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Low light improves ability of Appalachian oak seedlings to compete with mesophytes in nitrogen-rich soils

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ABSTRACT

Historically, oaks have dominated forests and woodlands in the eastern US, but oaks are being replaced by mesophytic tree species. Mesophication was likely triggered by moist, shaded conditions related to fire exclusion, and thus, moisture and fire have been the focus of prior research. However, forests undergoing mesophication also experience high soil nitrogen (N) availability, and timber harvests often create high-light conditions. Oaks may compete poorly with mesophytes in these resource-rich conditions due to their distinct strategies for growth and nutrient acquisition. Here, we examined how light and N influence competition among one of three oak species (*Quercus alba*, *Quercus montana*, and *Quercus rubra*) and their common mesophytic competitors (*Liriodendron tulipifera*). In a greenhouse, we grew seedlings for 12 weeks along a gradient of light and two levels of N, both alone and sharing a pot with two competitors. When grown individually, mesophytes consistently reduced their root:shoot biomass ratio relative to oaks under high N, which may allow mesophytes to overtop oaks in N-rich conditions. When grown in competition, all oaks were competitively viable with mesophytes at 40 % light transmittance and below when grown in low N conditions. However, under high N conditions, white, chestnut, and northern red oak were only competitive with mesophytes at 20 %, 40 % and 10 % light levels, respectively. Our findings suggest potential management strategies for creating conditions that favor oaks over mesophytes. The intensity of timber extraction could be adjusted based on soil N richness, while regular prescribed fire and/or limiting the dominance of early-successional N fixers may help reduce soil N richness.

1. Introduction

For the past century, oak species have been declining in abundance across eastern North America (Abrams, 2003) including in the southern Appalachians (Fei et al., 2011). Forests that were historically dominated by oaks now have a lower relative abundance of oak, and in some cases have lost oaks entirely (Fei et al., 2011). Oak decline was likely catalyzed by numerous interacting disturbances, including repeated logging, and hunting practices that decreased the predators of frugivores and herbivores that browse oak acorns and seedlings (McEwan et al., 2011). This decline been intensified by mesic conditions (Pederson et al., 2014), and the exclusion of fire, which have led to the rise of fire-sensitive, nutrient-acquisitive species (Jo et al., 2019) called mesophytes. In the process of mesophication, the decline of fire-adapted oaks and rising abundance of fire-sensitive mesophytes creates conditions that continue to favor mesophyte dominance (Nowacki and Abrams, 2008). As a result, eastern forests now have cool and damp conditions with less flammable fuel beds, as mesophytic species directly promote moist soil conditions (Alexander et al., 2021), and leaf litter of mesophytic species absorbs more water and/or dries more slowly than oak litter (Kane et al., 2021; Kreye et al., 2018, 2013). The loss of flammable fuel beds further deteriorates conditions for fire spread and oak reproduction (Brose et al., 2013). As a result, a large focus of research and management effort has been on the moisture and/or fire related feedbacks associated with the

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mesophication hypothesis (Abrams and Nowacki, 2015; Alexander and Arthur, 2010; Hanberry et al., 2020).

However, forests undergoing mesophication have simultaneously experienced altered nutrient regimes through two main pathways: changes in nitrogen (N) abundance and N acquisition strategies. First, N inputs and outputs have changed. Soils have become increasingly N-rich with less frequent fire, which volatilizes N (Hubbard et al., 2004), the loss of American Chestnut (*Castanea dentata*) and its nutrient-poor and flammable litter (Elliott and Swank, 2008; Kane et al., 2020), and with chronic N atmospheric deposition (BassiriRad et al., 2015; Li et al., 2016; Walker et al., 2023). Land use disturbance, such as timber extraction, can also lead to elevated inputs of N and light. High light conditions caused by fire or clearcutting can favor N-fixing trees, such as black locust, which can introduce large amounts of N in early succession (Boring and Swank, 1984; Ottinger et al., 2023; Wurzburger et al., 2023) and promote the growth of nearby mesophytic trees (Minucci et al., 2019).

The second way that nutrient conditions have changed in eastern forests is through a shift in biogeochemistry, driven by the dominant mycorrhizal association and the nutrient strategies of trees. Oaks and hickories generally associate with ectomycorrhizal (EM) fungi and tend to produce leaf litter that is chemically resistant to decay, which results in low nutrient availability in soils (Averill et al., 2019; Keller and Phillips, 2019). EM trees can persist in these nutrient-poor conditions because some EM fungi can mine organic N directly from organic matter (Frey, 2019). As a result EM trees tend to promote and are favored by soils with low nutrient availability, yet this mycorrhizal association comes with a high carbon cost to the host tree (Hawkins et al., 2023). In contrast, many mesophytic species (e.g., tulip-poplar (*Lireodendron tulipifera*) and red maple (*Acer rubrum*)) provide nutrient-rich, rapidly decomposing litter that promotes high mineralization and nitrification rates, and they associate with arbuscular mycorrhizal (AM) fungi that scavenge mineral N (Phillips et al., 2013). Of particular relevance to the issue of oak decline is the recent recognition that EM and AM dominated forests represent alternative stable states within the eastern broadleaf biome (Averill et al., 2019; Lu and Hedin, 2019; Steidinger et al., 2019). Based on a theoretical analysis, AM trees are competitively disfavored in low-nutrient conditions because AM fungi cannot mine organic nutrients, and EM trees are competitively disfavored in nutrient-rich conditions because of the higher carbon cost of supporting and maintaining the EM symbiosis (Lu and Hedin, 2019).

Most oak-hickory forests reside in the older age classes (Brown, 2018), which are currently targeted for timber extraction, and it will be critical that young oak forests develop to replace this resource. While shaded, nutrient dense, and moist conditions have facilitated the *establishment* of mesophytic species in the understory and regeneration layer (Fei et al., 2011; Nowacki and Abrams, 2008), high light conditions further reinforce mesophyte long-term dominance, particularly in nutrient and moisture rich ecosystems with high site indices (Cook et al., 1998).

Oak species generally do well in high light and can take advantage of canopy openings if they are followed by fire (Brose and Van Lear, 1998). However, when intensive forest management practices alter the oak-dominated canopy cover and create high-light conditions in the understory, resource-conservative species such as oak are disfavored, because they grow at slower rates as seedlings and saplings than do resource-acquisitive mesophytes such as maple and tulip-poplar (Alexander et al., 2021; Gottschalk, 1985; Kolb et al., 1990). While results from prior studies suggest that oak-mesophyte competition depends on light, nutrients such as nitrogen may further explain outcomes. After disturbances (e.g., clearcut, fire, shelterwood cut), oak reproduction is often high (Brose et al., 2013), and oaks can compete adequately after disturbance in high light on nutrient-poor sites (Swaim et al., 2018). However, when oak-dominated stands experience a disturbance resulting in moderate light conditions on mesic, nutrient-rich sites, oaks can retain only a fraction of their prior dominance (Cook et al., 1998). Without repeated fire in the landscape to suppress mesophytic species and control vegetation-fire feedback loops (Alexander et al., 2021), oaks become competitively excluded under high light and nutrient conditions as stands develop (Beck and Hooper, 1986; Brose et al., 2013), in part due to rapid height growth and overtopping by mesophytic species (Swaim et al., 2016). This suggests that oak reproduction may not be the main issue; rather, it suggests that light and nutrients interact to influence regeneration in latter stages. Young oaks struggle to compete with their mesophytic neighbors due to their distinct strategies for growth and acquiring nutrients.

