Developing Hazelnuts for the Eastern United States

T.J. Molnar, J.C. Goffreda and C.R. Funk Department of Plant Biology and Pathology Rutgers University 59 Dudley Road, Foran Hall New Brunswick, NJ 08901-8520 USA

Keywords: Corylus avellana, Corylus americana, hazelnut, eastern filbert blight, Anisogramma anomala, breeding

Abstract

Over the last century, many advances were made in the art and science of hazelnut improvement that clearly show the potential for developing well-adapted commercial quality hazelnuts for the eastern United States. At Rutgers University, we are using these advances to build an efficient and effective hazelnut breeding program. New Jersey's geographic location and climate make it well suited for assessing the major limiting factors of European hazelnut (*Corylus avellana* L.) culture in the northeastern U.S., which includes susceptibility to eastern filbert blight (*Anisogramma anomala* [Peck] E. Müller) and lack of cold hardiness. By utilizing previous eastern U.S. breeding efforts, access to a greatly expanded base of hazelnut germplasm, better understanding of eastern filbert blight, and recent advances in hazelnut genetics and breeding, it will be possible to significantly increase the usefulness of hazelnuts in New Jersey, the eastern U.S., and other climatically homologous areas.

INTRODUCTION

Commercial hazelnut production in the U.S. is done exclusively in the Pacific Northwest, with 99% of the U.S. crop produced in the Willamette Valley of Oregon (Mehlenbacher and Olsen, 1997). Four major components: 1) past eastern U.S. breeding and collection efforts, 2) expanded hazelnut germplasm resources, 3) improved understanding of eastern filbert blight (*Anisogramma anomala* [Peck] E. Müller), and 4) advances in hazelnut genetics and breeding, have set the stage for the dramatic expansion of hazelnut culture throughout eastern North America. At Rutgers University in New Jersey we are using these components to build an efficient and effective hazelnut genetic improvement program. This paper discusses these components in relation to supporting the development of a promising eastern U.S. hazelnut breeding program.

LIMITS TO HAZELNUT CULTURE IN THE EASTERN U.S.

It has been widely reported that two major factors, susceptibility to eastern filbert blight (EFB) and lack of cold hardiness, limit the culture of European hazelnut (*Corylus avellana* L.) in the eastern United States (Fuller, 1908; Morris, 1920; Barss, 1930; Slate, 1930; Reed, 1936; Lagerstedt, 1975; Thompson et al., 1996; Farris, 2000). EFB, caused by *Anisogramma anomala*, is a native, obligate, biotrophic fungal parasite of the wild American hazelnut, *Corylus americana* Walter, first described by C.H. Peck in 1874. Its symptoms, disease cycle, and epidemiology were reviewed by Johnson and Pinkerton (2002). EFB can be found associated with *C. americana* throughout its range, which covers much of the eastern U.S., from Maine to Saskatchewan, Canada, south to Georgia and Louisiana, and west to Oklahoma (Gleason and Cronquist, 1998). Consequently *C. americana*, which is described as being much more resistant (or tolerant) to EFB than its European relative (Fuller, 1908; Morris, 1920; Weschcke, 1954), acts as both a widespread host for EFB and a source of inoculum to infect *C. avellana* planted across its range.

Cold air temperatures typically limit *C. avellana* culture in two ways: 1) injury to woody tissues by extreme low air temperatures and 2) injury to staminate flowers.

Proc. VIth Intl. Congress on Hazelnut Eds.: J. Tous, M. Rovira & A. Romero Acta Hort. 686, ISHS 2005 Minimum air temperatures periodically occur in the northeastern U.S. with potential to cause extensive stem death or entire tree death of non cold-hardy cultivars (Slate, 1934, 1959). Injury to staminate flowers occurs more regularly (injury occurs at a warmer air temperature then injury to woody tissues) and is a limiting factor to hazelnut culture over a wider geographic area. According to L.H. MacDaniels, in parts of the east hazelnuts may appear to thrive but fail to fruit due to catkin killing and lack of pollination (1964). Catkin injury appears to result from desiccation during a combination of freezing air temperatures and wind (Slate, 1933; Reed and Davidson, 1958). Catkins are particularly sensitive to injury during bloom (Thompson et al., 1996) with cold hardy cultivars tending to be late blooming (Mehlenbacher, 2003).

