Rootstock Development in Temperate Nut Crops

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Abstract

The driving force behind the development of rootstocks for nut crops has been the solution of specific problems, often related to the presence of pests or the need for adaptation to particular sites. The use of interspecific hybrids as rootstocks has lead to increased appreciation for the contribution genetic diversity can make to orchard profitability in the face of site specific challenges. The past decade has seen dramatic increases in access to germplasm resources, while technological developments in molecular genetics have contributed to genetic characterization in some species. The focus on clonal propagation through tissue culture has been somewhat abated by the slow pace of nursery incorporation of available techniques, by challenges with anchorage of some clonal rootstocks, and by the recognition of the vulnerability inherent to a monoculture susceptible to an unsuspected root pest. Increased application of spatial analysis systems (GIS) may contribute to prescription use of site-specific rootstocks.

INTRODUCTION

Nut crops are relatively long-lived species whose performance reveals the integration over time of the plant’s genetic composition (both of the scion and the rootstock in grafted plants) with the effects of the site (composed of edaphic, climatic and other biotic variables), under the cultural system used for management. The development of improved rootstocks for nut crops requires an understanding, appreciation, and control of all of those potential sources of variation.

Rootstock influences are more obscure than scion effects. Systematic rootstock development through breeding requires the same commitment of time and resources needed for scion breeding while the demonstration of rootstock efficacy requires additional care in test establishment and long-term monitoring. Furthermore, various site-specific challenges within otherwise homogenous regions of cultivar adaptation introduce additional complexity while possibly limiting broad deployment. As a result there are few programs focused specifically on rootstock breeding for nut crops.

The historic pattern of rootstock development across nut crops has been one of dynamic interaction between a knowledgeable grower community comprised of nurserymen, traditional farmers (using local materials in seedling culture) and orchardists (using selected genetic materials in grafted configurations under intensive management), an active plant introduction program, and an observant scientific community, all riding a mounting wave of developing technology. In recent decades, the ingredients of that mix have been richly supplemented: the nursery industry has incorporated new techniques of propagation with an abundance of ever “improved” cultivars and rootstocks; traditional farmers have been the focus of unusual and increasingly complimentary attention; orchardists have had the expert consultation of multidisciplinary teams, organized by the wonders of computer technology to address management goals; the plant introduction program has provided increased access to international germplasm; and the scientific community has added the tools of molecular genetic characterization and spatial analysis to its arsenal. There is potential for great improvement in rootstock development for most nut crops. At the beginning of the 21st century we find ourselves with powerful tools to map new territory.
Possibly the greatest potential is associated with the development of molecular genetic techniques of characterization with which to map the crop genome. These tools are being used to characterize species, differentiate seedlings arising in different regions, as well as to fingerprint individual cultivars. The goal of many programs is the ultimate development of marker-aided selection. Observations made on one group of plants are being found pertinent to crop relatives, creating new opportunities for cooperative research by previously isolated researchers, and developing links of understanding and appreciation between the traditional farmers (whose materials are the focus of population genetic studies) and orchardists (who have had forensic verification of their materials and want ever improved cultivars).

The availability of global positioning systems (GPS) for mapping and integration into geographic information systems (GIS) holds great promise for agriculture in general and orchard management in particular. By integrating data from long-term orchard performance research into systems of spatial analysis, the precision of site evaluation and problem diagnosis should be facilitated. Coupled with molecular genetic analysis of local populations, techniques of spatial analysis will contribute to our understanding of population genetics and crop adaptations to their sites. Although valuable data is accumulated in soil, water, plant, and disease analysis labs of all land grant colleges, there are few programs recording those data in GIS. In our efforts to understand the distribution of cotton root rot, caused by *Phymatotrichum omnivorum* (Nesbitt et al., 1992), we found no institutional memory of the samples submitted over time, and may have faced limitations to access even if the data existed. Is the diagnosis of a devastating, long-lived, soil borne disease on one’s property public information or is it as private as a personal medical report? Will it be possible to map the distribution of nematodes? *Meloidogyne* *partityla* Kleynhans was first described in South Africa (Kleynhans, 1986) but was introduced on pecans from the U.S and is now increasingly being found as the dominant nematode on pecan (Starr et al., 1996). Will accurate maps of soil variation, coupled with accurate maps of associated organisms (including plants, fungi and nematodes) allow us to navigate our orchards better?

Excellent reviews of the extent and origin of genetic diversity for many nut crops have been published (Moore and Ballington, 1991; Duke, 2001), and a review of breeding objectives and methods for nut crops has also been recently provided (Janick and Moore, 1996). Rosenganter (1984) provides additional interesting ethnobotanical information for some nut crops. Detailed review of rootstock development for some nut crops was provided by Rom and Carlson (1987) which, in many cases still serves as an invaluable foundation. A brief description of plant biology and origin will be given here merely to establish the context of rootstock development. The purpose of this paper will be to explore recent advances in the development of rootstocks for the major temperate nut crops in the hope that the challenges being successfully addressed in some might guide efforts in others, while egregious mistakes might be avoided.

