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Black and Chestnut Oak Seedling Response to Glaciated Soil: Implications for Northward Expansion in Response to Climate Warming

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Species ranges are expected to move northward with climate warming. However, species will likely encounter soil conditions that differ from their historic ranges. Black (*Quercus velutina*) and chestnut (*Q. montana*) oaks are expected to do well in climates that are hotter and drier, but it is unknown as to how they respond to soils of different geological histories. At a glaciated and nonglaciated site in northwestern Pennsylvania, we compared the growth, biomass allocation, and mycorrhizal association for black and chestnut oak seedlings at two different levels of light. On nutrient-poor, nonglaciated soils at high light levels, both species had greater growth and biomass accumulation than on nutrient-rich, glaciated soils. However, at low light levels, these responses were greatest on glaciated soils, especially for chestnut oak. Although mycorrhizal association was beneficial on nonglaciated soil at high light levels, low light levels were associated with reduced growth when compared to glaciated soils. In low light and nutrient-poor soils, mycorrhizal association may result in a carbon sink with lower net photosynthesis, as carbon for plant growth is, instead, allocated to the mycorrhizae symbiont. Variable species response to soil types indicates reduced performance for black and chestnut oak seedlings on high-quality glaciated soils especially in high light environments.

Keywords: *Quercus*, biomass, mycorrhizae, roots, light, specific leaf area

Although plant distribution and community composition are determined by continental scale climate patterns (Woodward 1987, Neilson 1995), vegetation patterns at the local and regional scale are more strongly related to edaphic and topographic features (Ertsen et al. 1995, Iverson et al. 1997). As climate warms, many forest tree species are projected to expand northward (Woodall et al. 2009, Fei et al. 2017). Even with successful dispersal, species are likely to encounter soil and vegetation conditions that differ from their historic ranges (Lafleur et al. 2010). Understanding the role of soil factors in seedling performance will be important for understanding the consequences of migration to new locations and can also inform models for predicting the physiological response of a species in new competitive environments (Iverson and McKenzie 2013).

Black oak (*Quercus velutina* Lam.) and chestnut oak (*Quercus montana* Willd.) are two species in mixed-oak forests in eastern North America that may benefit from a warming and drying climate (McKenney et al. 2007, Landscape Change Research Group 2014). However, most models of suitable habitat do not often account for a species' physiological response to local ecological conditions from experimental data. Therefore, this study was initiated to explore the differential effects of glaciated versus nonglaciated soil on the growth of two oak species.

Black and chestnut oaks are considered drought-hardy, having ectomycorrhizal associates, with intermediate growth rates compared to other oak associates such as faster-growing northern red oak (*Q. rubra* L.) and slower-growing white oak (*Q. alba* L.). However, findings suggest that black oak seedling growth response is similar to that of white oak, whereas chestnut oak was similar to northern red or white oak at intermediate to high light levels (15 and 50 percent full sun) (Brose and Rebbeck 2017). Black oak has a broad geographic range primarily south of the last glacial maximum extent (Ehlers et al. 2011). Where their ranges overlap, chestnut

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oak has a more narrow site preference than black oak, and is typically found on drier ridge tops and less fertile sites (McQuilkin 1990). Climate-change predictors suggest that coarse-textured, erodible soils with a low pH will be drivers of the projected habitat for black oak, whereas high elevations and steeper slopes will have the greatest influence on chestnut oak (Matthews et al. 2011, Prasad et al. 2014). However, oak species' response to different soil types has not been well documented (Dey et al. 2009).

To determine the effect of glacial versus nonglacial soil on black oak and chestnut oak seedlings, we selected two sites representing distinct geological histories and soil conditions. The two sites were part of a broader silvicultural study investigating the effects of light level on oak seedling development and growth (Brose 2008, 2011, Brose and Rebbeck 2017). For this study, we measured growth, biomass, and mycorrhizal association across two levels of light intensity to compare seedling performance and morphology between these sites. We hypothesized that (1) in the absence of competition, both oak species would have a higher performance on nutrient-rich, glaciated soil because of greater resource availability; (2) mycorrhizal infection would be greatest on nutrient-poor, nonglaciated soil to aid in resource scavenging; and (3) measured morphological and physiological responses would reflect a greater shade tolerance and wider range adaptability of black oak than chestnut oak.