Here, we examine how light and N interact to affect the competitive dynamics of oak and mesophytic species relevant to southern Appalachian forests. In a greenhouse experiment, we measured the biomass and height of three oak species (*Quercus alba* (white oak), *Q. montana* (chestnut oak), and *Q. rubra* (red oak)) and two mesophytic species: tulip-poplar, a light-gap opportunistic species, and red maple a fire-sensitive, low light tolerant species. First, to understand how these species individually respond to nutrients and light resources we grew seedlings alone under four levels of light and two levels of N. Second, to understand the competitive interactions among oak species, red maple and tulip-poplar, we grew seedlings in competition sharing resources under the same treatments of four levels of light and two levels of N. The light treatments represent different intensities of harvest or forest disturbance, and the N levels represent modern N conditions and historical, low N conditions. Our experiment focused on the seedling/sapling stage when above-ground biomass and height is most critical for long-term competitive success. We addressed two questions and hypotheses in our study:

1. Under what light and N levels does each species grow best, individually? We hypothesized that mesophytic species, maple and tulip-poplar, would be more responsive to higher light and N levels in height and biomass compared to oaks.
2. Under what light and N levels are oak species able to maintain their competitive dominance over mesophytes? We hypothesized that oaks would only remain competitive with mesophytes under low N and moderate light.

2. Methods

2.1. Greenhouse experimental design

We conducted a greenhouse experiment at the USDA Forest Service, Coweeta Hydrologic Laboratory in western North Carolina, USA. The Coweeta Basin encompasses 1626 ha, elevations range from 675 to 1592 m, and slopes range from 30 % to over 100 %. Mean annual temperature is 12.6°C and mean annual precipitation is 1800 mm (Swift et al., 1988). Forests within and surrounding the Coweeta Hydrologic lab are mixed deciduous forests of the southern Appalachians. We were interested in the effects of five common tree species in eastern deciduous forests: red maple, tulip-poplar, northern red oak, chestnut oak, and white oak. Oak species were selected because they span hydrologic gradients, with the former two commonly found on side-slopes and towards ridges, and the latter commonly found in toe-slopes and valleys in the southern Appalachian Mountains (Swank et al., 2001). Red maple is ubiquitous throughout the Coweeta Basin at all aspects, elevations, and landscape positions and has been increasing in importance over time (Kloeppel and Clinton, 2003). Tulip-poplar is also a common species that is both early successional and old-growth and typically occupies more mesic landscape positions (Elliott et al., 1997).

In July–August 2020, we sourced healthy and representative oak and mesophyte seedlings from the field and acclimatized them in the greenhouse for 4–6 weeks before the start of the 40-week experiment. Seedlings (non-sprout origin) in their first year of growth were collected from the basin of the Coweeta Hydrologic Lab, Franklin, NC, and Knoxville, TN. We removed the majority of natural soil on the roots and planted seedlings in 4-L pots in media containing a 1:1 ratio by volume of peat and vermiculite with a trace amount of sand. After adjusting to greenhouse and potting mixture conditions, we randomized seedlings into treatments and experiments.

To test hypothesis 1, we planted oaks and mesophytes individually in 4-L pots, and to test hypothesis 2, we planted one oak with two mesophyte seedlings sharing the same soil volume in a 12-L pot as a proxy for competition. Both experiments had identical treatments, measurements, and response variables (Supplemental Fig. 1). They had a factorial design by crossing the fixed effects of light transmittance (four levels), N fertilization (two levels), and species (five species). Each table row contained 30 large 12-L pots with three tree species (red maple + tulip-poplar + chestnut oak or northern red oak or white oak; $n = 5$). For the competition experiment, there were five replicates each (2*5*5*4 total number of pots containing three seedlings = 200). Additionally, each table row contained ($n = 4$) individual trees in 4-L pots. For the individual pot experiment, there were four replicates each (2*4*5*4 total number of pots = 160). We note that we did not test three oak species in a pot together due to resource limitations.

The four levels of light were created by shade cloth (Shade Cloth Store, custom size knitted 100 % UV stabilized polyethylene) (100 %, 40 %, 20 %, 10 % transmittance), with one cloth suspended over the length and draping over the sides of one of four tables (not fully replicated). Our highest light level represented a clearcut forest, and our darkest light level (10 % transmittance) for understory conditions (Arthur et al., 2021). Because the response of photosynthesis to light is curvilinear (Elliott et al., 1997), we selected shade cloth that would confer relatively low light levels—levels above the light compensation point for these species and increasing such that we would likely see linear increases in growth with our treatment levels. We monitored photosynthetically active photon flux density (PPFD, μmol m^2 s^{-1}; LI-250A with LI-193 sensor, Li-Cor, Lincoln, NE) in each treatment to validate treatment levels.

Nutrient treatments included two levels of N (N addition 10 g m^{-2} y^{-1} and no N addition: 0) as a volumetric application rate, applied as ammonium nitrate in 100 mL every two weeks during the growing season (September–November and March–July). To ensure that other nutrients were not limiting seedling growth, the seedlings received one treatment of 50 % strength Hoagland's solution without N (Hoagland and Arnon, 1950) at the beginning of the experiment in September and another treatment in May 2021. Because pot surface area and volume differed between 12-L and 4-L pots in our study, our N additions were determined as a function of soil volume equivalent of the aerial rate of 10 g m^{-2} y^{-1} to a depth of 10 cm. This rate of mineral N addition (0.1 mg cm^{-3} y^{-1}) simulates the amount of N mineralized in disturbed watersheds in the Coweeta Basin (Motes et al. in prep) assuming a soil bulk density of 0.7225 g cm^{-3} (Boring and Swank, 1984).

