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Negative effects of belowground competition outweigh potential benefits of arbuscular mycorrhizal facilitation for seedling success in a managed temperate hardwood forest

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Abstract

Mycorrhizal facilitation and root competition interact to determine forest adaptability to global change, specifically the myriad stressors affecting trees in temperate hardwoods. As managers seek to apply forest adaptation strategies to climate change—including maintaining current canopy conditions, expanding representation of trees at their northern range limit, or moving future climate-adapted species to forests outside their current range—it is essential to understand how belowground interactions affect seedling success under different management scenarios. We planted three species of arbuscular mycorrhizal (AM) seedlings representing different adaptation strategies: *Acer saccharum* (sugar maple), *Prunus serotina* (black cherry), and *Nyssa sylvatica* (black gum) under selective pre-salvage harvests of *Fraxinus americana* and 0.1 ha harvest gaps at three levels of root access, assessing changes in growth, survival, and foliar nitrogen (seedling success). We found that while sugar maple in the selective harvests initially demonstrated higher AM fungal colonization, survival, and foliar N, root exclusion facilitated success of all three species after a second season, especially in the harvest gaps. These findings show that despite the potential loss of root access and AM fungal inoculum with increased harvest intensity, climate-adaptive management could improve AM seedling success through competition release.

Key words: arbuscular mycorrhizal fungi, belowground competition, seedling success, northern hardwood forests, climate-adaptive management

Introduction

Stressors to the temperate forests of North America are numerous, ranging from insect pests (Trotter and Shields 2009; Youngquist et al. 2017) and pathogens (Cale et al. 2017) to climate change-related threats of frost damage (Augspurger 2013), extreme weather (Rustad and Campbell 2012), and drought (Aubin et al. 2016; Isaac-Renton et al. 2018). To facilitate a transition towards more resilient future-adapted forests, we must ensure forest structural complexity to simultaneously maintain current species types, expand the representation of trees at their northern range limit, and facilitate the northward migration of future climate-adapted trees. This goal requires a range of silvicultural interventions, from selective harvests and canopy gaps that may promote current species to larger harvest gaps that yield the warmer, drier microclimates that may promote the population enrichment and assisted forest migration of more southern-adapted species (Nagel et al. 2017; Palik et al. 2022). However, the effects of these management strategies on belowground interactions are largely unexplored, despite their potential to alter competition among the roots of neighboring trees for water, space, and nutrients (root competition; Gerhardt 1996).

Despite decades of research on how root competition impacts seedlings (Connell and Slatyer 1977; Berkowitz et al. 1995; Chapin et al. 2011; Coomes and Grubb 2000), our understanding of how mycorrhizal facilitation may interact with belowground competition to drive forest successional dynamics remains limited (Lekberg et al. 2018; Ke and Wan 2020; Van Nuland et al. 2023). Mycorrhizal fungi can facilitate seedling success by transferring nutrients (van der Heijden et al. 2015) and water (Kakouridis et al. 2022) to roots in exchange for photosynthate, thereby helping trees overcome nutrient limitation (Phillips et al. 2013) and drought stress (mycorrhizal facilitation; Ruiz-Lozano 2003). These benefits may occur through independent mycorrhizal colonization or possibly by connecting seedlings to mature trees through common mycorrhizal networks (Simard et al. 1997). However, evidence for common mycorrhizal networks is sparse (Karst et al. 2023). Alternatively, mycorrhizal fungi may become parasitic in high-nutrient soil (Johnson 1993), low-light conditions (Hayman 1974; Daft and El-Giahmi 1978), and in soils with a high root density (Johnson et al. 1997). Thus, depending on the function of the mycorrhizal symbioses and the strength of root competition, access to roots of neighboring mature trees (hereafter called root access) could facilitate or inhibit seedling growth and survival (hereafter called seedling success).

Forming symbioses with 80% of land plants (Smith and Read 2008; Bonfante and Genre 2010), and colonizing trees such as maple (*Acer* spp.), ash (*Fraxinus* spp.), and cherry (*Prunus* spp.; Brundrett and Tedersoo 2020), arbuscular mycorrhizal (AM) fungi are ubiquitous in both the canopy and understory of temperate hardwoods (Genre et al. 2020); however, the degree of benefit AM fungi render to seedlings remains uncertain and context-dependent (Johnson 1993; Johnson et al. 1997), further complicating the role of mycorrhizae in belowground interactions (Karst et al. 2023). AM trees commonly exhibit conspecific negative density dependence (Brown et al. 2020), in which seedlings perform more poorly when grown near conspecifics (Bennett et al. 2017). Indeed, AM hosts can be susceptible to the accumulation of less beneficial host species-specific AM fungal communities (Bever 2002) and pathogens (Packer and Clay 2003).

Despite this tendency towards conspecific negative density dependence, AM trees are increasingly dominant in the forests of the eastern US (Abrams 1998; Jo et al. 2019). Furthermore, forest inventory data show 100% AM dominated forest stands are more commonly found than mixed stands (Averill et al. 2022; Delavaux et al. 2023). A con-mycorrhizal feedback wherein AM fungi create conditions to reinforce the dominance of their tree hosts has been hypothesized to explain these patterns (Averill et al. 2022; Delavaux et al. 2023). In particular, AM fungi and their tree hosts can perpetuate fast nitrogen cycles (Phillips et al. 2013), and AM fungi can be shared among heterospecific host plants, which have been found to be more beneficial than fungi shared amongst conspecifics (Bever 2002). However, it should be noted that AM dominance in the northeast has also been driven by a legacy of small gap and single-tree selection that strongly favors shade-tolerant AM trees like *Acer* spp. (Smith and Miller 1987; Leak and Smith 1996; Leak and Sendak 2002; Neuendorff et al. 2007; Premer and Froese 2022).

While it has been suggested that preserving large, mature ectomycorrhizal trees can bolster ectomycorrhizal seedling success (Simard 2009; Cortese and Horton 2024), it is an open question whether leaving adult AM trees behind facilitates AM seedling success. Root access in less intensively harvested stands may negatively affect AM seedling success due to increased competition between seedlings and neighboring mature tree roots and associated AM fungi for nutrients, water, and light (Coomes and Grubb 2000) and from increased pathogen exposure (Bennett et al. 2017). Furthermore, there is a higher potential for mycorrhizal parasitism in more dense, light-limited forests where trees may be more carbon-limited (Johnson et al. 1997). However, root access may facilitate AM seedling success via the increased likelihood of mycorrhizal fungi colonizing roots, the subsequent benefits of nutrient and water provision, and the potential for resource exchange with neighboring trees (Simard 2009). These benefits may be greatest in harvest gaps, where nutrients may be more scarce (Coomes and Grubb 2000). The balance of mycorrhizal facilitation and root competition can also vary depending on the identity and relative abundance of each AM tree species (Liang et al. 2015). For example, the strength of competitive versus facilitative effects on trees has been shown to vary dramatically based on species identity (Bennett et al. 2017), life history traits such as shade tolerance (Brown et al. 2020), and site richness (Berkowitz et al. 1995), underlining the importance of regional, species- and site-specific research on these drivers.