Methods and Materials

Study Sites and Data Collection

This study was conducted on two sites representing distinct geological histories with both occurring in the Appalachian Plateau Province of northern Pennsylvania (Schultz 1999). The Pittsburgh Low Plateau (41°18′26″N, 79°00′29″W; referred to as the "nonglaciated site" hereafter) was never glaciated, and the Glaciated Allegheny Plateau (41°50′51″N, 80°13′42″W; referred to as the "glaciated site" hereafter) was glaciated during the Wisconsin Glacial Episode (Figure 1). Soils at the nonglaciated site were characterized as Typic Hapludult, DeKalb stony loams (Zarichansky 1964), whereas soils at the glaciated site were characterized as Aeric Fragiaqualf, Venango silt loams (Yaworski et al. 1979). Northern red oak was the dominant canopy species at both sites, but other associates were sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), and yellow poplar (*Liriodendron tulipifera* L.) at the glaciated sites, whereas the associates at nonglaciated sites were red maple (*Acer rubrum* L.), sweet birch (*Betula lenta* L.), black cherry (*Prunus serotina* Ehrh.), white oak, and chestnut oak. The sites are located on broad, flat hilltops with minimal slope or aspect and have cool, humid summers and cold, snowy winters. Temperatures average 46° F (8° C) annually with means of 14° F (–10° C) minimum and 79° F (26° C) maximum, in January and July, respectively. Precipitation occurs throughout the year with a mean annual precipitation of 42 inches (1,060 mm) of rain and 72 inches (1,840 mm) of snow (Brose 2008). Snowfall is higher and the number of growing days longer at the glaciated site than at the nonglaciated site [snowfall: 93 versus 40 inches (2,370 versus 1,010 mm), respectively; growing days: 140 versus 116 days, respectively). The site index for northern red oak$_{50}$ averaged 75 feet (23 m) at the nonglaciated site and 89 feet (27 m) at the glaciated site.

In 2001, four oak stands, greater than 10 acres (4 hectares) and within 219 yards (200 m) of each other, were selected at each site. Two of these stands were heavily thinned, resulting in a high light understory averaging 54 ± 4 percent full sunlight. The remaining two stands were thinned lightly or uncut; creating a low light understory averaging 10 ± 1 percent of full sunlight at each site. The percentage full sunlight was determined with a ceptometer on uniformly overcast days with simultaneous measurements in fully open conditions. Within each stand, we established two separate 8 × 4 m species plots and, in the fall of 2001 or spring of 2002, planted 384 sound acorns of each species at a density of approximately 10 acorns per square yard (12 acorns/m^2). Black and chestnut oak acorns were selected from single, good form and quality, mother trees in northwestern Pennsylvania on nonglaciated soil and tested for soundness and uniformity prior to planting. Single source, half-sibling progeny was used to reduce seedling response because of genetics. Each plot was raked of leaf litter and tilled prior to planting. A wire mesh (0.25 inch [0.63 cm]) was placed over the plot to protect the planted acorns. Competing vegetation was managed with hand-pulling throughout the study duration.

Soil Sampling and Analysis

In 2001, five soil samples of the upper 12 inches (30 cm) were collected from the corners and center of each plot and composited into one sample to determine soil texture (percentage sand, silt, clay) (Bouyoucos 1961, Sheldrick and Wang 1993). Another portion was sent to the University of Maine Analytical Laboratory for chemical analysis. Soil pH was measured using distilled water. Organic matter (OM) was measured by loss on ignition at 375 °C. Nitrate (NO_3-N) and ammonium (NH_4-N) nitrogen were extracted in potassium chloride and measured colorimetrically by an autoanalyzer. Exchangeable acidity (acidity) was extracted in potassium chloride and measured by titration. All other nutrients were extracted in pH 4.8 ammonium acetate (Modified Morgan method) and measured by inductively coupled plasma atomic emission spectroscopy. Effective cation exchange capacity (ECEC) was calculated by the summation of milliequivalents of Ca, K, Mg, Na, and acidity.