**ALMOND* Prunus dulcis* [Miller] D.A. Webb, Rosaceae**

**Plant Biology**

The almond is a deciduous tree of the arid temperate zone. It grows to a height of 25–30' and has 1–1.5" white to pink solitary flowers that develop with or before the early foliage. The flowers of most almond cultivars are self-incompatible, although there is selection for self-compatibility, especially in Europe. Honeybees typically transfer the heavy pollen. The flower has a single pistil with two ovules. If both develop, an undesirable “double kernel” is produced. The fruit is a compressed, pubescent, oblong-ovoid drupe that splits at maturity to reveal the shallow pitted stone containing the seed (the edible kernel) (Kester, 1979).

Almonds are a concentrated source of energy, being relatively high in fat (~54%). The fatty acid in highest concentration is oleic acid (70–78%). Kernels are also relatively high in protein (~18%) (Adams, 1975). Seedlings vary in kernel quality, with some
producing bitter kernels due to high levels of the glucoside amygdalin. Amygdalin is hydrolyzed by the enzyme emulsin to form benzaldehyde and cyanide, which cause the bitter taste. Substrate and enzyme are both present in the seed and are united when cells are injured, as occurs during consumption. The trait has adaptive value as a protection against predation, and has been employed and maintained in traditional cropping systems by the use of bitter almond seedstocks (Kester and Gradziel, 1996).

History
Almonds originated in Asia and moved with the migrations of peoples, which were often caused by the upheavals of famine and warfare. In Genesis 43:11, the Hebrew patriarch Jacob (Israel) instructed his sons to carry almonds and pistachio nuts from their home in Canaan to Egypt when the family had to relocate during a period of extreme famine (ca. 1900 BCE). Archeological records corroborate extensive ancient use (Renfrew, 1973). The almond may have been introduced into Greece during the conquests of Alexander the Great (ca. 320 BCE) (Kester et al., 1991). From Greece, almonds spread into Italy and the Mediterranean region, a movement that can be traced in the etymology of the English word. “Almond” is derived from the French “amande,” from the Latin “amygdala,” which came from the Greek.

The Arab conquest of North Africa in the 6th and 7th centuries started another wave of almond introductions. The Moors took almonds with them when they conquered southern Spain. Almonds were then taken from Spain to California during the Spanish Mission Period (1800). The warm, dry climate of California, coupled with intensive agricultural systems, led to the preeminence of California in world almond production. Almonds are currently grown in regions characterized by a subtropical Mediterranean climate. Primary production centers are the central valleys of California, the Mediterranean region, and Central to Southwestern Asia (Kester et al., 1991).

Culture
In California, culture is intensive. Cultivars are selected for high production of soft-shelled kernels. Grafted trees of improved cultivars are propagated on rootstocks selected for the constraints of particular sites. Trees are planted in irrigated orchard configurations with densities of up to 331/ha. Two rows of the main cultivar to one row of a pollinizer are planted and hives of bees are maintained to aid pollination. Trees are heavily fertilized and protected with chemical pesticides, and yields of over 3,360 kg kernels/ha are achieved. Harvest operations are heavily mechanized, with specialized machines to shake nuts from the tree and others to collect them from the orchard floor.

In the Mediterranean region of production, culture is generally traditional, and many orchards are comprised of selected seedlings rather than grafted trees. Furthermore, most classes and cultivars are hard- or semi-hard-shelled. Orchards contain fewer trees than in California, with only 124–173 trees/ha being typical. Selection has occurred within particular regions that have become identifiable for the class of almonds produced, despite heterogeneity. For instance, the Spanish island Majorca is known for the Farmer Majorca class, composed of a multitude of related seedling trees. Recent selection has been for late-blooming cultivars that avoid frost damage, for self-compatibility, and for adaptation to the environmental stresses that are not as completely controlled as in California. Standardization accompanying globalization puts pressure on diversity. Increased uniformity allows increased mechanization, and may contribute to marketability and even profitability, but at the cost of genetic diversity. Small areas in the Mediterranean once comprised distinct landraces of selected almond seedlings. The diversity of those local populations is being reduced as grafted culture increases. Maintenance of ex situ germplasm collections cannot substitute for the continued selection of desirable seedlings by multiple local growers.

Rootstock Research
Rootstock selection criteria vary between traditional and intensive culture. In any
cultural system, the choices are primarily between almond seedling rootstocks (for dry, calcareous sites), peach seedling rootstocks (for acidic, irrigated sites), peach-almond hybrids (vigorous growth on calcareous, dry sites), and Marianna plums (for use on heavy soils). In traditional cultural systems, there is the perception that transplantation reduces survival and performance due to alteration of root morphology (Kester and Gradziel, 1996). Rootstocks are typically seedling almond, which has increased drought tolerance, and particular cultivars are used since their open-pollinated seed have been shown to be superior for certain regions. These include ‘Mission’ in the US, ‘Atocha’, ‘Garrigues’ and ‘Desmayo Roj’ in Spain, and ‘Chellaston’ in Australia (Kester and Grasselly, 1987).