Our 2-year study investigates how root access mediates the growth, survival, and foliar nitrogen of three AM seedlings—sugar maple (*Acer saccharum* Marsh.), black cherry (*Prunus serotina* Ehrh.), and black gum (*Nyssa sylvatica* Marsh.)—under two levels of canopy disturbance: selective pre-salvage harvesting of *Fraxinus americana* and 0.1 ha harvest gaps created through group selection—within the northern hardwood forests of Vermont, USA. Each species represents different applications of forest adaptation approaches to climate change (Palik et al. 2022), with sugar maple reflecting strategies to maintain current species densities (enrichment planting), black cherry representing assisted population expansion of a climate-adapted species, and black gum representing assisted range expansion of species expected to gain new habitat in the study region (Peters et al. 2020). We planted seedlings of these three species in selective harvests and 0.1 ha harvest gaps, and varied access to live roots through temporary root-severing and permanent trenching, a technique often used in studies aiming to eliminate both root competition (Coomes and Grubb 2000) and mycorrhizal facilitation (Simard et al. 1997). We hypothesized that increased access to live roots would ultimately benefit seedlings through mycorrhizal facilitation, especially in the harvest gaps where the soil may have less AM fungal inoculum and root competition is less intense.

Materials and methods

Plot establishment

Our experiment occurred at the Clement Woodlot Experimental Forest in Corinth, Vermont (Fig. S1; elev. 1200′/366 m, lat.: 44.05, long.: −72.32), a northern hardwood forest with nutrient-rich, high-calcium soils where sugar maple (*A. saccharum*) and white ash (*F. americana*) dominate, with lesser amounts of yellow birch (*Betula alleghaniensis*) and American beech (*Fagus grandifolia*) based on basal area. The mean annual temperature is 5.3 °C, while the mean annual precipitation is 110 cm (Rice et al. 2024). The woodlot was cleared for pastureland in the 19th century, which was subsequently abandoned and naturally reforested with primarily maple and ash prior to being given to Dartmouth College in the 1920s. Management of the area prior to this study consisted of single-tree selection harvests in 1992 and 1993 to convert stand conditions from even-aged to uneven-aged structure and encourage sugar maple dominance. The soils are predominantly sandy to coarse-loamy spodosols derived from glacial till and formed from carbonaceous phyllite and limestone (Rice et al. 2024). The soil is slightly acidic, moist, and well-drained, which explains why the trees that grew back after agricultural abandonment in the 19th century were primarily maple and ash, adapted to this rich, moist site.

To address how harvest type and root access affect seedling success, we utilized two main harvest types with different levels of canopy disturbance—harvest gaps and selective harvests (Figs. S1 and S2). The harvest gaps consisted of four 0.1 ha group selection openings in which all overstory trees within an 18 m radius were removed in co-produced adaptation treatments that align with other climate-adaptive forest management treatments in the northeast (Nagel et al. 2017). The selective harvests were four 0.1 ha circular plots of selective, pre-salvage harvesting focused on the removal of *Fraxinus americana*. The selective harvest resulted in a range of canopy opening sizes given ash was both scattered as individual trees and in groups across the site with an average basal area of 14 ± 1.6 m^2 ha^{-1} (ranged from 12.7 to 18.5 m^2 ha^{-1}) prior to harvest. Before harvesting, we measured the diameter at breast height (DBH) of stems >10 cm diameter in the harvest gap locations to ensure all plots were dominated by AM trees (Table S1). Initial surveys of the broader area showed that ash dominance ranged from 37% to 44% and sugar maple dominance ranged from 32% to 38%, based on importance values (relative basal area + relative density/2; Curtis and McIntosh 1951). Harvest took place between December 2020 and April 2021 using hand felling with chainsaws and a tractor with a winch for cable skidding. Soil in the harvest gaps was generally more disturbed as the litter layer was seldom present compared to the less invasive selective harvest treatment. All trees >10 cm DBH were measured and identified in August 2023 to characterize the selective harvest plots, which remained >95% AM due to maple (*A. saccharum*) dominance.

To create a range of seedling access to the network of roots and associated fungi of neighboring trees, we established six 0.75 m radius subplots in June 2022 within each of the eight 0.1 ha plots (Fig. S1). Of the six subplots, two were undisturbed controls (high root access), two were root-severed (medium root access), and two were trenched (low root access). There were 16 subplots of each treatment across the whole experiment (Table S2). Subplot locations were determined by scouting to find areas within the 0.1 ha plots that would accommodate a 0.75 m radius subplot, and randomly assigning treatments. In the low root access subplots, we dug a circular trench to a depth of 45 cm or until contacting bedrock, lined the trench with a 3 mm thick polyethylene rhizome barrier, and backfilled. As we only trenched along the perimeter, the structure of the soil inside the subplot remained intact. For the medium root access subplots, we severed the soil, roots, and hyphae in a continuous circle to a depth of 45 cm using a sharpshooter (a heavy, 45 cm long, straight shovel). This treatment was repeated halfway through the first summer (26 to 27 July 2022) to sever new root and hyphal growth. The control subplots were established with the same 0.75 m radius as the other treatments, but there was no root severing or barrier at the perimeter, yielding comparatively high root access.

We also implemented mowing and weeding treatments to maintain desired levels of root access and eliminate potential competition with volunteer woody and herbaceous species that grew in the plots. Mowing occurred in the control and root-severed subplots and consisted of cutting all woody and herbaceous growth to about 5 cm above the soil surface while leaving root networks untouched. Weeding occurred in the trenched subplots and consisted of pulling all woody and herbaceous vegetation up by the roots. These treatments helped to reinforce the gradient of root access among the subplots. Mowing and weeding was reinforced four times in 2022 (13 July, 26 to 27 July, 13 August, and 31 August), frequent enough to prevent weeds from overtaking and shading the seedlings in their vital first year of establishment. While some soil disturbance may have resulted from weeding in the trenched plots, this effect was minor compared to the disturbances caused by planting seedlings within each plot and by the soil scarification and root decay caused by harvest.

In each subplot, we planted four seedlings each of sugar maple, black cherry, and black gum for a total of 12 seedlings per subplot, and a total of 576 seedlings across the experiment. Bare-root, 6–12 in. seedlings from seed zones appropriate for the planting site were acquired from a nursery of a similar latitude as the Clement Woodlot (Cold Stream Farm; Free Soil, MI, USA) and stored in the dark at 4 °C prior to planting. We planted the seedlings between 9 and 17 June 2022. Eight of the 576 planted seedlings (1% of the total) were replaced due to a planting error by 29 June 2022.

We selected *A. saccharum* (sugar maple) as a species currently dominant in northern hardwoods and whose ecological, cultural, and economic significance incentivizes foresters to maintain the current population (Smith and Miller 1987; Leak and Smith 1996; Leak and Sendak 2002) making it a target in climate-adaptive management (Wikle and D'Amato 2023). Sugar maple (hereafter called "maple") is a shade-tolerant species that prefers moist, well-drained soils that can range from slightly acidic to slightly alkaline. It is commonly associated with fertile and calcareous soils (Burns and Honkala 1990), which explains its current dominance at the woodlot. We selected *P. serotina* (black cherry) as a species at the northern edge of its current range in our study region but expected to thrive in future climates, making it a target species for planting in other climate-adaptive management projects (Nagel et al. 2017). Black cherry (hereafter called cherry) grows on deep, moist, well-drained soil that is frequently acidic and infertile, although it can thrive in a variety of soil types (Burns and Honkala 1990). *Nyssa sylvatica* (hereafter called black gum) was selected for its potential for range expansion, being a more southern-adapted species that may find the climate of northern Vermont suitable for its growth in upcoming decades (Peters et al. 2020). Black gum can tolerate neutral to more acidic soil that can range from occasionally dry to saturated (Burns and Honkala 1990). All three seedlings are likely to respond differently to canopy disturbance as maples and black gum are late-successional and more shade-tolerant, while cherries are more early-successional and shade-intolerant (Burns and Honkala 1990).

