6 Black Walnut

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6.1 Introduction

6.1.1 Origin and History

Black walnut (*Juglans nigra* L.), also known as eastern black walnut or American walnut, is a fine hardwood species in the family Juglandaceae, section *Rhysocaryon* (Manning 1978). In general, *J. nigra* will not cross with species in the sections *Cardiocaryon* or *Trachycaryon*, but *J. nigra* will cross with *J. ailantifolia* (*Cardiocaryon*) (Williams 1990). *Juglans nigra* will also hybridize to some extent with other *Juglans* species (*Dioscaryon* and *Rhysocaryon*), and one hybrid is recognized: *J. nigra* × *J. regia* = *J.* x *intermedia* Carr. (USDA-NRCS 2004). Native to the deciduous forests of the eastern United States (USA), from Massachusetts to Florida and west to Minnesota and Texas, and occurring naturally in southern Ontario, Canada, black walnut is seldom found in pure stands, but rather in association with five mixed mesophytic forest cover types: sugar maple, yellow poplar, yellow poplar – white oak – northern red oak, beech – sugar maple, and silver maple – American elm (Williams 1990). Black walnut is a large tree and on good sites may attain a height of 30 to 38 m and diameter of 76 to 120 cm and can exceed 100 years of age (Williams 1990; Dirr 1998; USDA-NRCS 2004). Black walnut is shade intolerant, and control of competing vegetation is especially important in new plantations for the first 3 to 4 years. Black walnut grows best on moist, deep, fertile, well-drained, loamy soils, although it also grows quite well in silty clay loam soils or in good agricultural soils without a fragipan (Williams 1990; Cogliastro et al. 1997). These sites include coves, bottomlands, abandoned agricultural fields, and rich woodlands. Black walnut forms a deep taproot, wide-spreading lateral roots, and has been cultivated since 1686. A toxic chemical ‘juglone’ (5-hydroxy-1, 4-naphthoquinone), naturally occurring in the leaves, buds, bark, nut husks, and roots of black walnut, is a highly selective, cell-permeable, irreversible inhibitor of the parvulin family of peptidyl-prolyl *cis/trans* isomerases (PPIases) and functions by covalently modifying sullfhydryl groups in the target enzymes (Henning et al. 1998; Chao et al. 2001). Certain plants, especially tomato, apple, and several conifer species, are adversely affected (allelopathy; foliar yellowing, wilting, and even death) by being grown near the roots of black walnut trees (Goodell 1984; Dana and Lerner 1994). Horses can contract acute laminitis, an inflammation of the foot, when black walnut wood chips or sawdust is used for stall bedding or stables and paddocks are located too close to walnut trees (Galey et al. 1991). Historically, the bark of black walnut was used by several Native Americans, including the Cherokee, Delaware, Iroquois, and Meskwaki, in tea as a cathartic, emetic, or disease remedy agent, and chewed or applied for toothaches, snake bites, and headaches (Moerman 1998, 2003). *Caution*: *the bark should be used cautiously in medicine because it is poisonous*. The Cherokee, Chippewa, and Meskwaki also used the bark to make a dark brown or black dye (Moerman 1998, 2003). The Comanche pulverized the leaves of black walnut for treatment of ringworm, the Cherokee used leaves to make a green dye, and the Delaware used the leaves as an insecticide to dispel fleas (Moerman 1998, 2003). The nut meats were also a food source for Native Americans, and the nuts are still consumed today by people and are an important food source for wildlife.

6.1.2 Botany

Juglans nigra (section *Rhysocaryon*, Fig. 1) is the largest and the most valuable timber tree of the *Juglans*

Genome Mapping and Molecular Breeding in Plants, Volume 7
Forest Trees
C. Kole (Ed.)

