department of Agriculture (USDA) in Beltsville, MD, and G.H. Slate of the New York Agricultural Experiment Station in Geneva, NY. All three primarily used 'Rush', an EFB-resistant *C. americana* selection from Pennsylvania, as their wild parent. While these breeders made valuable progress in improving cold tolerance and nut quality, no commercially viable cultivars were ever produced (Molnar, 2011; Thompson et al., 1996). Some of their breeding selections are still available today from the USDA National Clonal Germplasm Repository (NCGR) (USDA, 2013). Additional grower reports and research efforts have shown that some of the 'Rush' hybrids and 'Rush' itself have remained free of EFB over many decades of exposure, demonstrating some of the potential for breeding cold-hardy, EFB resistant hazelnuts adapted to the East. The efforts of these pioneers have been built upon by a number of nurseryman and private breeders over the years. The most notable include C. Weschcke, C. Farris, J. Gordon, and J. Gellatly (Farris, 1974, 1989, 2000; Gellatly, 1950, 1966; Gordon, 1993; Weschcke, 1954). Their efforts have expanded the breeding stock and genetic resources available to current breeders, and some private breeders still remain who are currently working towards adapted, EFB-resistant hybrid plants for the eastern U.S. and colder regions (Molnar et al., 2005).

Although commercial hazelnut production in the East has been mostly prevented by EFB, historically the causal fungus was not found west of the Rocky Mountains (the western edge of *C. americana's* native range). This, in addition to a complementary climate, allowed hazelnut production to flourish in the Pacific Northwest for over a century (Thompson et al., 1996). Unfortunately, EFB was introduced into southwestern Washington State in the late 1960s (Davison and Davidson, 1973). As control measures for the disease had not yet been established, EFB spread quickly throughout Washington and into Oregon, where 99% of the current U.S. crop is produced. Although control measures have since been developed, they add great expense to an otherwise low-input crop because of the cost of scouting for cankers, spraying fungicides, and therapeutic pruning (Johnson et al., 1996; Julian et al., 2008, 2009). Control of the disease is not always completely effective and, when combined with the high costs, this makes genetic disease resistance the best economic, long-term solution to the problem of EFB management (Mehlenbacher, 2005).

In the 1960s, a hazelnut breeding program was started at Oregon State University (OSU) to study *C. avellana* in order to develop improved plants for the local industry (Thompson et al., 1996). After the introduction of EFB into Washington, in 1975, a disease resistant C. avellana pollinizing cultivar 'Gasaway' was found in the middle of an infected orchard full of 'DuChilly', a highly susceptible production cultivar (Cameron, 1976). It was later determined that 'Gasaway' transmitted resistance to its progeny in a 1 resistant: 1 susceptible ratio, signifying that is heterozygous for a dominant resistance allele at a single locus (Mehlenbacher et al., 1991a, 2004). Since its discovery, 'Gasaway' has been used heavily in OSU breeding efforts, and is the source of resistance in several recently released EFB-resistant nut producers and pollinizers from OSU. These include the production cultivars Santiam (Mehlenbacher et al., 2007), Jefferson (Mehlenbacher et al., 2011), and Dorris (Mehlenbacher et al., 2013), and the pollinizers Delta (Mehlenbacher and Smith, 2004), Gamma (Mehlenbacher and Smith, 2004), and Theta (Mehlenbacher et al., 2012), among others. In Oregon, these cultivars can be grown without additional fungicidal sprays and are expected to greatly reduce production costs (Julian et al., 2009). Disease-resistant hazelnut cultivars, which have also been bred for higher nut quality and increased yields, are helping to expand and improve the Oregon hazelnut industry, which had been in decline since the introduction of EFB several decades earlier (S.A. Mehlenbacher, personal communication).

Although 'Gasaway' provided a strong starting point for resistance breeding, breeders at OSU did not want to rely on only one single gene and utilized their extensive germplasm collection and that of the NCGR to search for additional sources of resistance. Researchers inoculated hundreds of cultivars and clonal breeding selections with the EFB fungus and observed them for their response. After over a decade of work, it was determined that, although most of the plants were highly susceptible, a few accessions demonstrated a high level of tolerance or resistance to infection. These plants came from a variety of backgrounds, including *C. avellana* as well as other *Corylus* species and hybrids with *C. avellana* (Chen et al., 2005, 2007; Coyne et al., 1998; Lunde et al., 2000; Sathuvalli et al., 2010a, 2011). Complicating the scenario, however, is the fact that the EFB outbreak in Washington and Oregon is believed to stem from a single-point introduction of the pathogen (Pinkerton et al., 1998). The resistance screening conducted at OSU utilized only local isolates, which are believed to be of limited genetic diversity (Cai et al., 2013; Muehlbauer et al., 2013). The question still remained of how these plants found to be resistant in Oregon would hold up within the pathogen's native range.

In an attempt to address this question, researchers at Rutgers University collected isolates of *A. anomala* from many locations across its native range and inoculated clonal trees from Oregon. They reported that some accessions and cultivars found to be resistant in Oregon developed cankers when challenged in the greenhouse with isolates of *A. anomala* originating in the eastern U.S., including isolates from Michigan and New Jersey (Molnar et al., 2010a). These plants included 'Gasaway' itself in addition to the 'Gasaway' offspring VR20-11. Corroborating the greenhouse inoculations, field studies later confirmed the infection of 'Gasaway' and 'VR20-11' in New Jersey under natural field conditions (2010b). It should be noted, however, that these plants still maintained a useful level of tolerance, suggesting that the *R*-gene was not being fully overcome (T. Molnar, personal communication). This research suggests that plants deemed resistant in Oregon may not necessarily hold up in regions where the pathogen is native and different

isolates may be found. As such, a much wider collection of plants should be evaluated in the eastern U.S., including *C. avellana* and other *Corylus* species, to better identify more durable sources of resistance. These result also support that plants should be tested in new regions before being recommended to growers.

Further, there has been a dearth of systematic, recorded research on the EFB resistance or susceptibility of most wild species of hazelnut. Although *C. americana* and other species (like *C. heterophylla*, the Asian hazelnut) have been reported to possess high levels of EFB tolerance or resistance, most of these reports have either been anecdotal, used small sample sizes and limited selections, or were conducted outside of the native range of the pathogen (Chen et al., 2007; Coyne et al., 1998; Lunde et al., 2000; Sathuvalli and Mehlenbacher, 2011; Sathuvalli et al., 2010). This lack of systematic evidence reflects the need to observe and describe the disease response of hazelnuts in the region where they are to be grown, especially if they intend to be used in an interspecific hybridization program to develop plants adapted to regions within the endemic range of *A. anomala*.

Discovering disease resistance within the OSU and NCGR germplasm collections signifies that *C. avellana*, although most plants are highly susceptible to EFB, can carry a high level of genetic resistance. This has led to increased germplasm collection and screening efforts, especially in parts of the world where greater access in now available. Molnar et al. (2007) collected hazelnut germplasm from Russia and Ukraine. They grew out over 600 seedlings from 32 different seed lots, inoculated the plants with EFB, and observed them over several years. From this effort, thirteen seedlings from eight different seed lots were identified that showed little or no EFB after 3 years of exposure.

Of the remaining seedlings, over 98% had multiple cankers with nearly 90% experiencing severe symptoms or death. The resistant seedlings were screened for the presence of Random Amplified Polymorphic DNA (RAPD) markers linked to the 'Gasaway' gene to determine whether there was any relation. The RAPD markers were developed and are routinely used by researchers at OSU and are routinely used to help identify seedlings segregating for the presence of the 'Gasaway' gene (Mehlenbacher et al., 2004, 2006). Although one seedling was inconclusive, the remaining 12 failed to generate any of the 'Gasaway'-linked RAPD markers, showing them to be genetically distinct.

This collection effort demonstrates the positive benefits that can come with exploring foreign, untested germplasm in new regions. New, possibly novel resistance genes from diverse backgrounds are now available for incorporation in hazelnut breeding programs. Some of these genes can even be found in plants expressing good-quality nut characteristics, like large, well-filled kernels, especially compared to 'Gasaway' which produces extremely small, poor-quality nuts and has required several generations of breeding to produce commercial quality cultivars. Collections of germplasm from OSU have also resulted in new plants expressing resistance to EFB, including OSU 759.010 from the Republic of Georgia (Sathuvalli et al., 2011), 495.072 from southern Russia (Sathuvalli et al., 2010a) and Crvenje and Uebov from Serbia (Sathuvalli et al., 2010a). Demonstrating the novelty of the new resistance genes, genetic mapping efforts have shown that the EFB genes from 'Gasaway', 'Ratoli', and OSU 759.010 are located on different linkage groups [OSU 759.010 = linkage group 2 (Sathuvalli et al., 2010b)]. In

theory, these *R*-genes can be pyramided into one genotype to possibly confer a more durable form of resistance. Thus, collecting and studying plants from foreign regions can allow for the utilization of a greater diversity of germplasm and can often result in the discovery of novel traits that expand the possibilities available to breeders.

Establishing hazelnut production in a new region requires more than just EFBresistant, well-adapted plants. Production protocols need to be developed, although the standard Oregon field practices should be able to be adapted to the East (Olsen, 2013a). Another area that must be explored is pollination. Since hazelnuts are monoecious and self-incompatible, genetic compatibility and timing of pollination is critical to ensure high, consistent yields (Mehlenbacher et al., 2004, 2009). Hazelnuts exhibit a sporophytic self incompatibility system. This system is controlled at a single locus with multiple S-alleles deciding compatibility (Mehlenbacher, 1997; Olsen et al., 2000; Thompson, 1979). Allelic dominance or co-dominance is signified in the pollen, while all known S-alleles have been found to be co-dominant within the pistil (Mehlenbacher, 1997; Mehlenbacher and Thompson, 1988).

Hazelnuts are wind pollinated and bloom during the winter, and flowering phenology is highly climate-dependant. In mild, Mediterranean-like climates like those of the main commercial production regions, hazelnuts are typically protandrous, while in colder climates, protogyny is more common (Germain, 1994; Mehlenbacher, 1991b; Olsen et al., 2000; Piskornik et al., 2001). Thus, it is expected that a plant's behavior in Oregon may be very different than that of a plant in the eastern U.S., where the winter climate is much colder and also much more variable. In Oregon, the main pollination period falls between January and February (Olsen, 2013b), while in New Jersey most pollination occurs in early March (Capik, data not shown). The timing of staminate flowers (catkins) is especially important in colder regions, as catkins are generally more susceptible to cold than female flowers or vegetative buds (Hummer et al., 1986; Thompson et al., 1996). Colder regions are also expected to have delayed bud break and compressed windows of flowering (Črepinšek et al., 2012; Germain, 1994; Olsen et al., 2000; Piskornik et al., 2001; Solar and Stampar, 2009; Thompson et al., 1996). In areas with more variable climates, catkins may quickly respond to warm spells during the winter, increasing their susceptibility to cold injury, especially with wind (MacDaniels, 1964; Slate, 1933).

Cold tolerance in hazelnuts is not a topic that has been particularly well researched, but some studies have been done. Slate (1933) reported on several hazelnut cultivars after an observing a large amount of winter injury in Geneva, NY. He found that cultivars like Cosford, Early Globe, Medium Long, Red Lambert, Winkler, and Rush, among others, experienced significantly less catkin injury than over 40 other accessions, including widely used production cultivars Barcelona and Daviana. The hardy plants were placed in a group that experienced less than 20% catkin injury. He surmises that the winter injury was not caused by extreme cold, but instead by cumulative desiccation and early flowering. He notes that the winter climate was extremely mild, which may have spurred catkins to elongate earlier than normal and become more susceptible to winter injury. His earlier reports also note that 'Medium Long', 'Early Globe', and 'Red Lambert' showed less catkin winter injury than other plants (Slate, 1929, 1930).

Hummer et al. (1986) did controlled freezing experiments on stems, female flowers, and catkins of various *Corvlus* species, focusing mainly on *C. avellana*. As the researchers were using a controlled freeze chamber, they were able to take samples during all winter months. As expected, plant parts were less hardy in the warmer months (October, February) and hardier during the coldest months (December, January). At maximum hardiness, it was determined that vegetative buds of most C. avellana plants tested (13 production cultivars and 5 others) were hardy down to between -30 °C and -40 °C in the coldest months. Female flowers and catkins were slightly less hardy, typically down to -20 °C to -30 °C, although there were outliers on either side (Hummer et al. 1986). Elongating or pollen-shedding catkins were not tested, although cold-damaged catkins shed pollen up until severe injury was experienced. Their evaluations were also conducted primarily through visual observations. Tissues were dissected and rated (1-4, with 1 being natural color and 4 representing intense browning and mold), with ratings of 3 or above considered "dead". It is unclear if rooted plants in the field would behave in a similar manner.

A similar study conducted by Chozinski (1995) showed comparable results. Nearly 40 *C. avellana* cultivars, along with several other species and hybrids including *C. heterophylla*, *C. cornuta*, *C. avellana* × *C. colurna*, and *C. americana* × *C. avellana*, were sampled by collecting 1-year-old stems at several dates over the winter and subjecting them to controlled freezing. Vegetative buds, female flower buds, and catkins were all tested by visual evaluation, and stems were further tested by measurement of electrolyte leakage. They, like Hummer et al. (1986), determined that vegetative buds were the most cold hardy, followed by female flower buds and catkins. It was also found that vegetative buds keep their cold acclimation longest, as they likely have the highest post-rest heat requirements. Female buds were found to be less vulnerable when at the red dot stage (stigmas just beginning to emerge) than later stages of floral development, and catkins were observed to be highly sensitive to cold once elongation had begun. Field observations showed that a female flower could experience some stigma tip death, but stigmatic surfaces that have not yet been exposed can stay alive and receptive to pollen. It was also determined that using electrolyte leakage does not give a clear gauge of lethal cold temperatures. Overall, there was more variation in cold responses in the *C. avellana* plants than the other *Corylus* species and hybrids, although significantly more pure *C. avellanas* were tested.

Establishing commercial hazelnut production in a new region like the eastern U.S. requires many factors, the most critical being the development of EFB-resistant trees that are well-adapted to the area. Assessing resistance from known plants and discovering novel resistance genes within untested germplasm are two methods to increase the availability of EFB-resistant material for breeders to work with. Utilizing foreign germplasm may also yield resistant plants with improved-quality nuts to help speed up the breeding process. However, other components, like evaluation of cold hardiness for winter survival and flowering phenology to provide complete pollination, are still needed to ensure successful, productive annual crops on a yearly basis. Researching these topics in New Jersey is necessary to establish a baseline for the behavior of these plants, so that future efforts have a foundation to build upon.

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Assessment of Host (*Corylus* sp.) Resistance to Eastern Filbert Blight in New Jersey John M. Capik and Thomas J. Molnar^{*}

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Abstract. One hundred ninety-three clonal accessions of *Corylus*, including species and various interspecific hybrids of *C. avellana*, *C. americana*, *C. heterophylla*, *C. colurna*, and *C. fargesii* were assessed for their response to field exposure to the eastern filbert blight (EFB) pathogen, *Anisogramma anomala*, in New Jersey, where the fungus is native. Plants were obtained from the U.S. Department of Agriculture Agricultural Research Service (USDA-ARS) National Clonal Germplasm Repository (NCGR) and Oregon State University (OSU), both in Corvallis, OR, the University of Nebraska, Lincoln (UNL), and the National Arbor Day Foundation. Additional plant material was acquired from the Morris and Holden Arboreta and from private nurseries in Amherst, NY, and Niagara-on-the-Lake, ON, Canada. The accessions were chosen based on their resistance to EFB in Oregon, a region where *A. anomala* is not native, or anecdotal reports and grower observations of tolerance or resistance to the disease. Trees were

planted in the field from 2002 through 2009 in New Jersey where they were exposed to EFB yearly through field inoculations and natural spread. In Jan. 2012, they were visually evaluated for the presence of EFB. The cankers were measured, and the proportion of diseased wood was calculated for susceptible trees. Nearly all accessions reported to be resistant to EFB in Oregon maintained at least a useful level of tolerance in New Jersey, with a number remaining free of cankers. However, several accessions developed small to medium-size cankers and showed branch die-back, including offspring of C. avellana 'Gasaway'. Most C. americana and C. heterophylla accessions remained free of EFB, although variation in EFB response was found in hybrids of these species with C. avellana, ranging from no signs or symptoms to severe EFB. Nearly half of the C. colurna × C. avellana hybrids developed cankers, while each of the C. fargesii accessions and most grower selections developed in eastern North America remained free of EFB. The results document the existence of a wide diversity of Corylus germplasm that expresses resistance or a high level of tolerance to EFB in New Jersey, and confirms previous reports that C. americana is highly resistant to the disease. Interestingly, most C. heterophylla and the C. fargesii were also found to be resistant, despite originating in Asia where A. anomala has not been found. The various interspecific hybrids show the potential for incorporating EFB resistance from wild species through breeding. The results provide further evidence of differences in disease expression in Oregon and New Jersey, where isolates differ and disease pressure may be higher.

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Introduction

The genus Corylus represents a diverse group of temperate woody plants, all of which produce edible nuts. The genus comprises anywhere from 9–25 species depending on the taxonomic study, with current revisions suggesting 11–13 polymorphic species assigned to four subsections (Erdogan, 1999; Erdogan and Mehlenbacher, 2000a, 2000b; Thompson et al., 1996). In the genus, C. avellana is of the greatest economic importance due to its large nuts and high-quality kernels. Commercial production is currently restricted to regions with moderate, Mediterranean-like climates, despite having a very wide native range with a northern limit that extends from latitude 68°N in Norway to Helsinki to the Ural Mountains (Mehlenbacher, 1991). Turkey produces about 70% of the world's crop, totaling 888,328 Mg in 2010 [Food and Agriculture Organization of the United Nations (FAO), 2012]. Turkey is followed by Italy, which produces around 15% of the total, and the U.S., which is responsible for 3% to 5%. Other countries growing noteworthy crops include Azerbaijan, Spain, Georgia, Iran, France, and China (FAO, 2012). Ninety-nine percent of the U.S. crop is produced in the Willamette Valley of Oregon (Mehlenbacher and Olsen, 1997).

European hazelnut production has been attempted in the eastern U.S. since colonial times. However, the relatively cold climate—and more significantly, an endemic disease called eastern filbert blight caused by Anisogramma anomala —made these attempts futile (Halsted, 1892; Morris, 1915, 1920; Thompson et al., 1996). The fungus, an obligate, biotrophic ascomycete in the order Diaporthales, infects only plants of *Corylus*. It is native to the eastern half of North America, associated with its natural host C. americana, on which it has been reported to cause only minor damage (Fuller, 1908; Weschcke, 1954). However, the disease causes severe perennial cankers that lead to branch dieback and eventual death of nearly all commercially important cultivars of C. avellana within 4 to 8 years of exposure (Johnson and Pinkerton, 2002; Pinkerton et al., 1993). The causal fungus, whose ascospores penetrate actively growing shoot tips in the spring during periods of rain, expresses no disease symptoms in the host plant in the first year of infection. It is only after the host plant cycles through a period of chilling and dormancy that the cankers erupt in the bark of stems with conspicuous, football-shaped stromata visible by late summer (Johnson and Pinkerton, 2002).

Efforts began in the early 1900s to develop better-adapted, disease-resistant hazelnuts for the eastern U.S. through hybridizing *C. americana* with *C. avellana*. This work was pioneered by the nurseryman J.F. Jones of Lancaster, PA and was continued by C.A. Reed of the U.S. Department of Agriculture (USDA) at Beltsville, Maryland, and G.H. Slate of the New York Agricultural Experiment Station in Geneva, NY. Their breeding strategies were similar as they hybridized various *C. avellana* cultivars with *C. americana* 'Rush', a wild hazelnut selected in southeastern Pennsylvania (Crane et al., 1937; Molnar, 2011; Reed, 1936; Slate 1961; Thompson et al., 1996). While these early

breeding efforts used only a narrow germplasm base and were discontinued before commercially viable cultivars were developed, progress was made in combining EFB resistance, cold hardiness, and improved nut size. Some of the resulting hybrid plants remain available today from private nurseries and many are also held in the USDA-ARS NCGR in Corvallis, OR (USDA, 2011). Further, grower reports in the east suggest a number of selections related to *C. americana* 'Rush' have remained free of EFB over many decades of exposure, supporting a realistic potential to breed hazelnut plants adapted to colder regions that express durable EFB resistance. Fortunately, private breeders and nurserymen in Wisconsin (Weschcke, 1954), Minnesota (Rutter, 1987), Michigan (Farris, 2000), and New York (Gordon, 1993), as well as British Columbia (Gellatly, 1964, 1966) and Ontario (Grimo, 2011), Canada expanded on the early attempts to develop better adapted, EFB-resistant hazelnuts. The results of their efforts have contributed to the genetic resources currently available for breeding, with several private individuals still actively working towards this goal.

The lack of EFB west of the Rocky Mountains and a more amenable climate provided the environment for commercial hazelnut production to thrive in Washington and Oregon since its establishment in the late 1800s (Thompson et al., 1996). However, this scenario changed dramatically with the inadvertent introduction of *A. anomala* into southwestern Washington in the 1960s (Davison and Davidson, 1973). Since that time, EFB has eliminated much of the production in Washington and has subsequently spread throughout the Willamette Valley of Oregon, where its control (scouting for cankers, pruning, and application of fungicides) significantly increases production costs (Johnson et al., 1996; Julian et al., 2008, 2009). As control methods are not 100% effective and

hazelnuts are traditionally a low-input crop, genetic resistance would be the most economical, long-term means for disease management. In 1975, C. avellana 'Gasaway', an obsolete pollinizer, was discovered to be free of EFB in the middle of a heavily infected orchard of 'DuChilly' in Washington (Cameron, 1976). Despite its low yields of tiny, poor-quality nuts, 'Gasaway', in crosses with susceptible selections, transmits resistance to half of its offspring, suggesting that it is heterozygous for a dominant resistance allele at a single locus (Mehlenbacher et al., 1991, 2004). Since its discovery, 'Gasaway' has been used extensively in breeding efforts at OSU, culminating after more than 30 years in the release of the improved, EFB-resistant nut producing-cultivars Santiam, Yamhill, and Jefferson and several EFB-resistant pollinizers (Mehlenbacher and Smith, 2004; Mehlenbacher et al. 2007, 2009, 2011). They can be grown without fungicides and are predicted to significantly reduce production costs in Oregon (Julian et al., 2009). The ability to grow EFB-resistant cultivars, which have also been selected for improved nut quality and yields, is leading to an expansion and reinvigoration of the Oregon hazelnut industry, after several decades of decline (S.A. Mehlenbacher, personal communication).

Because of concern about the long-term durability of a single gene for resistance, research at OSU included screening many hundreds of plants held in their germplasm collections and that of the NCGR for their response to inoculations with *A. anomala*. While most plants were highly susceptible, the work at OSU, spanning more than two decades, identified a number of new EFB-resistant *C. avellana* accessions from a diversity of origins as well as resistant accessions of other *Corylus* species and interspecific hybrids, several of which are now being incorporated into breeding efforts (Chen et al., 2005, 2007; Coyne et al., 1998; Lunde et al., 2000; Sathuvalli et al., 2010, 2011a). Complicating the situation, however, is that plants identified as resistant in Oregon were challenged only with isolates of A. anomala found there, which are believed to originate from a single point introduction (Pinkerton et al., 1998). The question then remains of how these Oregon-resistant accessions would respond when exposed to A. anomala in the eastern U.S., where the fungus is native and a greater diversity of isolates would be expected. Shedding some light on this topic, recent greenhouse inoculations as well as field evidence in New Jersey using geographically different isolates of A. anomala, have shown that some cultivars and selections identified as resistant in Oregon—including 'Gasaway' and some of its offspring—may not hold up to multiple isolates of the pathogen (Molnar et al., 2010a, 2010b). While more work is needed to better understand the genetic diversity, population structure, and range of pathogenicity within A. anomala, these findings suggest that quarantine efforts to restrict the movement of *Corylus* material from the east into the Pacific northwestern U.S. be maintained to prevent the introduction of new A. anomala isolates. They also suggest it may be necessary to evaluate germplasm in and across the eastern U.S. to identify sources resistant to a diversity of A. anomala isolates.

Further, while historical reports and more recent research provide evidence that native *C. americana*, and to a more limited extent *C. heterophylla*, is tolerant or resistant to EFB (Coyne, et al., 1998; Fuller, 1908; Morris, 1920; Weschcke, 1954), these reports are based on anecdotal observations, a limited number of plant accessions assessed in trials, and/or exposure to the pathogen outside of its natural range. Therefore, as efforts increase to breed cultivars with durable EFB resistance and wider adaptation (Molnar et

al., 2005), there remains a need to better characterize EFB resistance found within wild *Corylus* germplasm and existing interspecific hybrids.

In this study, a wide diversity of clonal *Corylus* accessions, including pure species and various interspecific hybrids of *C. avellana*, *C. americana*, *C. heterophylla*, *C. colurna*, and *C. fargesii* were exposed to *A. anomala* in New Jersey over a span of 10 years through field inoculations and by natural spread of the disease. The accessions were obtained from the NCGR, OSU, and the UNL, as well as the National Arbor Day Foundation, Nebraska City, NE, the Morris Arboretum in Philadelphia, PA, the Holden Arboretum in Kirtland, OH, and private nurseries in Amherst, NY and Niagara-on-the-Lake, ON, Canada. The objectives were to evaluate these accessions for their response to EFB in the field to: 1) compare the EFB response observed in New Jersey to that previously reported in Oregon, 2) study wild accessions held in the NCGR and OSU collections that have not been previously exposed to EFB, and 3) validate anecdotal reports and grower observations of resistance in hybrid *Corylus* selections and cultivars in the eastern U.S.

Materials and Methods.