Measurements

Directly after planting (by 29 June 2022), we tagged all seedlings with a metal forester's tag, noted whether seedlings were alive or dead, and measured the height of each seedling directly after planting (by 29 June 2022). At the end of the growing season (7 to 11 September 2022), we re-measured the height and survival of all seedlings. Growth and survival measurements were repeated from 16 to 17 August 2023.

Three times throughout the 2022 field season (13 July, 26 to 28 July, and 13 August 2022), and once in 2023 (13 August 2023), we measured percent volumetric soil moisture and temperature at three locations within each subplot using a Teros 11 moisture probe (METER, Pullman, WA, USA). The probe was inserted 5.5 cm into the soil. We measured leaf area index (LAI) in all subplots on 11 and 12 August 2023 using a LAI-2200C LiCOR Plant Canopy Analyzer (Lincoln, NE, USA). We sampled soil from three randomly chosen points within each subplot from 8 to 11 September 2022 to determine soil nitrate/nitrite and ammonium availability. We removed leaf litter (when present) before sampling the top 15 cm of soil, which included O/A and B horizons. Soil samples were stored in a −20 °C freezer prior to analysis and were thawed for a KCl soil extraction. In brief, we mixed 8 g of thawed soil with 32 mL of 2 mol/L KCl, shook the samples on "low" for an hour, and then filtered the extractant through Whitman filter paper (52 nm and 110 mm diameter). Extracts were analyzed using the automated flow injection colorimetric analysis technique on a Lachat QuickChem 8500 (Denver, CO, USA).

To measure foliar N at the end of the 2022 growing season, we used a hole punch to obtain leaf samples of seedlings across all subplots between 2 and 7 September 2022. To get a representative sample, we punched holes from four different leaves per seedling, avoiding diseased spots and large veins. We did not collect foliar samples from seedlings that had not leafed out or those with only a few small leaves to avoid negatively affecting their growth and survival. We then dried the leaf samples at 60 °C and analyzed them with an elemental analyzer (EA; Thermo Scientific) for % N. A total of 284 seedlings were analyzed for nutrient content.

We characterized the effects of management type on plot-level live woody root density and seedling mycorrhizal colonization in the control treatment subplots. Between 22 and 23 July 2022, we dug one randomly located root pit in each of the eight harvest plots that was approximately 30 × 30 × 30 cm. All live woody roots from within the pit were taken back to the laboratory, dried, and weighed to determine live woody root density in the top 30 cm of soil. To determine management effects on mycorrhizal colonization, we quantified the AM fungal colonization of maple and cherry roots. A subsample of fourteen maple seedlings within control subplots (seven from the selective harvest plots and seven from the harvest gap plots) was obtained on 15 and 17 November 2022. In July 2023, we collected roots from three cherry seedlings within the control subplots of each harvest treatment by gently excavating the soil around each seedling.

To quantify AM fungal colonization, we washed roots to remove soil, subsampled 5 to 10 root tips (of approx. 2 cm in length) from each sample (either maple seedling or cherry roots), and stored root tips in 90-proof ethanol. Root tips were cleared, dyed, and stained using the ink and vinegar method (Vierheilig et al. 1998). We measured the proportion of root length colonized by AM fungi using a gridline intersection procedure (Giovannetti and Mosse 1980) on an Axioskop microscope (Zeiss, Germany) with 20× and 40× lenses. We also measured the % colonization of dark septate endophytes (DSE) on maple seedlings (Jumpponen and Trappe 1998; Jumpponen 2001; Mandyam and Jumpponen 2015), whose potential interaction with mycorrhizae, and effect on directing feedback loops, remains largely unexplored (Smith and Read 2008). Due to concerns with disturbing the seedlings and time constraints, we did not analyze AM fungal or DSE colonization on black gum seedlings or by root access treatment.

Statistical analyses

To determine the effects of management type and root access treatment on environmental factors, we ran linear mixed effects models using functions from lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017) in which management type, root access treatment, and their interactions were fixed effects (Table 1). For leaf area index and soil inorganic N measurements, we included plot ID as a random effect. Soil temperature and soil moisture additionally had subplot ID nested within plot ID as random effects and data from 2022 and 2023 were analyzed together. Multiple comparisons were performed when there were significant fixed effects or interactions using the emmeans package (Length 2023). To compare root density between harvest treatments, we performed an unpaired, one-sided *t* test weighted for unequal variances. AM fungi and DSE colonization of maple seedlings and AM fungal colonization of cherry seedlings were first summarized by seedling ID then analyzed using one-sided *t* tests to compare colonization between harvest types.

Survival data was summarized by species within each subplot to obtain the proportion surviving (Assad et al. 2022), then logit-transformed prior to statistical analyses (Berkowitz et al. 1995; Warton and Hui 2011). Seedling growth, survival and foliar % N were analyzed through a linear mixed effects model in which harvest type, root access treatment, seedling species and their interactions were fixed effects, and subplot ID nested within plot ID were random effects (Table 2). Variances in the growth and survival models were weighted by species to meet model assumptions. Survival through the growing season of 2022 and total survival from June 2022 to August 2023 were analyzed separately but according to the same model as initial effects did not carry over into the next growing season. As growth patterns remained consistent over both growing seasons, we only present total growth. All analyses were performed in R Version 4.2.3 (R Core Team 2023). We determined results to be significant if $p < 0.05$, and marginally significant if $0.05 > p < 0.08$. Results are reported in the following section with mean ± standard error.

Table 1. Linear mixed effects model results for soil moisture and temperature (2022, 2023), leaf area index (LAI; 2023), and soil total inorganic nitrogen (TIN), nitrate, and ammonium (2022) at the Clement Woodlot (Corinth, VT, USA).

Response variable	Fixed and random effects	numDF	denDF	*F*	*p*
Soil moisture	Harvest + 1|Plot/Subplot	1	6	0.202	0.70
	Access + 1|Plot/Subplot	2	36	2.88	0.069
	Harvest*Access + 1|Plot/Subplot	2	36	0.017	0.98
Soil temperature	Harvest + 1|Plot/Subplot	1	6	8.42	**0.027***
	Access + 1|Plot/Subplot	2	558	1.32	0.27
	Harvest*Access + 1|Plot/Subplot	2	558	1.88	0.15
LAI	Harvest + 1|Plot	1	5.5	2.72	0.15
	Access + 1|Plot	2	25	1.76	0.19
	Harvest*Access + 1|Plot	2	25	1.10	0.35
Soil TIN	Harvest + 1|Plot	1	6	0.146	0.72
	Access + 1|Plot	2	36	0.0990	0.91
	Harvest*Access + 1|Plot	2	36	0.0567	0.95
Soil nitrite/nitrate	Harvest + 1|Plot	1	6	2.09	0.20
	Access + 1|Plot	2	36	4.49	**0.018***
	Harvest*Access + 1|Plot	2	36	1.05	0.36
Soil ammonium	Harvest + 1|Plot	1	6	0.228	0.65
	Access + 1|Plot	2	36	2.11	0.14
	Harvest*Access + 1|Plot	2	36	0.205	0.82

Note: Asterisks indicate statistical significance at the level of $p < 0.001$ (***), $p < 0.01$ (**), and $p < 0.05$ (*). Significant *p* values ($p < 0.05$) are bolded.

