

# Plant Breeding Reviews



VOLUME 45

Edited by  
IRWIN GOLDMAN

WILEY



PLANT BREEDING REVIEWS

Volume 45

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# PLANT BREEDING REVIEWS

Volume 45

Edited by

**Irwin Goldman**

University of Wisconsin–Madison  
Madison, Wisconsin, USA

**WILEY**

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# Antoine: Slave, Creole Gardener, and Expert Grafter of Pecan Trees

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## ABSTRACT

Scientific advancements in any field are often the result of hard work by well-trained scientists whose productive lives and academic careers are well documented. Occasionally, advancements are made in a given field by those without the advantage of formal education or training, and about whom there is little documentation, but whose intellect and skill contribute greatly to the advancement of that field. In the mid-1800s, a man known only as Antoine grafted 126 pecan (*Carya illinoensis*) trees at Oak Alley Plantation in St. James Parish, Louisiana. Originally, a sugarcane plantation, dating back to 1836, Oak Alley is famously recognized by its plantation house adorned with large Tuscan columns and lying at the end of a double row of 28 large live oak trees. There is very little known of Antoine, in part because he was a slave whose rights were largely curtailed. However, his successful grafting of 126 pecan trees laid the foundation for the development of the first recognized pecan cultivar, 'Centennial'. Antoine's techniques would be used as the basis for the consistency that led to the development of the pecan industry, not only in the United States, but also throughout the world. That he was unheralded during his time is largely due to the horrors and repressive nature of American slavery. It is long past time that his accomplishments, and the contributions of so many unrecognized horticulturists to the betterment of our crops, were recognized.

**KEYWORDS:** Oak Alley, pecan, slavery, slave, *Carya illinoensis*

## OUTLINE

- I. BACKGROUND
- II. WORK AND RECOGNITION OF 'CENTENNIAL' PECAN
- III. SIGNIFICANCE
- LITERATURE CITED

### I. BACKGROUND

Prior to the late 1800s, though pecans (*Carya illinoensis*) had been utilized by Native Americans for centuries and were later a popular trade item among the early European settlers of North America, pecans were not viewed as having serious commercial potential due to their lack of uniformity (Wells 2017). In 1794, French explorer and botanist Andre Michaux first encountered the pecan near Louisville, Kentucky. Twenty-five years later, he would encounter stands of wild pecan trees being cultivated by Native Americans near Kaskaskia, Illinois. He wrote of the pecan as being “more delicately” flavored than the walnuts of Europe. He was concerned with the lack of precocity – fruit production at an early age – in the pecan and suggested the pecan could be improved by grafting onto wild black walnut (*Juglans nigra*) (Bryant 2004).

However, there are no records of successful attempts at the vegetative propagation of pecan trees until 1822 when Dr. Abner Landrum budded pecan onto a wild hickory (*Carya* spp.) rootstock in Edgefield, South Carolina. Landrum himself was a fascinating man in his own right. A physician, ceramic artist, amateur horticulturist, and publisher, Landrum produced the first alkaline-glazed stoneware pottery in the New World, combining the techniques of Europe and Asia and creating a viable alternative to lead-glazed pottery. This was significant because the lead glaze used on most earthenware pottery produced in the south during the 1700s and early 1800s was responsible for a rash of lead poisoning cases throughout the region during that same period. In addition, acids from the vinegar used in preserving seemed to accelerate the process. Landrum’s pottery would spread throughout the entire southern tier of states to Texas during the late 1800s, saving countless agonizing deaths in the region (Koverman 2009).

Landrum had previously attempted to bud both pecan and walnut to hickory rootstock. In an article published in *American Farmer* magazine, Landrum wrote “the pecan did not take so well as the walnut but my trials were made rather late in the season.” The following summer, he had better success, stating “I have this summer budded some dozens of pecan on the common hickory nut, without a single failure as yet;



and some of them are growing finely” (Landrum 1822). Despite his success, Landrum’s attempts at budding pecan failed to lead to any further development in the form of nursery production, orchard establishment, or cultivar development. As a result, the pecan was still considered too unpredictable and nonuniform in its production to be of any commercial value beyond those nuts gathered from the wild and sold or traded.