ADVANCES IN HAZELNUT IMPROVEMENT: PAST TO PRESENT

Since the early 1900s, unsuccessful attempts have been made to identify commercial quality European hazelnut cultivars suitable for growth in the eastern United States (Weschcke, 1954; Slate, 1961). Finding that most cultivars lacked the cold hardiness and EFB resistance needed to reliably produce nuts, early breeders turned to making interspecific hybrids between C. avellana and C. americana to meet their objectives (Reed, 1936; Slate, 1936; Crane et al., 1937; Wescheke, 1954). Breeders attempted to combine the superior nut qualities of *C. avellana*, which includes larger nuts with thinner shells and higher kernel percentage that fall free from the husk on maturity, with the cold hardiness and EFB resistance of C. americana. Cultivars and contributions made by early breeders J.F. Jones of Lancaster, Pennsylvania; C. Weschcke of St. Paul, Minnesota; C.A. Reed of the USDA Beltsville, Maryland; G.L. Slate of the New York State Agricultural Experiment Station, Geneva, New York; and S.H. Graham of Ithaca, New York are summarized in Thompson et al. (1996). For the most part, these breeders only produced hybrids from first generation controlled crosses of C. americana x C. avellana (Slate, 1969), never examining the potential of second and third generation hybrids of selected improved parents. Although not from controlled crosses, breeding work was continued by making selections from open-pollinated seedling populations of the original hybrids (Graham, 1936; Slate, 1961; Reich, 1980). While progress was made towards developing EFB resistant cold hardy cultivars, the lack of genotype diversity used in the controlled crosses (extensive use of the C. americana 'Rush' as a pistillate parent) and the discontinuation of focused breeding programs, left much room for improvement. Hybrids with large, high-quality nuts were developed, however they were not adequately productive and cold hardy to warrant commercial planting and the nuts did not drop from the husks when mature (Slate, 1961, 1969). In addition, selections related to 'Rush' were shown to be highly susceptible to bud mites, *Phytoptus avellanae* Nal. and Cecidophyopsis vermiformis Nal. (Ourecky and Slate, 1969; Thompson, 1977a).

In an attempt to develop cold hardy, early maturing hazelnuts suitable for British Columbia and the harsh Canadian prairies, nurseryman J.U. Gellatly made openpollinated crosses and identified hybrids between *C. avellana* and other *Corylus* species, including *C. cornuta* Marshall, *C. colurna* L., and *C. chinenesis* Franchet (Gellatly, 1956, 1964, 1966). Gellatly's breeding work resulted in the development of several cultivars and selections shown to be sufficiently cold hardy and resistant to EFB in the east (Leferve, 1958; Farris, 1970, 2000; E. Grimo, pers. commun.; J. Gordon, pers. commun.). After evaluating many of Gellatly's selections, C. Farris, of Lansing, Michigan, used the reported *C. avellana* x *C. colurna* hybrid 'Faroka' extensively in his breeding program. This resulted in the release of the noteworthy cultivar 'Grand Traverse' (Farris, 1989, 2000).

In 1963 private breeder and nurseryman John Gordon of Amherst, New York began selecting superior hazelnut hybrids from large open-pollinated seedling populations of 'NY 104' and 'NY 200' (selections originating from the New York Agricultural Experiment Station breeding program of G.L. Slate, Geneva, New York). In the 1980s he added seedlings of Gellatly's *C. avellana* x *C. colurna* selections 'Faroka', 'Morrisoka', 'Laroka' and '502' to the breeding population. Gordon's genetic improvement scheme

largely consists of allowing EFB to cull many of the susceptible plants, limiting their pollen shed, with the remaining large population inter-pollinating. Open-pollinated nuts are harvested from the best seedlings to plant successive generations for further evaluation. He has continued this selection procedure to the present day screening thousands of seedlings. This resulted in the identification of several superior selections that meet his requirements of being highly EFB resistant, cold hardy, and annually yielding of large, high quality kernels. These selections are currently under evaluation at different locations.