Plant material. Clonal hazelnut material was obtained or purchased from cooperating institutions or nurseries as bare-root dormant layers or scion wood, with scion grafting performed at Rutgers University. The accessions chosen for study were previously identified as resistant or tolerant to EFB at OSU and/or through grower observations in other regions, or were chosen based on anecdotal information suggesting that select clones, *Corylus* species, or interspecific hybrids (sometimes of unknown

parentage) were tolerant of EFB. Known EFB-susceptible cultivars were also included in the trials as controls to assess the presence of EFB on the farm and to later provide a reservoir of inoculum. The plant material evaluated, including species (when known), cultivar name, origin, date of establishment, and number of trees in the field, is presented (Tables 1 and 2). As a point of reference, some general attributes of the species evaluated are also provided in Table 3 and Figs. 1 and 2. Grafted plants were propagated in the greenhouse in March of each year using dormant C. avellana rootstocks obtained from nurseries in Oregon. Bare-root dormant layers were typically potted in the greenhouse into 3.7- or 7.4-L plastic containers. All plants were grown in a peat-based planting medium (Promix BX; Premier Horticulture, Rivière-du-Loup, Quebec) and maintained at 24/18 °C (day/night) with 16-h daylengths. Plants remained in the greenhouse until June, when they were moved outside under shade for acclimation prior to field planting in September or October. Most plants were field planted the same year they were propagated or obtained, although some were held over one additional year before planting. The location of the study was the Rutgers University Vegetable Research and Extension Farm in North Brunswick, New Jersey. In 2002, a replicated planting was established, consisting of 18 trees each of 8 accessions found to be resistant to EFB in Oregon, as well as the susceptible controls 'Barcelona' and 'Tonda di Giffoni' (Table 1 and 2). In subsequent years, plantings were smaller due to limited available field space and/or propagation wood for grafting. Thus, most other accessions were only represented by one or two trees. Suckers from the base of the grafted trees were removed several times per year, while layered trees were allowed to grow naturally, with little wood

removed from their canopies over the study to allow multiple infection points and to avoid removal of the infected branches needed for disease development and assessment.

Exposure to eastern filbert blight. All plants were exposed to EFB on a yearly basis, which included natural spread of the disease from infected susceptible trees in the trials, as well as from adjacent plots containing hundreds of susceptible trees with sporulating cankers. In addition, field inoculations, which consisted of tying infected hazelnut stems into the canopies of the trees each spring, as described in Molnar et al. (2007), were made on nearly all plants annually. Infected stems were collected from susceptible trees growing at the Rutgers University Vegetable Research and Extension Farm.

Evaluation of disease response. In Jan. 2012, a thorough visual inspection for the presence of EFB cankers was carried out (193 accessions for a total of 455 trees) and disease incidence was recorded. On each tree exhibiting EFB, the total number of individual cankers was counted and each canker was measured to calculate the average canker length and the total amount of diseased wood per tree. Branches that were dead at the time of measurement and contained obvious EFB cankers were included in the calculation of the total amount of diseased wood per tree. Then, the total amount of shoot growth (all branches over 2.5 cm in diameter) per tree was measured and used to calculate each tree's proportion of diseased wood. Of the 18 trees of each of the 10 accessions planted in 2002, disease incidence was recorded for all. Of those accessions expressing EFB, five randomly selected trees were assessed for the canker attributes described above with results subjected to analysis of variance (PROC MIXED) in SAS (version 9.2; SAS Institute, Cary, NC). In other cases where multiple trees of a

susceptible genotype were available, averages for the canker attributes were calculated (Table 1).

Results and Discussion

Corylus avellana. All trees of known EFB-susceptible accessions, amounting to eight cultivars totaling 50 trees planted over the years 2002 to 2009, developed disease (Table 1). These included 'Tonda di Giffoni' and 'Sacajawea', which express a high level of quantitative resistance to EFB in Oregon (Mehlenbacher et al., 2008; Pinkerton et al., 1993). Besides the known susceptible accessions, the remaining *C. avellana* evaluated here were first described as resistant to EFB at OSU. Of these, 10 accessions remained free of cankers and eight developed EFB. They are discussed in more detail below.

'Gasaway' and its offspring. Ten accessions carrying the dominant 'Gasaway' resistance allele, including 'Gasaway' itself, were evaluated in this study. Of these plants, 'Gasaway', VR 20-11, 'Gamma', 'Yamhill', and 'Jefferson' developed EFB, while 'Zimmerman', 'Santiam', 'Delta', 'Epsilon', and 'Theta' remained free of disease (Tables 1 and 2). 'Gasaway', VR 20-11, and 'Zimmerman' were included in the 2002 replicated trial (18 trees each) with significant differences observed in their disease incidence and severity. All 18 trees of both 'Gasaway' and VR 20-11 [('Barcelona' × 'Compton') × 'Gasaway'] developed EFB. Interestingly, the proportion of diseased wood based on five trees of each from the 2002 planting was 0.16 for both accessions. However, the individual and mean canker length differed with average 'Gasaway' cankers (14.4 cm) shorter than those on VR 20-11 (22.4 cm) (P<0.0001), suggesting 'Gasaway' is able to restrict the development of EFB to a greater degree than VR 20-11. Non-sporulating

cankers attributed to EFB were also observed on both cultivars. They were counted and measured separately, although they were later combined to calculate the averages for canker length, total amount of diseased wood per tree, and the proportion of diseased wood for each tree, because they were causing visible damage, including stem cracking and tissue death. Similar to the typical EFB cankers, the sunken, non-sporulating cankers differed in average length between 'Gasaway' and VR 20-11 at 17.9 and 27.4 cm, respectively. These field results are congruent with earlier greenhouse inoculations with A. anomala, where both accessions developed typical EFB on some trees, although 'Gasaway' was only infected by an isolate from Michigan, expressing typical EFB and sunken, non-sporulating lesions (Molnar et al., 2010a). As a point of comparison, the average canker length and proportion of diseased wood for 'Barcelona' and 'Tonda di Giffoni' from the same 2002 planting was 61.9 cm and 0.67, and 24.5 cm and 0.39, respectively. 'Gasaway' expressed significantly smaller cankers and less proportion of diseased wood than both 'Barcelona' and 'Tonda di Giffoni'. VR 20-11 and 'Tonda di Giffoni' shared a similar average individual canker length, although the proportion of diseased wood of VR 20-11 was considerably less (P < 0.005). Despite the presence of many small cankers on each tree of 'Gasaway' and VR 20-11, the level of tolerance appears useful and results in vigorous trees, in contrast to 'Barcelona' and 'Tonda di Giffoni' (Table 1). 'Barcelona' and 'Tonda di Giffoni' expressed considerable branch dieback and stem death that halted growth of the plants, whereas 'Gasaway' and VR 20-11 continued to grow vigorously since being planted. No branch dieback or dead stems (over 2.5 cm) were observed on any trees of 'Gasaway' and only a minor amount on VR 20-11 (data not shown). We hypothesize, however, that the minor dieback on VR 20-11

may be a contributing factor to the significant difference in average total tree growth between 'Gasaway' and VR 20-11, 128.4 and 90.4 m (*P*<0.003), respectively.

Interestingly, 'Zimmerman', a direct descendant of 'Gasaway' ('Gasaway' × 'Barcelona') (Gökirmak et al., 2009; Lunde et al., 2006) represented here by 18 trees also planted in 2002, developed no signs or symptoms of EFB. 'Zimmerman' also remained free of typical EFB after greenhouse inoculations with multiple isolates of *A. anomala*, although one tree developed a sunken lesion when exposed to the Michigan isolate (Molnar et al., 2010a).

Of the pollinizers 'Gamma', 'Delta', and 'Epsilon' (Mehlenbacher and Smith, 2004), all planted in 2006, only 'Gamma' developed EFB, expressed as one small (9.0 cm) canker. 'Theta', a more recently released pollinizer, remained free of EFB, although it was only planted in 2009. As such, strong conclusions cannot be drawn on its longterm resistance. However, this observation is noteworthy as the results of 'Theta' are in contrast to 'Yamhill' (Mehlenbacher et al., 2009) and 'Jefferson' (Mehlenbacher et al., 2011), also planted in 2009, where the one tree of 'Yamhill' and five of nine trees of 'Jefferson' developed EFB (Table 1). These finding are in line with recent reports from Oregon where some trees of 'Jefferson' were observed with very small EFB cankers in an orchard planted adjacent to a highly infected orchard. However, the cankers were described as having few to no sporulating stromata with some walled-off by callous tissue in subsequent years (Mehlenbacher et al., 2011; Pscheidt, 2011). Cankers observed here on 'Yamhill' contained typical stromata, while cankers on 'Jefferson' contained both typical stromata and non-sporulating sunken lesions. The variation in disease response between accessions carrying the 'Gasaway' resistance gene, exemplified by the difference between VR 20-11 and 'Zimmerman', suggests that modifying factors, in addition to the major 'Gasaway' allele, may be expressed in some plants that can augment their disease response. These factors have yet to be identified and studied. Similar variation in disease response has been observed in seedlings segregating for the 'Gasaway' resistance allele in field plots at Rutgers University (T.J. Molnar, unpublished). The ability to visualize the effects of modifying factors in addition to the major gene effect of the 'Gasaway' allele is probably due to a combination of the high disease pressure and the diversity of *A. anomala* present in New Jersey, a region where the fungus is native. Similar findings have not been reported from Oregon where the diversity of the fungus may be limited (Pinkerton et al., 1998), and where importation of other isolates could be devastating to the commercial hazelnut industry and threaten the world's largest *Corylus* collections, at the NCGR and at OSU, which contain many valuable but EFB-susceptible cultivars of *C. avellana*.

Eight additional *C. avellana* accessions previously shown to be EFB resistant in Oregon were evaluated. Five of these remained free of EFB, including 'Ratoli', OSU 408.040, OSU 495.072, 'Uebov', and Moscow #2. However, Moscow #1, OSU 759.010, and CCOR 187.001 developed EFB (Table 1).

'Ratoli', a minor cultivar from Tarragona, Spain (Lunde et al., 2000), represented by six trees, remained free of EFB through greenhouse inoculations using multiple isolates of *A. anomala* in a previous study (Molnar et al., 2010a). This cultivar was shown to transmit resistance to its progeny in a manner consistent with a dominant allele at a single locus (Molnar et al., 2009; Sathuvalli et al., 2011b), suggesting its usefulness as a source of resistance in addition to the 'Gasaway' allele [Sathuvalli et al. (2011b) showed that the resistance allele mapped to a different linkage group than that of the 'Gasaway' *R*-gene].

OSU 495.072, represented by 18 trees, was selected at OSU from a seed lot collected in southern Russia in 1989. This accession also developed no EFB cankers after greenhouse inoculation (Molnar et al., 2010a).

OSU 408.040, represented by 18 trees, was selected at OSU from a seed lot received from the University of Minnesota, Minneapolis, MN in 1987 (Chen et al., 2005). While OSU 408.040 remained free of EFB in the field trial, it developed a sunken lesion on one tree after greenhouse inoculation with a Michigan isolate of *A. anomala* (Molnar et al., 2010a).

'Uebov', also developing no EFB, was represented by only one tree planted in 2006 (no greenhouse inoculations were performed on 'Uebov' at Rutgers University). It is a clonal selection from the ARI Fruit and Grape Research Center in Čačak, Serbia (Sathuvalli et al., 2010).

Moscow #2 is a clonal accession represented by two trees planted in 2005. It originated at the Russian Research Institute of Forestry and Mechanization and was found resistant to EFB through greenhouse inoculations at OSU (Sathuvalli et al., 2010). Interestingly, Moscow #1, obtained from the same institute and identified as resistant by Sathuvalli et al. (2010), developed EFB on one of two trees in our study.

OSU 759.010 (identical to OSU 759.007) was sent as scions from the Republic of Georgia to OSU. It was later demonstrated that OSU 759.010 passes resistance to its offspring in ratios of 3:1 and 1:1 in Oregon, suggesting resistance stems from a single

dominant gene for which OSU 759.010 is heterozygous (Sathuvalli et al., 2011b). In contrast, four of six trees of OSU 759.010 established in the field developed EFB in our study. Similarly, 10 of 19 trees exposed to *A. anomala* isolates through greenhouse inoculations also developed EFB (Molnar et al., 2010a).

All three trees of CCOR 187.001 planted in 2006 developed EFB. This genotype is a seedling of wild *C. avellana* from Finland. These results are in contrast to the findings of Chen et al. (2007), where multiple trees of CCOR 187.001 developed no EFB after greenhouse inoculations.

While a direct comparison may be inappropriate due to the different planting dates, Moscow #1, OSU 759.010, and CCOR 187.001 developed fewer cankers with a lower proportion of diseased wood and less branch die-back than either 'Tonda di Giffoni' and 'Sacajawea', likely indicating a higher level of tolerance to EFB.

Corylus americana. Fifty-two of 54 *C. americana* accessions remained free of EFB (Table 2). These results, based on accessions originating from a wide diversity of geographic origins across the native range of the species in North America, confirm early reports that *C. americana* expresses an innate level of resistance. As early as the 19th century, *C. americana* was reported as tolerant. Halsted (1892) wrote that upon inspection, native hazels were found to show disease "only at rare intervals". Later, Morris (1920) described *C. americana* as becoming infected with the fungus, but not suffering much injury. Similar reports were also made by Fuller (1908), Barss (1930), and Weschcke (1954), supporting the premise that *C. americana* is highly tolerant of EFB while also acting as a source of inoculum to infect the much more susceptible *C*.

avellana when cultivated across its native range. However, no systematic evaluation of *C. americana* was reported until Pinkerton et al. (1993) included trees of *C. americana* 'Winkler', a wild selection originating from Iowa, in their evaluation of 45 *Corylus* clones for response to exposure to *A. anomala* in Oregon. In their trial, 'Winkler' displayed no symptoms or signs of EFB, corresponding to the findings in our study for this accession. Later, Coyne et al. (1998) subjected a progeny of *C. americana* seedlings from Manitoba, Canada, and six accessions from the NCGR collection to greenhouse inoculations with *A. anomala*. Of the 47 seedlings inoculated, only one seedling later showed signs of EFB, while two of the six clonal accessions expressed small cankers. These reports, together with our findings that nearly all *C. americana* accessions remained free of EFB, provide evidence that a high level of resistance exists in the species.

The *C. americana* accessions originated from germplasm holdings of the NCGR and OSU and were not previously evaluated for their response to EFB. Many of the plants are seedling selections made by S. Mehlenbacher. These were obtained from wild seed collected across the U.S. and southern Canada in the 1980s (Sathuvalli and Mehlenbacher, 2011). Improved plants were selected from a larger group of seedlings based on geographic origin, nut characteristics, and yield in the absence of EFB in Corvallis, OR (S.A. Mehlenbacher, personal communication).

Corylus americana hybrids. No signs or symptoms of EFB were found on the seven hybrid accessions related to *C. americana* 'Rush', besides 'Reed' ('Rush' \times *C. avellana* 'Halls Giant') (Table 1), which also was found susceptible in Oregon (Lunde et al., 2000). Our results corroborate those of Coyne et al. (1998), who evaluated eight 'Rush' hybrids, including NY 616, and found no EFB after greenhouse inoculation. The hybrid selection Yoder #5, while not tested here directly, is also believed to trace back to 'Rush' based on SSR marker analysis (Sathuvalli and Mehlenbacher, 2011). Yoder #5 was shown by Molnar et al. (2009) to transmit EFB resistance to its offspring in a ratio of 1 resistant: 1 susceptible in research plots at Rutgers University. These results further suggest the 'Rush' source of EFB resistance may hold up well in the eastern U.S. In addition, NY 398, NY 616, and Grimo 208P [the latter resulting from open pollination of NY 1329 (*C. americana* 'Rush' × *C. avellana* 'Cosford')] have shown no disease in Niagara-on-the-lake, ON, Canada for many decades in the presence of susceptible plants with EFB cankers (E. Grimo personal communication).

Besides offspring of *C. americana* 'Rush', the picture of EFB resistance in *C. americana* hybrids is less clear. 'Skinner', a hybrid of a *C. americana* seedling from the Hudson Bay area, Canada crossed with an open-pollinated seedling of (EFB-susceptible) *C. avellana* 'Italian Red', has been claimed to be EFB-resistant and was propagated and distributed around the eastern U.S. (Ashworth, 1970). 'Skinner' was susceptible to EFB in our trials and recently in field trials at the UNL (T. Pabst personal communication).

Six out of the 10 National Arbor Day Foundation hybrid accessions evaluated developed EFB cankers. These plants are high-yielding selections identified from a large population (5000) of seedlings planted at the Arbor Day Farm in 1996 (Hammond, 2006). They were originally purchased from Badgersett Research Corporation in Canton, MN (Rutter, 1987) and are believed to be advanced-generation hybrids of *C. americana* and *C. avellana*. These accessions were not previously exposed to EFB in Nebraska. Sathuvalli and Mehlenbacher (2011), using SSR markers, showed that most of the Arbor Day accessions evaluated here clustered with *C. americana* 'Winkler'. Their results are logical as 'Winkler' was used extensively by Weschcke (1954) in his breeding efforts. Rutter (1987, 1991) relied heavily on Weschcke's material in establishing plantings at Badgersett Research Farm. Hybrid seedlings from Badgersett have been distributed throughout the midwestern and eastern states, with related material now being distributed by the National Arbor Day Foundation.

OSU 401.014 and OSU 532.014 are hybrid accessions selected at OSU, which were derived from open-pollinated seed collected in New Carlisle, Ohio, though from two distinct sources believed to be unrelated (Sathuvalli and Mehlenbacher, 2011). Their response adds further confusion to understanding inheritance of EFB resistance from *C. americana* when crossed with *C. avellana*. Both accessions were found to be free of EFB in Oregon trials (S.A. Mehlenbacher personal communication), but they developed EFB in New Jersey after only two seasons of exposure. In contrast, the hybrid CCOR 507.001, derived from open-pollinated seeds collected from a *C. americana* (Minnesota) accession in the NCGR collection, remained free of EFB since being planted in 2007.

Our findings support the existing premise that EFB resistance from *C. americana* can be successfully transmitted to offspring when crossed with susceptible *C. avellana*. However, only a limited number of *C. americana* parents (largely 'Rush' and 'Winkler') have been used in past interspecific breeding efforts, and few studies have been conducted to document the inheritance of resistance from the wild species. While the use of *C. americana* in breeding looks very promising, especially considering its wide native range and adaptation to harsh environments, in addition to EFB resistance, further study is needed to better understand inheritance of EFB resistance, which should include the use of a much wider diversity of wild parents.

Corvlus heterophylla. Fourteen of 16 accessions of C. heterophylla remained free of EFB (Table 2). Those included in this study represent multiple geographic origins, including northeastern China (Dalian and Yanji City) and central South Korea (Suweon), suggesting resistance to EFB may be a relatively common trait associated with the species. Supporting this idea, a previous report by Coyne et al. (1998) found that all three Korean C. heterophylla accessions remained free of EFB following greenhouse inoculations. Further, while not a planned part of our clonal study, positive results were also visualized in a population of 66 seedlings planted at Rutgers University in 2007, which were purchased from Lawyer Nursery (Olympia, WA) in 2006 as seed of C. heterophylla collected in China, although information on the geographic origin was not available. The plants were phenotypically C. heterophylla, as all had the conspicuous truncated and variable leaf shape of the species, as described in eFloras (2012), and were very similar in appearance to the *C. heterophylla* accessions obtained from the NCGR. These seedlings were exposed to A. anomala over 4 years in the field, and upon evaluation in 2012, the group showed a high level of tolerance to EFB with only 14 of 66 expressing cankers, all of which were typically small (<20 cm in length) and caused only minor stem damage (data not shown). While additional testing of a broader range of germplasm is needed to better understand the resistance in this species, the EFB response of the diverse C. heterophylla accessions and the unselected seedlings, along with that reported by Coyne et al. (1998), make a strong case that *C. heterophylla* possesses a high

level of tolerance or resistance to EFB, despite evolving in a region devoid of *A*. *anomala*.

Corvlus heterophylla hybrids. Five of the 13 *C. heterophylla* × *C. avellana* hybrid accessions evaluated in this study developed EFB (Table 1). Of these susceptible plants, four were from a group of eight accessions obtained from the UNL. They were originally imported to the U.S. from Dalian, China as dormant rooted layers in 1995 or 1996 by William Gustafson and are believed to be selected hybrids between C. heterophylla and C. avellana (T. Pabst personal communication). The plants were obtained from the Economic Forestry Institute of Liaoning Province, Dalian, China where a hybridization and selection program between C. avellana and C. heterophylla was initiated in the 1980s and is still in operation today (Ming et al., 2005; Weijian et al., 1994). Unfortunately, records were lost at UNL on their identity. However, based on morphological characteristics, the authors are confident of their interspecific hybrid nature. Interestingly, Sathuvalli et al. (2010) also included four C. heterophylla \times C. avellana accessions from Dalian, China in their greenhouse inoculation study (the relationship between our accessions from UNL is unknown), and all four were found to be susceptible.

OSU 526.041 is the result of a cross made in 1989 of *C. heterophylla* 'Ogyoo' and a mixture of three *C. avellana* pollens (OSU 55.129, Birk 5-6, and OSU 226.122), where the male parent has yet to be determined. OSU 526.041 was identified as EFB-resistant at OSU (S.A. Mehlenbacher personal communication). At Rutgers University, trees of OSU 526.041 developed no EFB after greenhouse inoculations with a variety of *A*.

anomala isolates (Molnar et al., 2010a), and all 18 trees evaluated in this field study have remained free of EFB since 2002. It should be noted that its parent *C. heterophylla* 'Ogyoo' also expressed no EFB in this study. OSU 526.030, an additional offspring of *C. heterophylla* 'Oygoo' crossed with *C. avellana* OSU 226.122 ('Tonda Gentile delle Langhe' x OSU 67.026) has shown no sign of EFB at Rutgers University, although it was established several years later than OSU 526.041 and is represented by only two trees.

'Estrella #1', from a cross of a selection of *C. heterophylla* var. *sutchuensis* × *C. avellana* 'Holder' and selected by Cecil Farris in Michigan (Farris, 1974), showed no sign of disease in this study. 'Estrella #1' was also found to be resistant in Oregon (Chen et al., 2007). Its sibling, 'Estrella #2' (Farris, 1974), was found to be susceptible to EFB in Oregon (Chen et al., 2007) and was not included in our study.

Grimo *Heterophylla* Hybrid #3 was selected by E. Grimo (Niagara-on-the-lake, ON, Canada) from open-pollinated seed collected from a *C. heterophylla* (possibly hybrid) seedling originating from Quebec in the 1970s. It remained free of EFB in our study. Conversely, Grimo *Heterophylla* Hybrid #2, a seedling from the same mother plant, developed EFB. Recent communications with their developer (E. Grimo personal communication) confirm our EFB response, as the original tree of Hybrid #3 remains free of EFB in Ontario, with Hybrid #2 later succumbing to the disease. Further evidence of EFB resistance transmitted from *C. heterophylla* in crosses with susceptible *C. avellana* is provided by Coyne et al. (1998). In addition to evaluating pure *C. heterophylla*, they also inoculated select accessions that originated from a cross of *C. heterophylla* 'Ogyoo' (resistant) × *C. avellana* 55.129 (susceptible). Two of the hybrid selections proved resistant to greenhouse inoculations, while the third was susceptible. Our results from a limited number of accessions support the premise that EFB resistance can be transmitted from *C. heterophylla* selections to some offspring, although the genetic control remains unclear. Regardless, these findings show that *C. heterophylla* may hold significant potential for breeding for EFB resistance, as well as for enhanced climatic adaptation. *Corylus heterophylla* is native across a wide section of Asia, including very cold parts of northeastern China (Mehlenbacher, 1991). Access to a wider germplasm base and more controlled crosses with select, EFB-resistant *C. heterophylla* parents should lead to further edification concerning the overall genetic resistance of the species.

Corylus colurna hybrids. Eight of 13 *C. colurna* hybrids showed no signs or symptoms of EFB (Table 2). While the results are positive, strong conclusions on the presence of EFB resistance in *C. colurna* cannot be drawn. No pure *C. colurna* accessions were available for evaluation and most of the hybrid plants originated directly or indirectly from the breeding program of J.U. Gellatly in British Columbia, Canada (Gellatly, 1950, 1956, 1964, 1966). This includes the accessions Gellatly Chinese Trazel #6 (CCOR 138.001) and #11 (CCOR 173.001) and Gellatly Turkish Trazel #3 (CCOR 407.001), which, contrary to their names, all appear to be of *C. colurna* descent and were shown to be EFB resistant in Oregon (Chen et al., 2007). The Rutgers University seedling selection H2R5P21, an open-pollinated seedling of Gellatly Chinese Trazel #6 originating from seed collected by C.R. Funk at the NCGR in 1995, has also shown no EFB in our plots or in greenhouse inoculations at OSU (S.A. Mehlenbacher personal communication).

Also included in our study were Gellatly's 'Chinoka', 'Erioka', and 'Faroka'. Two trees each of 'Chinoka' and 'Erioka' were found to be highly susceptible to EFB, dying within 5 years of planting. 'Chinoka' and 'Erioka' were also found to be EFB susceptible in Oregon (Chen et al., 2007). Interestingly, 'Faroka' became infected with *A. anomala* in Oregon trials where its presence was detected through the use of an enzymelinked immunosorbent assay (ELISA) following greenhouse inoculations (Lunde et al., 2000), as well as through the visualization of sunken lesions lacking stromata (Chen et al., 2007). Similarly, both trees of 'Faroka' in our trials each exhibited a single sunken lesion lacking stromata, although overall the trees remain very healthy in appearance.

Despite showing evidence of susceptibility to infection by *A. anomala*, 'Faroka' is believed to have transmitted a high level of EFB resistance to its offspring 'Grand Traverse' [reported as 'Faroka' × *C. avellana* 'Royal' in Farris (1989)]. The male parent of 'Grand Traverse' was disputed in Lunde et al. (2000) based on incompatibility alleles. Eighteen trees of 'Grand Traverse' remained free of EFB in our field study, as well as after greenhouse inoculations using multiple isolates of *A. anomala* (Molnar et al., 2010a). Similar results with 'Grand Traverse' were found at OSU (Lunde et al., 2000) and in Michigan where it was originally developed (Farris, 1995b, 2000). 'Grand Traverse' was also shown to transmit EFB resistance to about 25% of its progeny in a field trial at Rutgers University (Molnar et al., 2009). 'Lisa', an offspring of 'Grand Traverse', was also found to be resistant to EFB at OSU (Chen et al., 2007) and remains free of EFB in our trials after two seasons of exposure.

