Black Walnut: Guidance for Seed Transfer Within the Eastern United States

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Abstract

Black walnut (*Juglans nigra* L.) is a shade-intolerant hardwood tree common in riparian forests across the Central United States. Commercial values for top-quality black walnut logs are the highest for any tree in North America. Production of juglone from walnuts may have phytotoxic effects on neighboring plant communities. Genetic diversity of this species is high due to seed dispersal and pollen flow characteristics,while population structure is low. Common garden studies revealed relatively weak clines for growth traits but strong latitudinal gradients for cold tolerance. Seed transfer distances of 200 mi (322 km) from south to north, or roughly 2 degrees latitude northward, is considered a safe recommendation to maintain growth. At the northern edge of the species' range, such as Minnesota, local sources are best. Leaf anthracnose is an important pest, and thousand cankers disease can be a concern, especially in drought-prone areas. Black walnut is likely to expand northward with climate change, but its migration may require human assistance, and such expansion may be limited by soil conditions, site availability, deer browse, or drought.

Introduction

Black walnut (*Juglans nigra* L.) is a highly valued, long-lived, early successional hardwood tree species that grows in riparian areas (bottomlands) across much of the Central and Southern United States into upstate New York and New England, spanning plant hardiness zones 3 through 9 (U.S. Department of Agriculture, Agricultural Research Services 2012). While it is classified as a shade-intolerant species, saplings can survive under light to medium shade, although growth under these conditions is not suited for commercial production (Carpenter 1974). Black walnut grows best on well-draining sandy or silt loams (Losche 1973) and may also grow on mineland soils or spoils if nutrition and drainage are adequate (Ashby 1996). On optimal sites, black walnut exhibits rapid growth, but is notoriously sensitive to site and soil conditions. On sub-par sites, black walnut grows slowly, and mortality is high. Natural regeneration is severely impacted by heavy grass competition, especially fescue (*Festuca* spp.) (Krajicek 1975). Therefore, both careful site selection and control of competing grass vegetation is critical for black walnut plantings to be successful (Smith 1983), especially for those grown for timber (figure 1).

Black walnut's darkly colored bark and deep fissures distinguish it from the lighter gray bark plates of butternut (*Juglans cinerea* L.) (Farlee et al. 2010).

Figure 1. A plantation of black walnut managed for future timber requires intensive care to ensure that it will thrive. (Photo by M. Coggeshall, USDA Forest Service, 2005)