In more intensive agricultural systems, other rootstocks can contribute necessary attributes: peach seedling rootstocks such as ‘Nemaguard’ have resistance to nematodes and may have an advantage on well-drained, acidic, irrigated sites. Peach-almond hybrids combine the characteristics of both parent species with exceptional vigor. 'Marianna' plums are used specifically on heavy textured soils that might have drainage problems. The beneficial role of mycorrhizal inoculation on tree performance has been established by research in Spain (Estaun et al., 1999), with implications for nursery management practices such as choice of inoculum and fungicide (Fontanet et al., 1998).

Molecular genetic techniques using microsatellite markers have been developed for peach that are effective for almond, extending the development of marker-aided selection broadly in Prunus (Dirlewanger et al., 2003; Testolin, 2003). Other molecular genetic techniques, such as RAPDs are illuminating the species composition of interspecific hybrids of plum used in crosses for almond rootstocks (Boonprakob and Byrne, 2003).

CHESTNUT Castanea spp., Fagaceae

Plant Biology

Chestnuts are deciduous trees with simple, alternate leaves that have serrate to dentate margins. They are monoecious, with separate male and female flowers on the same tree. Male flowers are borne as unisexual catkins at the terminal end of shoots and as bisexual catkins on the lower shoots. Female flowers appear singly or in clusters of two or three at the base of the bisexual catkins and become the nut-bearing burrs. Male flowers tend to shed pollen prior to female receptivity, creating a tendency to cross-pollination. Pollen is primarily wind disseminated. The fruit is a spiny burr that dehisces into four valves at maturity to reveal three nuts. Chestnuts are rich reddish brown with a conspicuous pale oval scar at the base. The shell is relatively thin and is not as protective as the burr. When the shell is removed, a hairy pellicle (seed coat) covers the embryo and two irregular cotyledons. Chestnuts have the highest water content, the lowest fat content, and the highest carbohydrate (starch) content of any nut crop (Adams, 1975). If chestnuts dry after harvesting, some of the starch converts to sugar and viability of the seed is lost. As a result, post-harvest handling dramatically affects both the edible quality of the product as well as its viability for seed. In addition to the nuts, chestnuts produce very valuable, insect resistant wood.

Three species account for the majority of world production: the Chinese chestnut (Castanea mollissima Bl.), the European chestnut (C. sativa Mill.), and the Japanese chestnut (C. crenata Sieb & Zucc.). All species have a somatic chromosome number of $2n=24$ and hybridize freely.

History

Seven species of Castanea are found around the world in the temperate zone, and each has a long history of utilization. The Japanese chestnut is native to the Japanese islands and Korea and has been cultivated for over 2,000 years, with some cultivars being maintained since 750 CE. The species is considered the most domesticated, with the largest fruit, the most precocious seedlings, and the smallest mature tree size. Unfortunately, some of them produce nuts that are not very palatable until they have been cooked.

Most chestnuts consumed in Europe and the United States are derived from the
European chestnut, which has been cultivated in southern Europe and Asia Minor since the Roman Empire. Increasingly, hybrids between the European and Japanese chestnuts are grown commercially because the latter species is resistant to ink disease.

American chestnuts \([C.\ dentata\ (Marsh.)\ Borkh.]\) were a dominant tree in the eastern forests of North America until ink disease \((Phytophthora\ cinnamomi)\) eliminated them from the Gulf states in the early 1800s, and chestnut blight disease \([Cryphonectria\ parasitica\ (Murr.)\ Barr]\) came into the United States in the late 1800s (Anagnostakis, 2001). Ink disease probably came in on cork oak trees from Portugal, which were planted in the south before 1823. Blight disease was introduced in the 1880s, with Japanese chestnut planting stock. It was spread up and down the eastern seaboard with nursery stock, and then moved into the forest by other vectors, until by 1950 almost all large chestnut trees were infected. Ink disease is considered the most significant challenge to chestnut culture in Europe, and also causes serious losses in China, Japan, Turkey and the US, especially on heavy, wet soils. Ink disease is lethal to chestnuts, but the blight fungus does not kill roots, so trees continue to sprout, are reinfected, and die back. There is good evidence that, in the southern United States, heavy shading, competition, grazing, and continued infections often kill the trees completely, but this is not the case in northern forests, where canopy type, competition, and predation are quite different (Anagnostakis, 2001).

In addition to the two diseases, chestnuts in the United States are also threatened by the Oriental Chestnut Gall Wasp \((Dryocosmus\ kuriphilus)\), another introduced pest that has become established and is damaging native chestnut species. The gall wasp is believed to have been introduced from Asia into Georgia in 1974 on scion wood that did not pass through proper quarantine. It infested orchards of Chinese chestnuts in Georgia, and has also been found in wild trees of the American chestnut along the Appalachian Trail (Anagnostakis, 2001).