Furthermore, 'Faroka' is the female parent of the accessions Farris 88BS, Grimo 208D, and Grimo 186M. The latter two are seedling selections made by E. Grimo

derived from the germination of open-pollinated nuts from 'Faroka' (Grimo, 2011). Both Grimo selections remained free of EFB in our trials, while 88BS developed one single EFB canker (8 cm) on one of two trees after 5 years of exposure.

Chinese Trazel J-1, a hybrid obtained from the NCGR, developed EFB in our trial. It was developed in Oregon in 1972 by O. Jemtegaard (USDA, 2011) and is the only *C. colurna* hybrid evaluated in this study unrelated to Gellatly material, although the exact background is not known. Our results with the *C. colurna* hybrids suggest the likely presence of heritable EFB resistance in the Gellatly-derived material, especially from 'Faroka'. However, many of the accessions evaluated here were developed through the collection and germination of open-pollinated seeds. Thus, without further work including the use of molecular fingerprinting tools, we cannot be certain that they share a common ancestor or the same EFB resistance genes.

Gordon *Corylus* hybrids. Forty of the 42 accessions originating from John Gordon (John Gordon Nursery) in Amherst, NY remained free of EFB. The two infected plants, Gordon R21P1and R30DP2, developed one typical canker and one sunken lesion, respectively (Table 1). Gordon selected these accessions for our study based on their EFB-free survival for many years in his heavily EFB-infected nursery plots. He began his hazelnut breeding/selection efforts in 1963 with the planting of open-pollinated seeds of 'NY 104' (*C. americana* 'Rush' × *C. avellana* 'DuChilly') and 'NY 200' (*C. americana* 'Rush' × *C. avellana* 'Hall's Giant') with the objective of selecting improved seedlings. In the 1980s, he added open-pollinated seedlings of Gellatly's *C. avellana* 'Hall's Giant', as well as the *C. cornuta* × *C. avellana*

hybrid Gellatly 502 (Farris, 1978, 1982; Gellatly, 1950, 1966), to the breeding population, which at one time numbered many thousands of plants. Open-pollinated nuts were then harvested from the best seedlings surviving in his nurseries to plant successive generations for further evaluation. The accessions evaluated here are the result of several generations of selection by Gordon, although their parentage is unknown. Based on Gordon's starting material, it is likely that most of the resistance in the accessions stems from some combination of *C. americana* 'Rush' and the *C. colurna* × *C. avellana* hybrid 'Faroka'. However, the parental origins of these accessions are unknown.

Corylus fargesii. None of the six *C. fargesii* accessions developed EFB (Table 2). The scions were collected from healthy trees at the Morris and Holden Arboreta in Philadelphia, Pennsylvania and Kirtland, Ohio, respectively, where EFB was present on nearby *C. avellana*. The original plants were from open-pollinated seed collected by members of the North American China Plant Exploration Consortium in 1996 from Shaanaxi and Gansu provinces in the People's Republic of China (Aiello and Dillard, 2007). Few earlier records of introductions of the species have been reported in the U.S., besides that of Farris (1995a). Farris (1995a) reported that no symptoms or sign of EFB were observed on his introductions of *C. fargesii* under field conditions in both Michigan and Tennessee, for 13 and 8 years, respectively.

Conclusion

The field response to exposure to *A. anomala* of over 190 clonal *Corylus* accessions, representing a wide diversity of species and genetic backgrounds, was

assessed. From these accessions we identified many that remained free of EFB under very high field disease pressure, where known susceptible accessions succumbed to EFB, including some with known tolerance to infection in Oregon. The diversity of resistant *Corylus* germplasm should prove useful in developing improved cultivars expressing durable resistance to this disease.

While additional study is needed to determine the inheritance of resistance when crossing EFB-resistant wild *Corylus* with susceptible *C. avellana*, the relatively large number of interspecific hybrids remaining free of EFB confirms earlier reports and strongly supports interspecific hybridization as a breeding option. The relatively high inter-fertility that exists between C. avellana, C. americana, and C. heterophylla (Erdogan and Mehlenbacher, 2000a) will facilitate the development of new hybrids, and the diversity of EFB-resistant wild germplasm identified should make a good starting point for further breeding. While their nuts tend to be smaller and thicker-shelled than cultivated C. avellana (Fig. 1), the wild species may contribute, in addition to EFB resistance, traits for wider adaptation including extreme cold hardiness and drought tolerance. For example, C. americana is adapted to a very wide region of the U.S. and southern Canada and some C. heterophylla are adapted to the cold and dry winters of northeastern China. Other Corylus, like the single-trunk tree species C. colurna, although more challenging to cross with C. avellana (Erdogan and Mehlenbacher, 2000a), merit further investigation for breeding EFB-resistant plants that are better adapted to stress, possibly with non-suckering growth habits (Mehlenbacher, 1991; Molnar, 2011).

Furthermore, many of the accessions included in this study are held in the NCGR collection and are freely available for use in research and breeding. The EFB response

results from this study will be added to the descriptor data in the National Plant Germplasm System's (NPGS) Germplasm Resources Information (GRIN) database.

Differences in EFB response were found for a number of accessions in New Jersey compared to that reported from OSU, including accessions of *C. avellana* and hybrids. As discussed earlier, these differences can be attributed to the potentially wider diversity of *A. anomala* found in the eastern U.S., some of which may express increased virulence (Molnar et al., 2010a), as well as the high disease pressure. These results reinforce the need to maintain the quarantine now in place to restrict the movement of *Corylus* material from the east into the Pacific northwestern U.S. to prevent the introduction of new *A. anomala* isolates. They also demonstrate the usefulness in evaluating germplasm in and across the eastern U.S. to help identify sources of resistance able to hold up to a diversity of *A. anomala* isolates.

To better verify the resistance of some accessions, longer field evaluations are recommended and will be continued at Rutgers University. Some accessions were only evaluated in the field for 3 years (two seasons of exposure). While our experience shows this time can be sufficient to suggest tolerance to EFB, longer-term field testing is necessary to reduce the incidence of escapes, to confirm that resistance is stable, and to evaluate levels of tolerance, a component of which includes the annual rate of expansion of the perennial cankers. Regardless, the presence of EFB on plants from only two seasons of exposure is a clear indicator of their susceptibility.

Future studies of the resistant accessions identified or confirmed in this trial include evaluating the genetic relationships using microsatellite (SSR) markers, as well as studying transmission of resistance to offspring when crossed with susceptible plants.

Many of the accessions have been characterized with SSR markers by Gökirmak et al. (2009), Gurcan et al. (2010), Sathuvalli and Mehlenbacher (2011), and others (GRIN, 2012). However, those of C. heterophylla and C. colurna origin, as well as the accessions from UNL, John Gordon, and Grimo Nut Nursery, have yet to be fingerprinted. Knowing relationships between these plants in addition to their geographic origins and morphological traits could help breeders maintain high genetic diversity in breeding lines as well as helping to distinguish between plants that share a common lineage [and possibly the same EFB resistance gene(s)] or those that are distantly related. Further, work to place identified resistance gene(s) on the hazelnut genetic linkage map (Mehlenbacher et al., 2006) and the identification of closely linked DNA markers [as was done by Sathuvalli et al. (2011a, 2011b) for 'Ratoli' and OSU 759.010] would be of great value to breeding efforts, with gene pyramiding a practical option for developing durable EFB resistance. Future research will also include the evaluation of other hazelnut species not included in this study, including C. cornuta, C. californica, C. chinensis, C. *jacquemontii*, C. *ferox*, and others, especially as more germplasm from Asia becomes available.

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 Table 1. Disease attributes of Corylus accessions expressing eastern filbert blight (EFB) caused by Anisogramma anomala. Organizations mentioned

 in the table are located as follows: Oregon State University, Corvallis, OR; National Arbor Day Foundation, Nebraska City, NE; University of

 Nebraska, Lincoln, Lincoln, NE; Grimo Nut Nursery, Niagara-on-the-lake, ON, Canada; and John Gordon Nursery, Amherst, NY.

| | | | | | Avg | Total | Total | |
|----------------------------------|---------|--|-----------|---------------------|-------------------|----------|---------|-------------|
| | | | | EFB | canker | diseased | shoot | Proportion |
| | Year | | Disease | cankers | length | wood | growth | of diseased |
| Accession and species | planted | Origin or parentage | incidence | (no.) ^y | (cm) ^y | (m/tree) | (m) | wood |
| Replicated planting ^z | | | | | | | | |
| 'Barcelona'× | 2002 | Spain | 18/18 | 20.4 a ^v | 61.9 a | 12.63 a | 18.9 a | 0.67 a |
| 'Gasaway'w | 2002 | Washington, PI 557042 | 18/18 | 141.6 b | 14.4 b | 20.38 b | 128.4 b | 0.16 b |
| 'Tonda di Giffoni'* | 2002 | Italy | 18/18 | 39.0 a | 24.5 a | 9.55 a | 24.5 a | 0.39 c |
| 'VR20-11'wu | 2002 | Oregon, ('Barcelona' × 'Compton') × 'Gasaway' | 18/18 | 65.4 c | 22.4 a | 14.64 a | 90.4 c | 0.16 b |
| Corylus avellana | 11 | | | | | | | |
| 'Contorta'× | 2008 | England | 2/2 | 3.5 | 38.6 | 1.35 | 2.8 | 0.49 |
| 'Gamma'w | 2006 | Oregon, 'Casina' × VR 6-28 | 1/1 | 1.0 | 9.0 | 0.09 | 15.0 | 0.01 |
| 'Italian Red', CCOR 30.001× | 2006 | Germany, PI 557034 | 2/2 | 17.0 | 31.1 | 5.29 | 14.0 | 0.38 |
| 'Jefferson' ^{wt} | 2009 | Oregon, Oregon State University (OSU) 252.146 \times | 5/9 | 1.2 | 13.0 | 0.16 | 3.7 | 0.04 |
| | | OSU 414.062 | | | | | | |
| 'Losovskoi Sharovdnii'× | 2009 | Kharkiv, Ukraine | 1/1 | 2.0 | 19.5 | 0.39 | 1.0 | 0.39 |
| Moscow #1 ^w | 2007 | Moscow, Russia | 1/2 | 1.0 | 27.0 | 0.27 | 4.5 | 0.06 |

| 'Red Majestic' | 2008 | Netherlands, Plant Patent #16048 | 5/5 | 8.4 | 22.7 | 1.91 | 4.1 | 0.47 |
|---|------|--|-----|------|------|------|------|------|
| 'Restiello', CCOR 280.002× | 2006 | Spain, PI 557129 | 1/1 | 12.0 | 55.6 | 6.67 | 13.5 | 0.49 |
| 'Sacajawea'× | 2008 | Oregon, OSU 43.091 × 'Sant Pere' | 3/3 | 7.7 | 21.5 | 1.65 | 7.7 | 0.21 |
| 'Yamhill' ^Y | 2009 | Oregon, OSU 296.082 × VR 8-32 | 1/1 | 1.0 | 8.0 | 0.08 | 4.0 | 0.02 |
| CCOR 187.001** | 2006 | Finland, PI 557080 | 3/3 | 12.3 | 21.3 | 2.63 | 24.3 | 0.11 |
| OSU 759.010 ^w | 2002 | Republic of Georgia | 4/6 | 5.0 | 2.9 | 0.14 | 11.0 | 0.01 |
| Corylus americana | 1 | | | 1 | 1 | 1 | | |
| OSU 403.003 | 2007 | Minnesota | 1/1 | 4.0 | 30.5 | 1.22 | 6.0 | 0.20 |
| OSU 532.025, CCOR 679.001 | 2007 | West Virginia, PI 617246 | 2/2 | 11.0 | 25.8 | 2.84 | 6.8 | 0.42 |
| Corylus americana × C. avellana hybrids | | | | | | | | |
| 'Reed', CCOR 383.001* | 2005 | C. americana 'Rush' × C. avellana 'Hall's Giant', PI | 1/1 | 12.0 | 25.5 | 3.06 | 11.0 | 0.28 |
| | | 557392 | | | | | | |
| 'Skinner' | 2006 | C. americana (Hudson Bay, Canada) × Open pollinated | 1/1 | 2.0 | 22.8 | 0.46 | 5.0 | 0.09 |
| | | (OP). seedling of <i>C. avellana</i> 'Italian Red' | | | | | | |
| NADF #11 (14-30) | 2005 | National Arbor Day Foundation | 1/1 | 5.0 | 29.2 | 1.46 | 4.0 | 0.37 |
| NADF #2 (9-31) | 2005 | National Arbor Day Foundation | 3/3 | 2.7 | 15.5 | 0.41 | 3.8 | 0.11 |
| NADF #5 (13-55) | 2005 | National Arbor Day Foundation | 2/2 | 8.5 | 27.8 | 2.36 | 4.0 | 0.59 |
| NADF #6 (25-146) | 2005 | National Arbor Day Foundation | 1/1 | 5.0 | 15.0 | 0.75 | 2.0 | 0.38 |
| NADF #8 (20-122) | 2005 | National Arbor Day Foundation | 2/2 | 3.0 | 6.8 | 0.21 | 4.0 | 0.05 |
| NADF#9 (11-56) | 2005 | National Arbor Day Foundation | 1/1 | 7.0 | 48.6 | 3.40 | 4.0 | 0.85 |
| OSU 401.014 ^w | 2009 | OSU selection, seeds from K. Bauman, New Carlisle, | 2/2 | 2.0 | 19.5 | 0.39 | 1.5 | 0.26 |
| I | 1 | | | 1 | 1 | 1 | 1 | |

| OSU 532.014 ^w | 2009 | OH OSU selection, seeds from K. Bauman, New Carlisle, OH | 1/1 | 5.0 | 14.4 | 0.72 | 2.0 | 0.36 |
|--------------------------|------|--|-----|-----|------|------|-----|------|
| Corylus heterophylla | | | | | | | 1 | I |
| CCOR 467.002 | 2008 | South Korea, PI 557323 | 1/1 | 5.0 | 29.2 | 1.46 | 5.5 | 0.27 |

1/1

17.5

0.35

1.0

0.35

2.0

Clonal selection from Dalian, China

Corylus heterophylla × C. avellana hybrids

2008

D80-190

| | Dailan, China via University of Nebraska, Lincoln | | | | | | |
|------|---|--|--|--|---|---|--|
| 2006 | (UNL) | 1/1 | 4.0 | 10.5 | 0.42 | 2.0 | 0.21 |
| 2006 | Dailan, China via UNL | 1/1 | 4.0 | 19.0 | 0.76 | 4.0 | 0.19 |
| 2006 | Dailan, China via UNL | 1/1 | 4.0 | 24.0 | 0.96 | 3.5 | 0.27 |
| 2006 | Dailan, China via UNL | 1/1 | 7.0 | 17.4 | 1.22 | 2.5 | 0.49 |
| 2005 | Grimo Nut Nursery | 1/1 | 15.0 | 30.1 | 4.51 | 10.0 | 0.45 |
| | 2006 2006 2006 | 2006(UNL)2006Dailan, China via UNL2006Dailan, China via UNL2006Dailan, China via UNL | 2006 (UNL) 1/1 2006 Dailan, China via UNL 1/1 | 2006 (UNL) 1/1 4.0 2006 Dailan, China via UNL 1/1 7.0 | 2006 (UNL) 1/1 4.0 10.5 2006 Dailan, China via UNL 1/1 4.0 19.0 2006 Dailan, China via UNL 1/1 4.0 24.0 2006 Dailan, China via UNL 1/1 4.0 24.0 2006 Dailan, China via UNL 1/1 7.0 17.4 | 2006 (UNL) 1/1 4.0 10.5 0.42 2006 Dailan, China via UNL 1/1 4.0 19.0 0.76 2006 Dailan, China via UNL 1/1 4.0 24.0 0.96 2006 Dailan, China via UNL 1/1 7.0 17.4 1.22 | 2006 (UNL) 1/1 4.0 10.5 0.42 2.0 2006 Dailan, China via UNL 1/1 4.0 19.0 0.76 4.0 2006 Dailan, China via UNL 1/1 4.0 24.0 0.966 3.5 2006 Dailan, China via UNL 1/1 7.0 17.4 1.22 2.5 |

Corylus colurna hybrids

| Chinese Trazel J-1, CCOR | 2006 | Jemtegaard, C. columa hybrid (hyb.), PI 557263 | 1/1 | 16.0 | 24.3 | 3.88 | 5.5 | 0.71 |
|---------------------------|------|---|-----|------------------|------|------|------|-------|
| 170.001 | | | | | | | | |
| 'Chinoka', CCOR 199.001×5 | 2005 | Gellatly, C. columa hyb., PI557387 | 2/2 | N/A ^r | N/A | N/A | N/A | N/A |
| 'Erioka', CCOR 201.001*5 | 2005 | Gellatly, C. columa hyb., PI557389 | 2/2 | N/A | N/A | N/A | N/A | N/A |
| 'Faroka', CCOR 405.002×q | 2005 | Gellatly, C. columa hyb., PI 557393 | 2/2 | 1.0 | N/A | N/A | N/A | N/A |
| Farris 88BS | 2006 | 'Faroka' × C. <i>avellana</i> via Grimo Nut Nursery | 1/2 | 1.0 | 8.0 | 0.08 | 18.0 | <0.01 |

John Gordon collection

| Gordon R21P1 | 2006 | John Gordon Nursery selection | 1/1 | 2.0 | 27.5 | 0.55 | 4.0 | 0.14 |
|---------------|------|-------------------------------|-----|-----|------|------|-----|------|
| Gordon R30DP2 | 2008 | John Gordon Nursery selection | 1/2 | 1.0 | 17.0 | 0.17 | 7.0 | 0.02 |

²Canker attributes were measured for five randomly selected trees per accession of those in the replicated trial.

^y For a given attribute, means followed by a different letter in the same column are significantly different at P<0.05 according to a mean least square difference test

^x EFB susceptible in Oregon.

W Resistant to EFB in Oregon.

v 'Gasaway' expressed both typical sporulating EFB cankers and sunken lesions attributed to the disease. Of the average (from five trees) of 141.6 cankers per tree, 48.2 were

sunken, non-sporulating lesions.

^u VR 20-11 expressed both typical sponulating EFB cankers and sunken lesions attributed to the disease. Of the average (from five trees) 65.4 cankers per tree, 22.8 were sunken,

non-sporulating lesions.

¹3/5 infected 'Jefferson' plants had non-sporulating sunken lesions and 3/5 had typical cankers, with one plant expressing both.

⁵ Trees died from EFB in 2010

^r Trees were not available for measurement in 2012 or cankers healed over and were not able to be measured

^q Each tree of 'Faroka' developed one sunken, non-sporulating lesion that was subsequently walled off and rendered immeasurable.

Table 2. Corylus accessions showing no signs or symptoms of infection by Anisogramma anomala. Organizationsmentioned in the table are located as follows: Oregon State University, Corvallis, OR; National Arbor Day Foundation,Nebraska City, NE; University of Nebraska, Lincoln, Lincoln, NE; Grimo Nut Nursery, Niagara-on-the-lake, ON, Canada;John Gordon Nursery, Amherst, NY; Morris Arboretum, Philadelphia, PA; and Holden Arboretum, Kirtland, OH.

| | Year | Trees | |
|--|------------|-------|---|
| Accession | planted | (no.) | Origin or parentage |
| Corylus avellana ^y | | | |
| 'Zimmerman' ^z | 2002 | 18 | Oregon, C. avellana 'Gasaway' × 'Barcelona' |
| Oregon State University (OSU) 408.040 ^z | 2002 | 18 | Minnesota, PI 617266 |
| OSU 495.072 ^z | 2002 | 18 | Russia (southern) |
| 'Ratoli' | 2004, 2006 | 6 | Spain, PI 557167 |
| 'Uebov' | 2006 | 1 | Cacak, Serbia |
| Moscow #2 | 2005 | 2 | Moscow, Russia |
| 'Santiam' | 2006 | 6 | Oregon, OSU 249.159 × VR 17-15 |
| 'Delta' | 2006 | 3 | Oregon, OSU 249.159 × VR 17-15 |
| 'Epsilon' | 2006 | 1 | Oregon, OSU 350.089 × 'Zimmerman' |
| 'Theta' | 2009 | 2 | Oregon, OSU 561.184 × 'Delta' |

Corylus americana

| 'Winkler', CCOR 99.001 [×] | 2005 | 2 | Indiana, PI 557019 |
|-------------------------------------|------|---|--------------------------|
| | 2005 | 2 | |
| OSU 366.088, CCOR 180.002 | 2008 | 1 | Indiana, PI 495606 |
| OSU 531.017, CCOR 675.001 | 2007 | 1 | Indiana, 617242 |
| OSU 531.043, CCOR 677.001 | 2008 | 1 | North Dakota, 617244 |
| OSU 532.028, CCOR 680.001 | 2008 | 1 | West Virginia, PI 617247 |
| OSU 532.046, CCOR 681.001 | 2007 | 1 | Kentucky, PI 617248 |
| OSU 400.033, CCOR 684.001 | 2007 | 1 | Indiana, PI 617251 |
| OSU 405.057, CCOR 694.001 | 2007 | 1 | Minnesota, PI 617261 |
| OSU 557.122, CCOR 710.001 | 2007 | 1 | Wisconsin, PI 617273 |
| OSU 557.136, CCOR 711.001 | 2007 | 1 | Wisconsin, PI 617274 |
| OSU 557.138, CCOR 712.001 | 2008 | 1 | Massachusetts, PI 617275 |
| OSU 557.153, CCOR 713.001 | 2007 | 1 | Wisconsin, PI 617726 |
| OSU 557.190, CCOR 714.001 | 2008 | 1 | Massachusetts, PI 617277 |
| OSU 558.178, CCOR 715.001 | 2007 | 1 | Michigan, PI 617728 |
| OSU 366.060, CCOR 59.002 | 2007 | 2 | Mississippi, PI 433984 |
| OSU 366.078, CCOR 117.002 | 2007 | 1 | Minnesota, PI 557020 |
| OSU 400.027 | 2007 | 2 | Indiana |
| OSU 400.030 | 2007 | 1 | Indiana |
| | l | l | |

| OSU 400.039 | 2007 | 1 | Indiana |
|---------------------------|------|---|--------------------------|
| OSU 400.040 | 2007 | 1 | Wisconsin |
| OSU 400.043 | 2007 | 1 | North Dakota |
| OSU 401.006, CCOR 686.001 | 2007 | 1 | Pennsylvania, PI 617253 |
| OSU 403.040 | 2007 | 1 | Nebraska |
| OSU 403.046 | 2007 | 1 | Nebraska |
| OSU 403.053 | 2007 | 1 | Nebraska |
| OSU 405.038 | 2007 | 2 | New Jersey |
| OSU 405.043 | 2007 | 1 | New Jersey |
| OSU 405.060, CCOR 695.001 | 2007 | 1 | Minnesota, PI 617262 |
| OSU 405.084, CCOR 225.001 | 2007 | 1 | Indiana, PI 557021 |
| OSU 531.006 | 2007 | 1 | Michigan |
| OSU 531.016 | 2007 | 1 | Michigan |
| OSU 531.017, CCOR 675.001 | 2007 | 1 | Indiana, PI 617242 |
| OSU 531.027 | 2007 | 1 | Indiana |
| OSU 531.037, CCOR 676.001 | 2007 | 1 | Wisconsin, PI 617243 |
| OSU 531.038 | 2007 | 1 | Wisconsin |
| OSU 531.043, CCOR 677.001 | 2007 | 1 | North Dakota, PI 617244 |
| OSU 532.028, CCOR 680.001 | 2007 | 1 | West Virginia, PI 617247 |
| | | | |

| OSU 532.076, CCOR 682.001 | 2007 | 1 | Michigan, PI 617249 |
|---------------------------|------|---|---------------------|
| OSU 533.069 | 2007 | 2 | Pennsylvania |
| OSU 533.072 | 2007 | 1 | Pennsylvania |
| OSU 533.074 | 2007 | 1 | Pennsylvania |
| OSU 536.013 | 2007 | 1 | South Dakota |
| OSU 537.058, CCOR 683.001 | 2007 | 1 | Indiana, PI 617250 |
| OSU 537.061 | 2007 | 2 | Wisconsin |
| OSU 537.064 | 2007 | 1 | Virginia |
| OSU 557.026 | 2008 | 2 | Virginia |
| OSU 557.046 | 2007 | 2 | North Dakota |
| OSU 557.075 | 2007 | 2 | Pennsylvania |
| OSU 557.125 | 2007 | 1 | Wisconsin |
| OSU 557.128 | 2007 | 1 | Wisconsin |
| OSU 558.044 | 2007 | 1 | Illinois |
| OSU 559.026 | 2008 | 1 | Nebraska |