Management and Policy Implications

Managing for new species compositions, including facilitated species movements to future climate-adapted locations, may require consideration of seedling performance on different site-specific soil types or other plant–habitat interactions. For example, practitioners are becoming increasingly interested in moving seed zones or species to new habitats that are more adapted to future climates to maintain ecosystem health and forest productivity. Although oak species are expected to do well in regions with warming and drying climates, other abiotic and species-specific factors may alter how new species interact and compete with existing vegetation. As indicated by our study, black and chestnut oak have different growth responses when established on glacial soil; further, growth varied by understory light level. Managers wishing to establish species along the leading edge of existing species ranges should consider field trials and experimental approaches to evaluate growth and performance at the local scale and within an anticipated management context. Further, robust monitoring programs across the expected future range may aid in the identification of source populations and locations with a high likelihood of success, as well as the management of new species assemblages.

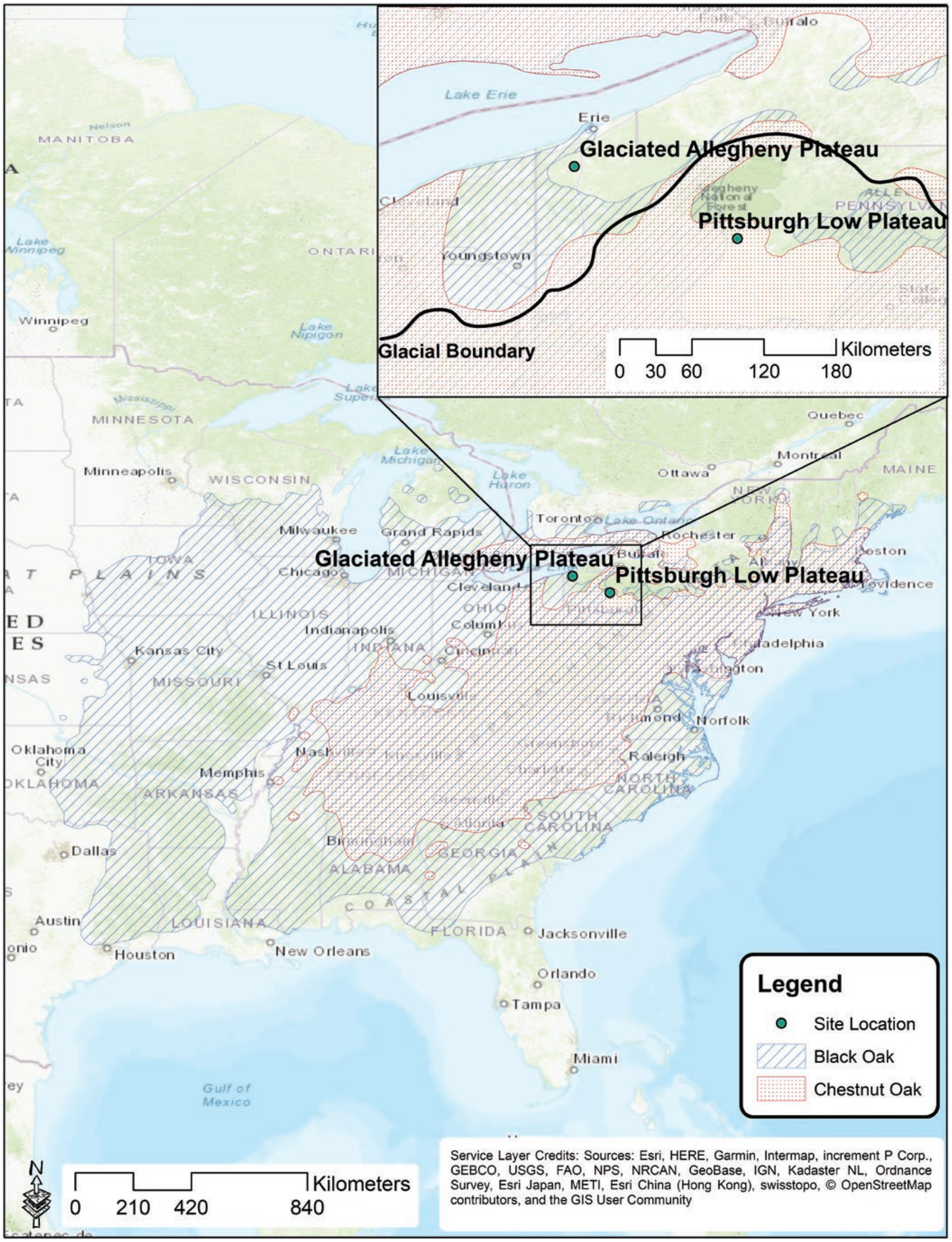

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Figure 1. Historical range of black and chestnut oak, study site locations, and glacial boundary (glacial boundary is approximated from Ehlers et al. 2011).