In 1978 private breeder Phil Rutter of Canton, Minnesota began selecting nuts from superior seedlings of C. Weschcke's (1954) extensive plantings of C. americana x C. avellana hybrids. Rutter later added material to his breeding program originating from hybrids developed by G.L. Slate, J.U. Gellatly, and C. Farris. In a breeding scheme similar to Gordon's, inferior genotypes are naturally eliminated by the harsh climate of Minnesota and the presence of EFB. Superior seedlings are identified and nuts harvested to plant successive generations, which then undergo similar evaluations. Pollinations are controlled to some degree by emasculating inferior plants prior to anthesis. Large numbers (over 50,000) of seedlings are currently being evaluated by Rutter, with experimental plantings of his hybrid seedlings being undertaken by growers in Minnesota, Nebraska, Wisconsin, and other states. In addition to cold hardiness and high resistance to EFB, the main breeding objectives are overall kernel productivity and cropping potential. Rutter has identified seedlings expressing very high blight resistance and cold hardiness that are segregating for high nut productivity and quality. In cooperation with the University of Minnesota, Rutter is currently exploring the potential of hazelnuts as a mechanically harvested oil crop used for making biodiesel fuel (Rutter, pers. commun.).

Although the early eastern breeding programs released no widely used commercial quality cultivars, EFB resistant and cold hardy hazelnuts were developed that merit attention. These cultivars clearly show the potential for the genetic improvement of hazelnuts in the eastern U.S. Private breeders and amateur horticulturists have continued selecting from open-pollinated seedlings of these original cultivars, potentially identifying genotypes superior to their parents. In spite of using inefficient methods (absence of biparental controlled crosses of selected parents and limited diversity of original *C. americana* sources), their breeding efforts maintained large, segregating, diverse populations, preserving a pool of genetic resources vital to continuing breeding efforts. The existing eastern U.S. collection of hazelnut germplasm, made up of original clones and their seedlings, along with new germplasm being introduced, will play a major role in the development of well-adapted commercial quality cultivars and the overall expansion of hazelnut culture in the eastern U.S.

Extensive efforts have been and are being made by the U.S. Dept. of Agriculture, Agricultural Research Service National Clonal Germplasm Repository (USDA, ARS-NCGR) and Oregon State University (OSU), both at Corvallis, Oregon, to develop and preserve a worldwide collection of *Corylus* genetic resources (Erdogan and Mehlenbacher, 2000; Hummer, 2001). The repository currently holds 623 accessions originating from 39 countries, including representatives of the nine major *Corylus* species. Out of these, 364 are named cultivars and selections, and 600 of the 623 accessions are available for distribution as scion wood (J. Postman, pers. commun; USDA ARS-NCGR database). Early eastern U.S. breeders did not have access to the broad base of *Corylus* germplasm currently available. These expanded genetic resources, along with continuing *Corylus* collection efforts, will be essential for developing superior cultivars adapted to the eastern U.S.

Due to the discovery of EFB in commercial orchards in Washington in the early 1970s and its subsequent spread (Davidson and Davidson, 1973; Pinkerton et al., 1992; Pinkerton et al., 2001), collection efforts have been combined with an urgent need to locate and develop EFB resistant commercial quality cultivars for the current hazelnut production region of the U.S. (Mehlenbacher et al., 1994; Thompson et al., 1996; Coyne et al., 1998; Lunde et al., 2000). Prior to the 1970s, little research was done on the biology

and pathology of EFB. Past reports were limited to field observations and basic morphological and anatomical descriptions (Peck, 1874; Halsted, 1892; Humphrey, 1893; Fuller, 1908; Morris, 1920; Barss, 1930). Due to the obvious financial perils EFB could impart on the hazelnut production region of the U.S. (Willamette Valley of Oregon), starting in the 1980s the Oregon Hazelnut Commission, OSU, and the USDA Agricultural and Cooperative States Research Services funded extensive research towards better knowledge of the destructive pathogen (Johnson, 1996). Since that time, major advances have been made in the understanding of EFB. A comprehensive study of the developmental morphology and cytology of Anisogramma anomala was completed by Gottwald and Cameron (1979). Detailed accounts of its natural infection period (Stone et al., 1992; Johnson et al., 1994), mode of infection (Pinkerton et al., 1995), development in host (Gottwald and Cameron, 1979 & 1980a) and discharge and spread of spores (Gottwald and Cameron, 1980b; Pinkerton et al., 1998a, b; Pinkerton et al., 2001) were also completed. These new understandings allowed breeders and pathologists to develop more effective and efficient EFB resistance evaluation techniques, ultimately leading to the identification of additional sources of resistance (Coyne et al., 1998, Lunde et al., 2000). Techniques were developed to reliably identify genotypes with high quantitative resistance to EFB in 16-24 months, using artificial field inoculations, which shortened screening time from the 5-7 years needed when using standard field trials (Pinkerton et al., 1993; Coyne at al., 2000). Greenhouse inoculation procedures were developed that identify genotypes expressing very high degrees of resistance (Johnson et al., 1994; Osterbauer et al., 1997; Coyne et al., 1998; Lunde et al., 2000), which when combined with the use of ELISA (enzyme-linked immunosorbent assay), would reduce the time required for identification to 3-5 months (Coyne et al., 1996). Techniques using RAPD (random amplified polymorphic DNA) based marker-assisted selection for the identification of seedlings carrying the 'Gasaway' single dominant gene for EFB resistance (Mehlenbacher, 1991a) were developed that provide the potential to greatly increase the efficiencies of breeding for resistance (Davis and Mehlenbacher, 1997; Mehlenbacher et al., 2004). The above stated resistance screening techniques, not available to early breeders, can greatly reduce the time required to identify sources of high resistance to EFB and subsequently incorporate them into a genetic improvement program.