The experimental treatments occurred during the growing season from September to November 2020, then, from March to July 2021 for a total of 40 weeks of treatment. All seedlings over-wintered in the greenhouse under their respective shade cloth light treatments and were watered as needed but otherwise were without climate control. Every two weeks during the growing season, seedling positions were rotated within their treatment to minimize spatial greenhouse effects. Insecticidal soap and copper fungicide were applied as needed, and growth and biomass of trees were not affected by pests during the experiment. If a tree died during the treatment period, we replaced the seedling with a spare either from a bank of "spare" seedlings in the greenhouse, or, a first-year seedling from the local area around the Coweeta Basin. We stopped replacing seedlings after leaf-out in March 2021. Most oak fatalities occurred during the 2020 portion of the growing season, likely due to stress from transplanting. The majority of tulip poplar and maple deaths occurred when they did not come out of winter dormancy in March of 2021. Approximately 26 trees were replaced throughout the experiment with 14 replacements in 2020 and 12 replacements in 2021. Tree mortality was similarly distributed throughout the light and nitrogen treatments.

During the growing season of the experiment, the average greenhouse air temperature was 19.9 ºC (range 10.8–35.4 ºC). Average soil moisture (θ) was 43 % v/v (CS655, Campbell Scientific Inc., Logan UT; $n = 1$ per treatment). Daily minimum θ differed between treatments and pot types (4-L and 12-L) and ranged from 29 to 40 %. Despite some pots having lower daily minimum θ, a whole treatment group's average never dropped below 29 % over the course of the experiment. Average air relative humidity was 65 % (HMP50, Campbell Scientific Inc., Logan, UT; $n = 1$ per light treatment). Air temperature and relative humidity did not differ among the treatments.

2.2. *Destructive harvest*

We destructively harvested seedlings over four consecutive days (July 6–9, 2021), and seedlings were harvested evenly from all treatments in replicate groups. Each seedling was photographed, then cut at the base of the stem using shears, and the above and belowground biomass was washed of potting material and packaged in paper bags for drying and weighing. Pots were carefully inverted into a closed container, and soil was loosened to minimize any loss of fine roots prior to gentle shaking and rinsing with tap water. In competition pots, roots were visually distinguished by species and disentangled using forceps.

To measure above and belowground biomass, stems and leaves and roots were dried at 65 °C until weights were stable and then weighed to the nearest 0.01 g. To measure final height, seedling height was estimated using imaging software (Image J version 10.14.07) using reference photos taken at harvest and the standard pot height as scale in each photo. Soil pH at the end of the experiment was similar between treatments and ranged from 4.8 to 5.5.

To verify mycorrhizal colonization, we sampled three 2–3 cm segments of the fine root system of seedlings in the highest and lowest light treatments and preserved them in 90 % ethanol. From at least three individuals from each of the high and low light treatments, we assessed mycorrhizal colonization. For AM seedlings (tulip-poplar and red maple), root segments were cleared in KOH and stained with trypan blue to visualize AM fungal structures (i.e. arbuscules and vesicles) with a compound microscope (Wurzburger and Wright, 2015). For oak seedlings, we determined if root tips possessed a fungal mantle and a Hartig net using a dissecting scope and a compound scope, respectively. We observed AM colonization on red maple and tulip-poplar and EM colonization on all oaks, demonstrating that seedlings had access to viable soil inoculum. We did not examine if oaks also possessed AM fungal colonization, which can occur at the seedling stage (Dickie et al., 2001).

2.3. *Statistical analysis*

We fit separate generalized linear mixed models (GLMM) in SAS for the individual pot experiment and for the competition experiment. We chose this class of models because our data were not normally distributed—they most closely resembled a gamma distribution with non-negative values and very few zero values—and because our design had random effects—seedlings in the competition experiment in the same pot were not independent. Response variables included final height, aboveground biomass, belowground biomass, and total biomass, and root:shoot ratio. All GLMMs used a gamma distribution with a log link. Fixed factors were N (two levels), light transmittance (four levels), and species (five levels). Due to space and resource constraints, we realize that light was not fully replicated. The positions of the light treatments themselves remained fixed in position in the greenhouse and could theoretically experience spatial differences in light, moisture, and temperature. To help to minimize this effect, all benches were a similar distance to climate control fans pots were consistently rotated within the light treatment. Temperature, light, and moisture were continuously monitored throughout the greenhouse.

All possible effects and interactions were modeled and evaluated at the $\alpha = 0.05$ level. Least-squares (LS) means, and standard errors are presented below unless otherwise noted. All figures show back-transformed means and standard errors. Differences in the LS means were tested post-hoc at $\alpha = 0.05$. We chose not to use a Tukey-Kramer adjustment to the P values, because we only tested certain combinations of LS means, not all combinations.

For the competition experiment, we created a new variable to account for random effects that was a combination of the target species and the oak species; for example, LITU-QURU would identify a tulip-poplar seedling that was growing in a competition pot with a northern red oak seedling.

Two seedlings had zero aboveground biomass at the end of the experiment due to mortality. To avoid calculation errors in root:shoot ratio, these data were omitted from that analysis. Further, in all models, actual zero data were considered missing because they used a log link prior to fitting.

3. Results

3.1. Total, above-, and belowground biomass, root to shoot biomass ratio, and height of seedlings grown individually

Total biomass varied by species (Table 1). White oak had 95 % more total biomass than the average tulip-poplar, chestnut oak, and northern red oak, which had similar total biomass; and white oak had three times more total biomass than red maple. Light increased total biomass across all species similarly, but N increased total biomass in some species more than others. Tulip-poplar responded more to N than any other species, with 2.4 times more total biomass than unfertilized tulip-poplar seedlings. Fertilization only increased total biomass in the highest light environment, and this was the case for all species.

Aboveground biomass responses to N, light, and species were similar to those of total biomass (Table 1). Aboveground biomass varied by species. White oak seedlings had more aboveground biomass than the average tulip-poplar, chestnut oak, and northern red oak, which had similar total biomass; and white oak had 2.5 times more total biomass than red maple. Light increased aboveground biomass across all species similarly, but N increased aboveground biomass in some species more than others. Tulip-poplar and chestnut oak aboveground biomass responded more to N than any other species, with 2.7 times more aboveground biomass than their unfertilized counterparts. Fertilization only increased aboveground biomass in the two highest light environments, and this was the case for all species.

Belowground biomass responses were also similar to total and aboveground biomass responses (Table 1). Belowground biomass varied by species. White oak had 7 times, and the other oaks had ~3 times the amount of belowground biomass than red maple. Light increased belowground biomass across all species similarly, but N affected some species more than others. Fertilization increased belowground biomass in tulip-poplar but decreased belowground biomass in red maple. Fertilization only increased belowground biomass in the highest light environments, by 68 %, which was the case for all species.

Some species were taller with increased N and light (Table 1, Fig. 1). Only tulip-poplar and chestnut oak were taller (170 % and 124 %, respectively) when fertilized compared to controls. This was similar in height growth, however tulip-poplar and chestnut oak species grew taller when fertilized, and red maple (ACRU) grew taller at 20–40 % light, followed by 100 % light, compared to 10 % light (Supplemental Fig. 2ab, Supplemental Table 1).

