Northern Red Oak: Guidance for Seed Transfer Within the Eastern United States

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Abstract

Northern red oak (*Quercus rubra* L.) is a large-seeded hardwood that grows in forests across eastern North America. Genetic diversity of this species is high due to high levels of seed dispersal and pollen flow and from hybridization with other species in the red oak section. Hybridization occurs readily across its range except in the northern parts of the range where other species in the red oak family are less common. Northern red oak is expected to thrive in a future climate because of its genetic diversity and inherent plasticity. Common garden studies revealed relatively weak clines for growth traits. No empirical transfer distances have been suggested, but distances of 200 mi (322 km), or roughly 3 degrees latitude northward, is a safe recommendation to avoid phenological mismatches. Oak wilt, a pathogen of concern, is slowly spreading across its range and may become more problematic in the future. Several insects impact northern red oak but are generally more problematic in older stands or stands that are weakened by other causes.

Introduction

Northern red oak (*Quercus rubra* L.) is a long-lived, mesic hardwood that is widely distributed across the eastern half of North America from Maine and the Canadian Maritimes, west to Minnesota, and as far south as Arkansas, Alabama, and Georgia. Studies of pollen records suggest that *Quercus* refugia were likely scattered across the lower Mississippi Valley and northern Florida followed by rapid recolonization concurrent with ice sheet retreat 18,000 years before present (Davis 1983). Northern red oak is associated with deep, well-draining soils but can tolerate a range of soil textures from loams to silty clay loams. Northern red oak is generally associated with north or easterly aspects and lower elevations. Regeneration of northern red oak can occur from seed (acorns) (figure 1), and stumps can also coppice. Leaves of northern red oak have pointy tips (figure 2) which are readily distinguished from the rounded tips of white oak (*Quercus alba* L.) leaves.

Figure 1. Acorns of northern red oak are oblong with a flat, scaly cap. (Photo by Carolyn C. Pike, 2018)