Since the OSU breeding program was initiated in 1969, major advances have been and are being made in the knowledge of hazelnut genetics and breeding. The genetics of the sporophytic pollen-stigma incompatibility system within *C. avellana* has been elucidated (Thompson, 1979), along with the identification of 25 unique self-incompatibility alleles (S-alleles) and the determination of dominance relationships among them (Mehlenbacher, 1997a). Early breeders lacked knowledge of this system, which is needed to efficiently identify compatible parents for use in controlled crosses and to determine suitable pollenizers for orchard plantings. Work has also begun towards understanding the incompatibility systems in wild *Corylus* species (Erdogan and Mehlenbacher, 2001). In addition, research has been done towards the development of marker-assisted selection techniques useful for identifying desired S-allele genotypes. RAPD markers have been identified for the S₁ and S₂ alleles (Pomper et al., 1998). This tool will allow breeders to identify S-alleles in seedlings at a much earlier stage, saving time and resources, since the previous methods require seedlings be grown until they flower (Mehlenbacher, 1997b).

In addition to the self-incompatibility system, interspecific hybridization potentials of *Corylus* species were examined. Erdogan and Mehlenbacher intercrossed eight different *Corylus* species revealing genetic relationships and clarifying hybridization possibilities between species that were disputed or not previously attempted (2002). Increased knowledge of hybridization possibilities and a continually expanding base of genetic resources will allow breeders to incorporate characteristics lacking in *C. avellana* (such as non-suckering growth habit, extreme cold hardiness, early maturity and seedling precocity, disease and pest resistance, and tolerance to various abiotic stresses) from

many different *Corylus* species, developing advanced cultivars of interspecific origin.

Adding to the tools and knowledge available to present hazelnut breeders, the genetic control of many qualitative and quantitative traits has been studied. Inheritance of qualitative traits examined includes red leaf color (Thompson, 1985), chlorophyll deficiency (Mehlenbacher and Thomson, 1991b), cutleaf leaf shape (Mehlenbacher and Smith, 1995), pollen color (Mehlenbacher and Smith, 2002), style color (Mehlenbacher and Thompson, 2004), contorted growth habit (Smith and Mehlenbacher, 1996), and non-dormancy (Thompson et al., 1985). Heritability of quantitative traits examined includes bud mite resistance (Thompson, 1997a), pellicle removal (Mehlenbacher and Smith, 1988), nut and kernel defects (Mehlenbacher et al., 1993), and other morphological and developmental characteristics important to nut production (Thompson, 1977b; Yao and Mehlenbacher, 2000). Early breeders did not have access to this information, which is important for the efficient identification of suitable parents to use in controlled crosses to meet breeding objectives, as well as in directing the selection criteria of progeny.