Results

Characterization of experimental treatments

Environmental conditions displayed minimal variation by harvest or root access treatment (Fig. 1 and Tables 1 and 3). Soil moisture was marginally affected by root access treatment ($F_{[2,36]} = 2.88$, $p = 0.069$), with higher average volumetric water content (VWC) in the root-severed (28.7%) and trenched (28.4%) than control treatment (25.2%). Soil VWC did not vary by harvest type ($F_{[1,6]} = 0.202$, $p = 0.70$) or the harvest*root access interaction ($F_{[2,36]} = 0.017$, $p = 0.98$). Soil temperature varied by harvest type ($F_{[1,6]} = 8.42$, $p = 0.027$) with soil in the selective harvests (23.6 ± 0.16 °C) 2.8 °C cooler than in the harvest gaps (26.4 ± 0.26 °C). LAI varied little by root access treatment (Tables 1 and 3), although LAI in the harvest gaps (2.07 ± 0.24), was lower than LAI in the selective harvests (3.09 ± 0.23). While total inorganic nitrogen and ammonium in the soil remained consistent across harvest type and root access treatment, nitrate and nitrate varied by root access treatment ($F_{[2,36]} = 4.49$, $p = 0.018$; Tables 1 and 3), with concentrations in the trenched treatment (16 ± 3 ug/g soil) over two-fold higher than in the control (7.5 ± 1 ug/g soil; $p = 0.0138$).

Live woody root density and mycorrhizal colonization

Harvest type affected live woody root biomass and % mycorrhizal colonization (Fig. 2). Live root mass, a proxy for root density, was five times higher in selective harvests versus harvest gaps ($t_{4.66} = 3.14$, $p = 0.014$), averaging at 141 ± 90.8 g m^{-2} in the harvest gaps and 733 ± 165 g m^{-2} in the selective harvests. Mean AM fungal colonization of maple seedling roots in control subplots of selective harvests (51.7 ± 4.0%) was two-fold higher than in the harvest gaps (24.7 ± 4.3%; $t_{11.9} = 2.89$, $p < 0.001$). Total AM fungal and DSE colonization of maple roots was also higher in the selective harvests (88.4 ± 1.8%) than in the harvest gaps (59.8 ± 5.0%; $t_{6.49} = 4.09$, $p = 0.0027$). Similarly, AM fungal colonization of cherry seedling roots in the control subplots was higher in selective harvests (58.1 ± 7.1%) relative to the harvest gaps (43.9 ± 4.5%; $t_{5.08} = 1.69$, $p = 0.076$).

Seedling survival

Harvest type interacted with species to affect seedling survival in 2022 (Fig. 3*a*, Table 2; Harvest Type*Species Interaction, $F_{[2,84]} = 3.71$, $p = 0.029$). Maple survival was higher in the selective harvests (90.6 ± 3.0%) than in the harvest gaps (67.7 ± 6.5%; $p = 0.034$). Cherry and black gum survival did not vary significantly between harvest types, although mean survival was lower in the harvest gaps (68.8 ± 5.9% for black gum and 96.9 ± 1.7% for cherry) than in the selective harvests (78.1 ± 5.5% for black gum and 100% for cherry). Overall seedling survival from June 2022 to August 2023 exhibited a significant three-way interaction between harvest type, root access treatment, and species type (Fig. 3*b*; $F_{[4,68]} = 2.72$, $p = 0.037$). While the differences in maple survival between the harvest gaps and selective harvests was near significance ($p = 0.081$), 56.2 ± 9.2% of maples in root-severed subplots survived in the harvest gaps while 87.5 ± 8.5% survived in the selective harvests. Cherry seedling survival was higher than that of maple ($p < 0.001$) or black gum ($p < 0.001$) in both 2022 ($F_{[2,84]} = 45.3$, $p < 0.001$) and 2023 ($F_{[2,68]} = 42.1$, $p < 0.001$). By

Table 2. Linear mixed effects model results for initial seedling survival (2022), overall growth and survival (2022–2023) and foliar N (2022) at the Clement Woodlot (Corinth, VT, USA).

Response variable	Fixed and random effects	numDF	denDF	F	p
Initial survival	Harvest + 1|Plot/Subplot	1	6	1.10	0.33
	Access + 1|Plot/Subplot	2	36	1.77	0.18
	Species + 1|Plot/Subplot	2	84	45.3	**$<0.001^{***}$**
	Harvest*Species + 1|Plot/Subplot	2	84	3.71	**0.029^{*}**
	Species*Access + 1|Plot/Subplot	4	84	0.994	0.42
	Harvest*Access + 1|Plot/Subplot	2	36	1.77	0.19
	Species*Access*Harvest + 1|Plot/Subplot	4	84	1.07	0.38
Overall survival	Harvest + 1|Plot/Subplot	1	5	2.08	0.21
	Access + 1|Plot/Subplot	2	68	42.1	**$<0.001^{***}$**
	Species + 1|Plot/Subplot	2	29	0.0788	0.92
	Harvest*Access + 1|Plot/Subplot	2	68	0.189	0.83
	Harvest*Species + 1|Plot/Subplot	2	29	0.234	0.79
	Access*Species + 1|Plot/Subplot	4	68	0.687	0.60
	Harvest*Access*Species + 1|Plot/Subplot	4	68	2.72	**0.037^{*}**
Overall growth	Harvest + 1|Plot/Subplot	1	6	4.46	0.079
	Access + 1|Plot/Subplot	2	34	9.61	**$<0.001^{***}$**
	Species + 1|Plot/Subplot	2	350	370	**$<0.001^{***}$**
	Harvest*Access + 1|Plot/Subplot	2	34	1.19	0.32
	Harvest*Species + 1|Plot/Subplot	2	350	31.9	**$<0.001^{***}$**
	Access*Species + 1|Plot/Subplot	4	350	10.2	**$<0.001^{***}$**
	Harvest*Access*Species + 1|Plot/Subplot	4	350	0.936	0.44
Foliar N	Harvest + 1|Plot/Subplot	1	7.3	0.180	0.68
	Access + 1|Plot/Subplot	2	44	15.5	**$<0.001^{***}$**
	Species + 1|Plot/Subplot	2	240	132	**$<0.001^{***}$**
	Harvest*Access + 1|Plot/Subplot	2	46	1.23	0.30
	Harvest*Species + 1|Plot/Subplot	2	240	8.66	**$<0.001^{***}$**
	Access*Species + 1|Plot/Subplot	4	240	7.91	**$<0.001^{***}$**
	Harvest*Access*Species + 1|Plot/Subplot	4	240	0.0724	0.99

Note: Asterisks indicate statistical significance at the level of $p < 0.001$ (***), $p < 0.01$ (**), and $p < 0.05$ (*). Significant p values ($p < 0.05$) are bolded.

the end of the study, mean cherry survival was the highest at 96.2 ± 1.69%, followed by maples at 70.2 ± 4.57%, then black gum at 58.1 ± 5.32%.