Nitrogen and light shifted allocation between above- and belowground biomass pools, but this depended on the species (Table 1, Fig. 2). Oaks invested more than twice (2.2x) as much biomass in roots relative to shoots than tulip-poplar, and almost four times (3.7x) the amount compared to red maple. For tulip-poplar, fertilization generally decreased allocation belowground, and light generally increased it. In contrast, red maple had similar belowground investment in all unfertilized seedlings, and in fertilized seedlings at the lowest light level. Belowground investment was lower in fertilized red maples, but only from 20 to 100 % light levels, which generally increased with light. Oaks also tended to invest less belowground when fertilized at higher light levels, but because variability was high, these trends were not always significant.

3.2. Comparing total biomass, AGB, BGB, and height between experiments

We expected all seedlings grown in individual pots to outperform those grown with competitors. To test this, we compared growth metrics

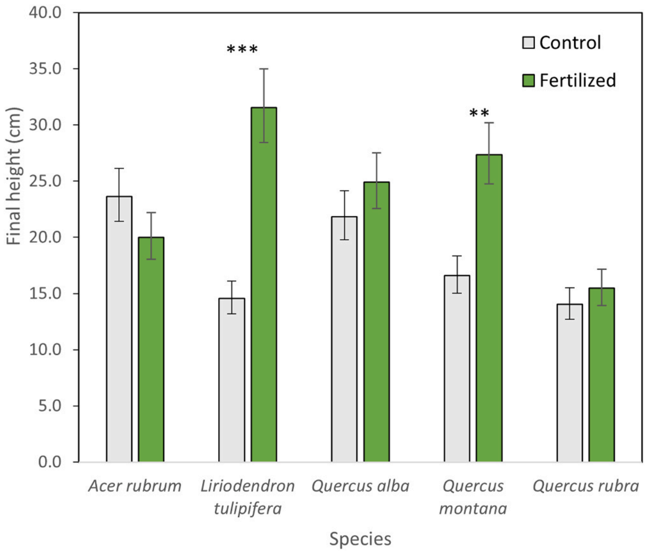

Fig. 1. Final seedling height of species across all light levels. Tulip-poplar (*Lireodendron tulipifera*) and chestnut oak (*Quercus montana*) species were taller when fertilized. White and northern red oaks respectively showed no significant height response to fertilization. Pairs of bars in within species with **, or *** are significantly different from each other at $P \leq 0.01$, 0.001, respectively. Means and standard errors are back-transformed.

Table 1

Results for total, aboveground, and belowground seedling biomass; ratio of root to shoot biomass; and final height in individual pots. F values in bold are significant at $P < 0.05$. NDF and DDF are numerator and denominator degrees of freedom, respectively. Asterisk indicates 117 DDF only for final height due to missing data.

			Total Biomass	Above-ground Biomass	Below-ground Biomass	Root to Shoot Biomass Ratio	Final Height
Effect	NDF	DDF*	*F*	*F*	*F*	*F*	*F*
N	1	119	**4.4**	**24.5**	0.1	**67.1**	**17.5**
Light	3	119	**32.7**	**28.2**	**32.4**	**6.2**	**6.9**
NxLight	3	119	**2.7**	**4.5**	**2.7**	**3.0**	1.4
Species	4	119	**18.7**	**10.1**	**31.3**	**74.8**	**6.5**
NxSpecies	4	119	**3.7**	**5.0**	**3.3**	0.8	**6.7**
LightxSpecies	12	119	1.0	1.1	1.5	**5.9**	1.7
NxLightxSpecies	12	119	1.0	1.4	0.9	**2.8**	1.2

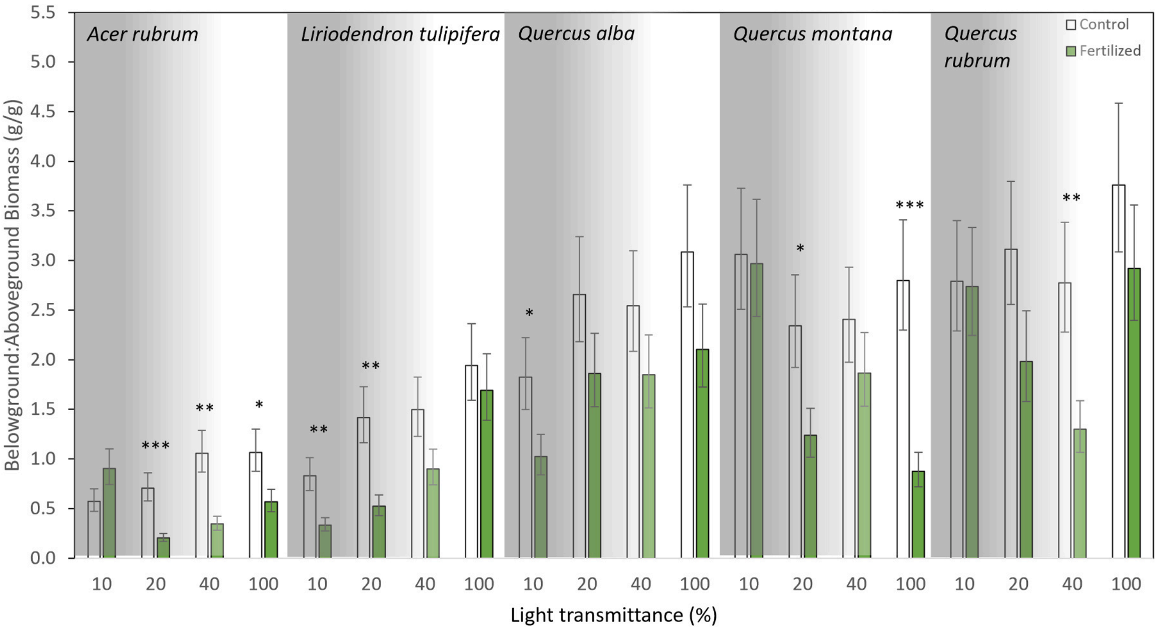

Fig. 2. The three-way interaction effect on mean (SE) root:shoot biomass ratio. Generally, red maple (*Quercus rubrum*) and tulip-poplar (*Lireodendron tulipifera*) invested less belowground biomass in fertilized seedlings compared to unfertilized seedlings, and investment belowground tended to increase as light increased. All three oaks didn't conform to this pattern; instead, depending on oak species, fertilization decreased belowground investment at low to intermediate light levels. Groups of control and fertilized bars within species and light level with *, **, or *** are significantly different from each other at $P \leq 0.05, 0.01, 0.001$, respectively. Means and standard errors are back-transformed.

between individuals of each species within each light and N level (e.g., tulip-poplar individual pot biomass in all light and N treatments compared to those in competition pots). Regardless of the measure, seedlings grown individually performed better than their counterparts in competition (Table 2). Seedlings produced 1.5x more total biomass, 1.4x more aboveground biomass, 1.5x more belowground biomass, and grew 1.4x taller (not shown) when grown individually compared to when they were grown with other species. This is notable given that the fertilization rates per seedling, the initial pot growing volume, and the treatment duration were identical among experiment (pot) types.