When sugarcane planter, Jacques Telesphore Roman, the owner of Oak Alley Plantation, died in 1848 of tuberculosis, an inventory of his estate was conducted. This inventory provides the only written record of a man named Antoine, who, in the distasteful context of that time, was considered a part of the inventory of Roman’s estate. Roman had acquired the 9000 acre sugarcane plantation in 1836 and promptly built the main house between 1837 and 1839. The plantation later acquired the name Oak Alley, referencing the 28 massive live oak trees lining the entrance to the main house. A hospital, an overseer’s house, a 100-stall horse stable, a sugarhouse, and sawmill were also built. Aside from these outbuildings and the opulence of the main house, the plantation was home to 24 simple, wood-frame cabins, which housed the 113 people enslaved by Roman to serve him and his family in the home and in the fields. Antoine was listed among the 93 field slaves at Oak Alley. The 1848 ledger records Antoine’s age at 38 years, which suggests he was born in 1810. The notation beside his name states that Antoine was “a Creole Negro gardener and expert grafter of pecan trees.” According to Roman’s ledger, this man’s life was valued at \$1000 (Anonymous 2010) (Figure 1.1).

## II. WORK AND RECOGNITION OF ‘CENTENNIAL’ PECAN

In the early 1840s, a pecan tree growing on the Nita Plantation on the east bank of the Mississippi River, just around a bend and upstream from Oak Alley Plantation, consistently produced large, thin-shelled pecans that were favored by a local dentist, Dr. A.C. Colomb, who attempted to graft cuttings from the tree onto other pecan trees. Failing in this endeavor, Colomb collected graftwood cuttings from the tree and gave them to J.T. Roman so that Roman’s gardener, Antoine, could graft the wood onto trees across the river at Oak Alley Plantation (Flack 1970).

Antoine began grafting Colomb’s cuttings onto trees near the main house of Oak Alley. Initially, he was successful in grafting 16 trees. Although the exact grafting method used by Antoine is unknown (most likely some form of bark graft), he would continue this work until 110



**Fig. 1.1.** Main house, Oak Alley Plantation. *Source:* Photograph courtesy of Oak Alley Plantation.

pecan trees were successfully grafted in a large pasture near the river on Oak Alley Plantation. All 126 trees were bearing pecans by the end of the Civil War. Following the war, Oak Alley went through a succession of owners, who cut down most of these trees to plant sugarcane. By 1902, only two of the original trees grafted by Antoine were still alive (Flack 1970).

In 1876, the famed Centennial Exhibition was held in Philadelphia. This was the first official World's Fair held in the United States, and such novel items as Alexander Graham Bell's telephone, the Remington typewriter, Heinz ketchup, and the Wallace–Farmer electric dynamo, a precursor to electric lighting, were displayed alongside the torch of the as-yet-to-be completed Statue of Liberty. One of Oak Alley's prior owners, Hubert Bonzano, happened to serve on the Centennial Exposition's board of managers. Bonzano, a proud resident of Louisiana, began to encourage the state to submit everything of interest that it had to offer for display at the exhibition (Kilcer, personal communication). Bonzano's boosterism resulted in the submission of a few pecans



**Fig. 1.2.** ‘Centennial’ pecan, the first recognized improved pecan cultivar. *Source:* USDA Yearbook of Agriculture (1904).

gathered from the remaining pecan trees grafted by Antoine. Professor William Brewer, chair of Agriculture at Yale’s Sheffield Scientific School, awarded Bonzano a certificate for the pecans, commending their “remarkably large size, tenderness of shell and very specific excellence” (Taylor 1905). While this was a triumph for Bonzano and generated recognition of the pecan, it is a shame that the man known only as Antoine received no recognition for his invaluable contribution.