Culture
Chestnuts need well-drained, slightly acidic \((pH\ 5.5–6.5)\) soils for optimum performance, and have little tolerance for alkaline soils. They seem to be particularly well adapted to mountainous regions. Trees are quite precocious, and some species may produce flowers within months of seed germination (Rutter et al., 1991). Grafted orchards are managed in China, Japan and Europe, but graft failure has promoted seedling culture in the US, with associated problems of crop uniformity and quality.

China produces most of the world’s chestnuts. They are exported in large numbers from Italy, Spain, Australia, China, and Korea. Japan and the United States are primarily importers, although these markets are partially satisfied by locally grown chestnuts. New cultivars are being registered at an increasing rate, and interest in the crop is increasing.

Rootstock Development
Japanese chestnuts may be a source of resistance to \(Phytophthora\) (Rutter et al., 1991, Miller et al., 1996). The major limitation to the commercial development of chestnut production in the US is graft incompatibility. Current recommendations call for using seedling rootstocks of the cultivar intended for use as scion. This severely limits the evaluation and incorporation of new cultivars. Greg Miller (pers. commun.) notes that chestnut has ring-porous wood in which the spring wood has very large vessels that are long, with high conductance. Part of the graft compatibility challenge may be mechanical. Furthermore, the major diseases of chestnuts all relate to xylem conductance, an area of apparent vulnerability in the plant.

Molecular genetic techniques are used for characterization of the genetic diversity of the species as well as for characterization of the pathogens plaguing them. Dane et al. (1999) used RAPDs to characterize diversity of chinquapins, contributing to information necessary for the establishment of regional in situ repositories. Botta et al. (2002) developed microsatellite markers for use in characterizing diversity of both wild and cultivated \(Castanea\ sativa\) populations in France, Italy and Greece. The highest levels of
diversity were found in wild populations that were most distant from each other, giving tacit support to the strategy of using locally collected materials as rootstocks on the basis of greater site adaptation. The identification of pollen sterility in cultivated materials increases the need to characterize and conserve local wild populations.

The chestnut exemplifies both the dangers and benefits of globalization. The devastation of the North American forest by introduced diseases and insects argues in favor of the careful regulation of genetic materials moving between countries. Breeding programs are succeeding in developing resistance to these pests by the use of interspecific hybrids that were created using introduced germplasm, illustrating the value of carefully sharing genetic resources.

HAZELNUT *Corylus avellana* L., Betulaceae

**Plant Biology**

Hazelnuts, also known as filberts, are produced on small, shrubby, often multitrunked trees that usually grow to heights of fifteen to twenty-four feet. They have simple, alternate, round-oval leaves with toothed margins. Hazelnuts are monoecious, with both male and female flowers on the same plant, but they are not self-fruitful. Flowers appear before the leaves. Male flowers are borne in catkins at nodes on one-year-old wood, and their wind-disseminated pollen is shed in midwinter. Female flowers are inconspicuous clusters of tiny flowers enclosed within bud scales, visible at the time of pollination as bright red stigmas extending from buds. Fruit matures from early September to October, with the ovoid or oblong nut inside a leafy husk. There is wide diversity in fruit and husk shape, and that diversity is reflected in the common names: “hazel” is from the Old English word for hood or bonnet (“hæsel”), which referred to a nut whose husk was shorter than the nut; “filbert” may be derived from the German for “full beard,” which referred to a long husk (although the name may also be derived from St. Philbert) (Rosengarten, 1984). In some countries long nuts are called “filberts,” while shorter, round nuts are called “hazels.”

The nuts are composed of a shell that has variable amounts of pubescence, especially at the tip. Inside the shell, the kernel is encased in a more-or-less-fibrous seed coat (pellicle) that is usually removed by blanching. Kernels are high in fat (~62%), with the predominant being oleic acid. Hazelnut kernels are also high in Vitamin E, averaging 400 mg/100 g (Adams, 1975).

**History**

The European hazelnut was the first plant of the temperate deciduous forest to move into areas vacated by receding glaciers at the close of the last ice age, due primarily to its great climatic tolerance. Nuts are recovered at European archeological sites in conjunction with prehistoric human settlements, indicating a long history of food usage (Renfrew, 1973). Hazelnuts are one of Europe’s oldest cultivated plants. They have been grown for centuries in Turkey, Italy, Spain, France, Germany, and England, although different conventions have arisen for their culture in each country. Hazelnuts were introduced into North America by shipments of seed sent in 1629 to the Massachusetts Company (Rosengarten, 1984). Due to the Eastern Filbert Blight (EFB) caused by *Anisogramma anomala* [Peck] E. Muller, the culture of hazelnuts in the United States is concentrated in the coastal valleys of Oregon and Washington.