Corylus americana × C. avellana hybrids

| OSU 541.147 ^{zx} | 2002 | 18 | 'NY 110' (<i>C. americana</i> 'Rush' × <i>C. avellana</i> 'DuChilly') × OSU 226.118 |
|--|------|----|--|
| CCOR 507.001 | 2007 | 1 | Minnesota, PI 557023 |
| 'Medium Long', CCOR 701.001 [×] | 2005 | 1 | <i>C. avellana</i> × <i>C. americana</i> (likely) from the New York Agricultural |

| | | | Experiment Station, PI 617265 |
|--------------------------------------|------|---|---|
| NY 398 | 2007 | 3 | <i>C. americana</i> 'Rush' × <i>C. avellana</i> 'Red Lambert', PI 557382 |
| NY 616 ^x | 2002 | 1 | <i>C. americana</i> 'Rush' × <i>C. avellana</i> 'Barcelona', PI 557341 |
| 'Potomac', CCOR 377.001 [×] | 2005 | 1 | C. americana 'Rush' × C. avellana 'DuChilly', PI 557391 |
| Weschcke-TP1 ^x | 2009 | 1 | Selection from C. Weschcke Farm, Wisconsin |
| NADF #1 (10-50) | 2005 | 3 | National Arbor Day Foundation |
| NADF #3 (11-51) | 2005 | 5 | National Arbor Day Foundation |
| NADF #4 (15-74) | 2005 | 3 | National Arbor Day Foundation |
| NADF #7 (25-60) | 2005 | 2 | National Arbor Day Foundation |
| NADF #10 (11-55) | 2006 | 3 | National Arbor Day Foundation |
| Grimo 208P | 2006 | 2 | 'NY 1329' (<i>C. americana</i> 'Rush' × <i>C. avellana</i> 'Cosford') × Open pollinated (OP). |

Corylus heterophylla

| 'Ogyoo' | 2008 | 1 | South Korean cultivar, HF13, PI 557323 |
|--|------|---|---|
| CCOR 703.005 | 2007 | 1 | Yanji City, Jilin, China PI 608046 |
| CCOR 703.009 | 2007 | 2 | Yanji City, Jilin, China, PI 608046 |
| CCOR 703.011 | 2007 | 1 | Yanji City, Jilin, China, Pl 608046 |
| OSU 373.056, CCOR 124.001 ^w | 2008 | 1 | OSU seed selection from Jilin, China, PI 557310 |
| CCOR 688.001 | 2008 | 1 | South Korea, PI 617255 |
| Korean Het. 001 | 2008 | 1 | Clonal selection Suweon, South Korea |
| | | | |

| OSU 402.050 | 2008 | 2 | OSU seed selection from Dalian, China |
|-------------|------|---|---|
| OSU 404.009 | 2008 | 1 | OSU seed selection from Dalian, China |
| OSU 404.010 | 2008 | 1 | OSU seed selection from Suweon, South Korea |
| OSU 404.026 | 2008 | 2 | OSU seed selection from Suweon, South Korea |
| OSU 404.037 | 2008 | 1 | OSU seed selection from Suweon, South Korea |
| OSU 404.042 | 2008 | 2 | OSU seed selection from Suweon, South Korea |
| D81-10 | 2008 | 1 | Clonal selection from Dalian, China |

Corylus heterophylla × C. avellana hybrids

| OSU 526.041 ^{zx} | 2002 | 18 | C. heterophylla 'Ogyoo' × C. avellana |
|--|------|----|---|
| China #1 | 2006 | 1 | Dailan, China via Nebraska-UNL |
| China #13 | 2006 | 2 | Dailan, China via Nebraska-UNL |
| China #20 | 2006 | 1 | Dailan, China via Nebraska-UNL |
| China #23 | 2006 | 1 | Dailan, China via Nebraska-UNL |
| 'Estrella #1', CCOR 139.001 [×] | 2006 | 3 | <i>C. heterophylla var.</i> sutchuenensis × <i>C. avellana</i> 'Holder' via C. Farris, Pl |
| OSU 526.030 | 2008 | 2 | 557351 C. heterophylla 'Ogyoo' × C. avellana OSU 226.122 |
| Grimo Het. Hazel Hybrid #3 | 2005 | 1 | Grimo Nut Nursery selection |

Corylus colurna hybrids

| 'Grand Traverse' ^{zx} | 2002 | 18 | <i>Corylus</i> hybrid (hyb.). 'Faroka' × <i>C. avellana</i> , PI 617185 |
|---|------|----|---|
| Chinese Trazel #11, CCOR 173.001 [×] | 2005 | 3 | Gellatly <i>C. colurna</i> hyb., PI 557264 |

| Chinese Trazel #6, CCOR 138.001 [×] | 2005 | 3 | Gellatly C. colurna hyb., PI 557261 |
|---|---------------|---|---|
| Grimo 186M | 2006 | 1 | <i>C. colurna</i> hyb. 'Faroka' × OP |
| Grimo 208D | 2006 | 1 | <i>C. colurna</i> hyb. 'Faroka' × OP |
| 'Lisa' ^x | 2008 | 1 | 'Grand Traverse' ('Faroka' × <i>C. avellana</i> 'Royal') × OP |
| Rutgers H2R5P21 | 2006, 2009 | 2 | Chinese Trazel #6 × OP |
| Turktrazel Gellatly #3, CCOR 407.001 [×] | | | Gellatly C. colurna hyb., PI 557395 |

John Gordon collection

| [| 'Auger' | 2007 | 3 | John Gordon Nursery selection |
|---|-------------------|------|---|-------------------------------|
| | 'Slagel' | | 1 | John Gordon Nursery selection |
| | Gordon #8 V | 2005 | 2 | John Gordon Nursery selection |
| | Gordon Neighbor N | 2004 | 1 | John Gordon Nursery selection |
| | Gordon R02P1 | 2006 | 1 | John Gordon Nursery selection |
| | Gordon R03P1 | 2006 | 1 | John Gordon Nursery selection |
| | Gordon R06P1 | 2006 | 2 | John Gordon Nursery selection |
| | Gordon R06P2 | 2006 | 1 | John Gordon Nursery selection |
| | Gordon R08DP1 | 2006 | 1 | John Gordon Nursery selection |
| | Gordon R08DP2 | 2006 | 1 | John Gordon Nursery selection |
| | Gordon R09P1 | | 1 | John Gordon Nursery selection |
| | | | | |

| Gordon R10P1 | 2006 | 1 |
|---------------|------|---|
| Gordon R10P2 | 2006 | 1 |
| Gordon R12DP1 | 2006 | 1 |
| Gordon R12DP3 | 2006 | 1 |
| Gordon R12PP2 | 2006 | 1 |
| Gordon R13P1 | 2006 | 1 |
| Gordon R15P1 | 2006 | 1 |
| Gordon R15P2 | 2006 | 1 |
| Gordon R16P1 | 2006 | 1 |
| Gordon R17P2 | 2006 | 1 |
| Gordon R17P4 | 2006 | 1 |
| Gordon R18P1 | 2006 | 1 |
| Gordon R22P1 | 2006 | 1 |
| Gordon R24DP1 | 2006 | 1 |
| Gordon R25P1 | 2006 | 1 |
| Gordon R26P1 | 2006 | 1 |
| Gordon R27P2 | 2006 | 1 |
| Gordon R28P1 | 2006 | 1 |
| Gordon R29P2 | 2006 | 1 |
| | l | I |

John Gordon Nursery selection John Gordon Nursery selection

| 1 | John Gordon Nursery selection |
|---|---|
| 1 | John Gordon Nursery selection |
| | 1 1 1 1 1 1 1 1 1 1 1 |

Corylus fargesii

| C. fargesii 96-574-D Morris | 2004 | 1 | Morris Arboretum, Shaanxi and Gansu provinces, China |
|------------------------------------|------|---|--|
| C. fargesii 96-574-E Morris | 2004 | 1 | Morris Arboretum, Shaanxi and Gansu provinces, China |
| C. fargesii 96-574-F Morris | 2004 | 1 | Morris Arboretum, Shaanxi and Gansu provinces, China |
| C. fargesii 96-574-I Morris | 2004 | 1 | Morris Arboretum, Shaanxi and Gansu provinces, China |
| <i>C. fargesii</i> 96-574-J Morris | 2004 | 1 | Morris Arboretum, Shaanxi and Gansu provinces, China |
| <i>C. fargesii</i> 97-298-C Holden | 2004 | 2 | Holden Arboretum, Shaanxi and Gansu provinces, China |
| C. fargesii 97-298-C Holden | 2004 | 2 | Holden Arboretum, Shaanxi and Gansu provinces, China |

^zIncluded in the 2002 replicated trial.

^vAll *C. avellana* listed were found to be resistant to EFB in Oregon.

^xResistant to EFB in Oregon.

^wOSU 373.056 was potentially mislabeled at OSU and could be a *C. americana* selection from Montana.

Table 3. General attributes of hazelnut (*Corylus* sp.) species evaluated for their response to eastern filbert blight (EFB). With the exception of *C. fargesii*, which has been largely untested, the species included below can be hybridized with *C. avellana*, the hazelnut of commerce (Erdogan and Mehlenbacher, 2000a). Descriptions are derived from Mehlenbacher (1991) and eFloras (2012). Characteristics of the hybrid accessions are typically intermediate between the two parent species with selection made towards the nut characteristics of *C. avellana*.

| Species | Growth | Tree size | Husk (involucre) | Nut characteristics | Origin | Major breeding |
|--------------|---------|--------------|----------------------|-------------------------|-------------------------|--------------------------|
| | form | | type | | | attributes |
| Corylus | Multi- | 3-10 m, | Some forms release | Quite variable; some | Europe and Asia minor; | Large, thin-shelled nuts |
| avellana | stemmed | occasionally | nuts upon maturity, | horticulturally | north from Norway to | with high quality |
| | shrub | to 15 m | other are clasping | important cultivars | Finland east to Ural | kernels; nuts that fall |
| | | | and retain nuts | have thin shells with | Mountains, south to | free from husk at |
| | | | | nuts of over 3.0 g with | Morocco, bounded in the | maturity |
| | | | | kernels reaching >1.5 | west by Atlantic Ocean; | |
| | | | | g, wild accessions | commercially cultivated | |
| | | | | much smaller with nuts | in regions with | |
| | | | | <1.5 g and kernels | Mediterranean climates | |
| | | | | <0.7 g | | |
| C. americana | Multi- | 1-3 m | Clasping and very | Thick shells, nuts <1.5 | eastern North America | Resistance to EFB; |
| | stemmed | | fleshy, retains nuts | g with kernels <0.5 g | from Saskatchewan, | cold hardiness; |

| | shrub | | at maturity | | Canada and Maine | attractive fall color |
|--------------|--------------|--------------|----------------------|-------------------------|-------------------------|------------------------|
| | | | | | south to Georgia, and | (omamental) |
| | | | | | west to eastern | |
| | | | | | Oklahoma | |
| <i>C</i> . | Multi- | 1-3 m, | Some forms release | Thick shells, nuts <1.5 | Korea, Japan, China, | Resistance to EFB; |
| heterophylla | stemmed | occasionally | nuts upon maturity, | g with kernels <0.5 g | eastern Mongolia, and | cold hardiness |
| | shrub | to 7 m | others are clasping | | the Russian far east | |
| | | | and retain nuts | | | |
| C. colurna | Single trunk | 20-40 m | Clasping and very | Thick shells, nuts <1.5 | Balkan Peninsula, | Resistance to EFB; |
| | tree | | fleshy, retains nuts | g with kernels <0.5 g | Turkey, the Caucuses, | cold hardiness; non- |
| | | | at maturity, | | and northern Iran | suckering growth habit |
| | | | although some | | | |
| | | | selections release | | | |
| | | | nuts at maturity | | | |
| C. fargesii | Single trunk | Up to 25 m | Clasping, retains | Thick shells, nuts <1.5 | China, including Gansu, | Resistance to EFB; |
| | tree | | nuts at maturity | g with kernels <0.5 g | Guizhou, Henan, Hubei, | non-suckering growth |
| | | | | | Jiangxi, south Ningxia, | habit; peeling bark |
| | | | | | Shaanxi, and northeast | (omamental) |

Figure 1. Representative samples of nuts and kernels of hazelnut (*Corylus* sp.) species and interspecific hybrids evaluated in this study. Accessions included are as follows (in order from left to right, top to bottom): *C. avellana* 'Barcelona', *C. avellana* 'Tonda di Giffoni', *C. avellana* 'Gasaway', *C. americana* 'Winkler', *C. americana* Oregon State University (OSU) 532.076 from Michigan, *C. americana* × *C. avellana* hybrid Nebraska #1 (10-50), *C. americana* × *C. avellana* hybrid NY 398, *C. heterophylla* OSU 404.026, *C. heterophylla* × *C. avellana* OSU 526.041; *C. heterophylla* var. *sutchuensis* × *C. avellana* 'Estrella #1', *C. colurna* (unnamed seedling selection), *C. colurna* × *C. avellana* 'Faroka', *C. colurna* × *C. avellana* 'Grand Traverse', Gordon *Corylus* hybrid (unknown parentage) 'Auger', Gordon *Corylus* hybrid (unknown parentage) GR10P2, *C. fargesii* (seed collected from Morris Arboretum, Philadelphia, PA). A millimeter ruler is located at the bottom of the image to show scale.



Figure 1.

Figure 2. Example of morphological difference observed in the nut husks (involucres) of the hazelnut (*Corylus* sp.) species and interspecific hybrids evaluated in this study. Species or hybrid included are as follows (in order from left to right, top to bottom): *C. avellana* (unnamed seedling selection), *C. avellana* Russian H3R13P40, *C. avellana* Russian H3R14P26, *C. americana* (unnamed seedling selection), *C. americana* × *C. avellana* hybrid Nebraska #1 (10-50), *C. heterophylla* (unnamed seedling selection), *C. colurna* × *C. avellana* hybrid Nebraska #1 (10-50), *C. heterophylla* (unnamed seedling selection), *C. colurna* × *C. avellana* 'Grand Traverse', *C. fargesii* (unnamed seedling selection). Pictures were taken in the field in late July 2011 at Rutgers University, with the exception of the *C. colurna* photo which was taken at the U.S. Department of Agriculture Agricultural Research Service National Clonal Germplasm Repository in Corvallis, OR. The *C. avellana* pictures were chosen to demonstrate the variation in husk length found in this species. The other images are representative of the species in general. Note that the separate husk images are not to scale and are for comparison of morphological characteristics only. However, for reference, the general range of all the husks shown span 5 to 8 cm in diameter from the smallest (*C. heterophylla*) to the largest (*C. colurna*).



Figure 2.

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Eastern Filbert Blight Resistant Hazelnuts from Russia, Ukraine, and Poland

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Abstract. Stable genetic resistance to the fungal disease eastern filbert blight (EFB), caused by *Anisogramma anomala*, is vital for sustainable production of European hazelnut (*Corylus avellana*) in eastern North America. In this study, new hazelnut germplasm from the Russian Federation, Ukraine, and Poland (a total of 1,844 trees from 66 seed lots) was subjected to *A. anomala* under field conditions over at least 5 years in New Jersey. Plants were then rated for the presence of EFB using an index of 0 (no disease) through 5 (all stems containing cankers). Nuts of the resistant trees were evaluated to identify plants with improved kernel characteristics. Genomic DNA of these trees was also screened with sequence characterized amplified region (SCAR) markers generated by the primers BE-03, BE-33, and BE-68, which are closely linked to the

single dominant *R*-gene of 'Gasaway', to assess the resistant seedlings for the presence of this well known source of resistance. At final evaluation, 76 trees remained free of disease, with nine expressing only minor symptoms (rating 1 or 2). The resistant trees spanned 24 different seed lots representing all three countries. The remaining trees ranged from moderately to severely infected, with 81% of the total collection rating 5. Several of the resistant trees were found to produce commercial-size (\approx 12 mm diameter), round kernels that blanched well. While the results of the 'Gasaway' SCAR primers were inconclusive, the diverse collection origins and disease phenotypes provide evidence that novel sources of resistance were likely identified in this study. These new plants should broaden the genetic base of EFB-resistant *C. avellana* hazelnut germplasm available for breeding.

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Introduction

Eastern filbert blight (EFB), caused by the ascomycete fungus *Anisogramma anomala*, is an endemic disease of the wild American hazelnut, *Corylus americana*. This

pathogen is associated with *C. americana* throughout its native range, which spans much of the United States and southern Canada, east of the Rocky Mountains (Gleason and Cronquist, 1998). While EFB is typically inconsequential to *C. americana* (Capik and Molnar, 2012; Fuller, 1908; Weschcke, 1954), it causes severe cankering, branch dieback, and eventual death of most cultivars of the commercially important European hazelnut, *C. avellana* (Johnson and Pinkerton, 2002). This disease is considered to be the principle limiting factor of hazelnut production in the eastern U.S. (Thompson et al., 1996).

Today, 99% of U.S. hazelnut production occurs in the Willamette Valley of Oregon, representing $\approx 5\%$ of the world crop, which was 857,759 t in 2010 (Food and Agricultural Organization of the United Nations, 2012). When the hazelnut industry began in the Pacific northwestern U.S. in the early 1900s, EFB was not present (Barss, 1930). The suitable climate of the region, combined with the lack of EFB, allowed for production to flourish for almost a century. This scenario changed dramatically with the introduction of A. anomala into southwest Washington in the 1960s (Davison and Davidson, 1973). In the early years following its introduction, EFB devastated orchards as effective control measures were not yet developed (Gottwald and Cameron, 1980; Pinkerton et al., 1992). It was later learned that scouting for cankers, therapeutic pruning, and copious fungicide applications were necessary to continue production in the presence of the disease (Johnson et al., 1996). Due to the expense of these control measures and the fact that hazelnut was traditionally a low-input crop, the development and production of EFB-resistant cultivars has been recognized as a more cost-effective, long-term management solution (Julian et al., 2008, 2009; Thompson et al., 1996). Breeding for

EFB resistance is now a major objective of hazelnut breeding programs in the United States (Mehlenbacher, 1994; Molnar et al., 2005a).

Recent taxonomic studies suggest *Corvlus* contains 11 species (Bassil et al., 2012; Erdogan and Mehlenbacher, 2000). Of these species, cultivated forms of C. avellana produce the largest nuts with the most desirable kernel characteristics, with the remaining species generally producing tiny, thick-shelled nuts (Mehlenbacher, 1991). Therefore, the identification of EFB resistance within C. avellana holds promise for more efficient breeding of commercial-quality, EFB-resistant cultivars. This assumption is due to the likely need for fewer backcross generations if genes for EFB-resistance are identified in plants that also produce nuts of improved quality. The first identified C. avellana cultivar resistant to EFB was Gasaway, a late-blooming pollinizer that produces low yields of small, poor-quality nuts. Despite its horticultural deficiencies, 'Gasaway' was shown to transmit a dominant allele at a single locus that confers resistance to its offspring in a ratio of one resistant to one susceptible (Mehlenbacher et al., 1991). Since its discovery, it has been widely used in the Oregon State University (OSU), Corvallis, OR, hazelnut breeding program. After nearly 30 years of breeding, EFB-resistant cultivars that produce commercial-quality nuts were recently released from OSU, including Santiam (Mehlenbacher et al., 2007), Yamhill (Mehlenbacher et al., 2009), and Jefferson (Mehlenbacher et al., 2011).

Concern over the long-term durability of using only one source of resistance to the EFB pathogen led to the initiation of research at OSU to find additional resistant plants. This work eventually yielded a number of *C. avellana* cultivars and seedling selections, as well as other *Corylus* species and interspecific hybrids found to be resistant to EFB in Oregon (Chen et al., 2005, 2007; Coyne et al., 1998; Lunde et al., 2000; Sathuvalli et al., 2009, 2010). Along with 'Gasaway', a number of these new sources of resistance are being incorporated into advanced breeding selections at OSU, which is being facilitated by the use of marker-assisted selection (MAS) (S.A. Mehlenbacher, personal communication). Mehlenbacher et al. (2004) identified a number of random amplified polymorphic DNA (RAPD) markers tightly linked to the 'Gasaway' *R*-gene, with the primers UBC 152₈₀₀, UBC 268₅₈₀, and OP AA12₈₅₀ used routinely in the OSU breeding program. Recently, sequence characterized amplified region (SCAR) markers developed from the RAPD markers linked to the Gasaway *R*-gene have also been developed for use in fine mapping around the 'Gasaway' resistance locus and have shown application for MAS (Sathuvalli and Mehlenbacher, 2010). In addition to 'Gasaway', other PCR-based molecular markers have been developed that are closely linked to the R-genes found in C. avellana 'Ratoli' (from Spain), OSU 408.040 (from Minnesota), and OSU 750.010 (from the Republic of Georgia) (Chen et al., 2005; Mehlenbacher et al., 2004; Sathuvalli et al., 2011a, 2011b, 2012). Using these primers, one can identify seedlings that carry the specific resistance allele within weeks of germination, in the absence of the EFB pathogen. This technique provides a very significant time reduction over greenhouse inoculation methods, where trees are required to cycle through a period of plant dormancy before EFB cankers can be visualized and can take between 9 - 24 months (Johnson et al., 1994; Molnar et al., 2005b). In addition to offering a more efficient disease selection method, MAS can also facilitate the "pyramiding" of two or more resistance genes into one cultivar as a possible means to develop plants expressing more durable forms of disease resistance.

Recent work at Rutgers University, New Brunswick, NJ, has shown that pathogenic variation may exist in *A. anomala*. A number of hazelnut genotypes, including 'Gasaway' and some of its offspring known to be resistant to the isolates of the fungus present in Oregon, were recently found to be susceptible when exposed to eastern U.S isolates in greenhouse inoculations and through long-term field trials. Conversely, a number of other genotypes ('Ratoli', 'Zimmerman', OSU 495.072, 'Grand Traverse', and OSU 541.147) were exposed similarly and remained free of disease (Capik and Molnar, 2012; Molnar et al., 2010a, 2010b). These findings support the need to continue efforts towards the identification and study of new sources of genetic resistance to *A. anomala*, especially the assessment of new germplasm in areas where the pathogen is native and disease pressure is high.

The objective of this study was to evaluate new introductions of hazelnut germplasm from Russia, Ukraine, and Poland for their response to *A. anomala* under field conditions in New Jersey to identify new sources of resistance and tolerance to EFB. Nut and kernel attributes of the resistant and tolerant trees would then be characterized to identify improved, EFB-resistant seedlings expressing the greatest potential value for genetic improvement efforts.

Materials and Methods

Plant material and culture. Hazelnut germplasm in the form of nuts resulting from open pollination was collected from southern Russia in 2002 and 2004, the Crimean Peninsula of Ukraine in 2002, and Konskowli, Skierniewice, and Warsaw, Poland, in 2006. A total of 66 seed lots were obtained from horticultural institutes and breeding

stations, as well as purchased from local roadside vendors and outdoor markets in late August or early September of each collection year. Their origin and specific seed parent, when known, are listed in Table 1. Nuts collected from the institutes were largely harvested directly from the trees prior to nut fall, which helped to avoid the mixing of nuts from different parent plants. No background information (cultivar, previous storage conditions, etc.) was available from the seed lots purchased as fresh in-shell nuts from local markets and some obviously constituted mixtures of nuts from different genetic backgrounds. Nuts were held in mesh bags at ambient room temperatures (~ 20 °C) for 2 to 3 weeks to dry and were then placed in cold storage until undergoing moist-chilling at 4 °C from October to March. They were germinated in wooden planting boxes (61 cm \times 91 cm × 15 cm) containing a peat-based medium (Pro-mix® BX, Premier Horticulture, Rivière-du-Loup, Québec) in a greenhouse maintained at 24/18 °C (day/night) with 16-h daylengths. In 4 to 6 weeks, seedlings were transplanted to 3.7 L plastic containers using the same planting medium. Each plant was top-dressed with 5 g of 5 to 6 month timerelease fertilizer (Osmocote Plus 15N-9P₂O₅-12K₂O with micronutrients, The Scotts Co., Marysville, OH) and watered as needed. It must be noted that each seed source from the 2002 collection [RUS-1 to RUS-31, except RUS-2 (Table 1)] was divided after germination and transplanting. Half of the resulting plants were exposed to severe greenhouse inoculations with the EFB pathogen and were discussed in Molnar et al. (2007). The remaining plants forwent greenhouse inoculations to be evaluated under longer-term field exposure to A. anomala in this study, which provides a more effective means to identify levels of tolerance to EFB (Coyne et al., 2000). None of the seedlings from the 2004 and 2006 collection (seed lots 04018 R to 04041 R and 06050 P to 06085

P, respectively) were exposed to greenhouse inoculations. After transplanting, seedlings were maintained in the greenhouse until early June or July and were then moved outside under 40% shade cloth until field-planting in September or October. Trees were planted in blocks by progeny, with the progenies organized in a completely randomized design at a spacing of 0.45 or 0.91 m within rows by 3.66 m between rows at either the Rutgers Fruit Research and Extension Center, Cream Ridge, NJ or the Rutgers Vegetable Research and Extension Farm, North Brunswick, NJ. Weed control, irrigation, and fertilizer were provided as needed over the course of the study with no applications of fungicides or insecticides.

Exposure to eastern filbert blight. Plants were exposed to EFB through natural spread from adjacent breeding nurseries holding many hundreds of infected hazelnut plants in addition to field inoculations, which consisted of tying infected hazelnut stems into the canopies of each tree in early April annually. The infected stems were collected from the Rutgers Fruit Research and Extension Center and the Rutgers Vegetable Research and Extension Farm. Disease pressure increased as the study progressed and EFB spread amongst the susceptible plants, which later constituted a large majority of the overall plantings.

Evaluation of disease response. In January 2012, a thorough visual rating of disease incidence and severity was recorded for all trees in the study according to an index developed by Pinkerton et al. (1992): 0 = no detectable EFB; 1 = single canker; 2 = multiple cankers on a single branch; 3 = multiple branches with cankers; 4 = greater than 50 percent of branches have cankers; 5 = all branches containing cankers, except for basal sprouts. The ratings of the individual trees were then used to calculate a mean

disease rating for each seed lot with means separated with the Ryan-Einot-Gabriel-Welsch (REGWQ) test using the REGWQ option of PROC GLM in SAS [version 9.2; SAS Institute, Cary, NC (SAS Institute, 2012)]. As a general point of reference, trees rating 0 are considered resistant. Trees rating 1 or 2 are considered highly tolerant, as, in our experience, they typically do not develop large enough cankers over the long-term to impede normal growth or nut production. Trees rating 3 are regarded as moderately tolerant, where it is unlikely that tree death will occur, although branches continue to die leading to a reduction in nut yield over time. Trees rating 4 or 5 are regarded as susceptible, where they show significantly reduced growth within 2 years of exposure and typically die entirely within 5 to 7 years.