Seedling Sampling and Analysis

In the second (YR2; 2003) and third (YR3; 2004) growing seasons, six seedlings within each species plot were randomly selected for destructive sampling. In late August, each seedling was carefully excavated. Seedling height (inch), root collar diameter (RCD; inch), leaf number, leaf area (in^2), taproot length (inch), and the number of first-order (those attached directly to the taproot) lateral roots were measured and recorded. All root tips were assessed for visible mycorrhizal infection under magnification. The percentage of root tips with mycorrhizal infection was determined as the number of root tips with mycorrhizae divided by the total number of root tips for each seedling. Each seedling was dissected into stem, root, and leaves. Leaf area was determined with a LI-COR 3100 Leaf Area Meter (Lincoln, NE). Tissues were oven-dried at 122° F (50° C) to a constant mass, and dry biomass (g) was determined. The root-to-shoot ratio (RSR) was calculated as the dry root biomass divided by the woody shoot (without foliage) biomass. The specific leaf area (SLA; in.^{2} g dry mass^{-1}), the ratio of leaf area to unit leaf mass, was also determined.

Statistical Design and Analyses

Differences in soil chemical and textural properties were analyzed at the site level from plot means using an SAS GLIMMIX procedure (SAS Institute Inc., Cary, NC).

The experimental approach was a 2 × 2 factorial split-plot design with two replicates of each light condition at each soil type. We compared oak seedling growth, biomass, morphological characteristics, and mycorrhizal infection by soil type (glaciated and nonglaciated), species (BO and CO), year (YR2 and YR3), and their interactions among the two light levels ($n = 48$ in each level of light). Individual seedlings were treated as a random variable and nested within a split-plot, repeated-measures procedure in GLIMMIX using an unstructured covariance and maintaining all covariance parameters in the model. We analyzed the low and high light levels separately, as the effects of light on growth and allocation have been well documented elsewhere (Brose 2008, 2011, Brose and Rebbeck 2017).

Response distributions were determined prior to analysis, and those with a gamma or negative binomial distributions were fit within the GLIMMIX model. Using the SAS UNIVARIATE procedure, the residuals of each variable were tested visually for normality and using Shapiro–Wilk and Levene's homogeneity of variance test statistics. Effects were considered significant if $P \le .05$. Means and standard errors are reported in their original units.

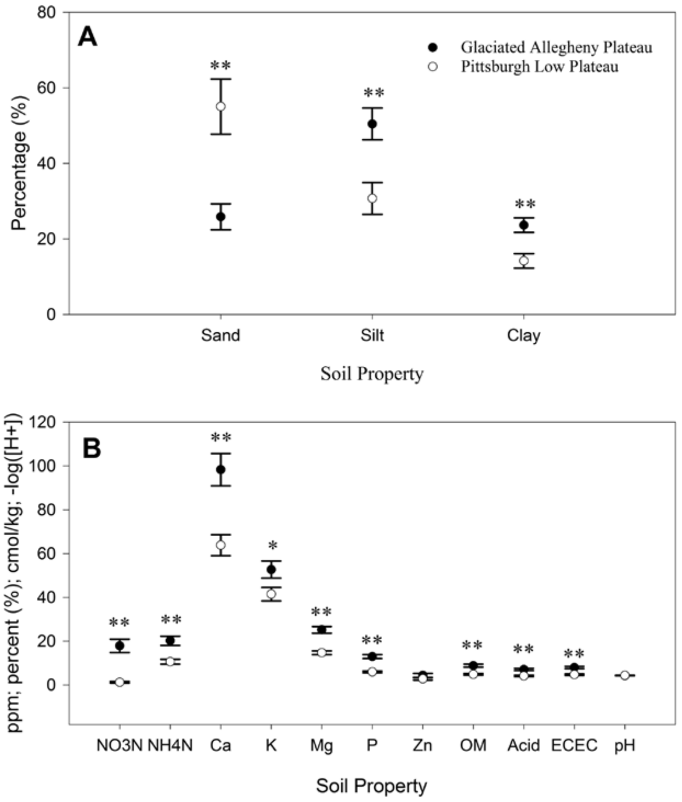

Figure 2. Soil physical (A) and chemical (B) properties at the glaciated soil type and nonglaciated soil type. Significant differences between sites are indicated with either a single asterisk (α = 0.05) or a double asterisk (α < 0.01).