3.3. Total, above-, and belowground biomass, and height of seedlings grown in competition

Similar to individual pots, all biomass pools from the competition experiment generally showed consistent directional responses to treatments. Two notable trends differed, however—the effect sizes of treatments were greater (i.e., even though seedlings grew more in individual pots, their responses to light and N were greater when grown in competition), and three-way interactions were significant (e.g., the N response depended on light *and* species).

Effect Sizes—Seedling biomass pools generally showed greater treatment effects when growing in competition. Total biomass roughly doubled with fertilization (1.93x competition effect, 1.26x individual effect) and increased more than 5.5 times from the lowest to highest light levels (vs. 2.9x individual effect) (Table 3). Total biomass increased with fertilization in the three highest light levels by 54 %, 145 %, and 194 % compared to the controls. In contrast, when grown individually, fertilization increased total biomass in the three highest light levels by 2 %, 19 %, and 111 %. Aboveground biomass more than doubled with fertilization in competition pots (2.6x competition effect, 1.7x individual effect), and more than quadrupled from the lowest to the highest light levels (vs. 3.3x in individual pots). Belowground biomass in competition pots increased 1.3x with fertilization, compared to no fertilization effect in the individual pots. Seedlings in competition increased belowground biomass with increasing light, with more than seven times greater biomass belowground in the highest light level compared to the lowest (individual effect was 3.9x from the 10 % to the highest two light levels).

The white oaks under lower light and N conditions could compete well, but none of the oaks competed well under higher N conditions, regardless of light. Under low N conditions, white oak typically had greater aboveground biomass than either competitor, except at 20 % light (Fig. 3a). When fertilized, white oak never had greater aboveground biomass than both competitors in any light condition (Fig. 3b). Under low N conditions, chestnut oak had greater aboveground biomass than either competitor in 10 % and 40 % light conditions (Fig. 3c). When fertilized, chestnut oak never had greater aboveground biomass than both competitors in any light condition (Fig. 3d). Northern red oak never had *greater* aboveground biomass than both its competitors at the same time, regardless of light or fertilization (Fig. 3e–f).

Similarly to aboveground biomass, the final height of white oaks

Table 2
Results for total, aboveground, and belowground seedling biomass, and final height in individual pots compared to competition pots (i.e., pot type). *F* values in bold are significant at $P < 0.05$. NDF and DDF are numerator and denominator degrees of freedom, respectively.

			Total Biomass	Above-ground Biomass	Below-ground Biomass	Final Height
Effect	NDF	DDF	*F*	*F*	*F*	*F*
Pot Type	1	234	**11.6**	**9.2**	**12.0**	**5.8**
Species	4	234	**30.1**	**12.4**	**58.4**	**8.2**
Pot Type x Species	4	234	0.6	0.5	0.9	2.1

Table 3
Results for total, aboveground, and belowground seedling biomass; root to shoot biomass ratio; and final height in competition pots. *F* values in bold are significant at $P < 0.05$. NDF and DDF are numerator and denominator degrees of freedom, respectively.

			Total Biomass	Above-ground Biomass	Below-ground Biomass	Root to Shoot Biomass Ratio	Final Height
Effect	NDF	DDF	*F*	*F*	*F*	*F*	*F*
N	1	190	**67.9**	**133.8**	**9.6**	**88.5**	**136.1**
Light	3	190	**79.8**	**53.0**	**99.2**	**27.2**	**16.0**
N x Light	3	190	**6.0**	**9.2**	**6.5**	**3.6**	**8.9**
Oak Species Competitor	8	190	**30.8**	**12.9**	**61.3**	**46.2**	**9.7**
N x Oak Competitor	8	190	**8.9**	**10.6**	**4.6**	**4.4**	**12.1**
Light x Oak Competitor	24	190	**4.1**	**2.8**	**6.2**	**5.1**	**4.7**
N x Light x Oak Competitor	24	190	**2.7**	**2.0**	**3.5**	**4.4**	**2.1**

