Sugar Maple: Guidance for Seed Transfer Within the Eastern United States

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Abstract

Sugar maple (*Acer saccharum* Marsh.) is a shade-tolerant hardwood tree native to forests across eastern North America. Genetic diversity of this species is high due to high levels of seed dispersal and pollen flow. Population structure is moderate along range edges where populations are isolated and gene flow may be limited. Sugar maple may hybridize with southern maple (*A. floridanum* [Chapm.] Pax), but hybridization events are considered rare. Common garden studies revealed relatively weak clines for growth traits and strong variation in phenological traits, although few common gardens exist. Seed transfer distances up to 200 mi (322 km), or roughly 2 degrees latitude northward, are considered a safe recommendation to avoid phenological mismatches. Widespread decline reported in New England and the Lake States has been attributed to insects and diseases on mature trees. Pear thrips, defoliators, *Eutypella*, and *Armillaria* fungi may impact seedlings and mature trees. Sugar maple is likely to expand northward with climate change, but southern populations may be subject to inbreeding from increased isolation among discontinuous stands.

Introduction

Sugar maple (*Acer saccharum* Marsh.) is a late-successional, shade-tolerant (Canham 1988), broad-leaved tree species, native to the United States and Canada. The bark is dark gray and exhibits different morphotypes ranging from flat plates, to raised shells, to elongated protrusions (Sajdak 1968). The species is renown for its colorful fall foliage that can vary from yellow to red (figure 1). Sugar maple occurs across eastern North America with disjunct populations in the tropics, occurring at high elevations as far south as Guatemala (Vargas-Rodriguez

Figure 1. Maple leaves vary from yellow to orange in the fall, creating a patchwork of colors that is a major attraction to tourists across the Northern United States. (Photo by Carolyn Pike, 2021)

et al. 2015). Sugar maple is believed to have had one southern glacial refugium that spread north and westward at the end of the last ice age (Miller and Parker 2009). A study that incorporated disjunct sugar maple populations, however, found that multiple glacial refugia may better explain the current geographic range in temperate and tropical forests (Vargas-Rodriguez et al. 2015).

Sugar maple has a broad ecological amplitude and can grow in northern hardwood (figure 2) and southern boreal forests on a variety of soil types and substrates (Barras and Kellman 1998) but grows best on well-drained loams (Godman et al. 1990). The species has high shade tolerance and is sympatric with basswood (*Tilia americana* L.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), and black cherry (*Prunus serotina* Ehrh.). In addition, its roots exude a leachate that has some allelopathic properties that may enhance its competitive ability in northern hardwood forests (Tubbs 1973). Sugar maple regeneration is most common from seed, which can successfully establish on a wide range of substrates, such as rotten wood, bare soil, and leaf litter (Caspersen and Saprunoff 2005). Artificial regeneration is relatively uncommon because of the species' propensity to regenerate naturally in the understory (figure 3).

Sugar maple is projected to adapt well to climate change because of its shade tolerance; ability to shift northward; plasticity (Peters et al. 2020, Prasad et al. 2020); and capacity to inhabit a wider climatic range than it currently occupies (Putnam and Reich 2017). Populations within the current southern range of sugar maple have not yet shown evidence

Figure 2. This mature stand of sugar maple in Wisconsin was recently thinned to allow light to reach the forest floor. (Photo by Christel Kern, USDA Forest Service, 2021)

Figure 3. Sugar maple is highly shade-tolerant and regenerates readily in full and partial shade of the understory. (Photo by Carolyn Pike, 2021)

of range contraction (Hart et al. 2014). Optimum temperatures for sugar maple germination may be higher than current norms, so the species should not be limited by germination temperature in the future (McCarragher et al. 2011). Wide-ranging dendrochronological studies failed to correlate radial growth with any single climate factor and concluded that the species is highly plastic, which bodes well for its ability to adapt to novel climates (Copenheaver et al. 2020).

Sugar production from sugar maple trees (figure 4) is, and has always been, a major food source for tribes (Chamberlain 1891) and an important commodity to rural economies across the species' range. Sugar production is likely to be impacted by climate change, leading to concerns about the sustainability of this resource (Oswald et al. 2018, Rapp et al. 2020). The zone of optimum production may shift north from the 43rd to the 45th parallel (Rapp et al. 2020), or syrup yield may remain relatively stable across a broad latitudinal and temperature gradient (Houle and Duchesne 2020). Researchers agree that the annual sap-collection season will begin and end earlier due to earlier freeze/thaw cycles (Rapp et al. 2020, Skinner et al. 2010). More information on this taxon can be found in Godman et al. (1990) and Nesom and Moore (2006).