Results

Soil Properties

Soil texture varied by site with glaciated soil having greater proportions of silt and clay than nonglaciated soil (Figure 2A). In contrast, nonglaciated soil had a greater proportion of sand. The glaciated soil was higher in nearly all soil chemical properties (NO$_3$-N, NH$_4$-N, Ca, K, Mg, P, percentage OM, acidity, and ECEC) than the nonglaciated soil (Figure 2B). However, the two soils did not differ in soil pH or Zn.

Seedling Response

As expected, many growth characteristics and mycorrhizal infection all increased from YR2 to YR3 regardless of light condition (Supplement 1, Tables 1 and 2). However, RCD at low light levels, remained constant from YR2 to YR3. In addition, interactions did occur between site, species, and year for stem, foliar, root, and total biomass (Supplement 2, Figure 2). Although general trends were still apparent, with increased biomasses from YR2 to YR3, and in high light, the nonglaciated site had larger biomasses, and in low light, the glaciated site had larger biomasses.

Hypothesis 1: Seedling Performance by Soil Type

Site was a significant factor in determining the relation for many growth characteristics including stem height, RCD, root tips with mycorrhizae, SLA, and stem, root, foliar, and total biomass. However, there were significant interactions between species and site for stem height in low light conditions and RCD at both levels of light (Supplement 2, Figure 1). At high light levels, seedlings grown at the nonglaciated site outperformed those grown at the glaciated site (Table 1). However, in low light levels, this relation was reversed (Table 2). SLA followed similar trends. At high light levels, SLA was highest at the nonglaciated site (Table 1), and at low light levels, SLA was highest in the glaciated site (Table 2).

Hypothesis 2: Mycorrhizal Associations by Site

At high light levels, mycorrhizal infection did not differ by site (Table 1). However, seedlings at low light levels had a higher percentage of root tips with mycorrhizae at the nonglaciated site than at the glaciated site (Table 2).

Hypothesis 3: Species Performance and Mycorrhizal Associations

There were few significant aboveground growth or biomass allocation differences between species (Supplement 1, Tables 1 and 2). At high light levels, chestnut oak had more first-order lateral roots than black oak (Table 1). At low light levels, biomass growth from Y2 to Y3 for chestnut oak was significantly suppressed at the nonglaciated site (Supplement 2, Figure 2). In general, chestnut oak had more root tips than black oak (Tables 1 and 2). At low light levels, black oak had a larger RSR and smaller SLA than chestnut oak (Table 2). In addition, chestnut oak at low light levels had a higher percentage of mycorrhizal infected roots tips than black oak (Table 2).

Table 1. Effect of site, species, year, and their interactions on mean (SE) seedling growth and development characteristics within the light environment, at high light levels.

	Site[a]		Species[b]		Year[c]	
	GAP	PLP	BO	CO	YR2	YR3
Aboveground						
Stem height (cm)	19.0 (2.5)^{2}	27.9 (3.6)^{1}	21.0 (2.7)	25.2 (3.3)	19.5 (1.9)^{2}	27.2 (2.3)^{1}
Root collar diameter (mm)	6 (0.3)^{2}	8 (0.4)^{1}	7 (0.3)	7 (0.3)	6 (0.2)^{2}	7 (0.3)^{1}
Leaves (#)	8 (2)	15 (5)	8 (2)	14 (3)	9 (2)	13 (2)
Below-ground						
Taproot length (mm)	248 (14)	285 (16)	254 (14)	278 (16)	252 (13)	281 (15)
Lateral roots (#)	46 (5)	44 (4)	34 (3)^{2}	59 (6)^{1}	44 (3)	46 (4)
Root tips (#)	227 (81)	483 (172)	164 (59)^{2}	669 (239)^{1}	354 (96)	310 (84)
Root tips with mycorrhizae (percent)	37.1 (6.1)	56.9 (9.3)	40.0 (6.5)	52.9 (8.7)	37.9 (4.9)^{2}	55.8 (6.5)^{1}
Biomass						
Stem biomass (g)	0.83 (0.2)^{2}	1.84 (0.4)^{1}	1.25 (0.3)	1.41 (0.3)	0.99 (0.2)^{2}	1.60 (0.3)^{1}
Root biomass (g)	0.87 (0.3)^{2}	3.76 (0.5)^{1}	2.65 (0.4)	2.73 (0.4)	1.92 (0.2)^{2}	3.67 (0.4)^{1}
Foliar biomass (g)	0.94 (0.3)^{2}	2.57 (0.6)^{1}	1.53 (0.4)	1.74 (0.5)	1.46 (0.3)^{2}	1.81 (0.3)^{1}
Total biomass (g)	3.59 (0.7)^{2}	8.05 (1.5)^{1}	5.03 (0.9)	5.74 (1.05)	4.24 (0.6)^{2}	6.82 (0.9)^{1}
Anatomy/physiology						
Root-to-shoot ratio	2.4 (0.3)	2.2 (0.3)	2.6 (0.3)	2.1 (0.3)	2.2 (0.2)	2.4 (0.2)
Specific leaf area (cm^{2}/g)	165.7 (33.1)^{2}	422.2 (97.0)^{1}	236.7 (54.4)	295.6 (67.9)	236.1 (39.7)^{2}	296.2 (50.1)^{1}