Antoine’s grafted trees were given the name ‘Centennial’ in honor of the exhibition and the 100th anniversary of the United States, becoming the first recognized pecan cultivar to be named. The tree was first catalogued under this name in 1885 by Richard Frotscher and William Nelson and was sold through their nursery in New Orleans (Flack 1970) (Figures 1.2 and 1.3).

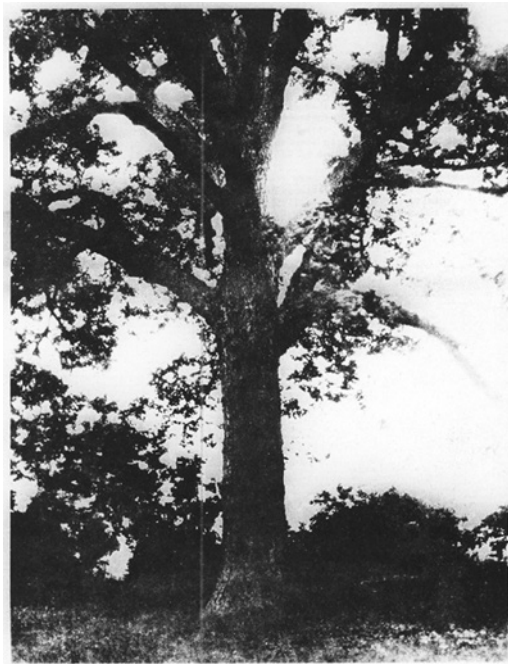
The original “mother” ‘Centennial’ tree, from which the graftwood used by Antoine was taken in the 1840s, was destroyed on March 14, 1890. The Nita Crevasse, a 15 ft deep gouge into the earth formed when a defective rice flume was used for routing water from the river to the rice fields, caused a breach in the levee. As the water flooded in, the tree was swept away with the earth beneath it (Taylor 1905) (Figure 1.4).

### III. SIGNIFICANCE

While ‘Centennial’ is no longer a commercially planted cultivar, it remains significant for the advancements made through its development as the first recognized pecan cultivar. Antoine’s successful grafting techniques brought the potential for uniformity to the industry. Pecan growers and nurserymen were shown the possibilities that exist in selecting and asexually propagating the best seedling trees.



**Fig. 1.3.** 'Centennial' pecan nuts. *Source:* Photograph by USDA ARS-Pecan Breeding and Genetics.



**Fig. 1.4.** One of the last remaining 'Centennial' pecan trees. *Source:* Oak Alley Plantation in 1941.

Prior to Antoine's success, pecan production was highly sporadic, and the variability between the nuts produced from one tree and the next, too great to entice any interest in commercial production. The term "seedling" often refers to a young tree, but to those familiar with pecans, a "seedling" refers to a non-improved tree grown from a nut. Although many cultivars such as 'Centennial' have arisen as chance seedlings, most seedlings are, in a sense, wild pecans arising from open pollination. As such, most of the pecans produced from an individual tree will grow into trees that produce pecans that bear little resemblance to their parents and siblings. As a result, pecans are found in a diversity of size, shape, shell thickness, and quality of kernel. The tree itself may also vary considerably from its relatives in its habit of growth, foliage density, leaf shape, time of budbreak, etc.

Most cultivated plants grown today are improved forms, which owe their continued existence to propagation by humans. In the case of pecan, selected individual trees are asexually propagated through grafting or budding, which allows shoots or buds (termed scions or graftwood) from a tree with desirable characteristics to be transferred or attached to an established tree called the rootstock. This allowed for the production of trees with reliably predictable characteristics, which could bring about consistency in production and uniform nut quality, both of which are requirements for successful commercialization of a potential horticultural crop.

Delayed in part by the Civil War, Antoine's breakthrough was later adopted by nurserymen such as Emil Borgeois, A.G. Delmas, Charles Pabst, and E.E. Riesen in Louisiana, Mississippi, and Texas, who further adapted these techniques on a commercial scale. This advance led to a profusion of new seedling selections, which would be developed into cultivars such as 'Alley', 'Van Deman', 'Pabst', 'Stuart', 'Schley', and 'Western Schley', which became the foundational cultivars of the early commercial pecan industry in the United States.