Nut and kernel evaluations. Nuts were harvested directly from the plants prior to nut fall to prevent loss of product due to predation from rodents. The harvest was carried out in late August through early September 2012 from nearly all plants rating 0 or 1. Thirteen EFB-resistant plants selected from related seed lots from Russia and Ukraine, identified in Molnar et al. (2007), were also included for comparison and documentation, as their nuts were not evaluated in the previous publication. Collected nuts were husked and dried indoors in mesh bags (~20 °C). They were placed on ventilated storage shelves with circulating fans run continuously for approximately 8 weeks prior to evaluation. Total intact nut weight and kernel weight of ten typical, individual nuts were recorded for each tree and used to calculate kernel percentage [(kernel weight/total nut weight) × 100]. Then, where available, 50 nuts were cracked and the number of good (free of defects) and substandard (blank, moldy, poorly filled, shriveled, or twinned) kernels were recorded and used to calculate the overall percentages of each of these defects. Presence of fiber on the kernels was rated using a scale of 1 = no fiber present to 4 = very fibrous (Thompson et al., 1978). The length, width, and thickness (depth) of ten typical kernels of each seedling were measured with a digital caliper to calculate average kernel dimensions. These dimensions were used to calculate the geometric mean diameter (*Dg*) and sphericity (index of roundness) (Φ) of the kernels using the formula $Dg = (LWT)^{1/3}$ and $\Phi = [Dg/L] \times 100$, where L= length, W = width, and T = thickness in mm (Mohsenin, 1970).

Further, using around 20 kernels, the ease of pellicle removal after dry heat $(130^{\circ}$ C for 13.5 minutes, then rubbing the cooled kernels with a terry cloth towel) was rated on a scale of 1 = complete pellicle removal to 7 = no pellicle removal (Mehlenbacher and Smith, 1988; Thompson et al., 1978). Nut and kernel attributes were subjected to statistical analysis using Analysis of Variance (ANOVA), including Fischer's least significant-difference test (PROC ANOVA) in SAS for all measurements with sufficient data points (Tables 2 and 3).

SCAR primer assessment. In May 2012, leaf samples were collected from 70 of the total 81 plants rating 0 or 1 as well as all 13 plants identified in Molnar et al. (2007) to undergo genomic DNA extraction and screening for the presence of SCAR markers BE-03, BE-33, and BE-68. These markers are closely linked (<1 cM) to the 'Gasaway' *R*-gene and were reported to be robust and useful for MAS (Sathuvalli and Mehlenbacher, 2010). Leaf tissue samples were stored at -80 °C until DNA extraction. For each sample, approximately 350 mg of frozen tissue was ground using a mortar and pestle and genomic DNA was extracted using a modified CTAB extraction protocol (Jobes et al., 1995; Saghai-Maroof et al., 1984). DNA was quantified with a NanoDrop

ND-1000 Spectrophotometer (Thermo Scientific Inc.) and diluted to a concentration of 25 ng/ μ l. PCR reactions followed the protocol developed by Honig et al. (2010). PCR products were run on an ABI 3500xl capillary electrophoresis genetic analyzer (Applied Biosystems, Foster City, CA) and sized using the GeneScan[™] Liz 1200[®] size standard. PCR reactions produced the expected single band products, with no non-specific amplification products. Sixteen control plants were included in the SCAR primer screening for comparison to the resistant seedlings. These included EFB-resistant cultivars and seedlings known to express the 'Gasaway' *R*-gene based on parentage (Gasaway, Santiam, Zimmerman, VR 20-11, and Rutgers breeding selections H3BR3P23 and H3BR3P10), EFB-resistant plants believed to be un-related to 'Gasaway' ('Ratoli', 'Culpla', OSU 408.040, and OSU 495.072), and several cultivars that are known to be susceptible to EFB (Barcelona, DuChilly, Ennis, Casina, and Cutleaf). Each 96-well plate sample run also included one well with a GeneScan installation standard (Applied Biosystems, Foster City, CA). Nearly all samples were replicated four times for each primer pair. Each genotype was scored using Genemapper 4.0 (Applied Biosystems, Foster City, CA) for the presence or absence of the specific peaks associated with each primer.

Results and Discussion. At final evaluation, 76 seedlings showed no signs of the pathogen or symptoms of the disease (rating = 0) with nine expressing only minor EFB (rating 1 or 2). Most other seedlings were highly susceptible, with 1780 out of 1844 (93%) rating 4 or 5 (Table 1). The resistant and highly tolerant seedlings spanned 24 of 66 seed lots representing all three countries (Russia, Ukraine, Poland). Five of these seed

lots (04030 R, RUS-2, RUS-4, RUS-11, and RUS-26) contained a higher proportion of resistant plants relative to the others. Together, they held a majority of the resistant/highly tolerant plants identified in the study (55 of the 85 total). The remaining 30 resistant/highly tolerant plants were sporadically distributed across the other seed lots.

Hazelnut is an obligate out-crossing, wind-pollinated species with a sporophytic self-incompatibility system (Mehlenbacher, 1997). All of the seedlings evaluated were derived from open-pollinated nuts, and we expect that the pollen parents were very diverse. A large number of the seed lots were harvested from germplasm collections holding many different, potentially intercrossing, cultivars and seedlings accessions. Further, C. avellana is a common understory shrub and a component of many landscape plantings and gardens across the regions where the nuts were collected. Thus, for many seed lots, pollen could have come from wild plants as well as a variety of locally grown trees, some of which themselves would have been propagated by seed. For the majority of seed lots holding only one or two resistant plants, such as 06080 P from Warsaw, Poland, based on the unknown female parent and diverse pollen sources, it is not possible to discern the origin of genes for resistance or speculate with any certainty on the genetic control of the resistance present. As a consequence, the results simply identify a number of new, potentially very valuable, hazelnut genotypes remaining free of EFB in New Jersey that merit further study. However, the significant clustering of resistant plants in five of the seed lots mentioned above, including the bimodal pattern of resistance observed within several of them (i.e. the presence of only clearly resistant or highly susceptible trees with few intermediate responses shown), provides an indication that dominant, simply inherited resistance genes may be present in some of their progeny. As

an example, seed lot 04030 R ['Moskovski Rubin' × open-pollination (O.P.)], 18 of 54 (33%) trees rated 0, one rated 4, and the remaining 35 rated 5. This pattern was very similar to that observed for RUS-2 ('Kudishovski' × O.P.), where 23 of 61 (38%) trees rated 0, two rated 4, and 36 rated 5. These seed lots were both collected from the hazelnut germplasm collection located at the Russian Academy of Agricultural Science Institute of Floriculture and Subtropical Cultures, Sochi, Russia, although in different years. Their results, especially when compared to the numerous other seed lots collected from cultivars at the same institute that held few or no resistant trees, suggest that a dominant, simply inherited resistance gene (or genes) is present in both 'Moskovski Rubin' and 'Kudishovski'. Both cultivars are believed to have originated from a breeding program located near Moscow, Russia (Kudasheva, 1965; Yablokov, 1962), where germplasm is still held by the Russian Research Institute of Forestry and Mechanization. They also share a major similarity in that both have purple leaves (their seedlings also segregated for purple leaves in our trials). Interestingly, Sathuvalli et al. (2010) identified five clonal accessions from the Russian Research Institute of Forestry and Mechanization that were also EFB-resistant: Moscow #1, #2, #26, #27, and #37. Several of this group, including Moscow #2, have purple leaves. Moscow #2 was also found to remain free of EFB after field exposure in New Jersey (Capik and Molnar, 2012). These commonalities, further supported by the general rarity of EFB resistance in C. avellana, make it is probable that our resistant seedlings from RUS-2 and 04030 R share a common ancestor or lineage with these Moscow resistant selections, and likely the same gene(s) for EFB resistance.

Seed lots RUS- 4 from Sochi, RUS-26 from Simferopol, Ukraine, and RUS-11 from Holmskij, Russia, also produced a relatively large proportion of resistant and highly tolerant trees, amounting to 32%, 31%, and 17% of each of their total, respectively. Their results also suggest that a dominant gene (or genes) for resistance is present in the progeny. Unfortunately, these seed lots represent nuts purchased at local markets and little is known of their origin, with some seed lots possibly consisting of mixtures of nuts from different parents. Due to the lack of information on the seed lots and few comparative progeny, it is hard to speculate on the origin of resistance. Regardless, the likely presence of simply inherited resistance genes is very promising. We suspect these nuts were harvested from local hazelnut sources based on the rural setting of the small, roadside markets in which the seed lots were purchased. If this assumption is correct, these plants probably represent germplasm not closely related to seedlings of 04030 R and RUS-2, which originate from near Moscow, and they may express novel genes for EFB resistance. Further testing, including the placement of *R*-genes on the hazelnut genetic linkage map (Mehlenbacher et al., 2006), will be necessary to draw stronger conclusions on the nature and relationships of genes for EFB resistance between these or any of the other resistant plants identified in this study.

Sufficient numbers of nuts were available for evaluation of nut and kernel attributes from 64 of the total 81 plants that were rated 0 or 1 for EFB response (Table 1) and all 13 EFB-resistant plants identified in Molnar et al. (2007). No nuts were collected from the Polish plants (a total of nine resistant/tolerant trees) because they were not yet bearing appreciable numbers of nuts or were subjected to heavy rodent predation in 2012. The ANOVA revealed significant differences in kernel attributes among plants (Tables 2 and 3). Table 3 provides kernel data for selected EFB-resistant plants and includes representation from 22 different seed lots [six of the plants from Molnar et al. (2007) originated from seed lots not holding resistant plants in this study] in addition to the EFBresistant cultivars Gasaway and Delta and susceptible Barcelona for comparison. Based on the nut evaluations, we identified several trees that produce nuts of improved quality, including round kernels that blanch well and have a low percentage of defects (Fig. 1). For example, selection H3R10P88 (RUS-28, Yalta, Crimea, Ukraine) produces nuts with a kernel to shell ratio of 50.3 % and round (average sphericity of 94.1), ≈ 12 mm diameter kernels that blanch almost completely (pellicle removal rating of 1). Selection CRRR05P32 (04026 R, Sochi, Russia) had an average kernel to shell ratio of 46.7%, with round (average sphericity of 93.1), ≈ 12 mm diameter kernels that also blanched almost completely (pellicle removal rating of 1). Further, selection H3R13P40 (RUS-9, Holmskij, Russia) produced nuts with an average kernel to shell ratio of 47.9% with round (average sphericity of 96.0), ≈ 14 mm diameter kernels that blanch well (pellicle removal rating of 2). It should be noted that these evaluations represent only one year of data and should be considered a preliminary assessment. However, a number of these traits have been previously shown to be under relatively strong genetic control, such as kernel weight, kernel dimensions, kernel to shell ratio, and presence of mold (Mehlenbacher et al., 1993; Thompson, 1977; Yao and Mehlenbacher, 2000), and would be expected to remain relatively consistent across years. Our results show a number of the new accessions represent significant improvements over 'Gasaway' in terms of kernel characteristics and presence of defects, supported by the fact that the plants were all grown in the same location where environmental variation across the site was negligible.

If resistance is found to be transmitted in a dominant manner, as is suggested by the disease response observed in some of the seed lots, some of these new accessions may prove to be of considerable value to breeding EFB-resistant hazelnuts with improved nut and kernel characteristics.

The results of the 'Gasaway' SCAR primer assessment were largely inconclusive. The SCAR marker primers proved capable of amplifying clear, distinct alleles for each marker; however, the presence/absence of alleles showed a poor correlation with known resistance or susceptible phenotypes. As expected, the six control plants known to express markers linked to the Gasaway *R*-gene amplified alleles from all three SCAR marker primers; however, two of the four known EFB-resistant control plants unrelated to 'Gasaway', OSU 408.040 (from Minnesota) and OSU 495.072 (from southern Russia), amplified alleles from BE33 and BE03, respectively. Additionally, of the five known EFB susceptible control plants included in the current study ('Barcelona', 'DuChilly', 'Ennis', 'Casina' and 'Cutleaf'), 'Casina' amplified alleles from two of the SCAR marker primers while 'Cutleaf' amplified alleles from all three SCAR marker primers. It is interesting to note that none of the 83 resistant seedlings amplified alleles from all three primers; however, a number of the seedlings amplified alleles by one or occasionally two of the primers (data not shown). From these results, it was difficult to draw strong conclusions on the presence of the 'Gasaway' *R*-gene in the seedlings. The goal of the SCAR marker screening was to ascertain information on the likely presence of the 'Gasaway' *R*-gene in the new germplasm. 'Gasaway' has been widely used in breeding EFB-resistant hazelnuts and unrelated sources of EFB resistance are desired to augment

prior improvement efforts and for the pyramiding of resistance genes to develop plants expressing more durable forms of resistance.

At the initiation of this study, the use of closely linked 'Gasaway' SCAR markers was considered a reasonable and valid approach to evaluate the seedlings for the potential presence of their target allele, especially based on the proven effectiveness of the 'Gasaway' RAPD markers for use in MAS within progeny segregating for presence of the allele at OSU. Our results showed the limitation of these markers when assessing a diverse and largely unknown pool of genotypes. Given our inconclusive results, recent findings may provide some insight into what may be occurring. Work by Sathuvalli et al. (2012) and Peterschmidt et al. (2012) showed that resistance derived from OSU 408.040, OSU 495.072, and 'Culpla' mapped to the same linkage group (LG6) and in close proximity to the 'Gasaway' *R*-gene locus, indicating a possible *R*-gene cluster associated with their resistant phenotypes. Under such a scenario, it is plausible to see amplification by one or more of the SCAR markers in other European hazelnuts showing resistance to EFB, if the 'Gasaway' *R*-gene represents a component of a cluster of conserved genes that provide a level of resistance or tolerance to infection by A. anomala. However, it was surprising to see amplification by all three markers in 'Cutleaf' and two of the three in 'Casina', which are known to be highly susceptible to EFB. Thus, the results remain inconclusive and point to a significant need to develop additional molecular tools (through map-based cloning, sequencing, and validating candidate *R*-genes, etc.) to assist in the identification and characterization of resistance alleles. Currently, very little is known about the mechanism of resistance associated with the 'Gasaway' *R*-gene or other

resistance genes in hazelnut. These understandings are vital when working with perennial crops such as hazelnut that have long generation times.

Regardless of the SCAR marker results, the field data shows that many of the new selections still remain free of EFB after many years in the field, whereas plants carrying the 'Gasaway' *R*-gene have shown an increased degree of susceptibility in New Jersey (Capik and Molnar, 2012; Molnar et al., 2010b). This includes several progeny segregating for a high level of resistance without individuals showing the tolerant phenotypes (EFB rating of 1, 2, and 3) observed in progenies segregating for the 'Gasaway' gene in New Jersey (Molnar, unpublished). As such, their phenotypes, in conjunction with the diverse origins of the plant material, suggest that novel sources of EFB resistance exist in some of the seedlings. Additional research, such as discovery of new genes/QTLs through developing mapping populations, test crosses, etc., will be needed to prove this hypothesis. Work along these lines is currently being conducted.

Conclusions. This study yielded a relatively large number of new seedlings of *C*. *avellana* shown to express resistance or a high level of tolerance to EFB. Some of these plants have remained disease-free or have expressed only very limited infections after nearly a decade of exposure to *A. anomala* in New Jersey under high disease pressure. While confounded by the fact that all of the seedlings are derived from open-pollinated nuts, the clustering of resistant seedlings in several seed lots suggests that some accessions may hold simply inherited, dominant genes for EFB resistance. More work is needed to better understand the EFB resistance expressed across the numerous seedlings identified in this study, including the relationships of the resistance alleles and how they are inherited. However, based on the diversity of origins represented in the collection and the out-crossing nature of hazelnuts along with the high-level of disease resistance observed, we hope that further research will reveal a number of novel genes for EFB resistance.

While the results of the 'Gasaway' SCAR primer assessment were largely inconclusive, they shed light on the challenges associated with breeding for disease resistance in a perennial, clonally propagated crop with a long generation time and support the great need for the development of additional molecular-based tools for use in such a system. Future work will include the characterization of the EFB-tolerant and resistant trees using simple sequence repeat (SSR) markers (Bassil et al., 2012; Boccacci et al., 2005; Gürcan et al. 2010). They will be analyzed alongside cultivars and accessions representing known geographic origins, such as those discussed in Gökirmak et al. (2009). This work will help us better determine origins and relationships within our collection and between other known EFB-resistant cultivars and selections, including OSU 495.072 from southern Russia and the aforementioned Moscow #1, #2, #26, #27, and #37 (Sathuvalli et al., 2010), as well as OSU 759.010 from the Republic of Georgia (Sathuvalli et al., 2011b).

The top EFB-resistant performers of this new collection will be assessed for use in the Rutgers genetic improvement program, including the study of inheritance of resistance of their progeny and the placing of resistance genes, where applicable, on the hazelnut genetic linkage map (Mehlenbacher et al., 2006). The most promising seedlings will also be propagated and made available to OSU and the United States Department of Agriculture, Agricultural Research Service, National Clonal Germplasm Repository in Corvallis, OR.

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| Seed | Year | | Trees | ^y Eastern filbert blight ratings | | | | | | | | |
|----------------------|---------|---|-------|---|----|---|---|----|----|----|--|--|
| lot | planted | Origin and parentage | (no.) | ^z Mean | 0 | 1 | 2 | 3 | 4 | 5 | | |
| ^x 04018 R | 2005 | 'Chikvistava' × Open pollinated (O.P)., Sochi, Russia | 59 | 4.98 _a | 0 | 0 | 0 | 0 | 1 | 58 | | |
| 04019 R | 2005 | 'Ata Baba' × O.P., Sochi, Russia | 8 | 4.88 _a | 0 | 0 | 0 | 0 | 1 | 7 | | |
| 04021 R | 2005 | 'Cherkeskii II' × O.P., Sochi, Russia | 38 | 4.89 _a | 0 | 0 | 0 | 0 | 4 | 34 | | |
| 04022 R | 2005 | 'President' × O.P., Sochi, Russia | 17 | 4.00 _{abc} | 2 | 0 | 0 | 3 | 1 | 11 | | |
| 04023 R | 2005 | 'Christina' × O.P., Sochi, Russia | 7 | 4.86 _a | 0 | 0 | 0 | 0 | 1 | 6 | | |
| 04024 R | 2005 | 'Zugdui' × O.P., Sochi, Russia | 45 | 4.07 _{abc} | 1 | 1 | 0 | 11 | 11 | 21 | | |
| 04025 R | 2005 | B-X-2 × O.P., Sochi, Russia | 36 | 4.97 _a | 0 | 0 | 0 | 0 | 1 | 35 | | |
| 04026 R | 2005 | Unknown seed mixture, Sochi region, Russia | 24 | 4.75 _a | 1 | 0 | 0 | 0 | 1 | 22 | | |
| 04027 R | 2005 | 'Akademik Yabokov' × O.P., Sochi, Russia | 31 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 31 | | |
| 04028 R | 2005 | 'Kavkas' × O.P., Sochi, Russia | 37 | 4.70 _{ab} | 2 | 0 | 0 | 0 | 1 | 34 | | |
| 04029 R | 2005 | 'Abhazki' × O.P., Sochi, Russia | 27 | 4.63 _{ab} | 1 | 0 | 0 | 0 | 5 | 21 | | |
| 04030 R | 2005 | 'Moskovskii Rubin' × O.P., Sochi, Russia | 54 | 3.31 _{bc} | 18 | 0 | 0 | 0 | 1 | 35 | | |
| 04031 R | 2005 | 'Victoria' × O.P., Sochi, Russia | 52 | 4.96 _a | 0 | 0 | 0 | 0 | 2 | 50 | | |
| 04032 R | 2005 | Unknown seed mixture, Sochi region, Russia | 59 | 4.81 _a | 0 | 0 | 0 | 1 | 9 | 49 | | |
| 04033 R | 2005 | 'Anastasia' × O.P., Sochi, Russia | 22 | 4.77 _a | 0 | 1 | 0 | 0 | 1 | 20 | | |
| 04034 R | 2005 | Unknown seedling, Sochi region, Russia | 39 | 4.64 _{ab} | 1 | 0 | 0 | 0 | 9 | 29 | | |
| 04035 R | 2005 | Wild C. avellana, Sochi region, Russia | 25 | 4.88 _a | 0 | 0 | 0 | 0 | 3 | 22 | | |
| 04036 R | 2005 | Unknown seedling, Sochi region, Russia | 3 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 3 | | |
| 04037 R | 2005 | 'Trapezund' × O.P., Sochi, Russia | 2 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 2 | | |
| 04038 R | 2005 | B-X-1 \times O.P., Sochi, Russia | 58 | 4.86 _a | 1 | 0 | 0 | 0 | 3 | 54 | | |
| 04039 R | 2005 | Unknown seedling, Sochi region, Russia | 12 | 4.58 _{ab} | 0 | 0 | 0 | 0 | 5 | 7 | | |
| 04040 R | 2005 | 'Rimskii' × O.P., Sochi, Russia | 49 | 4.86 _a | 1 | 0 | 0 | 0 | 2 | 46 | | |
| 04041 R | 2005 | B-X-3 × O.P., Sochi, Russia | 45 | 4.73 _a | 1 | 0 | 0 | 1 | 5 | 38 | | |

and Poland to eastern filbert blight (Anisogramma anomala).

| | | | 1 | 1 | | | | | | |
|---------|------|---|-----|---------------------|----|---|---|---|----|-----|
| 06050 P | 2007 | 'Garibaldi' × O.P., Konskowli, Poland | 15 | 4.87 _a | 0 | 0 | 0 | 1 | 0 | 14 |
| 06051 P | 2007 | 'Webba' × O.P., Konskowli, Poland | 29 | 4.86 _a | 0 | 0 | 0 | 0 | 4 | 25 |
| 06052 P | 2007 | 'Hall's Giant' × O.P., Konskowli, Poland | 8 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 8 |
| 06053 P | 2007 | 'Katalonski' × O.P., Konskowli, Poland | 27 | 4.81 _a | 0 | 0 | 0 | 1 | 3 | 23 |
| 06054 P | 2007 | Unknown seed mixture, Skierniewice, Poland | 157 | 4.64 _{ab} | 2 | 0 | 2 | 9 | 28 | 116 |
| 06077 P | 2007 | Warsaw Market #1, Warsaw, Poland | 18 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 18 |
| 06078 P | 2007 | Warsaw Market #2, Warsaw, Poland | 14 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 14 |
| 06079 P | 2007 | Warsaw Market #3, Warsaw, Poland | 21 | 4.86 _a | 0 | 0 | 0 | 1 | 1 | 19 |
| 06080 P | 2007 | Warsaw Market #4, Warsaw, Poland | 20 | 4.70 _{ab} | 1 | 0 | 0 | 0 | 1 | 18 |
| 06081 P | 2007 | Warsaw Market #5, Warsaw, Poland | 9 | 4.89 _a | 0 | 0 | 0 | 0 | 1 | 8 |
| 06082 P | 2007 | Warsaw Market #6, Warsaw, Poland | 12 | 4.92 _a | 0 | 0 | 0 | 0 | 1 | 11 |
| 06083 P | 2007 | Warsaw Market #7, Warsaw, Poland | 12 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 12 |
| 06084 P | 2007 | Warsaw Market #8, Warsaw, Poland | 16 | 4.81 _a | 0 | 0 | 0 | 1 | 1 | 14 |
| 06085 P | 2007 | Unknown seed mixture, Warsaw, Poland | 57 | 4.63 _{ab} | 4 | 0 | 0 | 0 | 1 | 52 |
| RUS-1 | 2003 | Unknown seed mixture, Institute of Floriculture and | 71 | 4.77 _a | 0 | 0 | 0 | 2 | 12 | 57 |
| RUS-2 | 2003 | Subtropical Cultures, Sochi, Russia 'Kudashovski' × O.P., Institute of Floriculture and Subtropical Cultures, Sochi, Russia | 61 | 3.08 _c | 23 | 0 | 0 | 0 | 2 | 36 |
| RUS-3 | 2003 | Sochi Market #1, Sochi, Russia | 13 | 4.15 _{abc} | 0 | 0 | 1 | 2 | 4 | 6 |
| RUS-4 | 2003 | Sochi Market #2,Sochi, Russia | 19 | 3.16 _c | 4 | 2 | 0 | 3 | 1 | 9 |
| RUS-5 | 2003 | Sochi Market #3, Sochi, Russia | 26 | 4.92 _a | 0 | 0 | 0 | 0 | 2 | 24 |
| RUS-6 | 2003 | Sochi Market #4, Sochi, Russia | 25 | 4.84 _a | 0 | 0 | 0 | 1 | 2 | 22 |
| RUS-7 | 2003 | Sochi Market #5, Sochi, Russia | 15 | 3.93 _{abc} | 1 | 0 | 1 | 2 | 4 | 7 |
| RUS-8 | 2003 | Sochi Market #6, Sochi Russia | 10 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 10 |
| RUS-9 | 2003 | Holmskij Market #1; Holmskij, Krasnodarskiy Kray, Russia | 10 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 10 |
| RUS-10 | 2003 | Holmskij Market #2; Holmskij, Krasnodarskiy Kray, Russia | 14 | 4.93 _a | 0 | 0 | 0 | 0 | 1 | 13 |
| RUS-11 | 2003 | Holmskij Market #3; Holmskij, Krasnodarskiy Kray, Russia | 24 | 4.04 _{abc} | 4 | 0 | 0 | 1 | 1 | 18 |
| RUS-12 | 2003 | Holmskij Market #4; Holmskij, Krasnodarskiy Kray, Russia | 7 | 4.57 _{ab} | 0 | 0 | 0 | 1 | 1 | 5 |
| RUS-13 | 2003 | Holmskij Market #5; Holmskij, Krasnodarskiy Kray, Russia | 9 | 4.78 _a | 0 | 0 | 0 | 0 | 2 | 7 |
| RUS-14 | 2003 | Holmskij Market #6; Holmskij, Krasnodarskiy Kray, Russia | 33 | 4.36 _{abc} | 0 | 0 | 0 | 4 | 13 | 16 |
| RUS-15 | 2003 | Mixed cultivars, Vavilov Research Institute of Plant Industry (VIR) | 66 | 4.76 _a | 1 | 0 | 0 | 1 | 9 | 55 |
| | | Breeding Station; Maykop, Russia | | | | | | | | |

| RUS-16 | 2003 | 'Badem'× O.P., Research Institute for Horticulture and Viticulture; Krasnodar, Russia | 19 | 4.26 _{abc} | 0 | 0 | 0 | 1 | 12 | 6 |
|--------|------|--|------|---------------------|----|---|---|----|-----|------|
| RUS-17 | 2003 | Krasnodar Market #1; Krasnodar, Russia | 9 | 4.78 _a | 0 | 0 | 0 | 1 | 0 | 8 |
| RUS-18 | 2003 | Krasnodar Market #2; Krasnodar, Russia | 18 | 4.72 _a | 0 | 0 | 0 | 0 | 5 | 13 |
| RUS-19 | 2003 | Krasnodar Market #3; Krasnodar, Russia | 35 | 4.86 _a | 0 | 0 | 0 | 0 | 5 | 30 |
| RUS-20 | 2003 | Krasnodar Market #4; Krasnodar, Russia | 17 | 4.88 _a | 0 | 0 | 0 | 0 | 2 | 15 |
| RUS-21 | 2003 | Simferopol Roadside Market #1A; near Simferopol, Crimea, Ukraine | 16 | 4.38 _{abc} | 1 | 1 | 0 | 0 | 1 | 13 |
| RUS-22 | 2003 | Simferopol Roadside Market #1B; near Simferopol, Crimea, Ukraine | 20 | 4.85 _a | 0 | 0 | 0 | 0 | 3 | 17 |
| RUS-23 | 2003 | Simferopol Roadside Market #2; near Simferopol, Crimea, Ukraine | 18 | 4.56 _{ab} | 1 | 0 | 0 | 0 | 3 | 14 |
| RUS-24 | 2003 | Simferopol Roadside Market #3; near Simferopol, Crimea, Ukraine | 16 | 4.16 _{ab} | 0 | 0 | 0 | 0 | 5 | 11 |
| RUS-25 | 2003 | Simferopol Roadside Market #4; near Simferopol, Crimea, Ukraine | 22 | 4.27 _{abc} | 1 | 0 | 0 | 1 | 9 | 11 |
| RUS-26 | 2003 | Simferopol Roadside Market #5; near Simferopol, Crimea, Ukraine | 13 | 3.08 _c | 4 | 0 | 0 | 1 | 3 | 5 |
| RUS-28 | 2003 | Nikita Botanical Garden #1; Yalta, Crimea, Ukraine | 35 | 4.89_{a} | 0 | 0 | 0 | 1 | 2 | 32 |
| RUS-29 | 2003 | Nikita Botanical Garden #2; Yalta, Crimea, Ukraine | 34 | 4.97 _a | 0 | 0 | 0 | 0 | 1 | 33 |
| RUS-31 | 2003 | Wild C. avellana, near Moscow, Russia | 5 | 5.00 _a | 0 | 0 | 0 | 0 | 0 | 5 |
| | | TOTALS | 1844 | 4.6 | 76 | 5 | 4 | 51 | 213 | 1495 |

^zProgeny means followed by a different letter in the column are considered significantly different (*P*<0.05) based on a Ryan-Einot-Gabriel-Welsch (REGWQ) test using the REGWQ option of PROC GLM in SAS [version 9.2; SAS Institute, Cary, NC (SAS Institute, 2012)]. ^yResponses were recorded as follows: 0 = no detectable EFB, 1 = single canker, 2 = multiple cankers on single branch, 3 = multiple branches with cankers, 4 = greater than 50% of the branches with cankers, and 5 = all branches containing cankers, excluding basal sprouts. The total number of plants observed in each disease category (0 through 5) for each progeny is listed in each column below the disease rating category.