Seedling growth

Total seedling growth from the onset of the study in June 2022 to the end in August 2023 also varied by harvest type (Table 2; Fig. 4; Harvest*Species Interaction; $F_{[2,350]} = 31.9$, $p < 0.001$), a trend driven by 207% higher cherry growth in the harvest gaps (71.9 ± 4.3 cm) than in the selective harvests (34.8 ± 2.7 cm; $p = 0.003$). Although not significant, maples grew over 10 cm more in the harvest gaps (13.4 ± 3.0 cm) than in the selective harvests (2.64 ± 0.96 cm), and black gum growth valued at −7.43 ± 2.2 cm in the harvest gaps while it valued at −13.4 ± 2 cm in the selective harvests, indicating initial dieback but more successful resprouting in the harvest gap. Species-specific growth also differed by root access (Species*Root Access Interaction; $F_{[4,350]} = 10.2$, $p < 0.001$). Cherry seedling growth across both harvest types was highest in the trenched treatment (74.3 ± 4.9 cm), lower in the root-severed (48.4 ± 3.8 cm) and lowest in the control (30.6 ± 4.0 cm; $p < 0.009$). Maples also grew almost 20 cm higher in the trenched (19.2 ± 2.7 cm) than control subplots (0.88 ± 2.0 cm; $p = 0.015$) and black gum seedlings grew approximately 10 cm higher in the trenched treatment (−5.12 ± 2.1 cm) than in the control (−16.0 ± 2.4 cm; $p = 0.064$). Total seedling growth was marginally higher in the harvest gaps (34.3 ± 3.4 cm) than in the selective harvest (12.4 ± 1.9 cm; Harvest, $F_{[1,6]} = 4.46$, $p = 0.079$). Seedling growth differed among all three root access treatments (Root Access, $F_{[2,34]} = 9.61$, $p < 0.001$) with highest growth in the trenched treatment (32.8 ± 3.6 cm), followed by the root-severed (20.6 ± 2.9 cm), and then the control subplots (10.2 ± 2.80 cm; $p < 0.043$). Growth varied by tree species identity (Species, $F_{[2,350]} = 370$, $p < 0.001$), with cherry seedlings demonstrating the highest growth (52.0 ± 2.8 cm), then maple (7.33 ± 1.5 cm), followed by black gum (−10.7 ± 1.5 cm) when averaged over harvest and treatment.

Foliar nitrogen

Seedling foliar N, collected at the end of the 2022 growing season, varied by species identity, harvest type, and root access (Tables 2 and 4). Foliar N varied by root access in a species-specific manner (Fig. 5; Species*Root Ac-

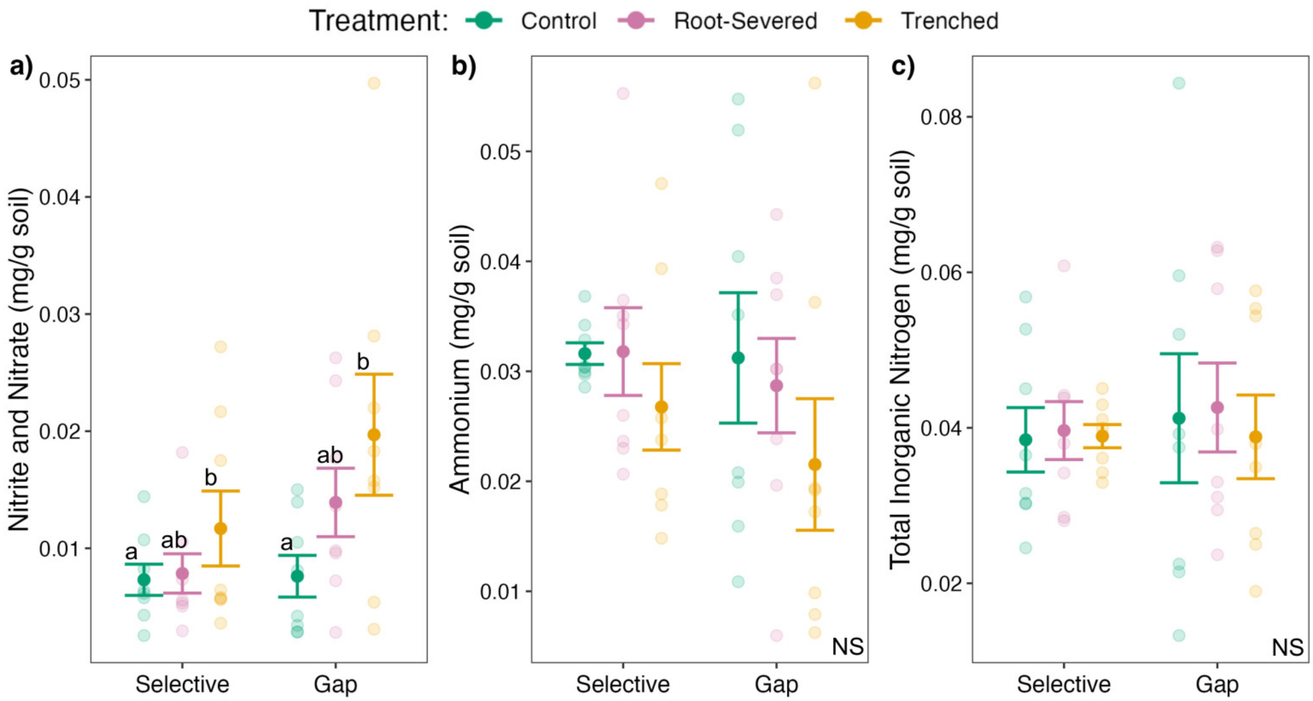


Fig. 1. Soil inorganic nitrogen values from the Clement Woodlot in Corinth, VT, USA in the summer of 2022 between harvest and treatment. (*a*) Total nitrite (NO_2) and nitrate (NO_3) concentrations vary by root access treatment, with higher nitrate and nitrate concentrations in the trenched plots. (*b*) There was no difference in ammonium (NH_4) concentrations by harvest or root access treatment, although there was a trend of decreasing ammonium availability with decreasing root access. (*c*) Total inorganic nitrogen (NO_2, NO_3, and NH_4) did not vary by harvest or by root access treatment. Letters not shared indicate significant differences between root access treatments ($p < 0.05$). The centerpoint indicates the mean, and the whiskers represent standard error. “NS” indicates no significant differences. Note the axes differ between panels.

Table 3. Means and standard errors for leaf area index (LAI; 2023) and soil characteristics, including volumetric water content (VWC) and temperature (*T*) from a probe inserted 5.5 cm into the soil (2022–23), and inorganic nitrogen concentrations, including nitrite and nitrate (NO_2/NO_3), ammonium (NH_4), and total inorganic nitrogen (TIN; 2022) at the Clement Woodlot (Corinth, VT, USA).