Note: Differences in superscript number indicate a significant difference ($\alpha = 0.05$).

[a] GAP: Glaciated Allegheny Plateau (glaciated); PLP: Pittsburg Low Plateau (nonglaciated).

[b] BO: black oak; CO: chestnut oak.

[c] YR2: second growing season; YR3: third growing season.

Table 2. Effect of site, species, year, and their interactions on mean (SE) seedling growth and development characteristics within the light environment, at low light levels.

	Site[a]		Species[b]		Year[c]	
	GAP	PLP	BO	CO	YR2	YR3
Aboveground						
Stem height (cm)	18.3 (0.4)^{1}	14.0 (0.3)^{2}	16.0 (0.3)	16.0 (0.3)	15.0 (0.3)^{2}	17.0 (0.5)^{1}
Root collar diameter (mm)	5.2 (0.1)^{1}	4.6 (0.1)^{2}	4.7 (0.1)^{2}	5.1 (0.1)^{1}	4.8 (0.1)	5.0 (0.1)
Leaves (#)	4 (0.3)	4 (0.3)	4 (0.3)	4 (0.3)	4 (0.2)	5 (0.3)
Below-ground						
Taproot length (mm)	188 (23)	206 (26)	206 (26)	188 (24)	181 (18)^{2}	214 (19)^{1}
Lateral roots (#)	46 (5)	42 (5)	42 (4)	46 (5)	41 (4)	47 (4)
Root tips (#)	253 (51)	268 (54)	125 (25)^{2}	540 (109)^{1}	239 (43)	283 (45)
Root tips with mycorrhizae (percent)	40.4 (5.1)^{2}	58.9 (7.5)^{1}	40.4 (5.1)^{2}	58.9 (7.4)^{1}	42.4 (4.4)^{2}	56.1 (5.0)^{1}
Biomass						
Stem biomass (g)	0.58 (0.02)^{1}	0.38 (0.02)^{2}	0.45 (0.02)	0.50 (0.02)	0.42 (0.02)^{2}	0.53 (0.03)^{1}
Root biomass (g)	1.25 (0.1)^{1}	0.88 (0.1)^{2}	1.15 (0.1)	0.97 (0.1)	0.81 (0.1)^{2}	1.33 (0.1)^{1}
Foliar biomass (g)	0.60 (0.06)	1.49 (0.06)	0.59 (0.06)	0.50 (0.06)	0.50 (0.04)^{2}	0.59 (0.05)^{1}
Total biomass (g)	2.42 (0.2)^{1}	1.74 (0.2)^{2}	2.17 (0.2)	1.96 (0.2)	1.73 (0.1)^{2}	2.44 (0.2)^{1}
Anatomy/physiology						
Root-to-shoot ratio	2.2 (0.2)	2.4 (0.2)	2.7 (0.2)^{1}	2.0 (0.2)^{2}	2.1 (0.1)^{2}	2.6 (0.2)^{1}
Specific leaf area (cm^{2}/g)	146.0 (16.3)^{1}	103.3 (11.5)^{2}	128.1 (14.3)	117.8 (13.1)	109.4 (9.1)	137.9 (13.2)

Note: Differences in superscript number indicate a significant difference ($\alpha = 0.05$).

[a] GAP: Glaciated Allegheny Plateau (glaciated); PLP: Pittsburg Low Plateau (nonglaciated).