^xAll seeds collected in 2004 (04018 R through 04041 R) and planted in 2005 were collected from the Institute of Floriculture and Subtropical Cultures, Sochi, Russian Federation, unless otherwise noted

Table 2. Analysis of variance (ANOVA) results of nut and kernel characteristics for allindividual plants (n = 80) in the dataset.

| Dependent Variable | df | Mean | Std Dev | F- value | Pr > F |
|-------------------------|----|-------|------------|-------------|----------------------|
| ^z Sphericity | 79 | 81.54 | 0.37 | 53.71 | < 0.0001 |
| Kernel length (mm) | 79 | 15.18 | 2.10 | 50.26 | <0.0001 |
| Kernel width (mm) | 79 | 11.82 | 1.25 | 19.48 | < 0.0001 |
| Kernel depth (mm) | 79 | 10.35 | 1.38 | 24.36 | < 0.0001 |
| Kernel weight (g) | 79 | 0.88 | 0.24 | 23.53 | < 0.0001 |
| Shell weight (g) | 79 | 1.16 | 0.37 | 31.67 | < 0.0001 |
| ^y Kernel % | 79 | 43.46 | 6.43 | 22.81 | < 0.0001 |

^zSphericity = $\Phi = [Dg/L] \times 100$, where $Dg = (LWT)^{1/3}$, L= length, W = width, and T =

thickness (depth) of kernel in mm.

^yKernel % = kernel weight/intact nut weight $\times 100$.

| | | kernel | kernel | average kernel dimensions | | | | | % of nuts in each category ^t | | | | | |
|-----------------------|----------|-------------------------|------------------|---------------------------|-------|-------|-------------------------|--------------------|---|------|-------|-------|------|-----|
| Plant ID | seed lot | wt. (g) ^y | ⁰∕₀ ^x | length | width | depth | sphericity ^w | fiber ^v | pellicle ^u | Good | Blank | Moldy | SH | PF |
| CRRR06P02 | 04024R | 0.72 | 47.72 | 13.91 | 11.38 | 10.01 | 83.9 | 1 | 4 | 42.5 | 50.0 | 2.5 | 5.0 | 0.0 |
| CRRR05P32 | 04026R | 1.01 | 46.72 | 13.73 | 12.84 | 11.84 | 93.1 | 2 | 1 | 82.0 | 8.0 | 2.0 | 0.0 | 8.0 |
| CRRR04P116 | 04028R | 0.81 | 33.46 | 13.79 | 11.66 | 10.54 | 86.9 | 3 | 4 | 76.0 | 16.0 | 0.0 | 6.0 | 2.0 |
| CRRR04P28 | 04030R | 1.35 | 50.97 | 18.16 | 13.04 | 11.12 | 76.0 | 2 | 3 | 70.0 | 8.0 | 8.0 | 8.0 | 6.0 |
| CRRR04P48 | 04030R | 1.09 | 43.79 | 15.92 | 12.75 | 11.22 | 82.6 | 3 | 2 | 86.0 | 2.0 | 2.0 | 10.0 | 0.0 |
| CRRR04P64 | 04030R | 0.96 | 42.94 | 14.02 | 12.73 | 11.23 | 89.9 | 1 | 6 | 84.4 | 6.3 | 3.1 | 6.3 | 0.0 |
| CRRR03P11 | 04034R | 1.05 | 42.49 | 14.86 | 13.51 | 11.18 | 88.1 | 3 | 6 | 58.0 | 16.0 | 2.0 | 16.0 | 6.0 |
| CRRR02P96 | 04038R | 1.00 | 44.15 | 17.41 | 10.99 | 9.35 | 69.6 | 3 | 1 | 86.0 | 2.0 | 0.0 | 8.0 | 4.0 |
| CRRR02P41 | 04040R | 0.96 | 35.58 | 15.26 | 13.17 | 11.06 | 85.5 | 3 | 6 | 54.0 | 28.0 | 0.0 | 16.0 | 2.0 |
| CRRR01P116 | 04041R | 0.60 | 32.72 | 13.77 | 10.22 | 8.35 | 76.7 | 1 | 6 | 78.1 | 3.1 | 0.0 | 9.4 | 9.4 |
| H3R10P94 ^s | RUS-1 | 0.71 | 41.67 | 12.83 | 12.01 | 9.59 | 88.8 | 2 | 7 | 82.0 | 6.0 | 4.0 | 4.0 | 4.0 |
| CRXR13P78 | RUS-2 | 1.17 | 47.52 | 18.22 | 12.28 | 11.22 | 74.6 | 4 | 6 | 84.0 | 0.0 | 6.0 | 10.0 | 0.0 |
| CRXR13P83 | RUS-2 | 0.95 | 51.83 | 13.72 | 12.20 | 11.24 | 90.0 | 1 | 6 | 58.0 | 30.0 | 0.0 | 10.0 | 2.0 |
| CRXR13P91 | RUS-2 | 1.26 | 52.26 | 17.90 | 12.68 | 11.28 | 76.5 | 4 | 7 | 64.0 | 8.0 | 12.0 | 10.0 | 6.0 |
| CRXR14P34 | RU2-4 | 0.79 | 41.36 | 12.40 | 12.01 | 11.40 | 96.3 | 2 | 2 | 78.0 | 14.0 | 4.0 | 4.0 | 0.0 |

Table 3. Nut and kernel characteristics of select eastern filbert blight (EFB)-resistant^z hazelnut (*Corylus avellana*) selections

 from Russia and Ukraine.

| CRXR14P117 | RUS-7 | 0.95 | 36.33 | 15.85 | 12.73 | 11.37 | 83.3 | 1 | 2 | 62.0 | 4.0 | 16.0 | 14.0 | 4.0 |
|------------------------|--------|------|-------|-------|-------|-------|------|---|---|------|------|------|------|------|
| H3R13P40 | RUS-9 | 1.31 | 47.87 | 14.94 | 14.30 | 13.78 | 96.0 | 1 | 2 | 72.0 | 8.0 | 4.0 | 12.0 | 4.0 |
| CRXR15P59 | RUS-11 | 0.86 | 38.71 | 13.44 | 12.62 | 11.90 | 94.1 | 2 | 6 | 62.0 | 20.0 | 4.0 | 12.0 | 2.0 |
| H3R07P25 | RUS-12 | 0.70 | 40.75 | 12.58 | 11.29 | 9.66 | 88.3 | 1 | 3 | 90.0 | 6.0 | 2.0 | 2.0 | 0.0 |
| H3R04P23 | RUS-13 | 0.91 | 43.38 | 12.93 | 11.98 | 11.39 | 93.5 | 1 | 6 | 86.0 | 8.0 | 0.0 | 0.0 | 6.0 |
| CRXR17P48 | RUS-15 | 0.94 | 46.28 | 15.73 | 12.65 | 10.95 | 82.4 | 4 | 4 | 40.0 | 30.0 | 24.0 | 6.0 | 0.0 |
| H3R14P26 | RUS-22 | 1.11 | 39.74 | 13.20 | 12.02 | 11.38 | 92.3 | 1 | 4 | 48.0 | 0.0 | 0.0 | 24.0 | 28.0 |
| H3R12P62 | RUS-23 | 0.78 | 41.08 | 15.11 | 10.62 | 9.73 | 76.8 | 4 | 4 | 90.0 | 2.0 | 4.0 | 4.0 | 0.0 |
| CRXR19P21 | RUS-25 | 0.51 | 34.07 | 12.37 | 11.03 | 8.83 | 86.0 | 3 | 3 | 56.0 | 18.0 | 8.0 | 16.0 | 2.0 |
| H3R07P07 | RUS-26 | 0.88 | 42.71 | 12.97 | 12.25 | 11.45 | 94.1 | 4 | 5 | 94.0 | 2.0 | 0.0 | 4.0 | 0.0 |
| H3R07P09 | RUS-26 | 0.72 | 40.71 | 12.43 | 11.51 | 10.74 | 92.9 | 3 | 5 | 86.0 | 2.0 | 0.0 | 12.0 | 0.0 |
| H3R10P88 | RUS-28 | 0.93 | 50.33 | 13.49 | 12.60 | 12.01 | 94.1 | 1 | 1 | 72.0 | 6.0 | 6.0 | 14.0 | 2.0 |
| Barcelona ^r | na | 1.48 | 42.26 | 16.73 | 15.34 | 14.41 | 92.5 | 3 | 3 | 63.6 | 6.0 | 2.6 | 1.6 | 21.8 |
| Delta | na | 1.17 | 49.83 | 13.98 | 13.38 | 12.62 | 95.3 | 2 | 5 | 60.0 | 30.0 | 8.0 | 2.0 | 0.0 |
| Gasaway | na | 0.44 | 43.12 | 13.81 | 10.39 | 8.56 | 77.5 | 3 | 7 | 72.0 | 10.0 | 0.0 | 6.0 | 12.0 |
| | LSD | | | | | | | | | | | | | |
| | (0.05) | 0.12 | 3.17 | 0.76 | 0.65 | 0.66 | 3.1 | | | | | | | |

^zCRRR06P02 and Gasaway were rated 1 (one small canker), while all other selections were rated 0 (no signs or symptoms of EFB).

^yAll kernel characteristics (weight, %, average kernel dimensions, sphericity, fiber, and pellicle) are based on 10 samples representing typical kernels from each plant.

^xKernel percent = kernel weight/total nut weight $\times 100$.

^wSphericity = $\Phi = [Dg/L] \times 100$, where $Dg = (LWT)^{\frac{1}{3}}$, L= length, W = width, and T = thickness (depth) of kernel in mm. = $\Phi = [Dg/L] \times 100$, where L= length, W = width, and T = thickness in mm.

^vFiber is rated on a scale of 1(no fiber) to 4 (very fibrous).

^uPellicle is rated on a scale of 1 (all pellicle is removed) to 7 (little to no pellicle is removed) after dry roasting at 130° C for 13.5 minutes.

^t% of nuts in each category [good, blank, moldy, shriveled (SH), and poorly filled (PF)] is based on 50 total nuts for each plant, except for CRR06P02 (40 nuts) and CRRR04P64 and CRRR01P116 (32 nuts each). CRRR03P11 also had one twinned kernel, which was not retained as a category in the table since there were no other twinned kernels found.

^sAccessions with an "H3R" designation were identified as being EFB-resistant in Molnar et al. (2007).

"Barcelona' % of nuts in each category (good, blank, etc.) is adapted from Mehlenbacher et al. (2011). In that report,

'Barcelona' also has 4% twin kernels and 1.5% brown stain (total is over 100%).

Figure 1. Whole nuts, raw kernels, and blanched kernels of select EFB-resistant hazelnut accessions. Top row left to right: H3R13P40, H3R14P26, and H3R10P88. Bottom row left to right: 'Santiam' (Mehlenbacher et al, 2007), 'Barcelona' (susceptible), and 'Gasaway'.



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Flowering Phenology of Eastern Filbert Blight Resistant Hazelnut Accessions in New Jersey

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Abstract.

Hazelnuts (*Corylus* spp.) are monoecious and wind-pollinated with reproduction limited by a sporophytic self-incompatibility system. They flower during the winter and are dichogamous with the dates of flowering ranging from December to March depending on the genotype, geographic location, and year. Successful, consistent nut production depends on both genetic compatibility and the appropriate timing of flowering between pollinizing and nut producing cultivars. While the disease eastern filbert blight (EFB), caused by *Anisogramma anomala*, once severely limited hazelnut production in the eastern U.S., resistant and tolerant genotypes are now available. However, little is known of their flowering phenology in the East. In this study, the flower and bud break phenology of 19 different EFB-resistant and -tolerant hazelnut accessions was evaluated over 4 years and the results compared to air temperature data collected during bloom. Results showed that the accessions followed a similar progression of bloom each year (both staminate and pistillate flowers), which allowed their placement into Early, Mid-, and Late flowering groups. However, the date of bloom and duration of bloom, especially for pollen shed, differed each year, largely corresponding to average air temperature trends. Confirming previous reports from other cold regions, it was shown that consistently colder average temperatures delayed bloom until later in the winter, which then led to a compressed period of flowering once temperatures warmed. In contrast, relatively warm temperatures over the season led to earlier flowering as well as a significant lengthening of the duration of bloom, similar to responses reported in Mediterranean climates. Our study is the first to document hazelnut flowering phenology under New Jersey's variable winter climate, and the results provide a benchmark for selecting suitable pollinizers and breeding parents for future nut production, flowering research, and/or genetic improvement in this region.

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Introduction.

European hazelnut (*Corylus avellana*) is an important world agricultural crop, ranking 5th in overall tree nut production. Turkey produced 430,000 t of hazelnuts in 2011, accounting for approximately 58% of total world production (742,997 t in 2011), followed by Italy (128,940 t), the U.S. (34,927 t, \approx 5%), Azerbaijan (32,922 t), and the Republic of Georgia (31,100 t) (Food and Agriculture Organization of the United Nations, 2013). Commercial production in the U.S. takes places almost solely in the Willamette Valley of Oregon, with 99% of U.S. hazelnut crop originating there.

The presence of the disease eastern filbert blight (EFB), caused by *Anisogramma anomala*, has historically prevented the commercial production of hazelnuts across much of eastern North America (Fuller, 1908; Thompson et al., 1996). *Anisogramma anomala* is an ascomycetous fungus native to east of the Rocky Mountains, where it is harbored by its natural host *C. americana*, the wild American hazelnut (Johnson and Pinkerton, 2002). Unfortunately, while *C. americana* is generally highly tolerant of EFB, nearly all *C. avellana* cultivars are highly susceptible (Capik and Molnar, 2012; Pinkerton et al., 1993; Thompson et al., 1996). The absence of this pathogen combined with a mild climate allowed hazelnut production to flourish in the Pacific Northwest for nearly a century (Thompson et al., 1996). However, *A. anomala* was inadvertently introduced into southwest Washington in the late 1960s. The resulting disease devastated hazelnut orchards in the state, as control methods were not yet established (Cameron, 1976; Davison and Davidson, 1973).

While it was later learned that scouting for cankers, therapeutic pruning, and copious fungicide applications could keep the disease under control (Johnson et al.,

1996), due to their associated expenses, the most cost-effective and sustainable approach for long term management was considered to be utilizing and developing genetic resistance to the pathogen (Julian et al., 2009; Mehlenbacher, 1994; Thompson et al., 1996). In the 1970s, 'Gasaway', an obsolete, late-blooming pollenizer, was found to be resistant to EFB. It was later shown to transmit this resistance to its offspring in a manner indicative of a dominant allele at a single locus (Mehlenbacher et al., 1991). 'Gasaway' has since been widely used in the Oregon State University (OSU) breeding program. To date, a number of cultivars carrying the gene have been released, including Yamhill (Mehlenbacher et al., 2009), Jefferson (Mehlenbacher et al., 2011), and Dorris (Mehlenbacher et al., 2013), as well as various pollenizers (Mehlenbacher and Smith, 2004; Mehlenbacher and Thompson, 1991; Mehlenbacher et al., 2012). These new cultivars have reinvigorated the hazelnut industry in Oregon, which, after decades of decline, has been expanding at a rate of ~1200 hectares per year for the past 5 years (S. Mehlenbacher, personal communication).

In addition to 'Gasaway', a number of other sources of EFB resistance have also been identified at OSU, and more recently at Rutgers University, which are now being used in breeding (Capik et al., 2013; Chen et al., 2007; Lunde et al., 2000; Molnar et al., 2009, 2010; Sathuvalli et al., 2010). Capik and Molnar (2012) examined the disease response of 190 clonal accessions of hazelnut in New Jersey, which spanned a wide diversity of origins, including multiple *Corylus* species and interspecific hybrids. While some plants previously reported as resistant to EFB in Oregon developed disease, including 'Gasaway' and some of its offspring, a large number of the accessions remained resistant or highly tolerant to EFB in New Jersey over more than 10 years of exposure.

Today, with access to a multitude of EFB-resistant cultivars and breeding selections, one of the major impediments to developing a commercial hazelnut industry in parts of eastern U.S. has been overcome. As such, it is important to examine other factors critical to consistent hazelnut production in this region. Since nut production is fully dependent on successful cross pollination, one factor of vital importance is flowering—a topic poorly studied and documented for hazelnut in the eastern U.S.

Hazelnuts are monoecious, wind-pollinated, and self-incompatible. Reproduction is restricted by a sporophytic self-incompatibility system, which is controlled by a single locus with various S-alleles determining compatibility (Mehlenbacher, 1997; Olsen et al., 2000; Thompson, 1979). Over 30 S-alleles have been identified to date (S. Mehlenbacher, personal communication). Dominance or co-dominance of the alleles is expressed in the pollen, while all known S-alleles are co-dominant in the pistil (Mehlenbacher, 1997; Mehlenbacher and Thompson, 1988).

Hazelnuts are also dichogamous. Male (catkins, staminate) and female (pistillate) flowers both have different chilling requirements to break dormancy, with catkins typically having lower chilling requirements than the female flowers [ranges of 100-860 h and 290-1550 h, respectively, as described in Mehlenbacher (1991)]. Normally, flowering occurs in winter, before vegetative bud-break, over a range of dates depending on the genotype, geographic location, and year. In traditional hazelnut production regions, which are primarily located adjacent to large bodies of water and have very moderated climates (Mediterranean Basin or Black Sea areas), hazelnuts can bloom over

an extended period from early December through March. In colder regions, bloom is compressed over a much shorter time frame in late winter or early spring in response to warming temperatures (Črepinšek et al., 2012; Germain, 1994; Olsen et al., 2000; Piskornik et al., 2001; Solar and Stampar, 2009; Thompson et al., 1996). Plants are typically either protandrous or protogynous depending on their genetic background and the climate of the region they are grown in. In regions with mild climates, protandry seems to be more common, whereas in regions with long, cold winters, protogynous or homogamous flowering typically occurs (Germain, 1994; Mehlenbacher, 1991; Olsen et al., 2000; Piskornik et al., 2001).

Female flowers are unique in that stigmatic surfaces can stay receptive to fertilization, if not pollinated, for up to three months (Thompson, 1979). When compatible pollen reaches a receptive female flower, the pollen grain germinates and develops a germ tube, which grows down to the base of the style where the sperm cell subsequently travels and then rests. At this time, the ovary is not yet fully-formed. After ovary formation is complete, usually in late spring, the pollen tubes begin to grow again and fertilization occurs (Beyhan and Marangoz, 2007).

Differences in cold-tolerance have also been reported for male and female flowers. In controlled freezing tests, Hummer et al. (1986) showed that female flowers of some *C. avellana* cultivars could survive temperatures below -40 °C. Catkins, however, were shown to be injured at warmer temperatures. The most cold-tolerant fully dormant catkins tested were hardy to -35 °C, although some cultivars (e.g. Ennis, Tonda Romana) displayed injury at temperatures reaching only -15 °C (Hummer et al., 1986). Catkins elongating prior to anthesis or fully elongated and shedding pollen were not tested. However, it should be noted that past experience of the authors suggests that elongating or shedding catkins are much more susceptible to cold damage than fully dormant ones (data not shown). Thus, in cold regions with unpredictable winter climates, such as that found across the Mid-Atlantic region of the eastern U.S., catkin survivability can present a significant challenge for consistent nut production. Once chilling requirements are met, the occurrence of atypical warm winter weather can signal the catkins to elongate prematurely, making them more sensitive to cold damage. This problem can be exacerbated by high winter winds, not uncommon in the eastern U.S., which appear to cause desiccation injury (Reed and Davidson, 1958; Slate, 1933). Past reports suggest that hazelnuts may appear to thrive in the East but fail to produce nuts due to catkin damage and lack of pollination (MacDaniels, 1964).

The density of pollinizers in orchards around the world ranges from 3% to 30%, with 10% pollinizer density as the standard in Oregon (Olsen et al., 2000). Recent recommendations in Oregon include planting at least three different pollenizers that shed pollen at different times during the period that female flowers of the main crop cultivar are receptive to ensure consistent orchard pollination (Mehlenbacher et al., 2009). In respect to meeting this recommendation, very little research has been done to document how fluctuating winter temperatures affect flowering phenology of hazelnut in the eastern U.S. For example, over a 10 day period from Dec. 22, 2008 to Jan. 1, 2009, winter temperatures in New Brunswick, NJ, varied from -11.1 °C to 18.9 °C then back to -8.3 °C (National Climate Data Center, 2013). Knowledge of how hazelnuts respond under these conditions is vital to developing orchards that produce nuts on a consistent yearly basis.

The objective of this study was to evaluate the flower and bud break phenology of 19 different EFB-resistant and -tolerant hazelnut cultivars and breeding selections over 4 years to better understand their response to New Jersey's climate and to provide a benchmark for selecting suitable pollenizers and breeding parents in the future.

Materials and methods.

Plant material.

Nineteen different cultivars and clonal breeding selections, representing various sources of EFB-resistance and disparate genetic backgrounds (Table 1), were observed over a period of 4 years to determine the timing of their pollen shed, pistillate flower emergence, and vegetative bud break. The trees were originally propagated at Rutgers University with scion wood provided by OSU or the United States Department of Agriculture (USDA) Agricultural Research Service National Clonal Germplasm Repository, Corvallis, OR, except for NADF #1 provided by the National Arbor Day Society, Nebraska City, NE. All of the trees were planted from 2002 to 2006 at the Rutgers University Horticultural Research Farm 3, North Brunswick, NJ, with specific planting dates listed in Table 1. A majority of the cultivars in the study were represented by three trees each, although OSU 587.044, 'Closca Molla', and 'Ratoli' were represented by two trees each, and 'Epsilon' and 'Gamma' only by one each.

Assessment of flower and vegetative bud break phenology.

During the winter and early spring periods of 2008/2009 through 2011/2012, observations of catkin and female flower development and vegetative bud break were

made and recorded twice weekly (every 3-4 days) from late December through mid-April for all trees included in the study. Catkin developmental stages were rated on a scale of 1 to 3, similar to that developed by Germain and Sarraquigne (2004) with images of the stages found in Figure 1. Stage 1 occurs when catkin elongation is initiated, and is represented by only minor pollen shed. Catkins were considered to have reached this stage as soon as any sign of stretching was apparent, which signifies a break in dormancy. They would likely be more susceptible to cold damage at this point. Catkins reach Stage 2 when elongation achieves its maximum point and significant pollen shed is taking place. Catkins were considered to have reached this stage when, upon inspection, a considerable amount of pollen was visibly released when the catkin was tapped with ones finger. Stage 2 was deemed the period of peak pollen shed. Stage 3 occurs when peak pollen shed concludes and the anthers within the catkins appear dry and withered, although minute amounts of pollen continue to be released for several days afterward.