Harvest type	Root access	LAI	VWC (%)	*T* (°C)	NO_2/NO_3 (ug/g soil)	NH_4 (ug/g soil)	TIN (ug/g soil)
Selective	Control	2.88 ± 0.29^{Aa}	25.2 ± 0.95^{Aa}	23.6 ± 0.26^{Aa}	7.3 ± 1^{Aa}	32 ± 1^{Aa}	39 ± 1^{Aa}
	Root-severed	2.72 ± 0.37^{Aa}	28.7 ± 0.75^{Aa}	23.5 ± 0.24^{Aa}	7.9 ± 2^{Aab}	32 ± 4^{Aa}	40 ± 4^{Aa}
	Trenched	3.71 ± 0.48^{Aa}	28.4 ± 0.70^{Aa}	23.7 ± 0.32^{Aa}	12 ± 3^{Ab}	27 ± 4^{Aa}	39 ± 4^{Aa}
Gap	Control	2.18 ± 0.51^{Aa}	24.9 ± 0.97^{Aa}	27.0 ± 0.46^{Ba}	7.6 ± 2^{Aa}	31 ± 6^{Aa}	39 ± 5^{Aa}
	Root-severed	2.22 ± 0.31^{Aa}	27.5 ± 0.84^{Aa}	26.5 ± 0.42^{Ba}	14 ± 3^{Aab}	29 ± 4^{Aa}	43 ± 6^{Aa}
	Trenched	1.86 ± 0.48^{Aa}	27.7 ± 0.82^{Aa}	25.8 ± 0.46^{Ba}	20 ± 5^{Ab}	22 ± 6^{Aa}	41 ± 8^{Aa}

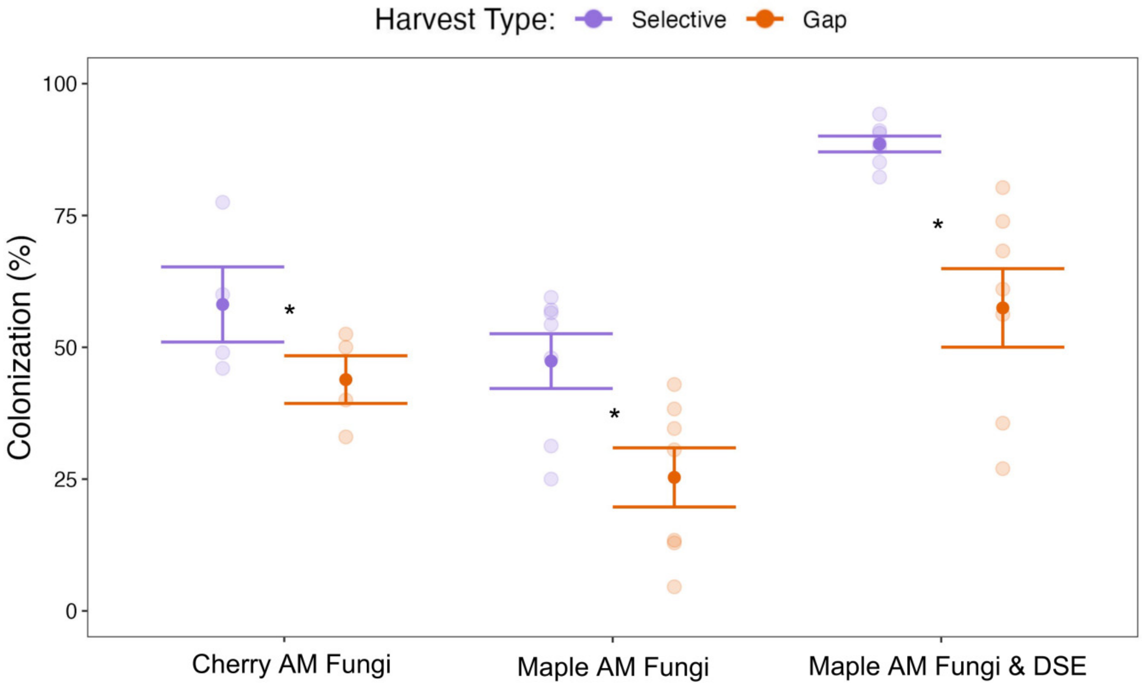
Note: $N = 72$ replicates for T and VWC, and 8 for nitrogen concentrations. Uppercase letters not shared indicate significant differences between harvest types, and lowercase letters not shared indicate significant differences among root access treatments ($p < 0.05$).

cess Interaction, $F_{[4,238]} = 7.91$, $p < 0.001$). Cherry foliar N was highest in the trenched (3.91 ± 0.084%), lower in root-severed (3.42 ± 0.08%), and lowest in the control subplots (2.9 ± 0.067%; $p < 0.001$). Maples had significantly lower foliar N in control subplots (2.36 ± 0.071%) than in root-severed (2.59 ± 0.08%) or trenched subplots (2.65 ± 0.078%; $p < 0.041$). Across all seedlings, there was a significant root access effect on foliar N (Root Access, $F_{[2,44.3]} = 15.48$, $p < 0.001$), with higher foliar N in the root-severed (2.88 ± 0.065%) and trenched subplots (3.00 ± 0.074%) than the control subplots (2.58 ± 0.051%; $p < 0.005$). Foliar N varied by species (Species, $F_{[2,239]} = 132$, $p < 0.001$), with higher foliar N in cherry (3.41 ± 0.061%) than in black gum (2.58 ± 0.052%) or maple seedlings (2.55 ± 0.046%; $p < 0.001$). Maple seedlings also displayed higher foliar N ($p = 0.034$) in the selective harvests (2.67 ± 0.06%) than in the harvest gaps (2.37 ± 0.063%; Harvest*Species interaction; $F_{[2,238.4]} = 8.66$, $p < 0.001$).

Discussion

Throughout this experiment, root access restricted seedling success. In the harvest gaps, where there were less woody roots, seedling growth and survival was higher

Fig. 2. Mean arbuscular mycorrhizal (AM) and dark septate endophyte (DSE) colonization of maple (harvested 2022) and cherry (harvested 2023) seedlings in control subplots was significantly higher in selective harvests versus harvest gaps at the study site in Corinth, VT, USA. The centerpoint indicates the mean, and the whiskers represent standard error. Asterisks indicate significant differences between harvest types ($p < 0.08$).