[b] BO: black oak; CO: chestnut oak.

[c] YR2: second growing season; YR3: third growing season.

Discussion

Tree species' response to climate change will be inherently complex because of the variable interactions of the principal components (soil, sunlight, and weather) that constitute the species' growing space (Potter et al. 2017). Additionally, alterations to the competitive environment will be the result of changes in physiology, phenology, and distribution of individual plant species, which will subsequently have an impact on local abundance and community composition (Lafleur et al. 2010). For example, in our study, oak seedling performance varied in response to soil type. Our results indicate that black and chestnut oaks are more adaptive to sites with low nutrient availability, indicative of their greater importance on low-quality sites in the eastern United States (Iverson et al. 2008). Specifically, in high light environments, both chestnut oak and black oak seedlings had more above- and below-ground growth at the nutrient-poor, nonglaciated site than at the nutrient-rich, glaciated site. However, at lower light levels, this effect was reversed, as increased available soil nutrients may have been more beneficial for growth than the cost associated with increased mycorrhizal infection at the nonglaciated site.

On the nutrient-rich, glaciated site, the seedling anatomy and physiology of both oak species suggested reduced physiological stress, especially at low light levels. SLA is often strongly correlated with measures of relative growth rate, photosynthesis, and leaf longevity, and can be related to the ecology of a species as well as its environment (Westoby 1998, Meziane and Shipley 1999). In low light, SLA was reduced in seedlings grown at the nutrient-poor, nonglaciated site when compared to those grown at the glaciated site. Similar to the patterns in growth between the two sites, the relation for SLA was reversed at high light. Although soil nutrients were higher on glaciated soils, differences in foliar nutrient accumulation, especially macronutrients such as nitrogen, calcium, and potassium, were not observed between the two soils. However, increased foliar accumulation of manganese on the nonglaciated soil did not impact seedling growth, as has been reported for other species, including northern red oak on nutrient-deficient soils (Horsley et al. 2000, St. Clair and Lynch 2005).

There were few significant growth differences observed between black oak and chestnut oak during the study period. However, differences observed between these two species did reflect various strategies for persisting under water and/or nutrient stress, or reduced available sunlight. Chestnut oak had more first-order lateral roots, root tips, mycorrhizal infection, and SLA than black oak. The rapid initial root development in chestnut oak may be important for survival on dry, infertile sites. Additionally, the larger SLA for chestnut oak at lower light levels corresponds to its higher tolerance to shade relative to black oak. In contrast, black oak had larger RSRs, specifically at lower light levels, which is indicative of its greater shade intolerance (Sander 1990).

As climate changes, so will the biotic competitive environment. Unlike the migration of species northward following glacial retraction, species that move to new locations in response to a changing climate will have to compete with already-established species (Lafleur et al. 2010). Further, new competitive interactions may complicate management objectives and may require new management strategies. It is widely recognized and practiced in reforestation that species perform best where they are locally adapted. However, assisted migration of species within their range, or somewhat beyond their leading edge, may help to reduce an adaptational lag whereby there is a mismatch between the genotypes in a population and the environment resulting from relatively fast environmental change and comparably slow evolutionary response (Matyas 1990). Under high emissions scenarios (tripling of preindustrial CO_2 levels over the next 100 years), climate models project that the range of both chestnut oak and black oak is expected to increase (Prasad et al. 2014). However, at low levels (a doubling of preindustrial CO_2), chestnut oak is expected to contract in its range and decline in its relative importance under both scenarios. Black oak, however, with its broader geographic range and site tolerance, is expected to increase in its relative importance value, regardless of low or high climate scenarios (McQuilkin 1990, Prasad et al. 2014).

As indicated by our study, black and chestnut oak may have different growth and competitive interactions when established on glacial soils. Additionally, the light environment will be an important factor affecting competitive interactions. Both species had reduced growth on glacial soil in high light environments. In contrast, in low light environments, growth was favored on glaciated soil. The variable response to light and soil environments for the two oak species in this study indicates that the competitive environment may change with northward expansion and novel species mixtures. Although this study is limited in its scope and scale, it provides a first step in studying the relation between growth and potential future species ranges. Future studies are needed to determine the effect of novel abiotic conditions including soil characteristics and mycorrhizal association on species growth, competitive interactions, and community dynamics.

Supplementary Materials

Supplementary data are available at *Forest Science* online.

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