Genetics

Sugar maple, a monoecious diploid (Kriebel 1957), is self-compatible, although selfing rarely produces viable seed (Gabriel 1967). Pollen, shed in the spring, is both wind- and insect-dispersed (Gabriel and Garrett 1984) and capable of long-distance dispersal (Khodwekar et al. 2015). The species is also highly dichogamic with male and female organs maturing at different time intervals: on some trees, males

Figure 4. Maple syrup is a major industry for residents of northern States and an important food source for tribes. In this image, a maple tap is testing for sugar content, in the early spring at a sugar maple forest in Michigan. (Photo by Paul Bloese, 2014)

mature before females (protandry), while on other trees, females mature before males (protogyny) (Gabriel 1968). This flowering asynchrony among trees within a stand may lower local gene flow or genetic diversity since not all combinations of outcrosses are likely (Gabriel 1968). Seeds are medium-sized double samaras, averaging 15,540 seeds per lb (7,030 per kg) and are dispersed in the fall (Zasada and Strong 2008). Usually, only one of the paired samaras contains a viable seed (Godman et al. 1990).

The taxonomy of sugar maple is not yet settled. Black maple (*Acer nigrum* F. Michx.), the closest relative to sugar maple (Jackson et al. 2020), is sometimes considered a subspecies (*Acer saccharum* ssp. *nigrum*) and may hybridize with sugar maple in the Central United States where their ranges overlap (Gabriel 1973, Skepner and Krane 1998). Florida maple (*Acer floridanum* [Chapm.] Pax or *Acer barbatum* Mich.), also known as southern maple, has relatively disjunct populations and is sometimes considered a subspecies (*Acer saccharum* var. *floridanum* [Chapm.] Small & A. Heller). Kriebel (1975) recognized sugar maple as a single species with multiple forms—saccharum, nigrum, and floridanum—which correspond to the species *A. saccharum*, *A. nigrum*, and *A. floridanum*. Despite its complicated taxonomy, hybridization of sugar maple with black maple or Florida maple is not known to widely occur.

The amount of genetic diversity and gene flow varies across the geographic range of sugar maple. Low to moderate genetic diversity is reported in tropical populations where stands are disjunct and isolated (Vargas-Rodriguez et al. 2015). Where sugar maple stands are contiguous, genetic diversity is high and rare alleles are uncommon (Foré et al. 1992, Foré and Hickey 1992, Graignic et al. 2016, Gunter et al. 2000, Khodwekar et al. 2015). Genetic diversity of southern populations in eastern Tennessee may exceed northern populations in Wisconsin (Gunter et al. 2000) due to the presence of rare alleles in the southern populations. Because sugar maple populations along the southern range edge are relatively isolated, rare alleles that evolve are not as readily dispersed to other populations. This low dispersal results in inflated estimates of genetic diversity, which may be an artifact of reduced gene flow or prior hybridization with *A. floridanum* or *A. nigrum*.

Across most of its range, even where populations are relatively continuous, moderate levels of spatial genetic structure have been reported for sugar maple, likely from occasional inbreeding and limited seed dispersal (Geburek 1993; Geburek and Knowles 1992; Perry and Knowles 1988, 1991; Young et al. 1993). Sugar maple's opportunistic nature may also explain this phenomenon. Sugar maple proliferates in the understory of uneven-aged stands resulting in cohorts that are uniquely positioned to take advantage of light gaps or other resource pulses. These cohorts contribute seeds during years when gaps or other favorable conditions are randomly created, resulting in their disproportionate representation. These synchronous cohorts are shaped by a combination of random events and natural selection (Mulcahy 1975).

Seed-Transfer Considerations

Sugar maple growth traits such as height, stem diameter, and leaf tannin content generally exhibit weak clinal (provenance) variation, as observed in both common gardens (Baldwin et al. 1987) and natural stands (Gunter et al. 2000). Conversely, phenological traits often follow predictable geographic patterns. For example, timing of fall coloration exhibited strong latitudinal trends, with sources from northern latitudes (from cooler climates) exhibiting coloration earlier than southern sources (from warmer climates). Similarly, northern sources tend to leaf out earlier in the spring and senesce earlier in the fall than southern sources (Kriebel 1957, Kriebel and Wang 1962, Putnam and Reich 2017, Ren et al. 2020). In common garden studies, sugar maple trees originating from northerly regions (relative to a common garden) are prone to damage from early spring frosts, while trees from southerly sources are more prone to damage from fall frosts (Kriebel 1975). Drought resistance is generally higher in sugar maple trees that originate from dry climates relative to seed sources from cool, moist climates. Sun scorch and leaf injury following extreme summer heat were more severe on northern genotypes than southern genotypes in a common garden trial (Kriebel 1975). Sun scorch also exhibited east-west clines in which sources from Ohio had more leaf damage than sources from Illinois.