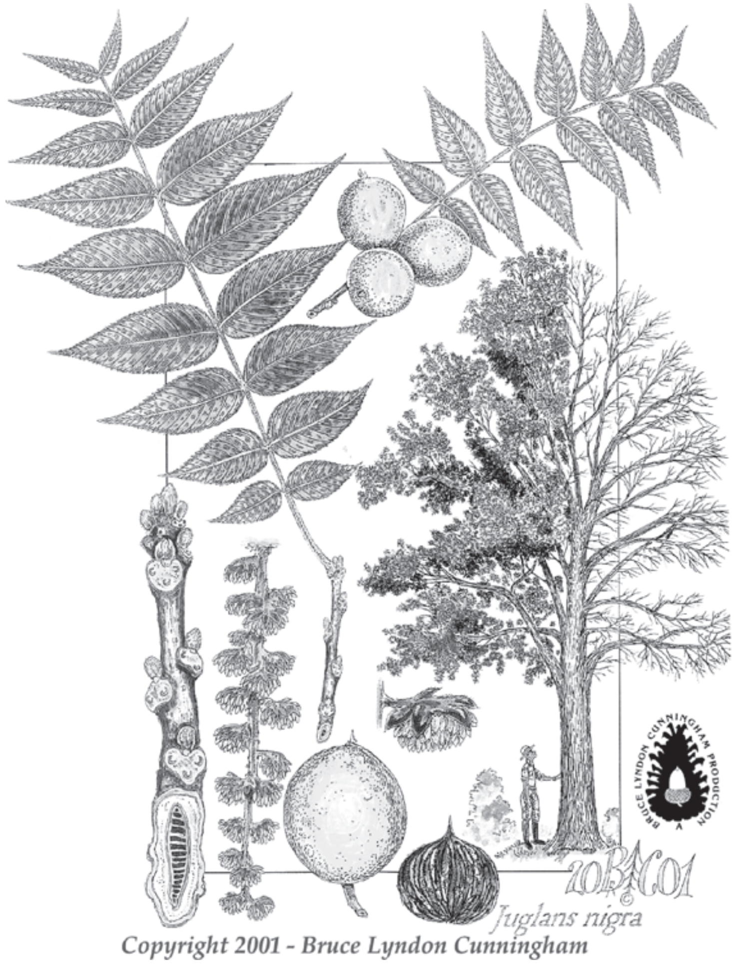

Fig. 1. Form, leaf shape, bud characters, and flower and fruit morphology of *Juglans nigra* L.

species and is hardy to USDA hardiness zone range of four to nine (Dirr 1998). Black walnut is monoecious with male and female flowers maturing at different times (McDaniel 1956). Staminate catkins (5 to 10 cm) develop from axillary buds on the previous year's wood and appear as small, scaly, conelike buds, and the female flowers occur in two- to eight-flowered spikes borne on the current year's shoots (Brinkman 1974; Williams 1990; Flora of North America Editorial Committee 1993+; Dirr 1998). The female flowers more commonly appear first (protogyny) and flowering occurs with or shortly after the leaves. Because flowering is dichogamous, self-pollination is unlikely, which promotes outcrossing. The fruit is a drupe-like, furrowed nut enclosed in a thick, indehiscent yellowish-green husk that develops from a floral involucre (Brinkman 1974). Fruits are subglobose to globose, rarely ellipsoid, 3.5 to 8 cm, warty, with scales and capitate-glandular hairs (Flora of North America Editorial Committee 1993+). The fruit occur singly or in clusters of two to three and are edible, sweet, oily, and high in protein (Reid 1990). The nut is subglobose to globose, rarely ellipsoid, 3 to 4 cm, and very deeply longitudinally grooved, and the surface between the grooves is coarsely warty (Flora of North America Editorial Committee 1993+). Leaves are alternate, pinnately compound, 30 to 60 cm long, with 9 to 23 leaflets, nearly glabrous and somewhat lustrous dark green, pubescent and glandular beneath, with petioles 6.5 to 14 cm long covered with glandular hairs (Flora of North America Editorial Committee 1993+; Dirr 1998). Black walnut stems are stout, densely grey-downy, smooth, and reddish buff, and they have a chambered light brown pith (paler than that of butternut, *J. cinerea*) and a distinctly notched leaf scar. Terminal buds are ovoid or subglobose, 8 to 10 mm long, and weakly flattened (Flora of North America Editorial Committee 1993+). Lateral buds are smaller, often superposed, and greyish in color. *J. nigra* has a dark grey or brownish bark, deeply split into narrow furrows and thin ridges, and the ridges are chocolate in color when cut, forming a roughly diamond-shaped pattern. The sapwood of black walnut is nearly white, and the heartwood varies from light to dark brown. The wood is heavy, hard, strong, stiff, normally straight grained, and has good resistance to shock (Forests Products Laboratory 1999). The chromosome number of black walnut is $2n = 32$ (Woodworth 1930). Black walnut trees produce seed at about 12 years of age, with good seed crops occurring every 2 to 3 years (Brinkman 1974). Seeds of black walnut, like most *Juglans* spp., have a dormant embryo, but dormancy can be broken by fall sowing or by moist prechilling of seeds at 1 to 5 °C for 3 to 4 months (Brinkman 1974).