**Culture**

In Turkey, which produces 65% of the world hazelnut production (USDA, 2001), hazelnuts are cultured in traditional systems that rely on hand labor. Multitrunk seedling trees are planted in clumps of four or five bushes, often arranged irregularly on steep hillsides. Stems are progressively removed as they grow too old, allowing younger shoots to come into production. Nuts in the husk are hand harvested before the crop drops (Mehlenbacher, 1991).
Italy follows Turkey in hazelnut production, accounting for about 23% of world production. Hazelnut culture in Italy is similar to that in Turkey, using clumps of multitrunck seedling trees, but with more uniform spacing. In Spain, where about 5% of world production originates, orchards are planted in still more regular rows, with a single bush at each location rather than a clump of separate bushes as in Turkey and Italy (Mehlenbacher, 1991).

The US produces about 3% of the world hazelnut production in systems that facilitate mechanization and maximize nut size and yield. Grafted trees of selected cultivars (mostly ‘Barcelona’) are grown as single-trunk trees in evenly spaced rows, with about 200 trees per acre. Trees are sprayed with chemicals to accelerate and concentrate ripening. Nuts fall to the ground and are mechanically windrowed and harvested (Mehlenbacher, 1991).

The European hazelnut, *Corylus avellana*, hybridizes with other species of *Corylus* that occur from China to the United States and that are largely untapped resources. The genetic diversity of the European hazelnut is well established, based on diverse seedling culture in the primary production centers. The potential is excellent for continued genetic improvement of hazelnuts through selection and breeding.

**Rootstock Development**

The primary factor determining hazelnut culture in the US is Eastern Filbert Blight, which has both cultural and genetic implications for rootstock development. Historically, there have been challenges with grafting hazelnuts, which were overcome to a certain extent by Lagerstedt’s development in the early 1980s of the hot-callusing pipe (Thompson et al., 1996). In addition, Lagerstedt worked to develop non-suckering rootstocks, releasing two *C. colurna × C. avellana* hybrids, (‘Newberg’ and ‘Dundee’) (Lagerstedt, 1993). Unfortunately, they are not being propagated due to susceptibility to EFB. There is a disadvantage to propagating any scion on a rootstock that suckers, since the suckers could be sources of infection with EFB. As a result, the nursery industry has returned to practices of layerage, producing self-rooted trees. No anchorage problems have been noted. Grafting has contributed to the speed with which new cultivars can be provided to the nursery industry. The effort to combat EFB led to the identification of ‘Gazaway’ as heterozygous for the single dominant resistance gene (Mehlenbacher et al., 1991). RAPD markers are used to identify resistant progeny in the breeding program (Mehlenbacher, pers. commun.). Pollenizers resistant to EFB have been released (Mehlenbacher and Thompson, 1991), and other sources of resistance in other species have been identified (Coyne et al., 1998). Patterns of interspecific hybridization have been clarified (Erdogan and Mehlenbacher, 2000), and future crosses should incorporate known sources of resistance, as well as other sources of non-suckering habit, toward the development of improved rootstock materials.

**PECAN *Carya illinoinensis* (Wangenh.) K. Koch, Juglandaceae**

**Plant Biology**

The pecan is a deciduous, temperate tree species native to North America. It is found in well-drained alluvial soils of the Mississippi River and its tributaries from Illinois and Iowa south to the Gulf Coast of Louisiana and west to the Edwards Plateau of Texas. Isolated populations are found as far east as southwestern Ohio, as far west as Chihuahua, Mexico, and as far south as Oaxaca, Mexico. In modern times, the distribution of pecans has been extended from the Atlantic seaboard west to California, with major commercial production in the non-native states of Georgia and New Mexico (Thompson and Grauke, 1991).

Trees are long-lived (to ~300 years) and grow to heights of over 120’. Leaves are alternate, odd-pinnately compound, with nine to fifteen serrate leaflets. Trees have a long juvenile period (~6–8 years). Trees are monoecious (male and female flowers are borne on the same tree) and heterodichogamous, each clone being either protandrous or
protogynous. Thus, male and female flowers mature at different times on the same tree and the timing of flower maturity varies from tree to tree. This system encourages out-crossing with other trees of complementary bloom period. Male flowers are borne on pairs of three stalked catkins that arise from buds of the previous season. Female flowers are borne as spikes at the tip of the current season’s shoots, usually with two to four flowers per peduncle, although clusters of up to 8 are not uncommon with some cultivars. Pollen is disseminated by wind (anemophily). The fruit is a “drupelike nut,” with the dehiscent husk splitting at maturity (usually September to November) to expose the elongated, relatively thin-shelled nut. Kernels are two-lobed, separated in the shell by an internal partition or septum. Kernels are high in oil (~70%), with the predominant oil being oleic acid (~60 to 70%)(Adams, 1975).

**History**

Early humans may have carried pecan nuts north as the Laurentide ice sheet retreated at the close of the last ice age. Nuts have been found in Illinois in association with the artifacts of early people dated to around 8900 BCE. There is a rich history of pecan use by Native American tribes recorded in the writings of Hernando de Soto, Cabeza de Vaca, and Oviedo. Dense groves of native pecan trees growing along the Guadalupe River of Texas were visited every other year, due to the alternate-bearing cycle. In years of heavy production, pecans were a major component of the people’s diet.