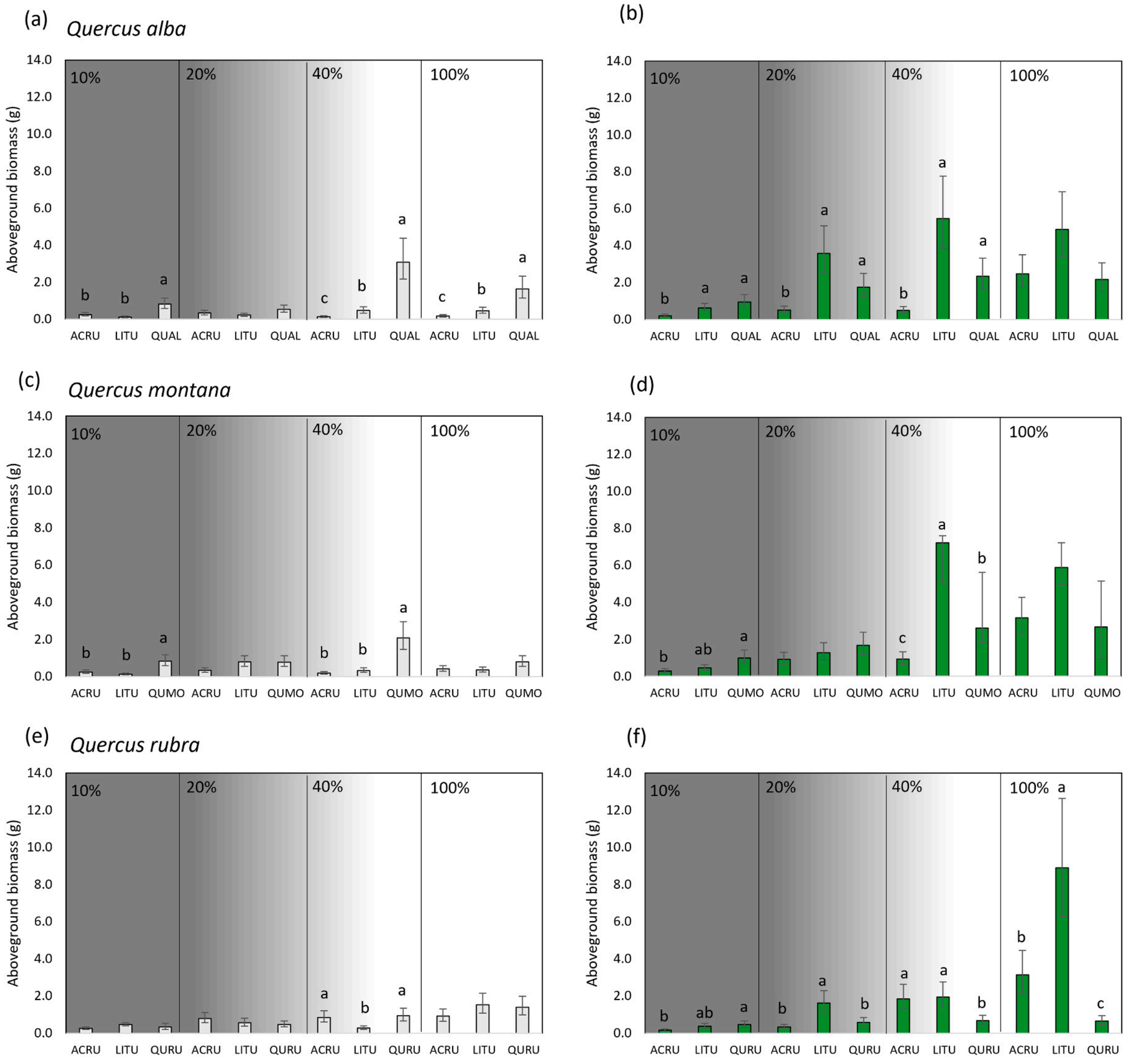

Fig. 3. The oak by light by N interaction on final aboveground biomass in competition pots. Differences between species within light and N levels not sharing the same lowercase letters on bars are significant at $P \leq 0.05$. Panels (a) and (b) are white oak (QUAL/*Quercus alba*), panels (c) and (d) are chestnut oak (QUMO/*Quercus montana*), and panels (e) and (f) are northern red oak (QURU/*Quercus rubra*). Gray bars represent unfertilized seedlings, and green bars represent fertilized seedlings. Light levels are indicated by transmittance level and shading across each panel. Mesophytes are identified as tulip-poplar (LITU/*Lireodendron tulipifera*) and red maple (ACRU/*Acer rubrum*). Generally, oaks grew more aboveground biomass in darker light levels but had more aboveground biomass than mesophytes at a wider range of light when unfertilized. White oak and chestnut oak had generally more aboveground biomass relative to mesophytes than northern red oak. Tulip-poplar had the greatest aboveground biomass in the higher light levels and when fertilized. Means and standard errors are back-transformed.

under lower light and N conditions could compete well against mesophytes (Fig. 4a). When fertilized, white oak only had greater final height than both competitors in the lower light levels (Fig. 4b). Under low N conditions, chestnut oak had final heights greater than or equal to their competitors in *all* light conditions (Fig. 4c). Like white oak, when fertilized, chestnut oak only had greater final height than both competitors in the lower light levels (Fig. 4d). While northern red oak had greater final height than both its competitors in lower levels of light when not fertilized, when fertilized it was only as tall or taller than its competitors at the darkest level of light (Fig. 4e–f). Tulip-poplar was

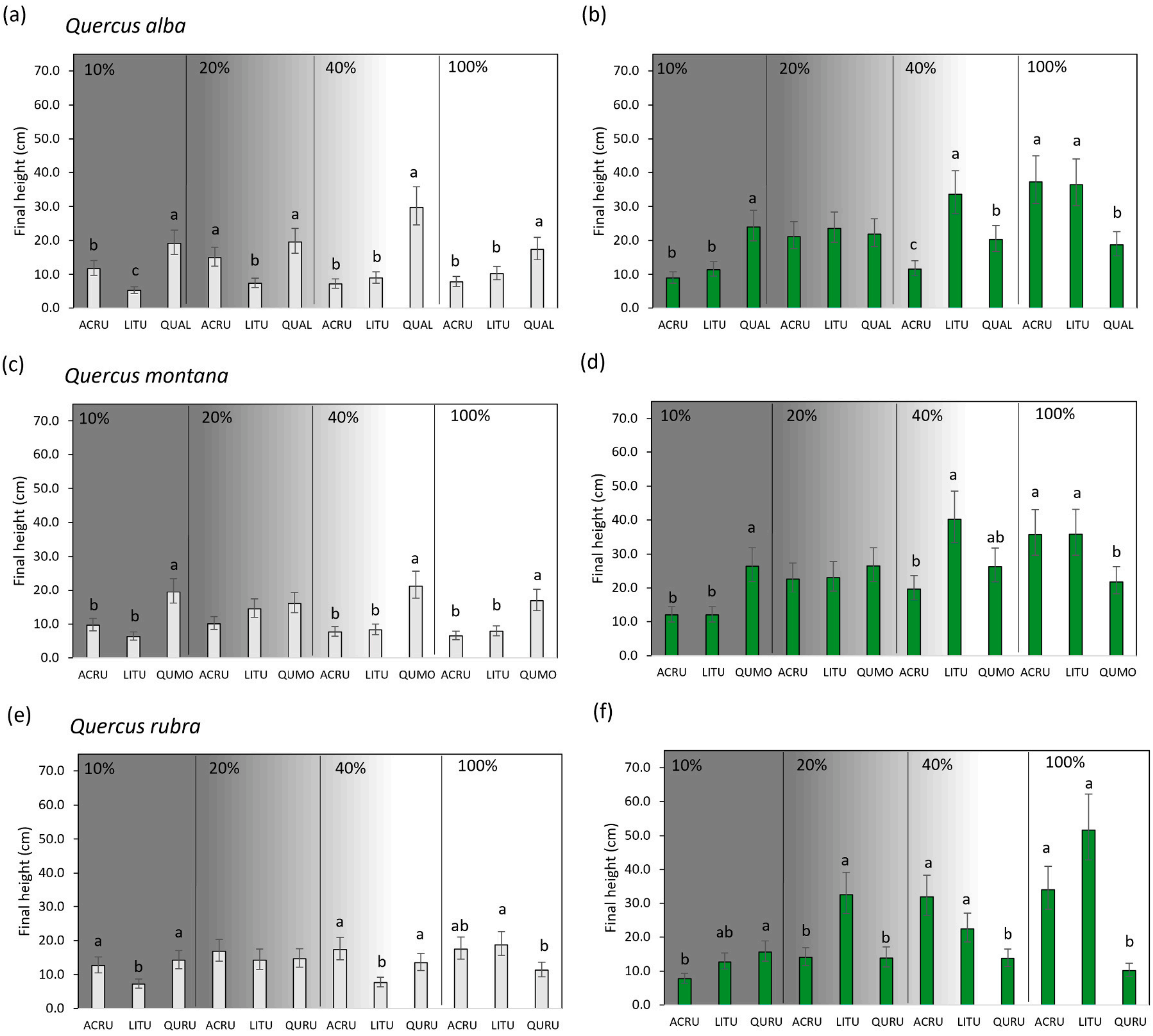

Fig. 4. The oak by light by N interaction on final height in competition pots. Differences between species within light and N levels not sharing the same lowercase letters are significant at $P \leq 0.05$. Panels (a) and (b) are white oak (QUAL/*Quercus alba*), panels (c) and (d) are chestnut oak (QUMO/*Quercus montana*), and panels (e) and (f) are northern red oak (QURU/*Quercus rubra*). Gray bars represent unfertilized seedlings, and green bars represent fertilized seedlings. Light levels are indicated by transmittance level and shading across each panel. Mesophytes are identified as tulip-poplar (LITU/*Lireodendron tulipifera*) and red maple (ACRU/*Acer rubrum*). Generally, oaks were as tall or taller than mesophytes in low light, but similarly to aboveground biomass, low N conditions granted the oaks a larger range of light in which they were competitive (10–40 % light). While white and chestnut oak were as tall or taller than competitors at up to 20 % when fertilized, northern red oak was only competitive at the lowest light level (10 %). Means and standard errors are back-transformed.

consistently taller than other seedlings when fertilized in the higher light levels, but this advantage immediately disappeared when N was low.