6.1.3 Economic Importance

Black walnut is one of the largest hardwood trees found in the USA and is valued economically and ecologically for its wood and edible nuts. Owners of quality black walnut wood receive high market prices, and the wood has many uses including furniture, veneer, cabinets, interior architectural woodwork, flooring, and gunstocks. Black walnut wood with figured grain gets even higher market prices. Curly and wavy figure can produce interesting characteristics in veneers, and these can arise from walnut butts, crotches, and burls. The nut is an important food source for wildlife and is also consumed by humans. The majority of black walnut trees occur in natural stands, with walnut plantations (ca. 13,800 ac) accounting for 1% of all the black walnut volume (ft^3) in the USA (Shifley 2004). There are 11 states that currently have the greatest volume of black walnut growing stock on timberland, and these include Missouri, Ohio, Iowa, Indiana, Illinois, Tennessee, West Virginia, Kansas, Pennsylvania, Virginia, and Michigan (Shifley 2004). Since the last (1997) comprehensive inventory and summary of the black walnut resource in the eastern USA, the number and volume of black walnut trees has increased, except in Michigan, Virginia, and Pennsylvania, where walnut volume is level or decreasing (Shifley 2004). In addition to the multimillion-dollar US market consumption of walnut wood, for the period 1999-2003, the USA exported walnut lumber to 67 countries (58,434.2 m^3; $40,964,481; averages per year) and walnut logs to 49 countries (62,897 m^3; $37,238,327; averages per year) (USDA-FAS 2004). Black walnut yields edible nuts that are used in baking (cookies, cakes, etc.) and ice cream products. The Hammons Products Company (Stockton, MO; http://www.black-walnuts.com) is the world's premier processor and supplier of American black walnuts for both food and industrial uses. Selection of black walnut trees for nut quality and production has developed slowly over the years, but over 700 cultivars have been named and the percent of edible kernel has improved to over 34% (Reid 1990; Reid et al. 2004). Black walnuts are low in saturated fats (3.4 g per 100 g edible nut), have zero cholesterol, and are high in polyunsaturated (35.1 g per 100 g edible nut) and monounsaturated fats (15 g per 100 g edible nut) (USDA-ARS 2004). Black walnuts are also a good source of protein (24.1 g per 100 g edible nut) and fiber (6.8 g per 100 g edible nut) containing low levels of sugar (1.1 g per 100 g edible nut) (USDA-ARS 2004). Ground black walnut shell (see Hammons Products Company, http://www.black-walnuts.com) is a hard, durable, nontoxic, biodegradable abrasive product used for blast cleaning and polishing. It is also used for industrial tumbling and deburring, as well as for uses in oil-well drilling, water filtration, and as explosive fillers.

6.2 Black Walnut Genetics

Black walnut genetic research has been focused on the practical improvement of the species for the production of timber or nuts. Although black walnut has a large native and commercial range, black walnut improvement has been largely a Midwestern preoccupation. The earliest recorded clonal selection of black walnut was the nut cultivar 'Thomas' (Corsa 1896, cited in Reid et al. 2004). New nut cultivars have been named, almost entirely by amateur breeders, throughout the 20th century. Now at least 700 such cultivars are recorded, although only a small number, perhaps 30 or 40, are suitable for inclusion in a contemporary nut-improvement program (Reid et al. 2004). The most important trait for selection for nut improvement is percent kernel. 'Thomas' averages 24% kernel, but the best of the newer selections routinely exhibit over 35% kernel. Other traits of interest include protandry, resistance to anthracnose (caused by *Gnomonia leptostyla* [Fr] Ces. & De Not.), high yield, low alternate bearing, and uniform fruit ripening. Protandry is important because black walnut, like all members of the genus *Juglans*, is dichogamous, and breeders would like to identify selections that can serve as pollenizers for the best nut-producing cultivars. There has been little published in refereed journals concerning the heritability or inheritance of important traits such as nut yield and percent kernel in black walnut, although these traits have been well studied in Persian walnut (*J. regia*) (Hansche et al. 1972). Observational studies related to almost every aspect of black walnut nut production have been published by scientists, hobbyists, and amateur breeders in the annual reports of the Northern Nut Growers, first published in 1910 and available through their Web site (http://www.nutgrowing.org).