There remain various forms of grafting and budding in use today to produce the trees that are planted into all commercial pecan orchards. While we don't know the exact form of grafting used by Antoine, nor where he learned this skill, the same basic concept of joining scion to rootstock is still used today to produce the improved cultivars grown by commercial pecan producers throughout the world.

Scientific advancements in any field are often the result of hard work by well-trained scientists whose productive lives and academic careers are well documented. Occasionally, advancements are made in a given field by those without the advantage of formal education or training, and about whom there is little documentation, but whose intellect and skill contribute greatly to the advancement of that field.

Antoine used his natural gifts along with the knowledge gained through hard-won experience to contribute to horticultural science in a manner few people can claim. The sole written record regarding this man from his own time exists only because he was deemed to have a certain value as the property of another man. This record describes him so very briefly in unflattering terms – “a Creole negro gardener and expert grafter of pecan trees.” Yet, Antoine was so much more than that. He was a human being with his own intrinsic value. Of how many contributions has the world been robbed through the mistreatment of others, through violence and oppression? How many others are out there who have made similar contributions, yet go unrecognized? Antoine was one of the major pioneers of early American agriculture and the commercial pecan industry. He was a horticulturist and indeed, a teacher.

Antoine’s success ultimately led to the propagation of more than 1,000 different pecan cultivars, which today are planted commercially on every continent except Antarctica. This is his legacy. America’s record of slavery cannot be forgotten. We should recognize that within this tragedy, there exist countless legacies, such as that of Antoine, which have been lost or obscured by the lens of history.

## LITERATURE CITED

- Anonymous. 2010. *Slavery at Oak Alley Plantation*. <http://www.oakalley-plantation.com/SlaveryResearchDatabase> (accessed June 14, 2010).
- Bryant, W.S. 2004. Botanical explorations of Andre Michaux in Kentucky: observations of vegetation in the 1790s. *Castanea* 2:211–216.
- Flack, J.R. 1970. *The spread and domestication of the pecan in the U.S.* Ph.D. dissertation, University of Wisconsin, Madison.
- Koverman, J.B. 2009. Clay connections: a thousand mile journey from South Carolina to Texas. American Material Culture and The Texas Experience: The David B. Warren Symposium. Bayou Bend Collection and Gardens at the Museum of Fine Arts, Houston, Texas. [http://scholarcommons.sc.edu/cgi/viewcontent.cgi?article=1022&context=mks\\_staffpub](http://scholarcommons.sc.edu/cgi/viewcontent.cgi?article=1022&context=mks_staffpub).
- Landrum, A. 1822. Letter to the editor, *Am. Farmer* 4:7.
- Taylor, W.A. 1905. Promising new fruits. p. 399–416. In *Yearbook of The Department of Agriculture*. United States Department of Agriculture, Washington, DC.
- United States Department of Agriculture. 1904. Washington. Government Printing Office, 1905.
- Wells, L. 2017. *Pecan: America’s native nut tree*. The University of Alabama Press, Tuscaloosa.

## Hazelnut Breeding

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### ABSTRACT

Hazelnut (*Corylus* spp.), also known as filbert, is an important temperate nut that has been used as a food crop since ancient times. There is a tremendous amount of genetic diversity in *Corylus* and more than 500 *Corylus avellana* cultivars have been described in the literature. World production is based on fewer than 20 ancient *C. avellana* cultivars that originated with the selection and clonal propagation of superior plants primarily in the Mediterranean Basin and along the Black Sea coast. Large nuts are sold in-shell, while the majority of the world's hazelnuts are sold as kernels for use by the confectionary industry. In Turkey, the most important producing country, nut clusters are picked from the tree by hand, often in orchards on very steep terrain. The husks of Turkish cultivars are long and clasping and retain the clusters on the tree for harvest. In other countries, nuts are mechanically harvested from the ground, and nuts that fall free of the husk at maturity are desired. As newer production systems are adopted, including high-density orchards of compact trees, appropriate cultivars, management practices, and machinery will be needed. Because of high demand for kernels, new orchards are being planted in many countries, including areas where the climate is less than ideal for the species. Interspecific hybridization offers an opportunity to expand production to new areas. Hazelnut has many arthropod pests, of which big bud mite (primarily *Phytoptus avellanae*) is a serious one. Many diseases affect hazelnut, of which eastern filbert blight (EFB) caused by the fungus *Anisogramma anomala* is the most severe threat in North America. Genetic resistance to big bud mite and EFB has been identified and incorporated into