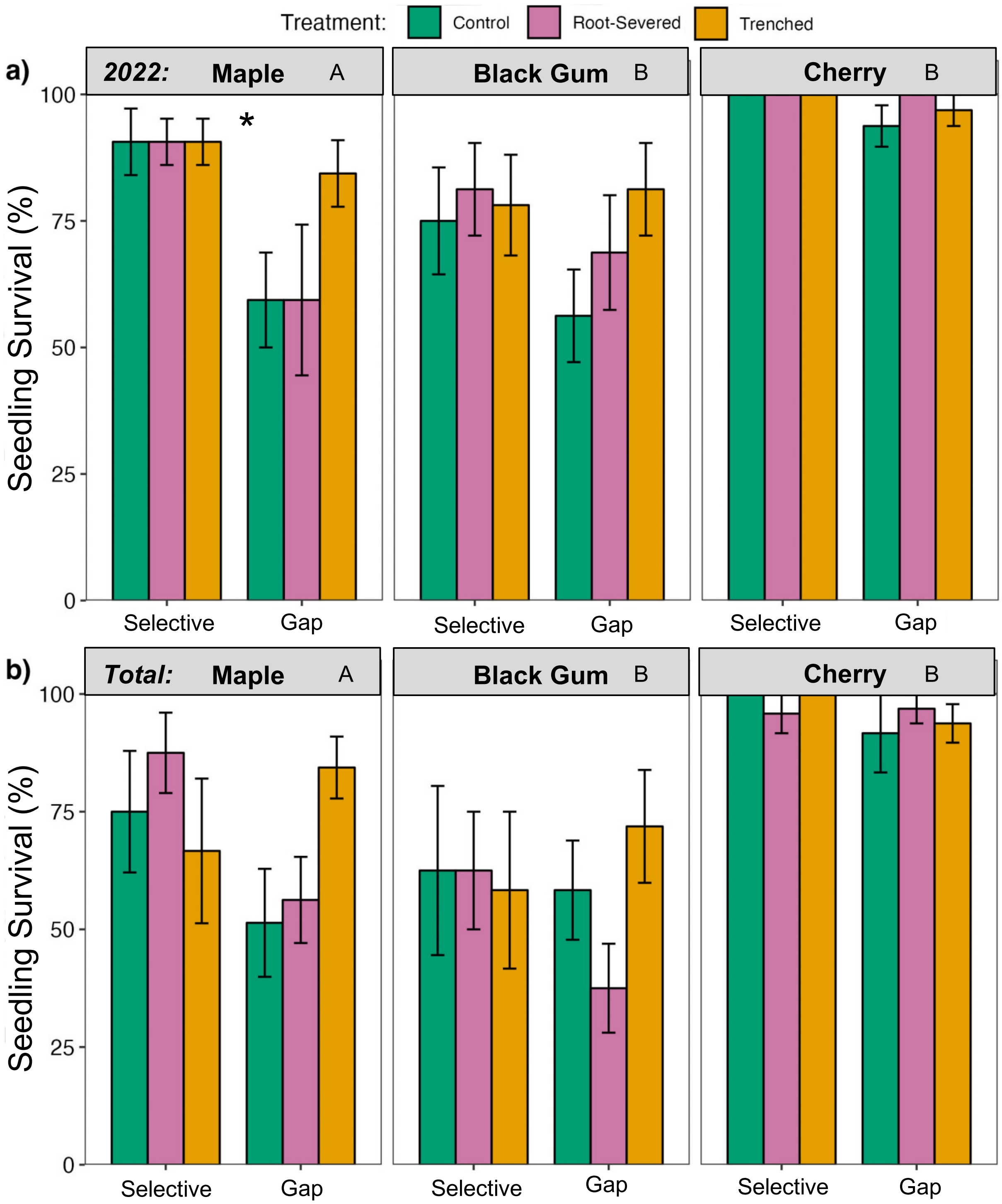


than in selective gaps, and often highest in trenched plots. These results oppose our hypothesis that root access would ultimately benefit seedlings through increased mycorrhizal facilitation, especially in harvest gaps. These positive effects of lower root access occurred despite increased mycorrhizal colonization of maple and cherry in the selective harvest plots. A number of studies demonstrate the benefits of mycorrhizal colonization to seedlings through nutrient (Bonfante and Genre 2010) and water provision (Kakouridis et al. 2022), and some have positive indications of common mycorrhizal networks at least for ectomycorrhizal seedlings (Van Der Heijden and Horton 2009). However, this study implies that for AM seedlings at our relatively rich site, the negative effects of root access—from root competition to potential pathogen exposure and mycorrhizal parasitism—outweigh any potential mycorrhizal benefit.

Potential experimental artifacts of our root access treatments may have affected seedling success, although the magnitude was likely minimal. A few seedlings were subject to deer browse, insect predation, and herbivory, which can alter AM fungal community assembly (Frew et al. 2024), but we noticed no shift in herbivory by management type or root access. Marginally higher soil moisture was found with lower root access, although pairwise comparisons revealed no significant differences, and this pattern was likely driven by less root uptake with root exclusion. Trenching and weeding may have affected seedling responses through soil disturbance and severed root decay (Coomes and Grubb 2000). However, we found no shift in total inorganic nitrogen, nitrate/nitrate or ammonium by harvest type (a much larger disturbance than weeding), and total inorganic nitrogen and ammonium remained consistent across root access treatments. Higher nitrite levels in the trenched subplots may have been a function of lower root demand as well as reduced competition between microbial communities and root systems since nitrate is a microbial product (Schimel and Bennett 2004). Finally, while seedlings in the trenched and root-severed treatments could still be colonized by AM fungi (Smith and Read 2008), treatments would invariably restrict seedling access to inoculum via live roots (Lang et al. 2021) and perhaps common mycorrhizal networks (Karst et al. 2023). Future studies investigating the effects of trenching and weeding on soil nutrients and microbial community composition would help disentangle the relative importance of root competition, mycorrhizal facilitation, and soil disturbance for seedling success in this system.

While root access did not appear to benefit seedling growth and survival after two growing seasons, maple seedlings in the first growing season displayed higher foliar N and survival with concurrent increases in mycorrhizal colonization in the selective harvests. It is possible that mycorrhizal colonization in the more root-dense selective harvests may provide an initial boost to maples. Indeed, sugar maple seedling density can plummet when less than a quarter of the root length is colonized by AM fungi (Tourville et al. 2023), and the presence of surrounding vegetation can facilitate maple survival (Berkowitz et al. 1995). However, maple seedlings also displayed minor gains in growth and foliar N with root exclusion, confounding these conclusions. Therefore, patterns in maple growth between selective and gap harvests are likely

Fig. 3. Maple seedling survival at the Clement Woodlot (Corinth, VT, USA) was higher in selective harvest plots than harvest gap plots in 2022, but initial gains were lost by the end of the 2023 growing season. Cherry seedlings demonstrated the highest survival, followed by maple and then black gum. Bars represent means and the whiskers indicate standard error. Asterisks indicate significant differences between harvest types within a species ($p < 0.05$), and capital letters indicate significant differences between species ($p < 0.05$).



explained by maple's shade-tolerant, late-successional status (Burns and Honkala 1990), and possibly by the high proportion of sugar maples in the overstory which may have selected for nutrient and fungal conditions favorable for other maples, as compared to black gum and cherry (Averill et al. 2022). However, any initial benefit maples derived in the selective harvests ultimately disappeared. By the end of the second summer, maple survival did not vary by harvest type and its growth increased with root exclusion, especially in the harvest gaps.

Fig. 4. Seedling growth at the Clement Woodlot (Corinth, VT, USA) varied by species type and by root access treatment. The centerpoint indicates the mean, and the whiskers represent standard error. Lowercase letters not shared indicate significant differences between root access treatments within a species and within each harvest type ($p < 0.08$), and capital letters indicate differences between species ($p < 0.05$). "NS" signifies that there are no significant differences in root access treatments within a species. The asterisk indicates significant differences between harvest types within a species ($p < 0.05$).