Although single-species plantations of black walnut for timber production date from as long ago as the late 1800s, modern efforts at genetic research were initiated by Johnathan Wright and Leon Minckler in the early 1950s (Minckler 1952, 1953; Wright 1954). Subsequent genetic research can be loosely divided into studies of heritability and selection age, local and regional adaptation, methods in black walnut breeding, genetic variance as measured by neutral genetic markers and other markers, the use of hybrids to improve black walnut, and the development of general genetic and breeding resources. Each of these areas is briefly reviewed below.

6.2.1 Heritability of Important Traits and Selection Age

Height and diameter growth are the most studied traits in black walnut, perhaps because they are easily measured traits in young trees and because they give an overall impression of a tree's vigor. Over the long term, these traits also reflect a tree's adaptation to the site on which it is growing. As expected, heritability estimates for these basic growth traits are very high in the early generations of selection. All the studies cited below are based on progeny from open-pollinated trees growing either in forests or grafted into "clone banks." Rink and Clausen (1989) summarized the results of three progeny tests after 13 years, finding that the narrow sense heritability for height was about 0.41, but that there were significant family × site interactions. This heritability estimate was similar to or slightly lower than those summarized in other studies (Beineke 1989). Kung et al. (1974) found h^2 for height growth of about 0.4 based on a study of twinned seedlings, and Rink (1984), Rink and Kung (1995), and Beineke (1974) indicated a value slightly higher (h^2 = 0.55), but in any case there is sufficient evidence that breeders can expect to make rapid progress in this trait in the first few generations of selection.

The heritability of diameter growth is in the same range as height (h^2 = 0.35 to 0.65) based on studies of clones (Beineke and Stelzer 1991), twins (Kung et al. 1974), and open-pollinated families (Rink and Kung 1995). Woeste (2002) found a somewhat lower value (h^2= 0.28) based on a 35-year-old progeny test. As was true for height, the heritability of this trait was near zero at outplanting, but increased over the first 10 years and did not appear to stabilize until about age 15 (Hammitt 1996; Rink 1997). Tree form is more difficult to measure than height or diameter; nevertheless, estimates of the heritability of this trait also range from 0.4 (Beineke 1989) to 0.5 (Beineke and Stelzer 1991). Other important traits are less well studied, but heritability estimates have been published for foliation date (h^2 = 0.92), defoliation date (0.73), sweep (0.32), number of crooks (0.24), branch angle (0.20), and branch number (0.41) (all reported in Beineke 1974). Black walnut geneticists have studied the heritability of phenological traits because of their role in the adaptation of seed sources to local environments (see below). Heritability estimates for multiple stems (0.18), leaf drop date (0.13; note the discrepancy between this value and that reported by Beineke), insect damage (0.27), and leaf angle (0.32) were reported by Bey (1970). Walnut anthracnose, described above, is the most important foliar disease of black walnut. Trees heavily infested with anthracnose appear to senesce and defoliate earlier than more resistant genotypes. Anthracnose resistance may be highly heritable (Funk et al 1981; Woeste and Beineke 2001), and this could be important in extending the growing season, and thus the growth, of black walnut, but attempts to associate anthracnose resistance with growth are not conclusive (Todhunter and Beineke 1984). The heritability of important wood-quality traits such as heartwood formation, heartwood color, and wound recovery is expensive to determine as these traits require destructive sampling of mature trees. Nelson (1976), Rink (1987a), and Woeste (2002) all report that heartwood area has a moderate to high heritability ($h^2 > 0.4$), perhaps because this trait is strongly associated with tree vigor (Woeste 2002). Rink (1987a) was unable to find any genetic component to heartwood color.

Because the rotation age for black walnut is more than 60 years, selection of juvenile trees for their anticipated rotation-age value is an essential part of any improvement program for the species. Juvenile-mature correlations and rank correlations for height and diameter growth based on progeny tests were reported by McKeand et al. (1979), Rink (1984), Beineke (1989), and Rink and Kung (1995). In general, these studies found family selection for the high heritability traits of height and diameter growth can begin by about age 8 years, but that within-family selection should be delayed until after age 12. The optimal age for selection depends on thinning schedules and site quality, as these factors influence selection intensity, intertree competition, and trait heritability (Kung 1973).