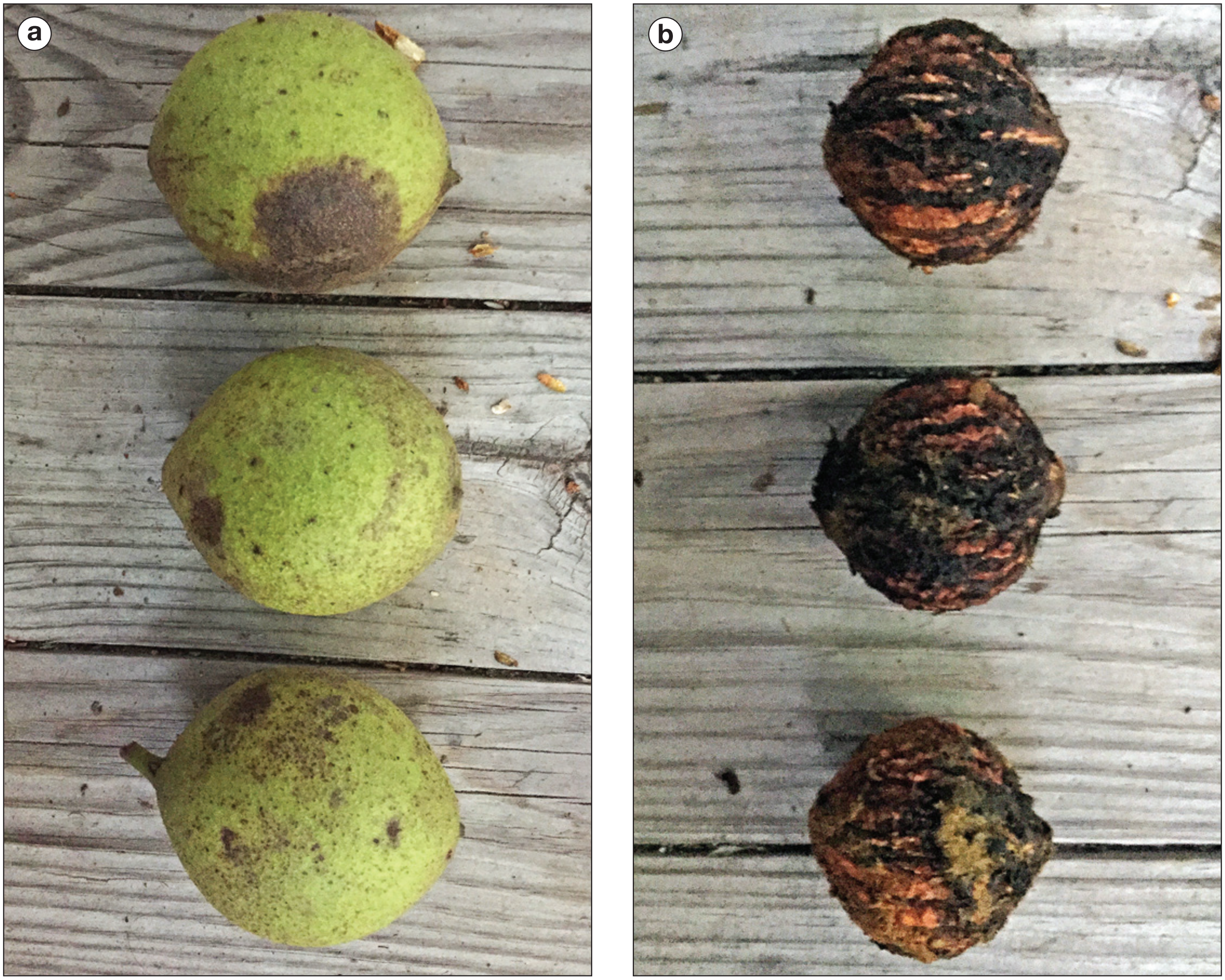

Figure 2. Three black walnuts are shown (a) before and (b) after the husk is removed. (Photos by Aziz Ebrahimi, Purdue University, 2021)

In addition, black walnut's fruits are generally round-shaped and hairless (figure 2) in contrast to the oblong, hairy, and sticky fruits of butternut (Farlee et al. 2010). Black walnut is valued for veneer (figure 3), with board-foot values frequently exceeding those for black cherry (*Prunus serotina* Ehr.) and nearly double those for oak (*Quercus* spp.), which, in many years, is the second most valuable hardwood in the central hardwood region (Settle and Gonso 2020). Black walnut is also cultivated for its edible nuts (Coggeshall 2011, Reid et al. 2009) (figure 4).

Black walnut is sympatric with other riparian, mesophytic hardwoods such as yellow poplar (*Liriodendron tulipifera* L.), white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), basswood (*Tilia americana* L.), beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marshall), oaks, and hickories (*Carya* spp.) (Williams 1990).

Black walnuts are notable for the production of juglone, a chemical that has allelopathic properties that can inhibit the growth of some neighboring plants, such as crimson clover (*Trifolium incarnatum* L.) and the nonnative amur honeysuckle (*Lonicera maackii* Maxim.) (Rietveld 1983). Phytoxicity on native trees is reported for white birch (*Betula papyrifera* Marshall) (Gabriel 1975) and, to a lesser extent, on eastern white pine (*Pinus strobus* L.), with such effects amplified on sites with poor drainage and lower plant vigor (Rietveld 1983). Juglone can inhibit growth of conifer seedlings, but in small quantities it can stimulate their growth (Funk et al. 1979).

Figure 3. This veneer of black walnut is a good representation of a highly valued timber product from this species. (Photo by M. Coggeshall, USDA Forest Service, 2009)

Figure 5. The immature catkins (male flowers) of black walnut will dry prior to opening and releasing pollen. (Photo by M. Coggeshall, USDA Forest Service, 2003)

The phylogeny of the genus *Juglans*, which includes both butternuts and walnuts, is complex because it traverses multiple continents and is divided into three sections based on origin, but not present locality. For example, black walnut occurs in the Rhysocaryon section which includes all New World walnuts, while butternut is part of the Cardiocaryon section, which is otherwise entirely Asian (Aradhya et al. 2006a, b; Aradhya et al. 2007). Although they co-occur, butternut and black walnut cannot hybridize because of their distinct phylogeny. One glacial refugium, in the lower Mississippi Valley, is supported by the genetics of extant trees, with no evidence of postglacial bottlenecks (Victory et al. 2006). Black walnut is likely to persist in its present range owing to its high genetic variation and its ability to produce and disperse seeds. Its shade and drought intolerance, however, may limit its growth or survival on sites where such conditions predominate (Morin et al. 2007).