new cultivars. Early genetic improvement efforts were largely by nurseries and growers. Over the past 60 years, 11 breeding programs have been active in different countries, but today there are only two relatively large programs, both in the USA. Standard methods to breed hazelnuts have been very effective although it takes 17 years from the time a controlled cross is made until a new cultivar is released. Biotechnology has added tools and knowledge to genetic improvement efforts. Thousands of DNA markers have been developed and scored, linkage maps have been constructed, and our knowledge of genetic diversity and the control of traits in *Corylus* have improved. To date, however, the use of marker-assisted selection has been limited to EFB resistance from 'Gasaway'. Genome sequences have been assembled into chromosome-length scaffolds and genes have been annotated, allowing efficient marker development for genetic studies and marker-aided breeding. The use of genome editing is limited by an inability to regenerate whole plants from single cells. The huge amount of genetic variability in *C. avellana* and other species can be exploited to develop improved cultivars with wider adaptation. Worldwide demand for hazelnuts continues to increase. With the proven effectiveness of traditional plant breeding approaches, the diverse genetic resources that have been collected and preserved, and the considerable promise of modern genetic and genomic tools, the future looks very bright for further genetic improvement of hazelnut.

**KEYWORDS:** *Corylus*, *Corylus avellana*, hazelnut, filbert, kernel, tree nut, pollinizer, incompatibility, climatic adaptation, genetic resources, floral biology

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## ABBREVIATIONS

ApMV	apple mosaic virus
BAC	bacterial artificial chromosome
BLAST	Basic Local Alignment Search Tool
cpSSR	chloroplast simple sequence repeat
ddRAD-seq	double digest restriction-site associated DNA sequencing
EFB	eastern filbert blight
ELISA	enzyme-linked immunosorbent assay
FAO	Food and Agriculture Organization of the United Nations
GBS	genotyping-by-sequencing
Hi-C	a chromosome conformation capture technique
HRI	Hazelnut Research Institute (Turkey)
HRM	high-resolution melting
INRA	Institut National de la Recherche Agronomique (France)
IRTA	Institut de Recerca i Tecnologia Agroalimentàries (Spain)
ISSR	inter-simple sequence repeat
LG	linkage group
MAS	marker-assisted selection
NCBI	National Center for Biotechnology Information
NCGR	National Clonal Germplasm Repository (USA)
Nr	non-redundant
NYSAES	New York State Agricultural Experiment Station (part of Cornell University)
OSU	Oregon State University
PacBio	Pacific Biosciences
QTL	quantitative trait locus

RAPD	random amplified polymorphic DNA
SAG	Servicio Agrícola y Ganadero (Chile)
SCDP	Statiunea de Cercetare-Dezvoltare pentru Pomicultura (Romania)
SNP	single nucleotide polymorphism
SSR	simple sequence repeat
TCA	trunk cross-sectional area
UMHDI	Upper Midwest Hazelnut Development Initiative
UNITO	University of Torino (Italy)
UPOV	International Union for the Protection of New Varieties of Plants
USA	United States of America
USDA-ARS	United States Department of Agriculture – Agricultural Research Service
USPTO	United States Patent and Trademark Office
USSR	Union of Soviet Socialist Republics