Female flower developmental stages were rated on scale of 1 to 4, also similar to that developed by Germain and Sarraquigne (2004), with images found in Figure 2. It should be noted that this scale is not considered to be absolute, as not all flowers on one tree progress at the same rate. Phenology ratings were taken on female flowers present on typical, mature branches and represent the stage in which a large majority of the flowers were in at the time of the rating. Stage 1, or the "red dot" stage, occurs when a single "dot" of red or purple color is observed emerging from the center of the floral buds. Stage 2 happens when the styles begin to noticeably emerge from the buds. The individual styles point straight out at this stage and have only just begun to separate.

begin to bend away from the center. The fully exserted styles have been referred to as "full spiders" at this stage, because of their superficial resemblance to arachnids (R. McCloskey, personal communication). Stage 4 is reached when greater than 50% of female flower are in the "full spider" stage. It should be noted that stigmas are receptive to pollen at all stages of exsertion (Thompson et al., 1996).

Vegetative bud break was recorded as the date that vegetative buds began to visibly swell, with clear separation of the bud scales, which indicates a breaking of dormancy. While vegetative bud break does progress through several stages up until full leaf development (Germain and Sarraquigne, 2004), and this information was observed and recorded, only the initial point of clearly breaking dormancy (Stage 1) was considered of most interest and discussed as part of the results in this study.

Data analysis and presentation.

The calendar dates when the male and female flowers (and vegetative buds) entered into each phenological stage, as described above, were converted to Julian days. The Julian day numbers were then averaged across the replicates of each cultivar/breeding selection to present the average date each cultivar/breeding selection reached that particular stage. This was repeated for each year of the study. The 4-year average was then calculated by taking the average date of progression into each stage for all trees per cultivar/breeding selection across all years. Individual years and the 4-year average were then graphically represented to help visualize the differences between the accessions and the year-to-year variation (Figures 3-7). The complete set of phenology data can be found in Supplemental Table 1.

Temperature data.

Maximum and minimum daily air temperature data were obtained from the New Brunswick 3 SE weather station, in New Brunswick, NJ, located less than 1 mile from the Rutgers University Horticultural Farm 3 (National Climate Data Center, 2013). Mean daily temperatures were estimated by taking the average of the minimum and maximum daily temperature recorded for each day. The 4-year mean daily temperatures were estimated by averaging all mean temperatures for each day of the 4 year study. It was previously shown that hazelnut phenology correlates better with daily mean and maximum temperatures than minimums (Crepinšek et al., 2012). Thus, estimated mean daily temperatures were included in the final phenology diagrams to provide a display of temperature trends across each year (and then the average of 4 years) for comparison between years and for discussion of phenology results.

Results and discussion.

The average floral and budbreak phenology for each accession over the past 4 years is shown in Figure 3 with averages for each individual year shown in Figures 3-7. Individual dates for each tree per year are shown in Supplemental Table 1. Overall, while the dates of male and female anthesis and vegetative bud break differed for each accession from year to year, the results show that the accessions tended to follow a similar, consistent pattern in their progression. Based on this repeating pattern, it was possible to place them into Early, Mid, and Late flowering groups (Tables 2-4). These groupings held true over all four years with only minor variation within and among them,

and they were largely similar across their respective male and female flower and vegetative bud groups, as discussed in more detail below.

Catkin development (pollen shed).

Early Group. 'Tonda di Giffoni' (TdG), 'Estrella #1', and 'Ratoli' were consistently the earliest accessions to shed pollen across the study each year. Their 4-year average dates of reaching Stage 1 were Jan. 23, Jan. 29, and Feb. 6, respectively (Table 2), although some year-to-year variation of this pattern was observed (Fig. 3-7). TdG was usually the first and held the record for the earliest initial pollen shed observed during the course of the study (Stage 1 on Dec. 20, 2011). It should be noted that catkins of TdG were estimated to have a chilling requirement between 170-240 hours by Mehlenbacher (1991), which was among the lowest of the cultivars tested. In Oregon, its first observed pollen shed date was Jan. 15, 8 days earlier than the average Stage 1 date in New Jersey. The only exception to it being the first to bloom in our study was in the 2008-2009 bloom period, when 'Estrella #1' reached Stage 1 first on Jan. 16. None of the other 16 accessions initiated pollen shed concurrently with TdG, 'Estrella #1', and 'Ratoli', except in the 2009-2010 bloom period when 'Closca Molla' reached Stage 1 on the same date (Feb. 18) as 'Ratoli'. However, that day was also the latest recorded date for 'Ratoli' reaching Stage 1 over the course of the study (TdG and 'Estrella #1' also reached Stage 1 later than normal that season) (Fig. 5). In general, one week separated the average Stage 1 bloom date of 'Ratoli', the latest plant from this group, from 'Closca Molla' (ave. date of Stage 1 was Feb. 13), the earliest plant from the Mid Group, discussed subsequently (Table 2).

Mid Group. 'Closca Molla', 'Grand Traverse', VR 20-11, OSU 526.041, OSU 541.147, 'Santiam', OSU 495.072, 'Zimmerman', 'Gamma', NADF #1, and 'Delta' consistently bloomed within close proximity to one another, largely in the order presented, and starting about 1 week after 'Ratoli' (Table 2). This grouping stayed very consistent over all 4 years, with a few exceptions. The earliest pollen shed for any of these accessions was in the 2011-2012 bloom period, when 'Grand Traverse' reached Stage 1 on Jan. 30 (Fig. 7). This early bloom was reflected in the fact that this period had the highest average monthly temperatures recorded for both December (4.8 °C) and January (1.5 °C) over the course of the study (Table 5). The latest blooming accession included in the Mid Group to reach Stage 1 over the 4 years was 'Gamma' on Mar. 6, 2009. This was also on the same date as 'Epsilon' and later than OSU 587.044 and OSU 408.040, which were generally very late blooming and are discussed below as part of the Late Group.

Late Group. 'Gasaway', OSU 408.040, OSU 587.044, 'Epsilon', and Finland CCOR 187 were consistently the latest group of plants to shed pollen and generally followed the order presented. These accessions typically did not reach Stage 1 until the first week of March, 5 days after the last accession included in the Mid group (NADF #1, ave. date Feb. 27) (Table 2). A member of this Late Group was always the last accession to reach Stage 1 each year. The latest record of any accession reaching Stage 1 was observed was on Mar. 6, 2012 with OSU 587.044. In contrast, the earliest pollen shed by a member of this Late Group, other than the anomalous 'Gasaway' behavior described in the following paragraph, was Feb. 28, 2009 by OSU 408.040 and Feb. 28, 2012 by Finland CCOR 187. On occasion, an accession from the Mid Group would overlap Stage 1 with one of these five accessions, like NADF #1 and 'Gamma' in the 2008-2009 period and 'Gamma', 'Santiam', 'Delta', and 'Zimmerman' in the 2009-2010 period. However, on average across all years and accessions, plants from the Late Group began Stage 1 nine days after plants from the Mid Group (Table 2).

It should be noted that, in the 2011-2012 period, 'Gasaway' reached Stage 1 during the first week of February (Fig. 7). Its female flowering during this period was also much earlier than normal, as discussed in its corresponding section. Although atypical, no obvious causes for this behavior were observed, other than the aforementioned higher than average winter temperatures. Mehlenbacher (1991) studied the chilling requirements of 'Gasaway' in Oregon and found that its requirements for catkins and flowers were between 600-680 and 1040-1170 hours, respectively. These requirements are higher than average for hazelnut, and do not provide any evidence as to why such early flowering was observed in 2011-2012. The other plants in the study with flowering dates similar to 'Gasaway' (which would be expected to have roughly similar chilling requirements) did not display abnormal flowering behavior during this year. This uncharacteristic year shifted the calculated average enough that the average Stage 1 date of 'Gasaway' was determined to be Feb. 28. Thus, based on its average, 'Gasaway' could be placed into the Mid Group; however, observations made over a decade at Rutgers University have consistently found it to be one of the latest blooming plants (data not shown). As such, we choose to keep it in the Late Group. This unexpected result gives a glimpse into the year-to-year variation observed under New Jersey's unpredictable climate and the need for greater understanding of the flowering patterns of hazelnut to choose appropriate pollinizers to ensure consistent yearly nut production.

General trends for catkin development

Based on the 4-year averages, those accessions placed in Early Group began Stage 1 between Jan. 3 (TdG) and Feb. 6 ('Ratoli'). The Mid Group began a week later, starting on Feb. 13 ('Closca Molla') and concluding on Feb. 28 ('Delta'). The Late Group (excluding 'Gasaway' in 2012) began with OSU 408.040 reaching Stage 1 on Mar. 3 and concluded with Finland CCOR 187 on Mar. 5 (Table 2). While these averages largely match the order in which the accessions progressed through bloom over each season, they provide only an approximate representation of flowering over the course of the study, as the date of pollen shed and the duration of bloom differed considerable from year-to-year. As an example, in the 2010-2011 period, 'Estrella' #1 reached Stage 1 on Feb. 18 (Fig. 6). In the following bloom season (2011-2012), it reached Stage 1 on Jan. 25, over 3 weeks earlier than the previous year (Fig. 7). Further, in the 2009-2010 period, TdG reached Stage 1 on Jan. 21. However, in the 2010-2011 period, TdG reached Stage 1 on Feb. 18, almost a month (28 days) later than the previous Though somewhat disparate, the wide ranging bloom dates tended to reflect vear. average monthly temperatures. For example, in the 2010-2011 period, estimated average monthly temperatures for December, January, and February were 2.4 °C, 1.7 °C, and 0.6 °C colder than the 4-year averages for those months, respectively (Table 5). Further, the overall mean temperature for the 2010-2011 period (average temperature across all days in December, January, and February) was 1.6 °C colder than the 4-year average. These colder than average temperatures were clearly reflected in a delay of catkin development until later in the season (Fig. 6). Across all accessions, in the 2010-2011 period, catkins reached peak bloom (Stage 2) on Mar. 4, which is 4 days later than the 4-year average of

Feb. 28. Additionally, as temperatures warmed, this delay was followed by a corresponding, tightly compressed window of pollen shed compared to the 4-year average, i.e. in the 2010-2011 period there were 31 total days from the earliest date of Stage 1 (TdG, 'Ratoli', 'Estrella #1') to the latest date of Stage 3 ('Gasaway', 408.040), whereas the 4-year average number of days was 64 (Table 5). One can visualize the impact of this compressed bloom period more clearly when the total cumulative number of pollen shedding days (sum of the total number of days each accession was shedding pollen) across all 19 accessions for each year is calculated. In the 2010-2011 period, only 263 cumulative days of pollen shed were observed, compared to the 4-year cumulative average of 362 days (Table 5). For comparison, the longest window of pollen shed was in the 2011-2012 period, the warmest year, when Stage 1 of the earliest accession to Stage 3 of the latest spanned 91 days, with 415 cumulative days of pollen shed observed (Table 5). These trends fit previous reports of a compressed period of bloom observed in cold regions (Thompson et al., 1996).

A similar pattern to the 2010-2011 period was observed in 2009-2010. Warm temperatures in mid January (ave. daily temperatures around 4-5 °C in the week leading up to initial pollen shed, reaching as high as 9.4 °C on Jan. 26) spurred TdG and 'Estrella #1' to begin pollen shed (Stage 1) in January. This warm trend was followed by a consistently cold February [monthly average -0.4 °C (4 year February average 1.3 °C)] (Table 5), which was reflected in the rest of the accessions remaining dormant until warmer temperatures (around 5.0 °C the 1st week of March, reaching as high as 10.0 °C the 2nd week) caused most plants to flower concurrently (Fig. 5). The overall earliest period for pollen shed was 2011-2012, probably due to the higher than average winter temperatures (December, January, and February, were 2.7 °C, 2.6 °C, and 2.3 °C higher than the 4-year averages, respectively). During this period, four separate accessions (TdG, 'Ratoli', 'Grand Traverse', and 'Estrella #1') reached Stage 1 before February, and all accessions but two (OSU 587.044 and 'Epsilon') reached Stage 1 before March (Fig. 7).

In the bloom periods of 2008-2009 and 2011-2012, there was greater variation in the pollen shed dates and durations of most accessions, which appears to follow the much more varied, inconsistent mean daily temperatures for those respective periods. In winter, inconsistent temperatures usually translate to periodic warm spells. If the temperatures are frequently warming and cooling, some plants may respond quickly to these fluctuations, causing variation in the pollen shed periods. In winters with less temperature fluctuation, plants seem to either stay dormant (cold, stable winter) until consistently warmer temperatures arrive in early Spring, or be active and flower earlier (warm, stable winter). Less stable winter temperatures appear to result in more startingand-stopping of flower development and seemingly lead to more varied windows of pollen dispersal.

In terms of the generalities of male flower bloom in New Jersey, when taking into account all of the accessions over all 4 years, the average date for Stage 1 was Feb. 21 with peak pollen shed (Stage 2) beginning Feb. 28. This stage lasted two weeks (on average), and Stage 3 was reached on Mar. 13 (Table 2). The latest average period for these stages for all accessions was 2009-2010, which reached Stages 1 through 3 six, six, and eight days later than the 4-year average, respectively. Interestingly, the 2009-2010

period was the second warmest by average winter monthly temperature (Table 5), although it did have the coldest February monthly average (-0.4 °C) of all years. 2011-2012 was the earliest average period of bloom, most likely due to its warmer than average winter temperatures. Over this period, the three stages of pollen shed were reached 13, 13, and 11 days earlier than the 4-year average.

Female flower development (pistillate bloom)

Early group. The earliest plants to reach Stage 1 of female flowering were 'Ratoli', TdG, and 'Closca Molla'. These three cultivars consistently bloomed in this order, except for in the 2008-2009 period, when TdG bloomed one day (Dec. 26) earlier than Ratoli (Dec. 27). 'Closca Molla', generally the latest of the three, bloomed on Jan. 13 on average (Table 3; Figure 3). This date was 2 weeks earlier than the 4-year average bloom date of the next earliest blooming accession (OSU 541.147, Jan. 27), which, similar to the male flower groups, was chosen to be the earliest blooming accession placed in the female flower Mid Group, to be discussed subsequently. The earliest incidence of female bloom was in the 2011-2012 period, when both TdG and 'Ratoli' began Stage 1 on Dec. 20 (Fig. 7), which directly reflects the warm temperatures recorded that month (4.8 °C average, reaching as daily averages as high as 15.6 °C on Dec. 7 and 11.4 °C on Dec. 22 & 23) (Table 5). The latest incidences of female bloom by a plant in this Early Group were in the 2008-2009 and 2010-2011 periods, when 'Closca Molla' reached Stage 1 on Jan. 16 in both years. During all 4 years, TdG and 'Ratoli' began Stage 1 in December, on average over a month before the nearest other accessions in the study, excluding 'Closca Molla' (Table 3). In Oregon, chilling requirements for female flowers of TdG were

estimated to be between 600-680 h, placing it amongst the lowest of all plants evaluated. TdG reached first reached Stage 1 in Oregon on Nov. 13 and displayed exserted stigmas (Stage 3) on Dec. 18 (Mehlenbacher, 1991). These dates are significantly earlier than those observed in New Jersey (Stage 1 - Dec. 25 and Stage 3 - Jan. 23 based on 4-year average) and provide a clear indication of how flowering behavior differs between the two regions.

Mid Group. Following the three earliest accessions in female bloom were: OSU 541.147, 'Zimmerman', 'Delta', 'Santiam', VR 20-11, OSU 526.041, 'Epsilon', 'Gamma', OSU 495.072, 'Grand Traverse', and 'Estrella #1'. These plants generally bloomed in the order presented, consistently 2 to 3 weeks after those discussed in the Early group (Table 3). Typically, there was a span of about 1 month separating the earliest of this group (OSU 541.147, 4-year average date of Stage 1 is Jan. 27) and latest ('Estrella #1', 4-year average date of Stage 1 is Feb. 25). The earliest start of female flowering for any accession in this group was Jan. 20, 2012 by 'Santiam'. The latest accessions to begin Stage 1 during any year were 'Grand Traverse' and 'Estrella #1', on March 3, 2009. Any outliers from this group are discussed in the Early and Late Group sections.

Late Group. The remaining group of accessions includes 'Gasaway', Finland CCOR 187, OSU 408.040, OSU 587.044, and NADF #1. These plants typically began Stage 1 around the beginning of March, with the exception of 'Gasaway', whose anomalous year is described in the preceding section. Excepting 'Gasaway', approximately 1 week separates the average bloom date of the earliest plant from this group (Finland CCOR

187, 4-year ave. date Mar. 1) from the latest plant included in the Mid group ('Estrella #1') (Table 3). Disregarding 'Gasaway' in 2012, the earliest date for reaching Stage 1 was Feb. 18, 2011 by Finland CCOR 187. This early date is reflected in the very high February temperatures reaching up to 12.2 °C the week of evaluations (February 4-year ave. temperature is 1.3 °C). The latest observation of female flowers reaching Stage 1 was on Mar. 8, 2009 by NADF #1. Temperatures the week leading up to this date dipped as low as -8.1 °C, while the temperature on Mar. 8 reached 13.1 °C. The 2008-2009 bloom period featured a consistently cold winter followed by fluctuating temperatures in February and March (Table 5).

Overall, the grouping of accessions in the Late Group was very consistent across all 4 years. The exceptions were limited to 'Estrella #1' and 'Grand Traverse' in the 2008-2009 and 2010-2011 periods. Both members of the Mid Group reached Stage 1 on Mar. 3, 2009, the same day as 'Gasaway' and OSU 408.040. Then, in the 2010-2011 period, both accessions again overlapped one of the Late Group plants, reaching Stage 1 on Feb. 21 ('Grand Traverse') and Feb. 22 ('Estrella #1'). These dates were later than that of Finland CCOR 187, which reached Stage 1 on Feb. 18. These exceptions also disregard the atypical 'Gasaway' data from the 2011-2012 period.

General trends for female flower development

Based on the 4-year averages, the accessions placed in the Early Group reached Stage 1 between Dec. 24 ('Ratoli') and Jan. 13 ('Closca Molla'). Accessions placed in the Mid Group reached Stage 1 ranging from Jan. 27 (OSU 541.147) to Feb. 25 ('Estrella #1'), while those in Late Group varied from Finland CCOR 187 on Mar. 1 to NADF #1 on Mar. 5 (excluding 'Gasaway' in 2012). Our placement of the accessions in these groups for the female flowers reflected those for male flower groups, with only minor differences. For both flower types, the Early Group holds three accessions, including TdG and 'Ratoli' in both. 'Closca Molla' was included in the Early Group for female flowers, whereas 'Estrella #1' was included in the male flower Early Group. For the late Group, both also held the same number of accessions with four in common ('Gasaway', OSU 408.040, OSU 587.044, and Finland CCOR 187). However, NADF #1 was the fifth member for the female flowers, whereas 'Epsilon' was included in the Late Group for the male flowers.

In terms of generalities for female flower development in New Jersey, when taking into account all of the accessions over all 4 years, the average date across the study for reaching Stage 1 was Feb. 13, followed by Feb. 19 for Stage 2, Feb. 29/Mar. 1 for Stage 3, and Mar. 8 for Stage 4 (Table 3). For all accessions, the 2008-2009 period had the latest female bloom, reaching Stages 1 through 4 three, five, five, and seven days later than their 4-year averages, respectively. In contrast, the 2011-2012 period was considerably earlier than the 4-year average, reaching Stages 1 through 4 eight, nine, seven, and five days earlier, respectively. As the 2011-2012 period was significantly warmer than the other years, this was not unexpected. However, by monthly average, 2008-2009 was not the overall coldest period (2010-2011 was), although it did have the coldest January (-2.9 °C, compared to an average of -1.1 °C) and March (4.7 °C, compared to an average of 6.8 °C) (Table 5; Supplemental Table 2), which likely corresponds to why it had the latest flowering dates.

Vegetative Bud Break. The dates of vegetative bud break for all accessions were loosely similar to the groupings for pollen shed and female flowering. 'Ratoli' and TdG were again the two earliest. 'Ratoli' and TdG broke bud dormancy considerably earlier than the other accessions, averaging Mar. 4 and Mar. 10, respectively across all 4 years (Table 4). In the 2008-2009 period, 'Ratoli' began bud break on February 18th, the earliest date recorded across the study. In contrast, in the 2010-2011 period, both 'Ratoli' and TdG did not begin bud break until Mar. 17, the latest date recorded for these plants. This trend was reflected across nearly all accessions by later than average bud break dates as well as male and female flowering dates that year (Fig. 6).

'Gasaway' had the consistently latest bud break dates, followed by OSU 408.040, NADF #1, and Finland CCOR 187. These four accessions each averaged bud break dates starting in April. All of the other accessions typically began bud break between Mar. 14-29, leading them to be classified as our Mid Group accessions (Fig. 3; Table 4). The latest date a plant began vegetative bud break was on Apr. 13, 2011 by 'Gasaway'. This year had by far the latest bud break for all accessions, with only five breaking dormancy in March, which is reflected in the colder than average monthly temperatures (Table 5). For example, the temperatures from Dec. 2010 through Mar. 2011 were consistently colder than the monthly averages, with the overall average of those months (0.7 °C) being 1.6 °C lower than the 4-year average (2.3 °C), while in April 2011 the average temperature rose to 10.0 °C, the second warmest April recorded in our study. The earliest breaking of bud dormancy by one of the four latest bud break plants was on Mar. 18, 2010 by Finland CCOR 187. Reflecting this point, the 2009-2010 period had the earliest overall bud break (avg. 1st day of budbreak was Mar. 17, 2010).

For vegetative bud break averaged over all 4 years, the Early Group accessions (TdG and 'Ratoli') broke dormancy on Mar. 4 and 10, respectively. The Mid Group began with 'Epsilon' on Mar. 14 and ended with both 'Grand Traverse' and 'Delta' on Mar. 28. The earliest plant in the Late Group was Finland CCOR 187 (Apr. 1), and 'Gasaway' was the latest plant in the entire study to break bud dormancy, on average, on Apr. 6.

Finally, in terms of generalities of vegetative bud break in New Jersey, average vegetative bud break across all of the accessions over the 4 years occurred on Mar. 24. The earliest average bud break happened in the 2009-2010 period (Mar. 17), while the latest took place in the 2010-2011 period (Apr. 3). The 2010-2011 was the coldest bloom period by monthly winter average, which makes its late bud break seem logical, while the 2009-2010 period had a warmer than average March (7.8 °C, 1.0 °C higher than average) but it did not seem significant enough to account for its earliest bud break date.

Conclusions.

This study was intended to provide a systematic, multi-year record of flower and vegetative bud break phenology of hazelnut in central New Jersey. Our results showed that the accessions followed a similar progression of bloom each year for both staminate and pistillate flowers, which allowed their placement into Early, Mid, and Late flowering groups. Despite one or two minor exceptions, these groups stayed consistent each year. However, the date and duration of bloom differed each year, which largely corresponded to average air temperature trends. The results of our study, in colder than average years, corroborated previous reports from cold regions (Črepinšek et al., 2012; Germain, 1994;

Piskornik et al., 2001; Solar and Stampar, 2009). For example, in the 2010-2011 period (our coldest period), bloom was delayed until later in the winter, which then led to a compressed period of flowering once temperatures warmed (Fig. 6). In contrast, relatively warm temperatures over the bloom period, as in 2011-2012, led to earlier flowering as well as a significant lengthening of the duration of bloom (Fig. 7), similar to responses reported in Mediterranean climates (Mehlenbacher, 1991; Thompson et al., 1996).

Olsen et al. (2000) states that 90% of cultivars evaluated in Oregon are protandrous. In contrast, our results show that most of the accessions examined in our study, across all years, were protogynous. Aside from 'Estrella #1', 'NADF #1', and 'Grand Traverse', which were consistently protandrous, the rest of the accessions were protogynous averaged across all years, with some minor year-to-year exceptions. OSU 587.044 was protandrous in 2008-2009 (by 5 days), Finland CCOR 187 was protandrous in 2008-2009 (by 2 days) and 2011-2012 (by 3 days), OSU 408.040 was protandrous in 2008-2009 (by 3 days), and OSU 526.041 was protandrous in 2008-2009 (by 1 day). These observations echo the conclusions of Thompson et al. (1996) and others in that protogyny is more common in regions with colder winters. However, our flowering windows were not as compressed as previously reported for cold region in most years (Crepinšek et al., 2012; Germain, 1994), possibly reflected by the fact that our climate is relatively mild [considered to be between zone 6B and 7A (USDA, 2012)]. Central New Jersey is only one to one and a half USDA cold hardiness zones colder than that of the Willamette Valley of Oregon (zone 8a to 8b) and is moderated to some degree by its close proximity to the Atlantic Ocean (~ 40 km away).

Our observation-based results provide a starting point for further research. A more detailed study on the chilling requirements of each accession, which for all but TdG and 'Gasaway' are currently unknown, and more specific climatic data collection and analysis combined with deeper field-based observation is necessary to strongly correlate particular climatic events to hazelnut phenological development. A thorough study on the cold hardiness of catkins across a wider collection of germplasm should also be conducted.