RUTGERS UNIVERSITY HAZELNUT BREEDING PROGRAM

The four major components advancing hazelnut improvement over the last century, as discussed in this paper, clearly show the potential for increasing the usefulness of hazelnuts in the eastern U.S. (and other climatically homologous areas of the world). At Rutgers we recognize these advances and are using them to build an effective and efficient hazelnut genetic improvement program. New Jersey's geographic location (latitude: 38°55'N to 41°21'N) and climate make it well suited for assessing the limiting factors of hazelnut culture in the northeastern U.S (excluding the shoreline, the average annual minimum temperature ranges from -17.8 to -23.3°C, USDA Plant Hardiness Zone Map). The Rutgers hazelnut breeding program is currently collecting and evaluating hazelnut cultivars and selections from the early eastern U.S. breeding programs, as well as more recent seedling selections made by nurserymen and private breeders. We are also evaluating accessions from the USDA ARS-NCGR, breeding material from OSU, and collections from arboreta and botanical gardens across the U.S. In addition, we are undertaking efforts in cooperation with OSU, to collect hazelnut germplasm from areas of the world currently lacking in U.S. collections. Plants will be evaluated for resistance to EFB, cold hardiness, nut quality (size, percent kernel, taste, etc.), cropping potential, insect resistance, growth habit, drought and heat tolerance, ornamental attributes, and other traits.

Since EFB is native to New Jersey and there is no established, economically important hazelnut industry, no quarantine restrictions are in place to control the importation and spread of EFB from other areas. This fact allows breeders to conduct research here that would be impossible to undertake in the Pacific Northwest, due to the presence of strict quarantine restrictions and the inherent risks to the hazelnut industry of importing new, potentially more-virulent, races of EFB. At present, no widely tested EFB resistant commercial quality cultivars are available, therefore identifying stable, high resistance to EFB is essential to any U.S. hazelnut breeding program. To rapidly evaluate collections at Rutgers for EFB resistance, we are using a combination of greenhouse and field inoculations. As a source of inoculum, we are using New Jersey EFB and EFB collected from various locations across the eastern U.S. By using EFB from different geographic locations, we can evaluate resistance to a diversity of possible strains or races of the disease (the presence of different races has not yet been determined, although research is now underway). We are also developing a "disease nursery" by allowing large numbers of hazelnuts, infected by EFB from around the country, to shed spores in the field. This will allow study of the stability of resistance under conditions of high disease pressure interacting with a diversity of EFB sources. Cultivars and selections found resistant under these conditions will be evaluated simultaneously for other important characteristics (cold hardiness, nut productivity and quality, growth habit, etc.) and the best used as parents in our genetic improvement program. Progeny will successively be evaluated under similar conditions by maintaining high disease pressure of diverse

sources of EFB in our nurseries. The top performing progeny will be clonally propagated and moved to replicated yield trials for further evaluation throughout New Jersey and other locations. From there, decisions will be made to recommend selections for release and/or for use as parents in successive generations of controlled crosses.

CONCLUSIONS

Hazelnut breeders now have at their disposal the tools necessary to develop a very efficient and effective genetic improvement program. In addition, much of the basic research has been initiated to further advance the science of hazelnut breeding. For example, the development of RAPD markers linked to the 'Gasaway' EFB resistance gene and the S₁ and S₂ incompatibility alleles both provide protocols for identifying additional markers for resistance genes and S-alleles, respectively (Pomper et al., 1998; Mehlenbacher et al., 2004). The techniques for culturing *Anisogramma anomala* have been identified (Stone et al., 1994), which will allow for further research to develop an even greater understanding of the pathogen and its genetic diversity.

At Rutgers, we hope to increase the usefulness of hazelnuts as both agricultural and ornamental plants for New Jersey, the eastern U.S., and other climatically homologous areas.

By combining present and continual research efforts and advances with an effective, focused genetic improvement program, it will be possible to develop productive hazelnut culture most anywhere in the temperate world.