Shell thickness and nut size were probably the two most important criteria of selection by early foragers, just as they are for modern pecan collectors. Trees producing large, thin-shelled nuts are more highly valued, more regularly visited, more extensively harvested, and (probably) more widely dispersed over time. About 1882, Edwin E. Risien of San Saba, Texas offered a prize for the best native pecan. His intention was to obtain nuts from the prize-winning tree and plant them to establish an orchard of superior seedlings. The tree that won the competition came to be known as the ‘San Saba’ pecan. Seedlings of that tree were selected and propagated, producing the ‘San Saba Improved’, and ‘Onliwon’ pecans, among others. In tree species characterized by additive traits with high heritability, the practice of planting locally selected seed would be very effective in the development of improved plants, as well as in the maintenance of genetically diverse, locally adapted populations.

The first report of successful asexual propagation in *Carya* was by Abner Landrum in 1822, who budded pecan onto hickory stocks. However, the first commercially viable orchard was established in 1846, when Antoine, a slave, successfully grafted ‘Centennial’ pecan scions at the Oak Alley Plantation in Louisiana. In the late 1800s several nurseries sold grafted trees, providing material for the first great boom in pecan orchard establishment, which occurred in Georgia in the early 1900s. The extensive acreage established at that time, largely using the ‘Stuart’ cultivar, quickly moved Georgia to the lead in production of improved pecans.

**Culture**

Native pecans are harvested from natural stands of minimally managed wild trees. Native trees produce fewer nuts per acre, of lower quality, and sell for less on the market than improved pecans. Native trees are being cut down at an accelerated rate, while the diversity of grafted orchards is comparatively narrow (Grauke et al., 1995).

Commercial pecans are grown in orchards of variable numbers of selected cultivars, grafted onto regionally adapted seedling rootstocks, in configurations that vary by geographic region. Tree density tends to increase from the East to the West, with many orchards planted on 15.2 × 15.2 m spacings in the East, with 10.7 × 10.7 m spacings common in Texas, and 9.1 × 9.1 m spacing common in New Mexico and farther west. Cultivar diversity tends to be greatest in the Southeast, while many western orchards contain large blocks of a single cultivar, ‘Western’. Rootstock usage is also regional, with ‘Riverside’ and ‘Burkett’ being the traditional seedstocks of choice in the west, while ‘Moore’, ‘Curtis’, and ‘Elliott’ are preferred in the east. Grafted trees begin to bear
between the fourth to eighth leaf, but orchards may not achieve a positive cash flow until
the 12th to 15th leaf. Cost of culture varies by region, with increased cost for pesticide
application in the Southeast, but increased irrigation expense in the arid West.

Rootstock Development

The genetic composition and performance of pecan seedlings (tree size and
seasonal growth patterns) varies based on the geographic origin of the seedstock families
(Wood et al., 1998). Particular seedstocks have been selected by nurserymen to optimize
performance within geographic regions (Grauke, 1998). Conner and Wood (2001) were
able to uniquely identify 43 individual cultivars of pecan using 100 Randomly Amplified
Polymorphic DNA (RAPD) markers. That technique may also be useful for population
level distinctions, given the tendency for related cultivars to form at least weak
associations in cluster analysis. Additional molecular genetic tools (Simple Sequence
Repeats, or SSRs) are being developed that distinguish species of the genus, provenances
within the range of pecan, and individual cultivars with precision (Iqbal et al., 1999;
Mendoza-Herrera et al., 2001). Recent research with those SSRs indicates that they
amplify across a broad range of species in other genera of the Juglandaceae (Carol
Loopstra and Azucena Mendoza-Herrera, personal communication) and collaborative
research is underway to identify a suite of primers that can be used in both walnut and
pecan (Keith Woeste & Malli Arudhya, pers. commun.).

Hanna’s (1987) review of pecan rootstock research noted the difficulty in
demonstrating statistically significant differences in performance due to open pollinated
seedstocks. In the authors’ experience, challenges in demonstrating significance are
typically due to inadequate control of site variables within test orchards. Hanna (1987)
suggested the need for clonal propagation to control rootstock variability. However, even
clonally propagated trees show patterns of variation that could be due to site (Vendrame
et al., 2000). Hanna (1987) also suggested the need for dwarf rootstocks. In the USDA-
ARS Pecan Breeding Program, we see a strong correlation between tree size, precocity,
and yield. We make controlled crosses designed to increase vigor for rootstock use,
consistent with patterns of selection by the nursery industry (Grauke and Thompson,
1996).

Interspecific hybridization is common in Carya. Some southeastern US nurseries
use seedstocks of C. aquatica or interspecific hybrids (Grauke and Thompson, 1995),
which can affect graft survival, tree size, and leaf color (evidently related to Fe uptake)
(Grauke and O’Barr, 1996). Interspecific hybrids performed better than C. aquatica, but
not as well as pecan on the well-drained site adapted to pecan. Other researchers found
improved performance of hickory and hybrids over pecan on sites adapted to water
hickory (Toliver and Stauder, 1982). The careful evaluation of site limitations is
necessary for the appropriate selection of rootstock.