4. Discussion

In the southern Appalachians, land managers are interested in restoring oak-dominated forests and identifying strategies to facilitate oak competition with mesophytes. While oak regeneration is influenced at multiple critical life stages (Arthur et al., 2012; Brose et al., 2013) seedling aboveground competition, without being overtopped by opportunistic competitors, represents a bottleneck (Kolb et al., 1990). Recruitment into the sapling stage requires high seedling survival and competitive ability (Brewer and Williams, 2025). Managing forests for oak regeneration first requires knowledge about how seedling oaks compete with mesophytes across the light and N regimes that represent contemporary forest conditions. Here, we investigated the effect of light and N on seedlings grown individually and in competition while experiencing the same nutrient and light resources. We expected mesophytes to outgrow oaks under high light and N. We generally found support for this hypothesis (Table 1, Fig. 1). We also hypothesized that oaks would only be competitive with mesophytes under low N and moderate light. We found that oaks were competitive under low to moderate light when unfertilized, but the addition of N narrowed the range of light conditions where oaks were competitive with mesophytes (Fig. 4, Fig. 5).

4.1. Mesophyte-oak competition

Managing forests for oak requires understanding the growth responses of their main competitors, mesophytes, to available resources. In our study, tulip-poplar and red maple showed greater responses in biomass or height to N and light, respectively, when grown individually. Specifically, tulip-poplar was most responsive to N. Mesophytes tend to grow rapidly under high light and nutrient availability, likely due to their nutrient acquisitive growth strategy. Mesophytes also associate with AM fungi, which scavenge mineral nutrients and come at a lower carbon cost than EM fungi (Lu and Hedin, 2019), making them better competitors in nutrient-rich conditions. In our study, mesophytes also demonstrated more flexibility in their proportional allocation of biomass, as they more consistently reduced their root:shoot biomass ratio compared to oaks under N fertilization (Fig. 2). Such flexibility

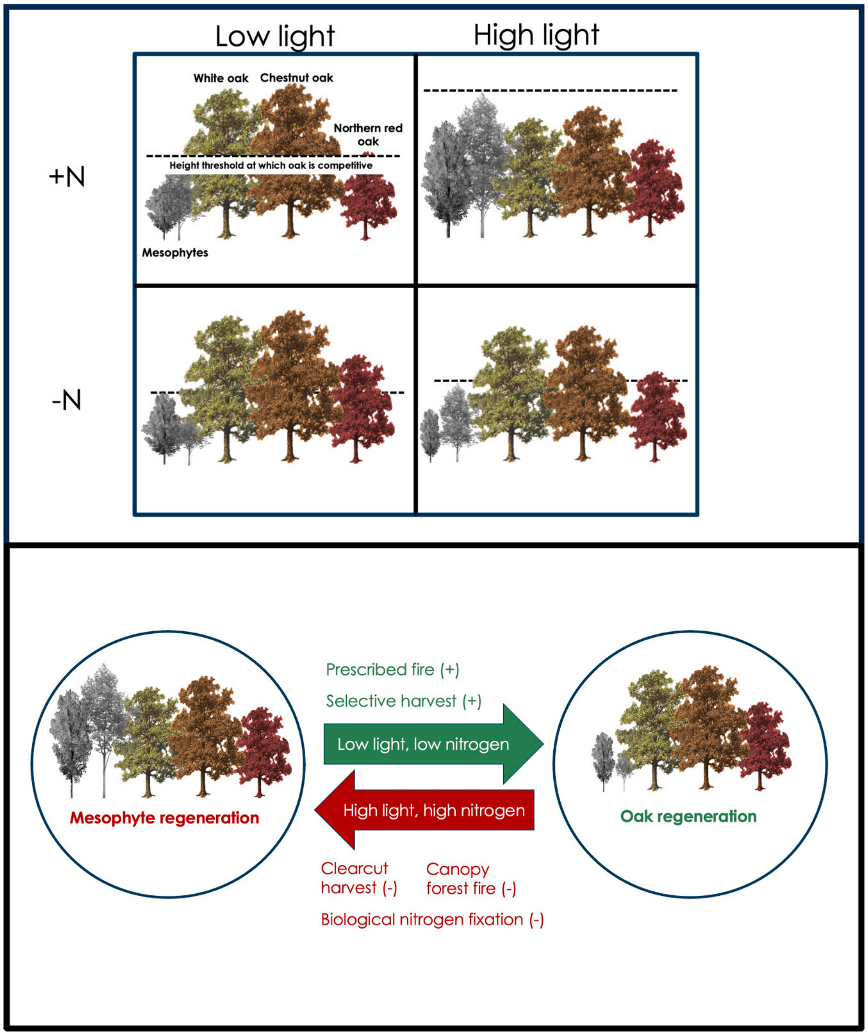

Fig. 5. Panel (a) depicts oak species heights relative to mesophyte competitors, red maple and tulip-poplar. Dotted line shows the height threshold at which oak is competitive with mesophytes. All three oak species are below this competitive threshold when nitrogen and light are high. Panel (b) shows management actions that impact light and nitrogen which ultimately aid or depress oak regeneration.

might allow mesophytes to allocate biomass aboveground and overtop oak competitors under nutrient rich conditions. Oak seedlings appear to more consistently invest in large root systems that store carbohydrates, allowing them to persist and resprout following stressful environmental conditions (Alexander et al., 2008) including shade (Loftis, 1990). However, oaks may also possess a certain flexibility in nutrient acquisition that we did not address in this study—they are occasionally colonized by both EM and AM fungi, particularly at the seedling stage. The carbon and nutrient trade-offs for dual-colonized oak seedlings and subsequent effects on competition with mesophytes is unknown and worthy of consideration.