Literature Cited

- Barss, H.P. 1930. Eastern filbert blight. California Dept. of Agriculture Bull. 19:489-490.
- Coyne, C.J., Mehlenbacher, S.A., Hampton, R.O., Pinkerton, J.N. and Johnson, K.B. 1996. Use of ELISA to rapidly screen hazelnut for resistance to eastern filbert blight. Plant Dis. 80:1327-1330.
- Coyne, C.J., Mehlenbacher, S.A. and Smith, D.C. 1998. Sources of resistance to eastern filbert blight. J. Amer. Soc. Hort. Sci. 124:253-257.
- Coyne, C.J., Mehlenbacher, S.A., Johnson, K.B., Pinkerton, J.N. and Smith, D.C. 2000. Comparison of two methods to evaluate quantitative resistance to eastern filbert blight in European hazelnut. J. Amer. Soc. Hort. Sci. 125(5):603-608.
- Crane, H.L., Reed, C.A. and Wood, M.N. 1937. Nut breeding. p.827-889. In: USDA Yearbook of Agriculture.
- Davidson, A.D. and. Davidson, Jr. R.M. 1973. *Apioporthe* and *Monchaetia* canker reported in western Washington. Plant Disease Reporter 57:522-523.
- Davis, J.W. and Mehlenbacher, S.A. 1997. Identification of RAPD markers linked to eastern filbert blight resistance in hazelnut. Acta Hort. 445:553-556.
- Erdogan, V. and Mehlenbacher, S.A. 2000. Interspecific hybridization in hazelnut (*Corylus*). J. Amer. Soc. Hort. Sci. 125(4):489-497.
- Erdogan, V. and Mehlenbacher, S.A. 2001. Incompatibility in wild *Corylus* species. Acta Hort. 556:163-169.
- Farris, C.W. 1989. Two new introductions: the 'Grand Traverse' hazelnut and 'Spartan Seedless' grape. Annual Report of the Northern Nut Growers Association 80:102-103.
- Farris, C.W. 1970. Inheritance of parental characteristics in filbert hybrids. Annual Report of the Northern Nut Growers Association 61:54-58
- Farris, C.W. 2000. The Hazel Tree. Northern Nut Growers Association, Inc.
- Fuller, A.S. 1908. The filbert or hazelnut. p.118-146. In: The Nut Culturist, Orange Judd Company, NY.
- Gellatly, J.U. 1956. Filazels. Annual Report of the Northern Nut Growers Association 47:112-113.
- Gellatly, J.U. 1964. Filazels. Annual Report of the Northern Nut Growers Association 55:153-155.
- Gellatly, J.U. 1966. Tree hazels and their improved hybrids. Annual Report of the Northern Nut Growers Association 57:98-101.

- Gleason, H.A. and Cronquist, A. 1998. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. The New York Botanical Gardens, Bronx, NY.
- Graham, S.H. 1936. Notes on an experimental planting in Central New York. Annual Report of the Northern Nut Growers Association 27:64-67.
- Gottwald, T.R. and Cameron, H.R. 1979. Studies in the morphology and life history of *Anisogramma anomala*. Mycologia 71:1107-1126.
- Gottwald, T.R. and Cameron, H.R. 1980a. Infection site, infection period, and latent period of canker caused by *Anisogramma anomala* in European filbert. Phytopathology 70:1083-1087.
- Gottwald, T.R. and Cameron, H.R. 1980b. Disease increase and the dynamics of spread of canker caused by *Anisogramma anomala* in European filbert in the Pacific Northwest. Phytopathology 70:1087-1092.
- Halsted, B.D. 1892. Report of the botanical department a serious filbert disease. New Jersey State Agricultural Experiment Station Annual Report 13:287-289.
- Hummer, K.E. 2001. Hazelnut genetic resources at the Corvallis repository. Acta Hort. 556:21-23.
- Humphry, J.E. 1893. A hazel fungus. Massachusetts State Agricultural Experiment Station (Amherst) Annual Report 10:242-243.
- Johnson, K.B., Pinkerton, J.N., Gaudreault, S.M. and Stone, J.K. 1994. Infection of European hazelnut by *Anisogramma anomala*: Site of infection and effect on host developmental stage. Phytopathology 84(12):1465-1470.
- Johnson, K.B., Mehlenbacher, S.A., Stone, J.K. and Pscheidt, J.W. 1996. Eastern filbert blight of European hazelnut: It's becoming a manageable disease. Plant Dis. 80:1308-1316.
- Johnson, K.B. and Pinkerton, J.N. 2002. Eastern filbert blight. p.44-46. In: B.L. Teviotdale, T.J. Michailides and J.W. Pscheidt (eds.), Compendium of Nut Crop Diseases in Temperate Zones. The American Phytopathological Society Press.
- Lagerstedt, H.B. 1975. Filberts. p.456-488. In: J. Janick and J.N. Moore (eds.), Advances in Fruit Breeding. Purdue Univ. Press, West Lafayette, IN.
- Lefevre, H.E. 1958. Hardiness of filberts in Huntington County, Quebec. Annual Report of the Northern Nut Growers Association 49:102-103.
- Lunde, C.F., Mehlenbacher, S.A. and Smith, D.C. 2000. Survey of hazelnut cultivars for response to eastern filbert blight inoculation. HortScience 35(4): 729-731.
- MacDaniels, L.H. 1964. Hazelnuts and Filberts. Horticulture 42(10):44-45, 53.
- Mehlenbacher, S.A. and Smith, D.C. 1988. Heritability of ease of hazelnut pellicle removal. HortScience 23(6):1053-1054.
- Mehlenbacher, S.A. 1990. Hazelnuts (Corylus). Acta Hort. 290:791-838.
- Mehlenbacher, S.A. and Thompson, M.M. 1991a. Occurrence and inheritance of resistance to eastern filbert blight in 'Gasaway' hazelnut. HortScience 26:410-411.
- Mehlenbacher, S.A. and Thompson, M.M. 1991b. Inheritance of a chlorophyll deficiency in hazelnut. HortScience 26(11):1414-1416.
- Mehlenbacher, S.A., Smith, D.C. and Brenner, L.K. 1993. Variance components and heritability of nut and kernel defects in hazelnut. Plant Breeding 110:144-152.
- Mehlenbacher, S.A., Pinkerton, J.N., Johnson, K.B. and Pscheidt, J.W. 1994. Eastern filbert blight in Oregon. Acta Hort. 351:551-556.
- Mehlenbacher, S.A. and Smith, D.C. 1995. Inheritance of the cut leaf trait in hazelnut. HortScience 30(3):611-612.
- Mehlenbacher, S.A. and Olsen, L. 1997. The hazelnut industry in Oregon. Acta Hort. 445:337-345.
- Mehlenbacher, S.A. 1997a. Revised dominance hierarchy for S-alleles in *Corylus avellana* L. Theor. Appl. Genet. 94:360-366.
- Mehlenbacher, S.A. 1997b. Testing compatibility of hazelnut crosses using fluorescence microscopy. Acta Hort. 445:167-171.
- Mehlenbacher, S.A. and Smith, D.C. 2002. Inheritance of pollen color in hazelnut. Euphytica 127(3):303-307.