PISTACHIO *Pistacia vera* L., Anacardiaceae

Plant Biology

Commercial pistachio nuts are produced by *Pistacia vera*, a deciduous tree that
grows to a height of twenty-five to thirty feet, with alternate, pinnately compound leaves,
each with 3–5 leaflets. Trees are dioecious, producing male flowers on some trees and
female flowers on others. Both male and female flowers are borne on panicles in the axils
of the previous year’s growth. Pollen is spread by the wind to the apetalous female
flowers. The fruit is a dry drupe with an outer hull and a dry, thin shell that splits upon
drying to expose the greenish kernels, each usually about 2.54 cm long by 1.3 cm wide.
Kernels have about 20% protein and over 50% fat, 65% of which is the monounsaturated
fat oleic acid (Adams, 1975).
History

The pistachio tree probably originated in western Asia and Asia Minor, but grows wild eastward to Pakistan and India. Pistachios have been recovered from archeological excavations in Jordan, dated to 6760 BCE (Renfrew, 1973; Rosengarten, 1984). The Hebrew patriarch Jacob (Israel) instructed his sons to carry pistachio nuts and almonds with them from their home in Canaan to Egypt, as gifts for their brother Joseph, when the family had to move during a period of extreme famine. Pliny reported that pistachios were introduced to Italy from Syria during the first century BCE, and spread from there throughout the Mediterranean area (Rosengarten, 1984).

Pistachios were first introduced to the United States around 1853–1854 by the Commissioner of Patents, who distributed seed for experimental purposes (USDA, 1896). The crop did not gain much interest until later introductions began to fruit, in about 1881. The cultivar ‘Kerman’ was introduced into Chico, California, by the USDA plant explorer W.E. Whitehouse in 1929, from collections made near Kerman, Iran. That cultivar is the basis of the California pistachio industry.

Culture

The major pistachio producing areas are Iran, Turkey, and the San Joaquin Valley of California. In Iran and Turkey, nuts are harvested from trees of improved cultivars growing in established orchards, but harvesting and processing methods are primitive. Nuts are harvested by hand and many are allowed to dry in the hull, which can stain portions of the shell red, making them unattractive. As a result, many imported nuts are dyed with a red vegetable dye to camouflage the stains. Pistachios produced in California are mechanically harvested, hulled, and dried, and are unstained. Technology ensures that they can usually be marketed in natural condition. Small, wild nuts with desirable green color are still harvested in Afghanistan, although destruction of forests by clearing, overgrazing, and producing charcoal has reduced wild populations. International political issues have resulted in barriers to marketing pistachios, which has influenced domestic crop value and crop area.

Rootstock Development

Ferguson et al. (2001) have demonstrated increased yield at three California locations associated with UCB-1 (P. atlantica × P. integerrima) seedling rootstocks, with other hybrids and P. integerrima stocks being intermediate, and P. atlantica rootstocks the least productive. Yield differences are accompanied by differences in Verticillium wilt tolerance, freeze tolerance, and micronutrient uptake. Rootstock differences did not affect the percentage of splits and blanks, nut size, or alternate bearing.

Another strategy for rootstock development in pistachio is the development of techniques of clonal propagation. Parfitt and Almehdi (1994) developed techniques of successful micropropagation and have recently worked to develop methods for direct rooting (Almehdi et al., 2001). Such techniques should capture the benefits of genotypic selection and reduce genotype by environmental interaction, facilitating evaluation and increasing the progress of rootstock development.

WALNUT Juglans regia L., Juglandaceae

Plant Biology

Nuts from several species of the genus Juglans are consumed worldwide, but the most horticulturally important is the Persian walnut. Persian walnut trees grow to heights of 75’ and have trunks with tight, silvery bark. Shoots have chambered pith, distinguishing Juglans from its sister genus Carya (which has a solid pith). Leaves are odd pinnately compound, with 5–9 elliptic-ovate to long elliptic leaflets with entire margins (while black walnuts have more leaflets (15 to 19) that have serrate margins. Male flowers are borne laterally as single catkins on shoots of the previous season. Female flowers are borne terminally on current season shoots and usually have 1–3 nuts.
Flowers are wind pollinated, and male and female flowers mature at different times of the season, promoting cross-pollination, which results in increased heterozygosity. Despite the predisposition to cross-pollinate, walnuts are self-fruitful. The fruit is a drupelike nut with a thick, irregularly dehiscent husk covering a shallowly fissured shell that encases the two kernels, each of which is deeply divided at the base. Walnut kernels are rich in oils (64%), making them a high-energy food. The primary fatty acid is linoleic (62%), a polyunsaturated oil (Adams, 1975).

History

Progenitor trees were originally distributed across mountainous regions of central Asia, from eastern Turkey to Xin-jiang province of western China. Walnuts have a long association with humans and have been found in archeological excavations of caves inhabited by prehistoric groups in China and the United States. Initial selection for large nut size and thin shell could have been unconscious, as seeds from unconsumed caches of preferred seed germinated and established seedlings near habitations. Over time, and in association with people, walnuts having large, relatively thin-shelled nuts were developed.