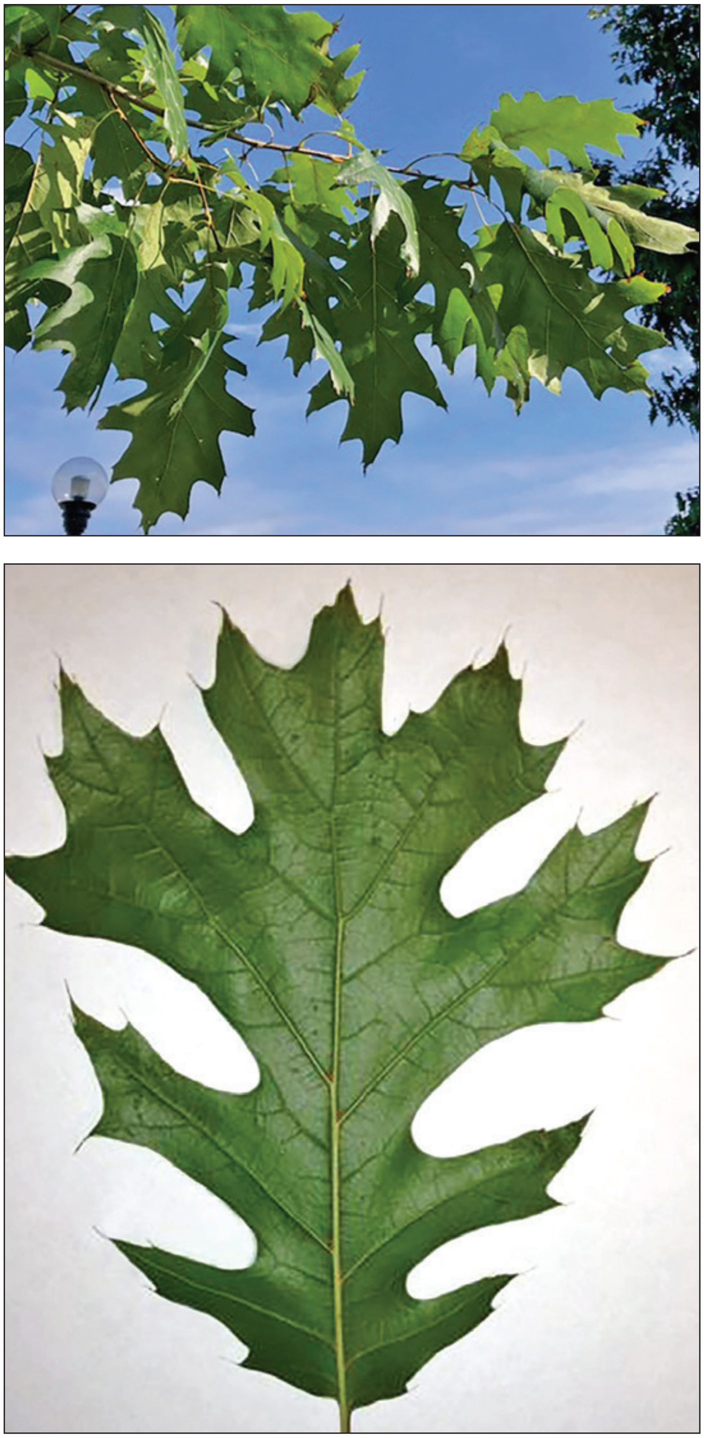

Figure 2. Leaves of northern red oak are oblong with toothed lobes and sharply pointed leaves. (Photos by Mark Coggeshall, 2021)

The bark of northern red oak trees is variable but is generally dark gray with shallow fissures (figure 3). Northern red oak readily hybridizes with other species in the Lobatae section including scarlet oak (*Q. coccinea* Muenchh.), northern pin oak (*Q. ellipsoidalis* E.J. Hill), bear oak (*Q. ilicifolia* Wangenh.), shingle oak (*Q. imbricaria* Michx.), blackjack oak (*Q. marilandica* Muenchh.), water oak (*Q. nigra* L.), pin oak (*Q. palustris* Muenchh.), willow oak (*Q. phellos* L.), black oak (*Q. velutina* Lam.), and Shumard oak (*Q. shumardii* Buckl.) (figure 4). Hybrids can sometimes be difficult to detect morphologically (Aldrich et al. 2003) and may require molecular assessments to confirm. Hybridization does not occur with species in the white oak section (Leucobalanus).

Northern red oak is intermediate in its shade tolerance and can tolerate light shade (Gottschalk 1994, Phares 1970). Shelterwoods are a common silvicultural practice in northern red oak stands (Dey and Parker 1996), though regeneration success can be unreliable if a strong cohort of seedlings is absent before, or immediately after, the first cut. Fencing is often required to protect seedlings from herbivory (Miller et al. 2004, Redick et al. 2020), while management to control competing vegetation (yellow poplar [*Liriodendron tulipifera* L.], red maple *[Acer rubrum* L.], or sugar maple [*Acer saccharum* Marshall]) may also be needed to enable northern red oak to survive or thrive (Morrissey et al. 2010). Northern red oak is the