Figure 4. This large bag of black walnuts was collected from a seed orchard. Black walnuts are best picked from the ground rather than directly from the tree. (Photo by M. Coggeshall, USDA Forest Service, 2004)

Genetics

Black walnut is a monoecious diploid, with outcrossing enforced by pronounced dichogamy (i.e., female and male flowers are produced at different times on a tree). Cultivars and clones may be distinguished by their consistent timing of peak male (figure 5) and female bloom (figure 6) (Ebrahimi et al. 2018, Pang et al. 2021), which has implications for breeders and may lead to Wahlund effects, or nonrandom breeding within stands or orchards (Robichaud et al. 2006). Black walnut is characterized by especially high genetic variation and low population structure based on nuclear microsatellites, with F_{ST} values (a ratio of genetic variation between subpopulations and the total population) near 0.017 (Victory et al. 2006). Despite the fruit's large size (figure 7), seeds and pollen are readily dispersed. Few detectable differences in fruit size occur among populations. One study showed that nuts from northern provenances had lower fresh weight than nuts from southern provenances, but no association was found between nut size and fresh weight or seedling vigor (Funk and Polak 1978).

Figure 6. After pollination, the female flowers of black walnut will develop into a nut inside an outer husk. (Photo by Keija Pang, Purdue University, 2011)

The success of black walnut seed and pollen dispersal may be attributed to several factors including small mammals (mainly squirrels), hydrochory (i.e., nuts can float and move long distances on rivers), and high levels of wind-dispersed pollen movement. Genetic diversity of neutral alleles is lower in northern populations compared with southern populations, but these latitudinal-based differences account for less than 10 percent of genetic variation (Victory et al. 2006).

Black walnut's high commercial value has led to decades of research on genetics and genetic improvement for artificial reforestation with this species (Beineke and Masters 1973, Mckenna and Coggeshall 2018, Mckenna and O'Connor 2014, Michler et al. 2004). Beineke (1972) speculated that inbreeding from high-grading could be a cause for concern, but merchantable value was not associated with rare alleles that would be lost by thin-from-above practices (Robichaud et al. 2010). Efforts to improve stem form (straightness for log quality), heartwood color, and growth continue today at the Hardwood Tree Improvement and Regeneration Center at Purdue University (West Lafayette, IN).

Figure 7. This abundant black walnut fruit crop is maturing on a grafted tree in a seed orchard. (Photo by M. Coggeshall, USDA Forest Service, 2003)

Seed-Transfer Considerations

A series of provenance trials highlighted clinal variation in black walnut, especially for variation between extreme sites (Bey 1976). Cold tolerance, which is a limiting factor for seed transfer, also varies clinally and latitudinally, with 40 percent of height growth attributed to latitude alone (Williams et al. 1974). Cessation of late-season growth is more differentiated than budbreak timing in the spring. Bey et al. (1971) found that southern sources started growing 3 days earlier and continued for 2 weeks longer than northern sources. Leaf fall is also strongly associated with latitude.

Optimal seed-transfer distances depend, in part, on the location of the planting site relative to the range edge. Populations along the southern range edge may experience insufficient chilling hours to break bud dormancy (Morin et al. 2007), especially if northern sources are moved south two or more USDA Hardiness Zones (e.g., from zone 5 to zone 7) (U.S. Department of Agriculture, Agricultural Research Service 2012). Published seed-transfer zones for black walnut have not been widely implemented (Deneke et al. 1980), but sources from up to 200 mi (322 km) south of the planting site are recommended for production forestry, except in extreme northern sites where local sources are best (Bey et al. 1971, Bey 1980, Bresnan et al. 1994, Clausen 1983, Rink and Van Sambeek 1988, Wendel and Dorn 1985). The improvement in growth attained by planting southerly sources may be due to an extended growing season because southern sources flush earlier and drop leaves later than northern (or local) sources when moved northward (Bey et al. 1971). For restoration, managers may consider combining local sources with sources from as far as 200 mi (322 km) south of the planting site to ensure that seedlings have sufficient cold tolerance to survive and thrive on the site. See table 1 for a summary of seed-transfer considerations.