6.2.2 Local and Regional Adaptation

Even mature black walnut trees bear a relatively small number of large seeds, and trees often only bear in alternate years. Seed-germination rates fall to near zero if seeds are stored more than 2 years (Beineke 1989). Consequently, seed from improved sources is typically expensive and subject to local shortages in supply, and provenance trials to measure the effects of long-distance seed movement have been a fundamental part of black walnut improvement. These provenance trials were established to characterize regional genetic variability and to determine the relationship between the latitude of seed sources and tree growth. The underlying rationale was that trees from southern sources would leaf out earlier and lose their leaves later than trees from more northern latitudes. This, in general, was what Bey (1970) concluded. Longer growing seasons, in turn, would translate into faster growth. Frost injury, which can cause poor form, and dieback from winter injury were considered potential drawbacks to the use of southern seed sources. Early reports (Bey and Williams 1975) indicated that trees from provenances to the south of the planting site would perform well compared to local sources. Bey (1979, 1980) and Bresnan et al. (1992, 1994) refined this analysis. The results from a large number of provenance studies have been summarized with a general guideline often called the "200 mile rule," i.e., plant seeds from sources 200 miles (322 km) to the south for optimal growth. In fact, the recommendations found in the reports of Bey and others were far more nuanced, recognizing that planting site climate is not strictly dependent on latitude. The use of grafted trees to evaluate site effects and adaptability is only now under way (Woeste and McKenna 2004).

6.2.3 Methods in Black Walnut Breeding

The publication "Genetics of Black Walnut" (Funk 1970) reviewed much of what was known at the time on the subject, including sections on micropropagation, seed orchard design, and the use of hybrids, topics that continue to be the subject of research. At the time Funk wrote his synopsis, Beineke was developing his own ideas for clonal seed orchards of black walnut (Beineke and Lowe 1969) as a means to improve the availability of improved seed (Beineke 1982). Beineke was the first to document the effects of inbreeding on black walnut seedling growth (Beineke 1972). He believed that wild stands of black walnut were genetically depauperate and that the species was suffering from dysgenic selection. Beineke published a justification of his approach and his own synopsis of black walnut breeding 13 years after Funk (Beineke 1983). Beineke, a fierce proponent of clonal forestry, became the first person in the USA to patent a tree (Beineke 1980).

Black walnut is not an easy species to vegetatively propagate (Coggeshall and Beineke 1997a, b), and the expense inherent in clonal approaches to improvement made Beineke's proposed improvement methods (McKeand and Beineke 1980; Lowe and van Buijtenen 1986) theoretically attractive but difficult and expensive in practice. Rink (1987b) focused on the practical problems related to seed production, including fertilization and thinning of seed orchards. A comparison of improved seed from seed orchards with elite clonal and nursery-run stock published by Hammitt (1997) indicated that the (patented) clones and improved sources were superior to 1-0 common nursery stock, especially with respect to form.

6.2.4 Genetic Variance Measured by Neutral and Other Markers

By the late 1980s, it became possible to determine the mating system parameters for black walnut using allozyme systems (Rink et al. 1989). The goal of the research was to determine the level of inbreeding and outcrossing of black walnut in native stands and the allocation of genetic variance at marker loci among and within populations. Forest fragmentation, overharvesting, and dysgenic selection were thought by many to have led to inbreeding and low genetic variance (Beineke 1972), but Rink found that black walnut had a high outcrossing rate (about 90%) and was highly heterozygous based on eight loci (Rink et al. 1989). The 26 maternal trees in Rink et al.'s 1989 study were significantly more heterozygous than their progeny, and Rink suggested this might have been caused by selection against inbred progeny. These findings would be substantiated by later research (Rink et al. 1994; Busov et al. 2002). These later studies also showed that the mating parameters of black walnut seed orchards were similar to those found in wild stands, and that as much as 94% of the variance in the isozyme marker loci was distributed within populations, i.e., that very little differentiation among populations could be detected at the level of allozymes. Fjellstrom (1993) found high levels of heterozygosity in black walnut using RFLPs, and unpublished research by one of the authors (Woeste) indicates that black walnut is highly heterozygous at microsatellite loci (Woeste et al. 2002) as well.