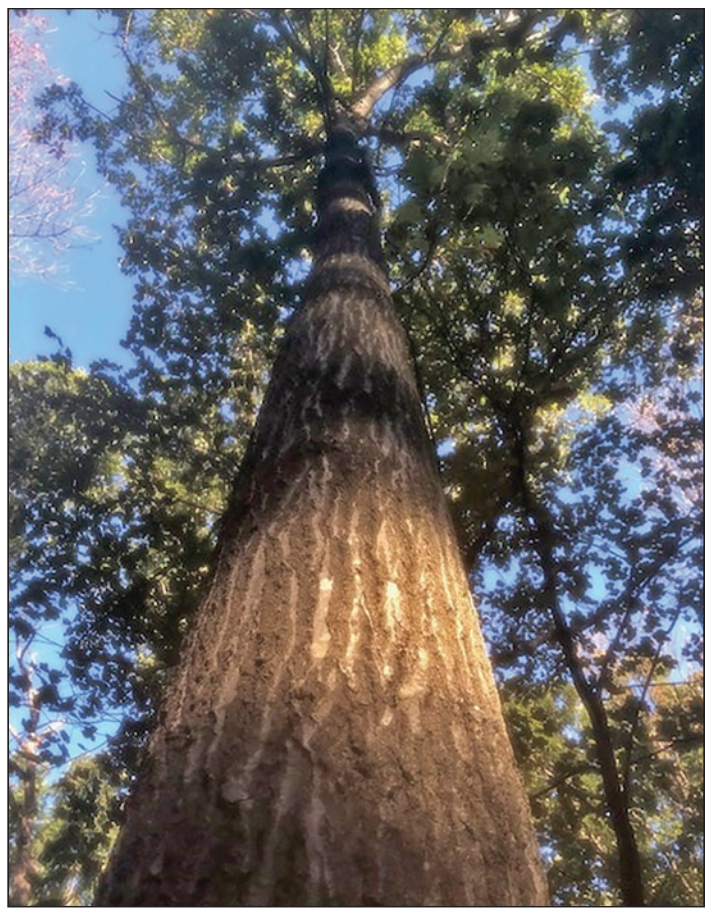

Figure 3. The bark of northern red oak is dark gray and scaly with ridges, but the species lacks the deeper fissures of others in the red oak family. (Photo by Mark Coggeshall, 2021)

most-planted hardwood tree in the Northeastern United States (Pike et al. 2018) and suitable for planting across a variety of site types including riparian areas and reclaimed minelands (Adams 2017). The species is more commonly propagated as a bareroot seedling because of its prodigious root system (figure 5).

Genetics

Genetic structure of neutral DNA markers in northern red oak is more prominent latitudinally than longitudinally (Birchenko et al. 2009, Magni et al. 2005), likely due to the northward re-colonization that followed glacial recession that was more rapid compared to other deciduous tree species (Davis 1983). Genetic diversity and gene flow in northern red oak is very high. The species is a complete out-crosser, and inbreeding is very low in natural stands (Schwarzmann and Gerhold 1991, Sork et al. 1993). The exceptionally high genetic diversity of northern red oak (compared to other hardwoods) is due, in part, to its ability to hybridize with other species in the Lobatae section, a feature that has resulted in weak phylogenetic structure, or weak differentiation, from other taxa in the red oak family (Magni et al. 2005). Despite its high gene flow, caching habits of its primary seed dispersers (squirrels) can create fine-scale genetic structure locally (Sork et al. 1993).

Northern red oak is monoecious, wherein trees may produce both male and female reproductive structures on the same individual. Pollen is wind-dispersed, and acorns can be animal dispersed, primarily by gray squirrels, fox squirrels, and blue jays. The timing of pollen shed and female receptivity may be asynchronized among trees within a seed orchard or stand. This asynchronous phenology, in which the same subset of trees share pollen from year to year, contributes to the presence of a Wahlund effect whereby pollen is not shared equally among trees (Alexander and Woeste 2017, Jones et al. 2006, Moran and Clark 2012). Such effects can reduce expected levels of genetic diversity but can be offset by mixing seed from many sources and stands within a seed lot.

Seed-Transfer Considerations

Phenotypic variation in northern red oak is generally not attributed to provenance of seed source (Deneke 1974, Kriebel et al. 1976, Kriebel et al. 1988, Leites et al. 2019) (figure 6). For example, family differences in acorn size and first-year seedling growth superseded differences among provenances, except for extreme far northern seed sources (Kriebel 1965). Even though provenance accounted for low levels of variation in older provenance trials, physiological differences in young seedlings planted in common gardens in Minnesota were detectable between northern seed sources (Etterson et al. 2020). Geographic clines (north to south) are also evident for phenological traits such as date of flushing and timing of leaf coloration in the fall, although elevation, and to a lesser extent longitude, of seed origin can also affect leaf flushing and coloration (Schlarbaum and Bagley 1981). Older northern red oak trees from southern and western provenances had thicker bark than those from northern and

Figure 4. Northern red oak can naturally hybridize with other trees in the red oak family, such as Shumard oak (*Quercus shumardii*). The hybrids, as shown in this image, can be difficult to detect morphologically as hybrids may resemble one parent or have traits of both. (Photo by Mark Coggeshall, 2021)

Figure 5. Northern red oak seedlings have prodigious root systems that thrive in bareroot culture but may also be grown in large containers. (Photo by Mark Coggeshall, 2013)

eastern provenances, which is likely a fire adaptation attributed to sources originating from drier portions of its range (Russell and Dawson 1994). Radial growth in natural stands was most significantly correlated with early-season moisture from May through July (LeBlanc and Terrell 2011).