- Mehlenbacher, S.A. 2003. Hazelnuts. p.183-215. In: D.W. Fulbright (ed.), A guide to nut tree culture in North America, Vol. 1, Northern Nut Growers Association, Inc.
- Mehlenbacher, S.A., Brown, R.N., Davis, J.W., Chen, H., Bassil, N.V., Smith, D.C. and Kubisiak, T.L. 2004. RAPD makers linked to eastern filbert blight resistance in *Corylus avellana*. Theor. Appl. Genet. 108:651-656.
- Mehlenbacher, S.A. and Thompson, M.M. 2004. Inheritance of style color in hazelnut. HortScience 39(3):475-476.
- Morris, R.T. 1920. Hazel nuts. Amer. Nut J. 11:57.
- Ourecky, D.K. and Slate, G.L. 1969. Susceptibility of filbert varieties and hybrids to the filbert bud mite, *Phytoptus avellanae* Nal. Annual Report of the Northern Nut Growers Association 60:89-91.
- Osterbauer, N.K., Johnson, K.B., Mehlenbacher, S.A. and Sawyer, T.L. 1997. Analysis of resistance to eastern filbert blight in *Corylus avellana*. Plant Dis. 81:388-394.
- Peck, C.H. 1874. Report of the Botanist. Annual Report of the New York State Museum. 28:31-92 (first distributed Dec. 1876).
- Pinkerton, J.N., Johnson, K.B., Theiling, K.M. and Griesbach, J.A. 1992. Distribution and characteristics of the eastern filbert blight epidemic in western Oregon. Plant Dis. 76:1179-1182.
- Pinkerton, J.N., Johnson, K.B., Mehlenbacher, S.A. and Pscheidt, J.W. 1993. Susceptibility of European hazelnut clones to eastern filbert blight. Plant Dis. 77:261-266.
- Pinkerton, J.N., Stone, J.K., Nelson, S.J. and Johnson, K.B. 1995. Infection of European hazelnut by *Anisogramma anomala*: Ascospore adhesion, mode of penetration of immature shoots, and host response. Phytopathology 85:1260-1268.
- Pinkerton, J.N., Johnson, K.B., Stone, J.K. and Ivors, K.L. 1998a. Factors affecting the release of ascospores of *Anisogramma anomala*. Phytopathology 88:122-128.
- Pinkerton, J.N., Johnson, K.B., Stone, J.K. and Ivors, K.L. 1998b. Maturation and seasonal discharge pattern of ascospores of *Anisogramma anomala*. Phytopathology 88:1165-1173.
- Pinkerton, J.N., Johnson, K.B., Aylor, D.E. and Stone J.K. 2001. Spatial and temporal increase of eastern filbert blight in European hazelnut orchards in the Pacific Northwest. Phytopathology 91:1214-1223.
- Pomper, K.W., Azarenko, A.N., Bassil, N., Davis, J.W. and Mehlenbacher, S.A. 1998. Identification of random amplified polymorphic DNA (RAPD) markers for self-incompatibility alleles in *Corylus avellana* L. Theor. Appl. Genet. 97:479-487.
- Reed, C.A. 1936. New filbert hybrids. J. Hered. 27:427-431.
- Reed, C.A. and Davidson, J. 1958. The Improved Nut trees of North America. Devin-Adir Company, New York.
- Reich, J.E. 1980. Geneva filbert research-Past and present. Annual Report of the Northern Nut Growers Association 71:110-111.
- Slate, G.L. 1930. Filberts. New York State Agricultural Experiment Station Bulletin 588.
- Slate, G.L. 1933. Notes on the filbert orchard at Geneva. Annual Report of the Northern Nut Growers Association 24:34-37.
- Slate, G.L. 1934. Winter injury of filberts at Geneva 1933-1934. Annual Report of the Northern Nut Growers Association 25:36-40.
- Slate, G.L. 1936. The filbert breeding project at Geneva. Annual Report of the Northern Nut Growers Association 27:62-63.
- Slate, G.L. 1959. Winter injury of filberts at Geneva, N.Y. 1958-59. Annual Report of the Northern Nut Growers Association 50:75-76.
- Slate, G.L. 1961. The present status of filbert breeding. Annual Report of the Northern Nut Growers Association 52:24-26.
- Slate, G.L. 1969. Filberts-including varieties grown in the east. p.287-293. In: R.A. Jaynes (ed.), Handbook of North American Nut Trees. Humphrey, Geneva, NY.
- Smith, D.C. and Mehlenbacher, S.A. 1996. Inheritance of contorted growth in hazelnut. Euphytica 89:211-213.
- Stone, J.K., Johnson, K.B., Pinkerton, J.N. and Pscheidt, J.W. 1992. Natural infection