Over the course of this study, only minor catkin injury was observed in one year and was not included as a component of this research. However, the 4-year span of our study does not represent the temperature extremes possible in the eastern U.S., where catkin damage is a more likely possibility over a longer period, as described by Slate (1933) and MacDaniels (1964). For example, the lowest temperature observed over the course of our study was -17.2 °C on Jan. 17, 2009. This low came at a time when nearly all catkins were fully dormant, and no damage was observed. In the warmer than average period of 2011-2012, when TdG flowered in December and 'Ratoli' and 'Estrella #1' flowered in early January, some catkin damage was noticed on them, although it was less than 25% of their catkins (data not shown). This damage could not likely be solely attributed to low temperatures (Jan. 2012 monthly average = 1.5 °C, the highest we recorded and 2.6 °C higher than the 4-year monthly average, -1.1 °C. The lowest temperatures came on Jan. 16 and 17, -12.2 °C), and was probably due, at least in small part, to wind injury. Further, this injury did not appear to significantly affect overall pollen shed. Even catkins suffering injury managed to shed considerable amounts of

pollen. However, our observations for this study were made only on healthy catkins on each plant. No cold injury to female flowers or vegetative buds was observed.

For current and prospective growers, our results provide both direct information on a number of available EFB-resistant cultivars and breeding selections and an overview of how flower and bud break phenology may respond to temperature fluctuations in our region. These results should aid growers in choosing appropriate plants (pollinizers and nut producers) for production in central New Jersey and other places with similar climates, which may include much of the Fruit Belt region in the northeast U.S., spanning locations where tree fruit are typically grown south and west of New Jersey, across southern Pennsylvania, to parts of coastal Michigan and southern Ontario, Canada.

Based on our observations, 'Estrella #1' may make a very useful early season pollinizer due to its complete EFB resistance (Capik and Molnar, 2012) and early, abnormally long pollen-shed period combined with its abundance of catkins (data not shown), although its incompatibility alleles and pollen viability are currently unknown and need to be examined. Further, TdG could also be suitable as an early season pollinizer, but it lacks a sufficient level of EFB resistance for production in the East without fungicide applications (Capik and Molnar, 2012). Fortunately, an abundance of EFB-resistant accessions are available to choose from in the Mid Group that express a diversity of S-alleles, many which may compliment new cultivars developed in the future. Most of these Mid Group accessions shed their pollen during times that overlap the female flowering periods (Stage 2 and 3) of a majority of all of the accessions in the study. As a late season pollinizer, 'Gasaway' performs well in New Jersey. It consistently produces large quantities of catkins and is always amongst the latest flowering plants in the entire Rutgers University germplasm collection. However, it produces low yields of very poor quality nuts and gets a small amount of EFB (Capik and Molnar, 2012) that would likely need to be addressed by pruning on a semi-regular basis to reduce its spread once infection is noted.

In summary, our study is one of the first to document hazelnut flowering phenology under New Jersey's variable winter climate. The results provide a benchmark for selecting suitable pollinizers for current and future production in central New Jersey and likely other similar climatic regions in the eastern U.S. Our results also present useful data to support selection of breeding parents for developing new cultivars adapted to this region and as a foundation for further flowering research.

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| Accession name ^z | Number of trees/ planting Year | Origin/parentage | Incompatibility alleles ^y | | |
|--|-----------------------------------|---|---|--|--|
| 'Ratoli' | 2 - 2002 | Spain (Tarragona), PI 557167 | S_2, S_{10} | | |
| 'Tonda di Giffoni' (TdG) | 3 - 2002 | Italy (Campania), PI 296207 | $S_2, S_{\underline{23}}$ | | |
| 'Closca Molla' | 2 - 2002 | Spain (Tarragona), PI 557109 | S ₂ , S ₅ | | |
| Oregon State University (OSU) 541.147 | 3 - 2002 | Oregon, 'NY 110' (<i>C. americana</i> 'Rush' × <i>C. avellana</i> 'DuChilly') × OSU 226.118 | S <u>8</u> , S <u>23</u> | | |
| 'Zimmerman' | 3 - 2002 | Oregon, 'Gasaway' × 'Barcelona' | S_1, S_3 | | |
| 'Delta' | 1 - 2003 2 - 2006 | Oregon, OSU 249.159 × VR 17-15 | $\overline{S_{\underline{1}}}, \overline{S_{\underline{15}}}$ | | |
| OSU 526.041 | 3 - 2002 | Oregon, <i>C. heterophylla</i> 'Ogyoo' × <i>C. avellana</i> | Unknown | | |
| VR 20-11 | 3 - 2002 | Oregon, [('Barcelona' × 'Compton') × 'Gasaway'] | S ₂ , S <u>3</u> | | |
| 'Santiam' | 3 - 2006 | Oregon, OSU 249.159 × VR 17-15 | S ₃ , S ₁₅ | | |
| OSU 495.072 | 3 - 2002 | Russia (southern) | S_{6}, S_{30} | | |
| 'Gamma' | 1 - 2006 | Oregon, 'Casina' × VR 6-28 | $S_{2}, S_{1_{0}}$ | | |
| 'Epsilon' | 1 - 2006 | Oregon, OSU 350.089 × 'Zimmerman' | $S_{\underline{1}}, S_{4}$ | | |
| 'Grand Traverse' | 3 - 2002 | Michigan, <i>Corylus</i> hybrid. <i>C.</i> <i>colurna</i> hybrid 'Faroka' × <i>C.</i> <i>avellana</i> , PI 617185 | S_{11}, S_{25} | | |
| NADF #1 (10-50) | 3 - 2005 | Nebraska, National Arbor Day Foundation selection | Unknown | | |
| 'Estrella #1' 3 - 2006 Michigan, C. h. sutchuenensis | | Michigan, C. heterophylla var. sutchuenensis × C. avellana 'Holder', PI 557351 | Unknown | | |
| OSU 587.044 | 2 - 2002 | Oregon, <i>C. californica</i> B0509 × OSU 278.113 ('Tombul Ghiaghli' × INRA H 105–28) | S ₂ , S _{<u>7</u>} | | |
| Finland CCOR 187.001 | 3 - 2006 | Finland, PI 557080 | S ₉ , S ₂₅ | | |
| 'Gasaway' | 3 - 2002 | Washington, PI 557042 | S <u>3</u> , S ₂₆ | | |
| OSU 408.040 | 3 - 2002 | Minnesota, PI 617266 | S_{20}, S_{27} | | |

Table 1. Hazelnut (*Corylus* spp.) accessions evaluated for flowering and bud break phenologyin New Jersey over the winter seasons of 2008-2009 through 2011-2012.

^zAll accessions are resistant or highly tolerant to eastern filbert blight (*Anisogramma anomala*), except for 'Tonda di Giffoni' and 'Closca Molla', which are considered to be only tolerant (Capik and Molnar, 2012). Plants are listed from top to bottom in the general order in which they flowered each year. ^yDominant alleles for each accession are underlined.

| | Accession | Accession Stage 1 | | St | age 2 | Stage 3 | Total # |
|----------|------------------|-------------------|-----------|--------|-----------|---------|---------|
| Group | Name | Date | # of Days | Date | # of Days | Date | of Days |
| > | Tonda di Giffoni | 23-Jan | 7 | 31-Jan | 17 | 23-Feb | 24 |
| Early | Estrella #1 | 29-Jan | 22 | 20-Feb | 21 | 12-Mar | 43 |
| | Ratoli | 6-Feb | 6 | 13-Feb | 11 | 23-Feb | 17 |
| | Closca Molla | 13-Feb | 11 | 25-Feb | 12 | 8-Mar | 23 |
| | Grand Traverse | 17-Feb | 7 | 24-Feb | 12 | 7-Mar | 19 |
| | VR 20-11 | 19-Feb | 7 | 26-Feb | 14 | 12-Mar | 21 |
| | OSU 526.041 | 20-Feb | 7 | 27-Feb | 13 | 11-Mar | 21 |
| _ | OSU 541.147 | 21-Feb | 7 | 29-Feb | 13 | 13-Mar | 20 |
| Mid | Santiam | 23-Feb | 4 | 27-Feb | 15 | 13-Mar | 19 |
| | OSU 495.072 | 24-Feb | 8 | 4-Mar | 10 | 14-Mar | 19 |
| | Zimmerman | 25-Feb | 6 | 3-Mar | 10 | 13-Mar | 16 |
| | Gamma | 27-Feb | 6 | 4-Mar | 11 | 15-Mar | 17 |
| | NADF | 27-Feb | 8 | 6-Mar | 9 | 15-Mar | 18 |
| | Delta | 29-Feb | 6 | 6-Mar | 11 | 17-Mar | 17 |
| | Gasaway | 28-Feb | 4 | 3-Mar | 11 | 14-Mar | 15 |
| 0 | OSU 408.040 | 3-Mar | 4 | 7-Mar | 11 | 18-Mar | 15 |
| Late | OSU 587.044 | 3-Mar | 5 | 8-Mar | 11 | 19-Mar | 16 |
| | Epsilon | 4-Mar | 4 | 8-Mar | 8 | 16-Mar | 13 |
| | Finland | 5-Mar | 4 | 9-Mar | 8 | 16-Apr | 12 |
| S | Early Group Ave. | 30-Jan | 12 | 11-Feb | 16 | 29-Feb | 28 |
| age: | Mid Group Ave. | 22-Feb | 7 | 29-Feb | 12 | 12-Mar | 19 |
| Averages | Late Group Ave. | 3-Mar | 4 | 7-Mar | 10 | 23-Mar | 14 |
| 7 | Overall Ave. | 21-Feb | 7 | 28-Feb | 12 | 13-Mar | 19 |

Table 2. Summary of staminate flower development (Stage 1-3) for 19 hazelnut accessions

 averaged across 4 years in New Jersey.

| | Accession | Stage 1 | | Stage 2 | | Stage 3 | | Stage 4 | Total # |
|----------|------------------|---------|-----------|---------|-----------|---------|-----------|---------|---------|
| Group | Name | Date | # of Days | Date | # of Days | Date | # of Days | Date | of Days |
| Early | Ratoli | 24-Dec | 10 | 3-Jan | 10 | 13-Jan | 15 | 28-Jan | 35 |
| | Tonda di Giffoni | 25-Dec | 18 | 12-Jan | 12 | 23-Jan | 15 | 7-Feb | 44 |
| | Closca Molla | 13-Jan | 16 | 28-Jan | 13 | 11-Feb | 14 | 25-Feb | 43 |
| | OSU 541.147 | 27-Jan | 8 | 5-Feb | 10 | 15-Feb | 12 | 27-Feb | 31 |
| | Zimmerman | 30-Jan | 10 | 10-Feb | 9 | 19-Feb | 12 | 2-Mar | 32 |
| Mid | Delta | 2-Feb | 18 | 21-Feb | 10 | 2-Mar | 10 | 12-Mar | 39 |
| | Santiam | 7-Feb | 13 | 21-Feb | 10 | 2-Mar | 7 | 9-Mar | 31 |
| | VR 20-11 | 13-Feb | 7 | 21-Feb | 12 | 4-Mar | 10 | 13-Mar | 29 |
| | OSU 526.041 | 14-Feb | 6 | 20-Feb | 11 | 2-Mar | 9 | 11-Mar | 26 |
| | Epsilon | 15-Feb | 9 | 23-Feb | 9 | 3-Mar | 8 | 11-Mar | 25 |
| | Gamma | 16-Feb | 9 | 25-Feb | 11 | 7-Mar | 6 | 13-Mar | 25 |
| | OSU 495.072 | 18-Feb | 8 | 26-Feb | 17 | 14-Mar | 4 | 17-Mar | 28 |
| | Grand Traverse | 24-Feb | 6 | 1-Mar | 9 | 10-Mar | 8 | 18-Mar | 23 |
| | Estrella #1 | 25-Feb | 8 | 4-Mar | 9 | 13-Mar | 5 | 18-Mar | 21 |
| | Gasaway | 24-Feb | 6 | 1-Mar | 8 | 9-Mar | 9 | 19-Mar | 23 |
| | Finland | 1-Mar | 7 | 8-Mar | 6 | 14-Mar | 3 | 17-Mar | 16 |
| Late | OSU 408.040 | 1-Mar | 5 | 6-Mar | 9 | 16-Mar | 5 | 20-Mar | 19 |
| | OSU 587.044 | 4-Mar | 6 | 9-Mar | 6 | 15-Mar | 5 | 21-Mar | 17 |
| | NADF | 5-Mar | 5 | 9-Mar | 5 | 14-Mar | 4 | 19-Mar | 14 |
| Averages | Early Group Ave. | 31-Dec | 14 | 14-Jan | 12 | 26-Jan | 15 | 10-Feb | 41 |
| | Mid Group Ave. | 12-Feb | 9 | 21-Feb | 11 | 3-Mar | 8 | 11-Mar | 28 |
| Aver | Late Group Ave. | 1-Mar | 6 | 7-Mar | 7 | 14-Mar | 5 | 19-Mar | 18 |
| A | Overall Ave. | 10-Feb | 9 | 19-Feb | 10 | 29-Feb | 8 | 8-Mar | 27 |

Table 3. Summary of pistillate flower development (Stage 1-4) for 19 hazelnut accessions

averaged across 4 years in New Jersey.

| | Accession | St | age 1 | St | age 2 | Stage 3 | Total # |
|----------|------------------|--------|-----------|--------|-----------|---------|---------|
| Group | Name | Date | # of Days | Date | # of Days | Date | of Days |
| Early | Ratoli | 4-Mar | 16 | 20-Mar | 12 | 1-Apr | 28 |
| Ea | Tonda di Giffoni | 10-Mar | 11 | 21-Mar | 9 | 30-Mar | 20 |
| | Epsilon | 14-Mar | 13 | 26-Mar | 14 | 9-Apr | 26 |
| | Zimmerman | 16-Mar | 11 | 28-Mar | 13 | 10-Apr | 24 |
| | OSU 541.147 | 19-Mar | 8 | 27-Mar | 14 | 10-Apr | 22 |
| | OSU 495.072 | 22-Mar | 8 | 30-Mar | 11 | 10-Apr | 19 |
| | OSU 526.041 | 22-Mar | 10 | 1-Apr | 13 | 13-Apr | 22 |
| _ | Closca Molla | 24-Mar | 10 | 3-Apr | 11 | 14-Apr | 21 |
| Mid | Estrella #1 | 25-Mar | 15 | 9-Apr | 11 | 20-Apr | 26 |
| | Gamma | 26-Mar | 12 | 7-Apr | 9 | 16-Apr | 21 |
| | OSU 587.044 | 26-Mar | 12 | 7-Apr | 13 | 20-Apr | 25 |
| | VR 20-11 | 26-Mar | 9 | 4-Apr | 12 | 15-Apr | 20 |
| | Santiam | 27-Mar | 9 | 5-Apr | 11 | 16-Apr | 20 |
| | Delta | 28-Mar | 15 | 11-Apr | 10 | 21-Apr | 24 |
| | Grand Traverse | 28-Mar | 14 | 11-Apr | 9 | 20-Apr | 23 |
| | Finland | 1-Apr | 13 | 14-Apr | 9 | 23-Apr | 22 |
| Late | NADF #1 | 2-Apr | 6 | 8-Apr | 9 | 17-Apr | 15 |
| Ľ | OSU 408.040 | 4-Apr | 12 | 16-Apr | 8 | 24-Apr | 21 |
| | Gasaway | 6-Apr | 12 | 18-Apr | 7 | 25-Apr | 19 |
| S | Early Group Ave. | 7-Mar | 13 | 20-Mar | 10 | 31-Mar | 24 |
| age | Mid Group Ave. | 23-Mar | 11 | 3-Apr | 11 | 15-Apr | 23 |
| Averages | Late Group Ave. | 3-Apr | 11 | 14-Apr | 8 | 22-Apr | 19 |
| + | Overall Ave. | 24-Mar | 11 | 4-Apr | 11 | 15-Apr | 22 |

 Table 4.
 Summary of vegetative bud development (Stage 1-3) for 19 hazelnut accessions

 averaged across 4 years in New Jersey.

| | | | | | | ^z Length of | | ^y Cumulative | |
|----------------|-----------------------|------|------|--------------|------|------------------------|-----|-------------------------|------------|
| Bloom | Monthly averages (°C) | | | bloom period | | bloom period | | | |
| period | Dec. | Jan. | Feb. | Mar. | Apr. | Staminate Pistillate | | Staminate | Pistillate |
| 2008-2009 | 2.4 | -2.9 | 1.3 | 4.7 | 8.5 | 74 | 101 | 450 | 571 |
| 2009-2010 | 1.6 | -0.3 | -0.4 | 7.8 | 15.6 | 61 | 90 | 320 | 471 |
| 2010-2011 | -0.3 | -2.8 | 0.7 | 5.3 | 10.0 | 31 | 95 | 263 | 471 |
| 2011-2012 | 4.8 | 1.5 | 3.6 | 9.6 | 9.9 | 91 | 98 | 415 | 572 |
| 4-year average | 2.1 | -1.1 | 1.3 | 6.8 | 11.0 | 64 | 96 | 362 | 521 |

Table 5. Monthly weather summary table and bloom period for staminate and pistillate flowers.

^zLength of bloom period represents the number of days between the first accession to reach Stage 1 and the last accession to reach Stage 3 (staminate) or Stage 4 (pistillate).

^yCumulative bloom period represents the total number of days each accession bloomed [number of days between Stage 1 and Stage 3(staminate) or Stage 4(pistillate)] added together.

Figure 1. Progression of staminate flower development in hazelnut. From left to right: dormant catkins, Stage 1 (catkin begins elongation), Stage 2 (full elongation, peak pollen shed), and Stage 3 (anthers dry out, pollen shed ends). Pictures are not to scale.



Figure 2. Progression of pistillate flower development of hazelnut. From left to right: Stage 1 ("red dot stage"), Stage 2, and Stage 3 ("full spider stage"). Stage 4 is reached when > 50% of all female flowers on the tree are in the "full spider" stage. Pictures are not to scale.



Figure 3-7. Graphical summary of the phenological development of the staminate and pistillate flowers and vegetative buds of 19 *Corylus* accessions over 4 years in North Brunswick, NJ. The yellow bars represent staminate flower development. The gradient of three yellow colors corresponds to the stages of development described in the manuscript (light yellow is Stage 1, yellow is Stage 2, and dark yellow is Stage 3. The pink/red bars represent pistillate flower development. Pink corresponds to Stage 1, magenta to Stage 2, Red to Stage 3, and maroon to Stage 4. Stage 1 of vegetative bud development is represented by a green square. Estimate daily average temperatures, which were calculated by averaging the daily high and low temperatures, are presented across the top of the figure. Cultivars from top to bottom: Ratoli (Rat), Tonda di Giffoni (TdG), Closca Molla (Cl M), OSU 541.147 (541), Zimmerman (Zim), Delta (Del), OSU 526.041 (526), OSU VR 20-11 (VR20), Santiam (Sant), OSU 495.072 (495), Gamma (Gam), Epsilon (Eps), Grand Traverse (G.T.), NADF #1 (NADF), Estrella #1 (Estr), OSU 587.044 (587), Finland CCOR 187 (Fin), Gasaway (Gas), and OSU 408.040 (408).

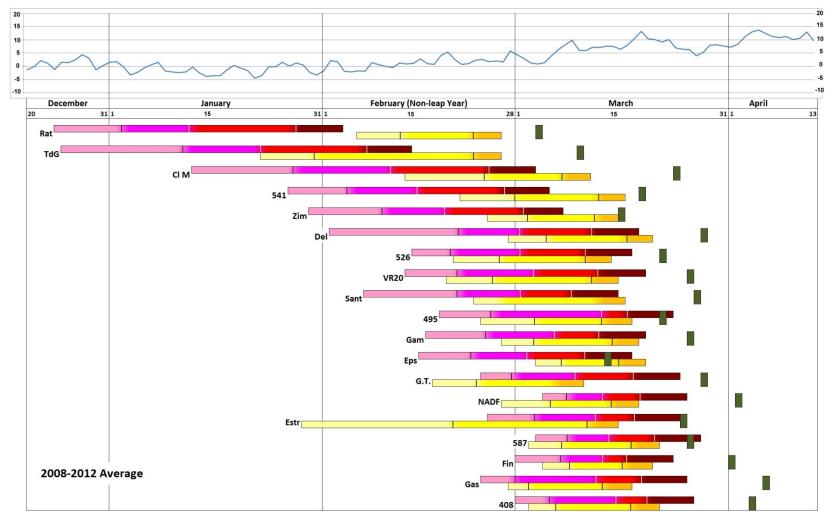


Figure 3. 4-year average flower and bud development for 19 Corylus accessions between Dec. 2008 and Apr. 2012.

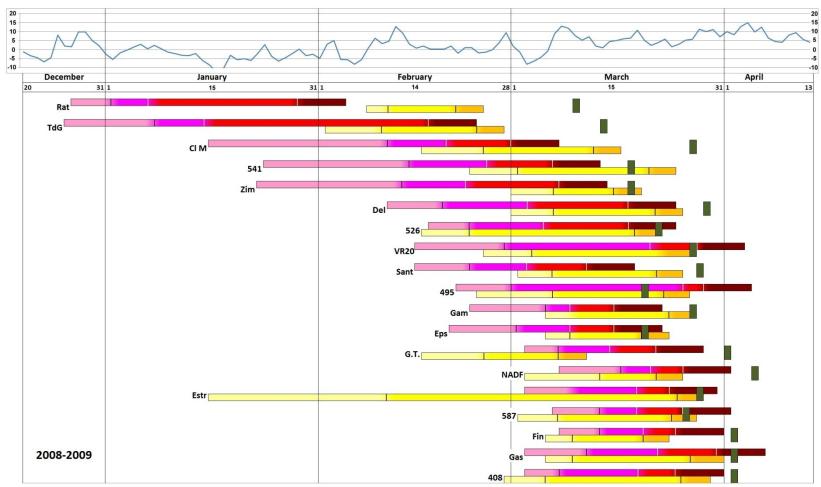


Figure 4. Flower and bud development for 19 Corylus accessions between Dec. 2008 and Apr. 2009.

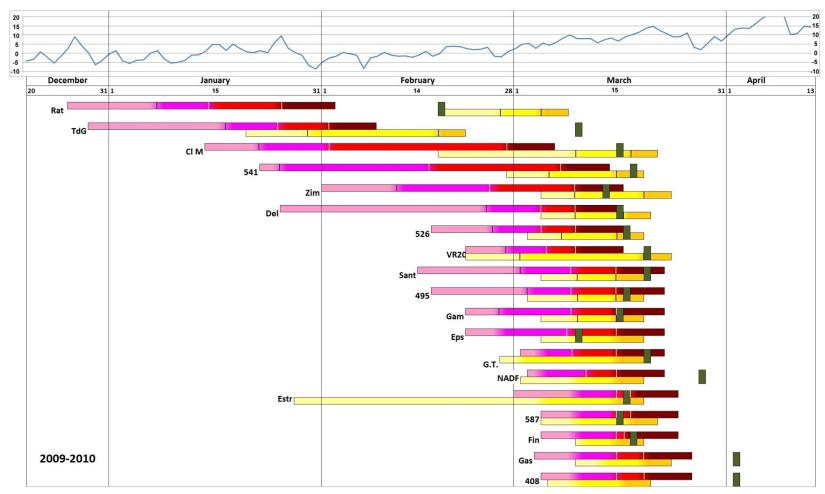


Figure 5. Flower and bud development for 19 Corylus accessions between Dec. 2009 and Apr. 2010.

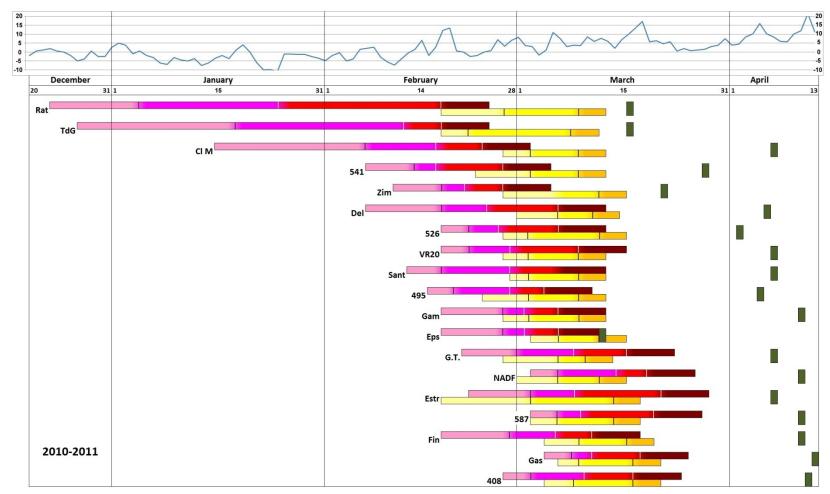


Figure 6. Flower and bud development for 19 *Corylus* accessions between Dec. 2010 and Apr. 2011. This period represent the overall coldest bloom period of the 4-year study.

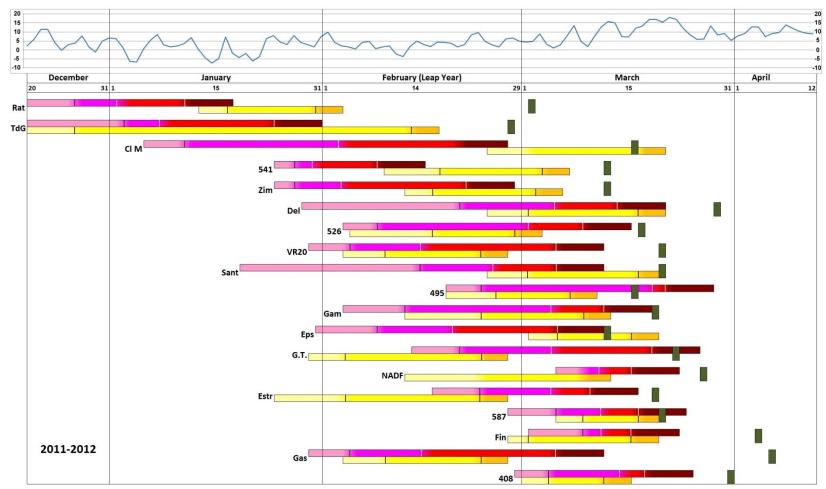


Figure 7. Flower and bud development for 19 Corylus accessions between Dec. 2011 and Apr. 2012. This period represent

the overall warmest bloom period of the 4-year study.