Kriebel (1975) defined three ecotypes of sugar maple corresponding to northern, central, and southern populations based on a variety of phenological traits (table 1). For these reasons, Kriebel (1975) defined a local seed source as one that originated within 100 mi (161 km) from the planting site. No other studies have assessed sugar maple seed-transfer distances empirically, so this recommendation may not apply to other parts of its range. Given that sugar maple is likely to expand its range northward with climate change (Caspersen and Saprunoff 2005) and is highly plastic (Guo et al. 2020), it is likely tolerant to seed-transfer distance up to 200 mi (322 km) in the Northern United States. Seed transfer guidelines are summarized in Table 2.

Table 1. A summary of traits for major subgroups of sugar maple based on Kriebel (1957).

Sugar maple population	Drought resistance	Susceptibility to leaf damage during summer	Cold resistance	Apical dominance
Northern	low	high	high	strong
Central	high	moderate	high	strong
Southern	high	high	low	weak

Insect and Diseases

Insects and diseases that impact growth and survival of mature sugar maple have been extensively studied, especially across New England. Defoliators are the most common insects that affect sugar maple, including native species such as forest tent caterpillar (*Malacosoma disstria* Hbn.) (Gross 1991), which affects sugar maple in New England and, to a lesser degree, across the Lake States (Minnesota and Wisconsin). The Bruce spanworm (*Operophtora bruceata* [Hulst]) and saddled prominent (*Heterocampa guttivitta* [Walker]), both native caterpillars, also feed on sugar maple (Houston et al. 1990). Pear thrips (*Taeniothrips inconsequens* [Uzel]) (Gardescu 2003) is the most important nonnative defoliator of sugar maple as its feeding can also introduce anthracnose fungi (*Discula campestris* [Pass.] Arx) (Brownbridge et al. 1999, Stanosz 1993). Sugar maple is not considered a primary host for the nonnative spongy moth (formerly gypsy moth) (*Lymantria dispar* L.) (Barbosa and Greenblatt 1979). Seedlings may also be defoliated by caterpillars in the Tortricidae including (*Clepsis melaleucana* Walker) (a native generalist caterpillar) and by European slugs (*Arion subfuscus* Draparnaud). Herbivory from a

Table 2. Summary of silvics, biology, and transfer considerations for sugar maple.

Sugar maple, *Acer saccharum* (Marsh.)	
Genetics	• Genetic diversity: high • Gene flow (pollen): high • Gene flow (seed): moderate to high
Cone and seed traits	• Medium-sized, winged seeds • 7,070 to 20,110 cleaned seeds per pound (3,200 to 9,100 per kg)
Insect and disease	• Forest tent caterpillar, pear thrips, sugar maple borer, and Asian longhorned beetle • Armillaria, anthracnose, and Eutypella canker
Palatability to browse	• Moderately palatable to deer browse
Maximum transfer distances	• Seed-transfer distances have not been tested across its range • Based on common garden studies, 100 to 200 mi (161 to 322 km) is the longest recommended seed-transfer distance
Range-expansion potential	• Northward potential is high • No evidence of southern range-edge contraction • Southern range-edge populations may become more disjunct and isolated

variety of other insects such as leafhoppers (*Typhlocyba* spp.) was reported as well (Gardescu 2003). Sugar maple borer (*Glycobius speciosus* [Say]) significantly impacts wood quality on mature trees with low vigor, especially after defoliation events (Wink and Allen 2003). Sugar maple is a preferred host of Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky), a large beetle native to Asia that travels on firewood and on pallets used for international shipping (APHIS 2022).

Mature trees and seedlings can be impacted by native *Armillaria calvescens* Bérubé & Dessureault (Bauce and Allen 1992), anthracnose (*Glomerella cingulate* (Stoneman) Spauld. & H. Schrenk), and leaf spot fungi such as *Cristulariella depraedans* (Cooke) Hohn (Gardescu 2003). Cankers caused by *Eutypella parasitica* Davidson and Lorenz usually occur on the lower bole (Kessler and Hatfield 1972, Kliejunas and Kuntz 1974). Other factors contributing to decline episodes in sugar maple stands include drought coupled with prior defoliation events (Horsley et al. 2002, Payette et al. 1996), climatic factors (Bauce and Allen 1991), and nutrient stress in New England (Bal et al. 2015) and Pennsylvania (Bailey et al. 2004).

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