Improved walnuts were sent to Greece from Persia “by the kings,” according to the Roman historian Pliny. From Greece, walnuts were introduced to Rome, where they were given the Latin name *Jovis glans* (“nut of Jupiter”), which was contracted to provide the genus name *Juglans*. The connection to Persian royalty is reflected in the specific epithet “regia”, meaning “royal.” Romans spread walnuts throughout the Mediterranean, where the trees readily adapted to the warm, dry climate. The trees spread across Europe and into England where they became known in Old English as “wealhnnutu” (“wealh” means “foreign” or “strange,” and “hnutu” is “nut”). Although the tree is not capable of bearing profitable crops in the cool, wet English climate, it was esteemed for its high-quality wood. Walnuts were carried around the world in English ships, and came to be known in commerce as “English walnuts” (Rosengarten, 1984). Walnuts came to the United States with the first settlers in New England, although the first established production was from Spanish materials introduced into California (Forde and McGranahan, 1996).

Culture

Walnuts are intensively cultured in California, with improved cultivars selected for high production and quality, grafted onto hybrid rootstocks. Pollinizer cultivars are included to provide adequate cross-pollination. Orchards are irrigated, with up to five acre-feet of water per acre being required to mature a crop. Trees are chemically protected from pests, and mechanically harvested and processed.

Initial Persian walnut introductions into southern California were made in 1867 by Charles Sexton, from Chilean sources, and were developed into the Santa Barbara soft-shelled walnuts (Forde and McGranahan, 1996). Introductions into northern California were by nurseryman Felix Gillet, who imported French cultivars in 1871. Those materials were developed into the University of California walnut cultivars (Forde and McGranahan, 1996).

In Europe and Asia, much production comes from seedling trees, although the use of grafted cultivars is increasing to the extent that it is perceived as a threat to some native populations (McGranahan and Leslie, 1991). Over centuries of cultivation, the selection of horticulturally valuable individuals and continued propagation by seed has resulted in distinct landraces in different regions. In Europe, the economic incentive to increase production and quality by establishing monocultures of a few genotypes is being balanced by the awareness that regionally distinct landraces provide a valuable source of genetic diversity. As more seedling trees are harvested for their valuable lumber, the need for conservation by in situ reserves has increased.
Rootstock Development

In 1877, Luther Burbank crossed *J. regia* with *J. hindsii* to produce the Paradox hybrid, which was noted for outstanding vigor, attaining 12" dbh in 10 years (USDA, Division of Pomology, 1896). Paradox hybrids were observed to impart vigor to grafted scions, were more resistant to crown gall caused by *Agrobacterium tumefaciens* Smith & Town, and they became the preferred rootstock for the California walnut industry (McGranahan and Catlin, 1987). Mircetich and Matheron (1983) reported that Paradox seedlings were more resistant to *Phytophthora* spp. than *J. regia* seedlings. Unfortunately, there has been nomenclatural ambiguity concerning what constitutes Paradox hybrid rootstocks, with complex hybrids between *J. regia* and several black walnuts (*J. hindsii*, *J. californica*, *J. major*, and *J. nigra*) being used as Paradox rootstocks (Potter et al., 2001). McGranahan et al. (1988) evaluated sources of *J. hindsii* and *J. californica* and noted patterns of difference between the species that justified continued recognition of distinctions, despite frequent hybridizations. They noted that some seed of *J. hindsii* required two seasons of stratification to germinate, a trait that might have survival value in the wild but that would be selected against by nurserymen. They also noted significant block and block by source interaction that implied species sensitivity to small variations in site conditions. McGranahan et al. (1988) cautioned that *J. hindsii* had potentially valuable traits for future walnut rootstocks, yet might be endangered due to introgression with the other walnut species with which it hybridizes. The need to protect isolated species from extinction brought about by hybridization with other more common species has been recently addressed by Levin (2002).

Greater success has been achieved using molecular genetics in walnut than any other nut crop: genetically transformed walnuts were developed with an *Agrobacterium* mediated transfer of marker genes and a Lepidopteran resistance gene from *Bacillus thuringiensis* (BT) (Forde and McGranahan, 1996). Recently, an elegant system using RNA interruption of the tumor causing system of crown gall was developed in *Arabidopsis* (Escobar et al., 2001) and may be established in walnut. The system may allow the development of durable crown gall resistance in walnut seedlings.

SUMMARY

Rootstock development in nut crops is being actively pursued, even though formal breeding may be limited. The foundation of appropriate regional rootstocks are often adapted local species. Some local species and populations are recognized as valuable, and at the same time are perceived as threatened. It is ironic that the successful cultivation of related crop plants could increase the threat to those genetic materials so valuable to their sustained development. The exchange of exotic genetic materials has created additional threats, both to the native materials and to other crop plants, accentuating the need for continued caution in introductions and deployments. The distance between conservation and breeding will grow smaller if we do our job well.

Literature Cited