## I. INTRODUCTION

Hazelnut (*Corylus* spp.), also known as filbert, is an important nut that has been used as a food crop since ancient times. The kernels of all *Corylus* species are edible. The use of hazelnut as a food by humans spans the geographic range of the genus in the northern hemisphere and dates back at least 8,400 BCE in western and central Europe, North America, and China (Holstein et al. 2018). In Europe, Turkey, and the Caucasus region, nuts were harvested from wild *C. avellana* (European hazelnut). Superior plants were selected and clonally propagated from the basal shoots also known as suckers. These activities gave rise to the cultivars grown today in the Mediterranean Basin and the Black Sea coast of Turkey and Georgia. In North America, native peoples collected hazelnuts from stands of *C. americana*, *C. cornuta*, and *C. californica*. In northeast China, humans continue to harvest large quantities of hazelnuts from wild stands of *C. heterophylla*.

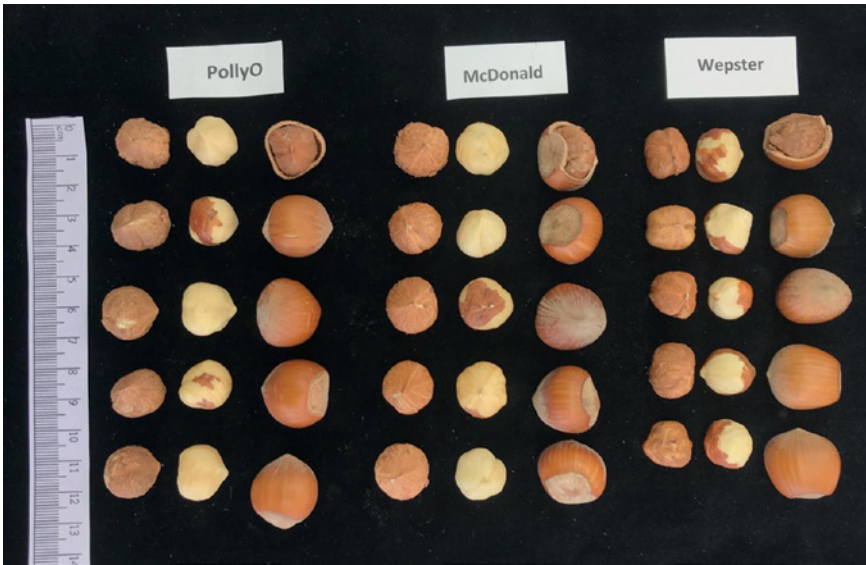
The world's most important cultivars were selected directly from the wide-ranging species *C. avellana*. World production remains based on these ancient *C. avellana* cultivars, with the exception of releases from breeding programs in the USA and France and the Ping'ou (*C. heterophylla* × *C. avellana*) interspecific hybrids being planted in northeastern China. Hazelnut kernels are in high demand by the confectionary industry, and new orchards are being planted in many countries. Wild species provide useful traits for breeding.

After the selection of superior plants from the wild vegetation, further improvements were made by nurseries, farmers, and gardeners who selected superior plants within seedling populations, as described in the history section. Long-term breeding programs were begun in the 1960s by universities and government agencies to improve yield and nut quality, climatic adaptation, and resistance to diseases. The objective of this chapter is to present information on the genetic resources available within the genus *Corylus*, some historical context on its genetic improvement, and the major breeding objectives and procedures used including applications of biotechnology.

## II. ECONOMIC IMPORTANCE, PRODUCING COUNTRIES, AND MARKETS

According to the Food and Agriculture Organization of the United Nations (FAO), hazelnut ranks fifth among the world's tree nut species for surface area harvested (about 672,000 ha in 2017), following cashew, walnut, almond, and pistachio. The average annual production of dried, in-shell hazelnuts in the world (2013–2018) is about 843,000 T, the majority of which are from only two countries, Turkey and Italy. Turkey produces about 65% of the world's hazelnuts, followed by Italy at 12%, and then the USA, Azerbaijan, and the Republic of Georgia at about 4% each. There are many new plantings in these countries as well as in Chile, Spain, France, Serbia, Ukraine, Russia, and Iran. In northern China, nuts continue to be harvested from wild stands of *C. heterophylla*, while new orchards are being planted to Ping'ou hybrid (*C. heterophylla* × *C. avellana*) cultivars (Wang et al. 2018).