6.2.5 Black Walnut Hybrids

Luther Burbank and others noticed the unusual vigor demonstrated by interspecies hybrids within the genus *Juglans*. Burbank's "Royal" hybrid (*J. hindsii* × *J. nigra*) has been cited by others as an exemplar of the phenomenon (Wright 1966). The "Royal" hybrid has been impractical in the Midwest because of poor cold tolerance, but in milder climates it is fruitful and appears to have excellent potential as a timber tree in California (Forde and McGranahan 1996) and the Pacific Northwest. Hybrids between the *J. nigra* × *J. regia* F_1 known as *J.* x *intermedia* Carr. have attracted the most interest in the United States (Wright 1966; Funk 1970), and Europe (Hussenforfer 1999; Germain 2004). Bey (1969) reported that researchers at the USDA Forest Service research unit at Carbondale, IL had begun to collect *Juglans* species with the intention of producing and testing hybrids. Funk (1970) summarized the hybridization research of McKay (1965) and others who found that, while *J.* x *intermedia* had variable vigor, it was always nearly sterile, and all attempts to restore fertility through the production of amphidiploids failed. The clonal deployment of *J.* x *intermedia* Carr. has not yet been pursued, although the possible uses of seedling hybrid rootstock for timber production in the Midwestern USA was discussed by Woeste and McKenna (2004). They cite the potential of *J. nigra* × *J. major* hybrids as a rootstock for drier sites. While seed availability previously limited research into the use of hybrids in *J. nigra* improvement (Bey 1969), *Juglans* hybrid seedlings can be produced on a commercial scale; seedling Paradox (*J. hindsii* × *J. regia*) rootstocks are routinely used in the Persian walnut industry in California (Forde and McGranahan 1996). The identity and parentage of *Juglans* hybrids can be verified using inter-simple sequence repeats (Potter et al. 2002).

6.2.6 General Genetic and Breeding Resources

There is no catalog of black walnut germplasm in the United States, but there are abundant resources. Germplasm collections or seed orchards of black walnut are maintained by at least one state agency (Vallonia Tree Nursery, http://www.in.gov/dnr/forestry/index.html?http://www.in.gov/dnr/forestry/nursery/&2), by universities (University of Missouri Horticultural and Agroforestry Research Center, New Franklin, MO; Purdue University Department of Forestry and Natural Resources, West Lafayette, IN; Southern Illinois University Department of Forestry, Carbondale, IL), private organizations such as the Arbor Day Foundation (Nebraska City, NE); state chapters of the Northern Nut Growers (e.g., Nebraska Nut Growers), and by at least two federal agencies in the United States (USDA Forest Service Hardwood Tree Improvement and Regeneration Center, West Lafayette, IN and the National Clonal Germplasm Repository, Davis, CA). A small number of *J. nigra* clones is also maintained by breeding programs in Europe (Germaine 2004).

There are few tools available for molecular genetic research in black walnut. There are no published, publicly available resources such as cDNA or genomic libraries; however, the National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov/) Web site has records for 88 nucleotide sequences including microsatellite loci, 19 proteins, and 22 population genetic data sets. This resource is likely to expand in the future.

6.3 Tissue Culture and Genetic Transformation

Important methods for capturing genetic gains from breeding programs include the use of vegetative propagation, both through rooted cuttings or grafting of elite clones and tissue culture. Beineke (1983) described optimum variables for grafting that included storage conditions for scion wood and rootstock condition. Although grafting success can be very high, this method is also extremely labor and resource intensive and not highly desirable for mass propagation. To date, success from rooted cutting propagation has been minimal, if not recalcitrant for most researchers (Coggeshall and Beineke 1997a, b). More promise has come from research on rooting of microshoots (Van Sambeek et al. 1990, 1997; Khan 1995; Long et al. 1995) as well as somatic embryogenesis (Neuman et al. 1993; Preece et al. 1995).

Genetic transformation can be used in lieu of conventional breeding when the desire is to either introduce a gene from another species or to circumvent long generation times as found in tree species such as black walnut. Only one report has been published to date on the successful genetic transformation of black walnut (Bosela et al. 2004). In this research, somatic embryo lines were established from cotyledons of immature zygotic embryos. From 16 embryo lines, transgenic callus was regenerated following infection with disarmed strains of *Agrobacterium tumefaciens* carrying transgenes for β-glucuronidase (GUS) and kanamycin resistance (uidA). GUS expression assays showed that the methods deployed resulted in high rates of gene transfer in all but two lines tested. When kanamycin was used for selection, the majority of the secondary embryos were transgenic. If these secondary embryos were kept on selection media, the chimeric embryos would regenerate fully transgenic embryos. These methods are now being used to generate transgenic lines with genes for herbicide resistance, insect resistance, and flowering control.

6.4 Future Scope of Works

To date, no genetic maps have been made for black walnut. Molecular markers previously developed have been used to begin to characterize population including estimation of genetic variation both in small stands and across large portions of the natural range. This type of genetic information was needed to aid in management of the genetics in fragmented stands and to guide movement of seed and seedlings in the Midwest USA. Once genetic maps have been developed, we will be able to target genes for cloning as well as to begin to identity quantitative trait loci, which could lead to marker-assisted breeding on an operational level.

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