Table 1. Summary of silvics, biology, and transfer considerations for black walnut.

	Black walnut, *Juglans nigra*
Genetics	• Genetic diversity: high • Gene flow: high
Cone and seed traits	• Large, hard, recalcitrant seeds can be freezer stored for 2 to 3 years; seeds can be sown with husk intact (Rink 1988) • 11 to 100 cleaned seeds per pound (25 to 220 per kg) (Bonner 2008)
Insect and disease	• Anthracnose (leaf disease) • Thousand cankers disease (vectored by walnut twig beetle) may become problematic with increasing drought • Shoot borers and ambrosia beetles can cause dieback and degrade form, especially in stressed trees
Palatability to browse	• Browse and antler rub slow growth and degrade value where white-tailed deer pressure is high
Maximum transfer distances	• 200 to 300 mi (322 to 483 km) from south to north is recommended to maximize growth • Local sources are recommended for reforesting along the northern range edge
Range-expansion potential	• Likely to migrate northward, but may be limited by soil and moisture conditions • Phytotoxicity of juglone may affect understory or adjacent plant communities

Black walnut exhibits sensitivity to local climate. Average July temperature and length of growing season were strongly correlated with height growth of 15-year-old trees, compared with other factors such as January temperature and annual precipitation (Smith 1983). Cold temperatures during the active growing season are more important than nadir winter temperatures because fully dormant tissues across provenances are cold hardy to extreme temperatures (George et al. 1977). Rainfall is an important determinant of height growth during periods of active growth (Bey et al. 1971), whereas temperatures of air and soil are more important for determining diameter growth (Bey et al. 1971). In provenance trials, mean annual temperature of the seed source also explained strong clines in tree heights (Leites et al. 2019).

Insects and Diseases

Black walnut has many minor pests and pathogens that feed on foliage, roots, fruit, and stems. These pests can reduce commercial value, but few currently pose major health risks. Several summaries of insect and disease pests have been published and are recommended for more detailed information (Katovich 2004, Mielke and Ostry 2004, Miller 1973).

Insect pests include shoot borers such as *Acrobasis demotella* Grote, which can reduce the dominance of the apical stem and degrade commercial value, but generally do not threaten survival (Katovich 2004). Other shoot borers (e.g., *A. caryivorella* Ragonot and *A. juglandis* LeBaron) feed on black walnut buds, emerging shoots, and leaves, but are usually less common than *A. demotella* (Miller 1973). Ambrosia beetles (*Xylosandrus germanus* [Blandford]), can attack healthy or declining trees causing dieback and sprouting from the tree's base (Katovich 2004). The shoot moth (*Gwendolina concitatricana* Heinrich) can injure or kill terminal buds, reducing commercial value. Walnuts are a favored food source for numerous other insects such as curculios, weevils (e.g., *Conotrachelus retentus* Say) and husk flies (*Rhagoletis suavis* Loew) (Miller 1973), which can become problematic in seed orchards. Lepidopterans may be commonly found on walnuts (Nixon and McPherson 1977), but usually pose few threats to tree health except for walnut caterpillar (*Datana integerrima* Grote & Robinson), which can become locally abundant in certain years and degrade tree vigor (Farris et al. 1982).

Anthracnose (*Gnomonia leptostyla* [Fr.] Ces. & De Not.), the most important foliar disease of black walnut, causes leaves to drop prematurely on susceptible trees, but its association with reduced growth is still not solidly established. Walnut bunch disease, or walnut witches'-broom, believed to be incited by a mycoplasma like organism (Chen et al. 1992), is less common than anthracnose but can lead to stunted crowns and mortality (Berry 1973). *Phytophthera citricola* Sawada, *Cyclindrocladium* species, *Pythium* species, and *Fusarium episphaeria* (Tode) W.C. Snyder & H.N. Hansen, are root pathogens generally associated with mortality of black walnut seedlings growing in nurseries. These root pathogens can be difficult to control even with fumigation (Berry 1973). Thousand canker disease (*Geosmithia morbida* M.Kolařík, E.Freeland, C.Utley, & Tisserat) vectored by walnut twig beetle (*Pityophthorus juglandis* Blackman) (Grant et al. 2011, Sitz et al. 2021) may pose a threat in the future in areas that experience persistent drought such as parts of the Western United States where black walnut is not native (Tisserat et al. 2011).

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