Hazelnuts are sold on two markets, kernel and in-shell, and the cultivars suited to each are different. The kernel market currently represents about 93% of the world crop, with most being used by the confectionary industry. Kernels are roasted and used to produce foods such as candies, baked goods, creams (nut butters), and other snacks. In response to the strong demand for kernels by the confectionary and baked-goods industry, the surface area and tonnage harvested have shown a trend of continuous growth from 1961 to 2017 (FAO 2020). This trend appears likely to continue in the coming years. The remaining 7% of the crop is sold in-shell for home cracking and consumption, including a very small percentage harvested from the tree and sold fresh in their green husks. 'Wepster', 'McDonald', and 'PollyO' are well suited to the kernel market (Figure 2.1). 'Barcelona' and 'Jefferson' are well suited to the in-shell market (Figure 2.2).



**Fig. 2.1.** Raw kernels, blanched kernels, and nuts of ‘PollyO’, ‘McDonald’ and ‘Wepster’ hazelnuts. All three have small- to medium-sized round kernels and the pellicle is easily removed with dry heat in the blanching process. They are well suited to the kernel market (see “Economic Importance, Producing Countries and Markets”).  
 Source: Rebecca L. McCluskey.

### III. TAXONOMY OF THE GENUS *CORYLUS*

The genus *Corylus* belongs to the order Fagales, family Betulaceae, and subfamily Coryloideae. Other families in the order Fagales include Juglandaceae (e.g., *Juglans* L. [walnut], *Carya* Nutt. [pecan and hickory]) and Fagaceae (e.g., *Fagus* L. [beech], *Castanea* Mill. [chestnut] and *Quercus* L. [oak]). The number of *Corylus* species ranges from 9 to 25, depending on the taxonomic authority. Recent revisions based on morphology supplemented by hybridization and molecular studies support 13 major species assigned to 4 subsections (Table 2.1). Molnar (2011) compiled detailed descriptions from the taxonomic literature. All *Corylus* species are native to the temperate zones of the northern hemisphere.

Photos present representatives of 12 *Corylus* species growing in Corvallis (Figures 2.3–2.8, 2.10–2.19, 2.21, 2.22a) and *C. sutchuenensis* (Franch.) Nakai (syn. *C. kweichowensis* Hu, *C. heterophylla* var. *sutchuenensis* Franch.) in Anhui province of China (Figures 2.9 and 2.20).



**Fig. 2.2.** Nuts, raw kernels, and blanched kernels of ‘Barcelona’ (top) and ‘Jefferson’ (bottom). Both cultivars have large nuts and are well suited to the in-shell market (see “Economic Importance, Producing Countries and Markets”). *Source:* Rebecca L. McCluskey.

Geographically, three species occur in North America (*C. americana* Marshall, *C. cornuta* Marshall, and *C. californica* Marshall), two in Europe and Asia Minor (*C. avellana* L. and *C. colurna* L.), one in the Himalayas (*C. jacquemontii* Decaisne), and the remaining seven in eastern Asia (*C. chinensis* Franchet, *C. fargesii* [Franch.] C.K. Schneid., *C. ferox* Wallich, *C. heterophylla* Fisher, *C. sutchuenensis* [Franch.] Nakai, *C. yunnanensis* A. Camus and *C. sieboldiana* Blume) (Whitcher and Wen 2001). Nine of them are shrubs that continuously produce shoots (suckers) from the crown of the plant, and four are tree species with a single stem (Table 2.1). Subsection *Corylus* includes five species (*C. avellana*, *C. americana*, *C. heterophylla*, *C. sutchuenensis*, and *C. yunnanensis*) whose major similarity is the leafy involucre (husk) that covers the nut. Photos of the three Chinese leafy-husked species are presented by Zhao et al. (2020). Subsection *Siphonochlamys* includes three species with tubular, bristle-covered involucre (*C. cornuta*, *C. californica*, and