For oak seedlings, growth and development is directly related to light availability (Arthur et al., 2021), however in our study, when oaks and mesophytes were grown together, competitive outcomes depended on light *and* N conditions. While we measured biomass (Fig. 3), we focus on height (Fig. 4) as a proxy for competitive success because taller seedlings intercept light from shorter seedlings (Schwinning and Weiner, 1998), and thus height often determines seedling competition and predicts future height growth (Swaim et al., 2016). For example, species such as tulip-poplar that display early height growth tend to maintain their dominance from seedling to sapling stage (Beck and Hooper, 1986). While oaks can grow taller with greater light resources and are smaller in dense shade, resource abundant conditions can stimulate competitors to rapidly grow and overtop oak seedlings (Brose and Van Lear, 1998, Fig. 5a). In our study, under high N conditions, oaks only remained competitively viable, that is, they were not significantly shorter than mesophytes, in low light conditions. Specifically, white oak, chestnut oak and northern red oak were competitive up to 20 %, 40 % and 10 % light levels, respectively (Fig. 4).

4.2. Oak harvesting practices based on soil N conditions

Forests persist along gradients of nutrient availability, and this could potentially guide management. Decades of atmospheric N deposition, fire exclusion and prior land use and disturbance have created N-rich soil conditions (Amos et al., 2018; Carpenter et al., 2021; Wurzburger et al., 2023), but soil nutrient availability is also dictated by parent material and topographic position (Knoepp et al., 2008; Knoepp and Swank, 1998), particularly in mountainous regions like the southern Appalachians. Our experiment may provide insight to how restoration and timber harvest practices can create light conditions that encourage oaks regeneration; the intensity of disturbance or harvest would need to be contingent on the N conditions of individual stands (Fig. 5b), or, targeted to reduce N.

We found that under low N, all oaks were competitively viable with mesophytes at 40 % light transmittance and below (Fig. 4). This suggests that it might be possible to maintain favorable oak conditions even after moderate levels of timber extraction on nutrient-poor sites, such as those on south-facing slopes or ridges, which tend to have drier, more shallow soils (Elliott et al., 1999). This is consistent with a forest clearcutting experiment where the dry mixed oak forest type, comprised of white, northern red and chestnut oak, eventually regained oak dominance decades later, but mesic and cove forests transitioned to dominance by tulip-poplar (Boring et al., 2014; Elliott et al., 2002). Contrastingly, at N-rich sites, our results suggest that maintaining favorable light conditions for oak would require removing a smaller proportion of canopy trees. This is consistent with a prior analysis of long-term data, where only low levels of selective cutting (<18 m^2 ha^{-1}) resulted in greater recovery of oak and hickory when black locust, an N-fixing tree had been dominant in early succession (Wurzburger et al., 2023). Other strategies on productive sites may include a combination of first shelterwood harvest followed by prescribed fire; this could allow oak to utilize light gaps to increase biomass and develop more robust root systems (Brose and Van Lear, 1998), while staving off competition from fire intolerant mesophyte seedlings that may have opportunistically utilized light gap resources.

Under the common practice of high basal area extraction (which creates extensive light gaps), oak may regenerate, but in N-rich conditions oak stems will likely be quickly overtopped by red maple and tulip-poplar (Alexander et al., 2008; Swaim et al., 2016, 2018). Harvesting recommendations are also likely to vary by species of oaks, and our results suggest that among the species in our study, chestnut oak might be a more robust competitor with mesophytes under N-rich conditions. In addition, post-harvest conditions often include resprouting stumps (Keyser and Zarnoch, 2014), which grow rapidly and can overtop seedlings and complicates our consideration of oak-mesophyte competition at the seedling stage.

4.3. Management strategies for reducing soil N

Our findings suggest that reducing soil N availability may benefit oak competitive outcomes in N-rich forests. While global change factors such as atmospheric N deposition and rising temperatures cannot be manipulated at the stand scale, prescribed fire and removal of early successional N-fixers may offer tools for reducing total N stocks in recovering forests. Infrequent prescribed fire or fire used alone, seems to minimally impact N stocks over the long term; but repeated burning, particularly when combined with selective felling may iteratively reduce N stocks and secure the continued recruitment of oak (Keyser and Loftis, 2021; Oakman et al., 2019; Fig. 5b). In some cases, frequent fire can increase rates of N mineralization even if total N stocks decline (Tierney et al., 2019), and thus fire should be considered as a tool to manage fuels, the N cycle and mesophyte competitors once oak is established in the understory (Dey and Schweitzer, 2018). Manipulating light through selective cutting paired with prescribed fire may also help ensure success of oaks (Hanberry et al., 2012). In southern Appalachian forests specifically, the use of mechanical thinning combined with prescribed fire may be necessary for reducing the dominance of ericaceous shrubs, which can inhibit oak reproduction (Lafon et al., 2022; Taylor et al., 2025).

Another potential strategy for reducing N richness is to reduce early successional N-fixing trees such as black locust, which introduce N through biological N fixation. In a field sapling experiment, black locust promoted the growth of mesophytes, but not oak, under high light conditions (Minucci et al., 2019), likely due to the positive effect of N fixation on available soil N. Analysis of long-term data suggests that early successional black locust can lead to mesophyte dominance, particularly after high levels of timber extraction (Wurzburger et al., 2023). Thus, management actions that can reduce the dominance of black locust in early succession are likely to have long-term benefits for oak.

5. Conclusions

As in many eastern forests, the southern Appalachian region experienced disturbances that drove species composition away from oak-hickory dominance. Today, in forests following intensive disturbance, opportunistic mesophytic species have little restriction on growth as they utilize available light and nutrients (Alexander et al., 2021; Nowacki and Abrams, 2008). Our study suggests that oak seedlings are most competitive in partial shade, but high N conditions narrow the range of light that oaks remain competitive with mesophytes.

Our findings suggest that maintaining oak dominance may require modified harvesting practices and management actions to create favorable conditions for oak seedings. For example, the intensity of timber extraction could be adjusted to a stand's soil N-richness, where basal area extraction could be reduced in the most mesic and nutrient-rich stands. Directly reducing N availability may also be possible through the use of prescribed fire and the reduction of N-fixing trees in early succession. Our work suggests that one facet of the problem of oak decline and the expansion of mesophytes relates to increasing light and N conditions that favor mesophytes over oaks, due to differences in their strategies for growth and nutrient acquisition. Further research is needed to investigate whether these light by N interactions extend to the sapling stage and beyond.

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CRediT authorship contribution statement

Sarah Ottinger: conceptualization, methodology, investigation, data curation, writing-original draft, writing-edits and review, visualization. **Chelcy Miniat:** conceptualization, methodology, validation, formal analysis, resources, writing-original draft, writing-review and editing, supervision, project administration. **Joel Scott:** investigation, resources, writing-original draft, writing-review and editing. **Nina Wurzburger:** conceptualization, methodology, validation, resources, writing-original draft, writing-review and editing, supervision, project administration, funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123300.

Data Availability

Data will be made available on request.

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