No studies to date have empirically assessed seed-transfer distances, but northern red oak is highly tolerant of long-distance seed transfers (Schlarbaum 2021). A reassessment of older provenance trials revealed local adaptation in which southern sources were best in mild environments and northern sources were most suited to cool environments (Leites et al. 2019). Height growth in common gardens was most strongly correlated with maximum summer temperatures; correlations with minimum temperatures and growing season length were not significant (Leites et al. 2019). Assisted migration (i.e., moving seed sources at least one zone northward) may help offset adaptation lags. Western edge populations that are adapted to drier climates may be favored for areas where droughts are predicted to be more prevalent. Northward transfer distances of 200 mi (322 km), or roughly 3 degrees latitude, is likely a safe recommendation to avoid phenological mismatches but has not been explicitly tested. This distance is also recommended for conifers such as white spruce (*Picea glauca* [Moench] Voss), where genetic diversity is high among families but low among provenances (Thomson et al. 2010). Considerations for seed transfer are summarized in table 1. Northern red oak is well suited for planting in the future because of its high genetic diversity, plasticity, fecundity from high seed production, and ability to regenerate from both stumps and seed. It also has strong juvenile growth allowing it to quickly establish on a new site.

Insect and Diseases

Red oak is often defoliated by insects, such as the nonnative gypsy moth (*Lymantria dispar*). Periodic outbreaks of native defoliators, such as fall cankerworm (*Alsophila pometaria*) and forest tent caterpillar (*Malacosoma disstria* Hubner), can feed on northern red oak in the spring leading to stress and predisposition to decline from other factors (Asaro and Chamberlin 2019). Drought events can stress northern red oak, rendering it more vulnerable to red oak borer (*Enaphalodes rufulus* [Haldeman]) and two-lined chestnut borer (*Agrilus bilineatus*), especially

Table 1. Summary of silvics, biology, and transfer considerations for northern red oak..

Northern red oak, *Quecus rubra* L.	
Genetics	• Genetic diversity: high • Gene flow: high to moderate • Does not readily inbreed and will not self-cross • Readily hybridizes with other oaks in the red oak section
Cone and seed traits	• Large seeded: 75 to 255 cleaned seeds per pound (165 to 561 per kg) (Bonner 2012) • Mammal dispersed
Insect and disease	• Defoliating insects: gypsy moth, two-lined chestnut borer • Pathogens: oak wilt is a growing threat
Palatability to browse	• High risk of browse from deer; seedlings often require protection
Maximum transfer distances	• No empirical transfer distances have been calculated • High tolerance to long-distance transfer • Transfer of 200 mi (322 km) (3° latitude from south to north) is likely well tolerated
Range-expansion potential	• Northward potential is high • Likely to maintain populations in current range

Figure 6. This range-wide provenance trial (17 years from planting) is one of several common gardens analyzed to study the geographic patterns of variation in northern red oak. (Photo by Mark Coggeshall, 2008)

following defoliation events. Oak wilt (*Ceratocystis fagacearum*) is also a concern and can limit management efforts from mid-March through mid-July due to activity of insect vectors like bark beetles and ambrosia beetles (*Scolytinae*) and picnic beetles and sap beetles (*Nitidulidae*). Oak borers (*Enaphalodes rufulus*) are active in late spring/early summer and will attack wounded (pruned) trees and others in close proximity. Bacterial leaf scorch (*Xylella fastidiosa*) of northern red oak has symptoms similar to oak wilt, but trees will decline in health over several years before they succumb and die.

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