- period and susceptibility of vegetative seedlings of European hazelnut to *Anisogramma anomala*. Plant Dis. 76:348-352
- Stone, J.K., Pinkerton, J.N. and Johnson K.B. 1994. Axenic culture of Anisogramma anomala: Evidence for self-inhibition of ascospore germination and colony growth. Mycologia 86(5):674-683.
- Thompson, M.M. 1977a. Inheritance of bud mite susceptibility in filberts. J. Amer. Soc. Hort. Sci. 102(1):39-42.
- Thompson, M.M. 1977b. Inheritance of nut traits in filbert. Euphytica 26:465-474.
- Thompson, M.M. 1979. Genetics of incompatibility in *Corylus avellana* L. Theor. Appl. Genet. 54:113-116.
- Thompson, M.M. 1985. Linkage of the incompatibility locus and red pigmentation genes in hazelnut. J. Hered. 76:119-122.
- Thompson, M.M., Smith, D.C. and Burges, J.E. 1985. Nondormant mutants in a temperate tree species, *Corylus avellana* L. Theor. Appl. Genet. 70:687-692.
- Thompson, M.M., Lagerstedt, H.B. and Mehlenbacher, S.A. 1996. Hazelnuts. p.125-184. In: J. Janick and J.N. Moore (eds.), Fruit breeding, Vol. 3, Nuts, Wiley, New York.
- USDA ARS-NCGR Database. 2004. National Plant Germplasm System, *Corylus* Resources. http://www.ars-grin.gov/cor/corylus/corinfo.html
- USDA Plant Hardiness Zone Map. 1990. USDA Miscellaneous Publication No. 1475
- Weschcke, C. 1954. Hazels and filberts. p.24-38. In: Growing nuts in the north, Webb, St. Paul, Minnesota.
- Yao, Q. and Mehlenbacher, S.A. 2000. Heritability, variance components and correlation of morphological and phenological traits in hazelnut. Plant Breeding 119:369-381.