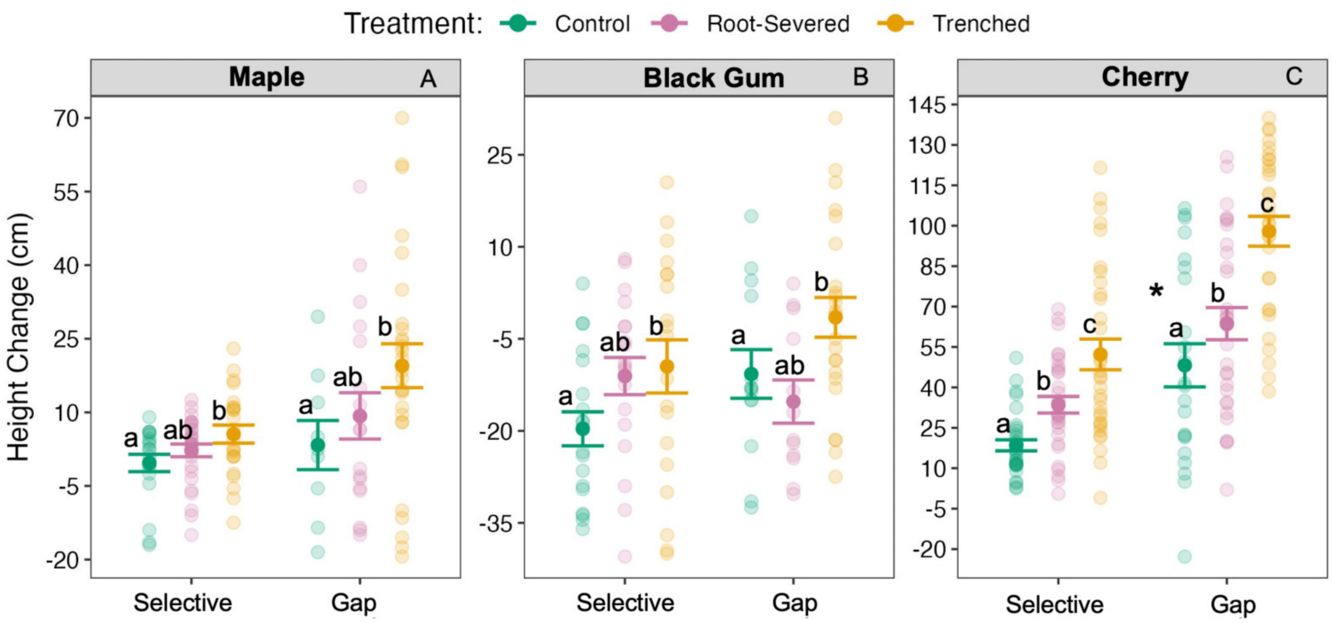


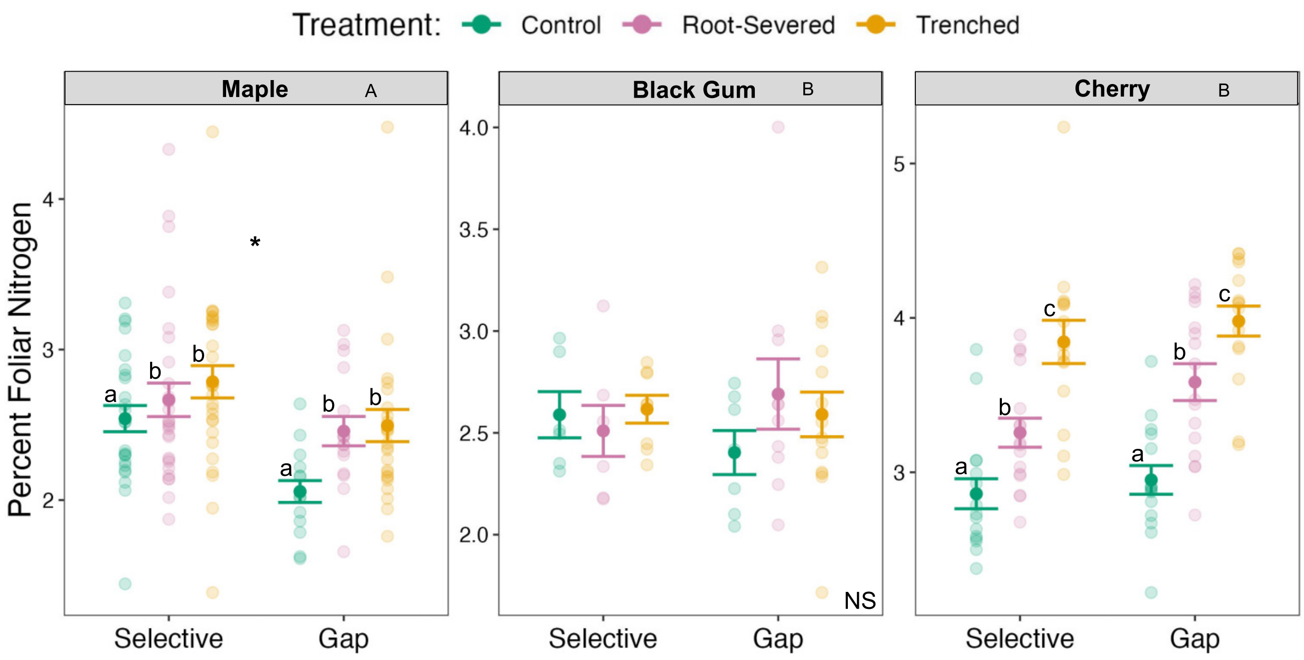
Table 4. Means and standard errors for % foliar nitrogen (2022) for seedlings at the Clement Woodlot (Corinth, VT, USA).

Harvest	Species	Root access	% Foliar N	N
Selective	Maple	Control	2.5 ± 0.09^{Aa}	25
		Root-Severed	2.7 ± 0.1^{Ab}	28
		Trenched	2.8 ± 0.1^{Ab}	28
	Black Gum	Control	2.6 ± 0.1^{Aa}	6
		Root-Severed	2.5 ± 0.1^{Aa}	7
		Trenched	2.6 ± 0.07^{Aa}	8
	Cherry	Control	2.9 ± 0.1^{Aa}	16
		Root-Severed	3.3 ± 0.1^{Ab}	16
		Trenched	3.8 ± 0.1^{Ac}	15
Gap	Maple	Control	2.1 ± 0.07^{Ba}	15
		Root-Severed	2.5 ± 0.1^{Bb}	16
		Trenched	2.5 ± 0.1^{Bb}	26
	Black Gum	Control	2.4 ± 0.1^{Aa}	7
		Root-Severed	2.7 ± 0.2^{Aa}	10
		Trenched	2.6 ± 0.1^{Aa}	14
	Cherry	Control	3.0 ± 0.09^{Aa}	15
		Root-Severed	3.6 ± 0.1^{Ab}	16
		Trenched	4.0 ± 0.1^{Ac}	16

Note: N values are the replicates within each harvest type, treatment, and species combination. Uppercase letters not shared indicate significant differences within a species between harvest types, and lowercase letters not shared indicate significant differences within a species among root access treatments ($p < 0.05$). Differences among species are not shown. However, there is a significant species effect on foliar N ($p < 0.05$).

While maples demonstrated initial gains in the selective harvest and only minor differences by root access treatment, cherries grew faster and had higher foliar N in the harvest gaps and with decreasing root access, despite mycorrhizal colonization being higher in the selective harvests than in the harvest gaps. Other literature suggests that among the dominant tree species of eastern North America, black cherry demonstrates strong conspecific negative density dependence (Bennett et al. 2017) which may be driven by cherry's high disease susceptibility (Packer and Clay 2003). Black cher-

Fig. 5. Each tree species displayed varying responses in % foliar nitrogen to root access treatments in 2022 at the Clement Woodlot (Corinth, VT, USA). The centerpoint indicates the mean, and the whiskers represent standard error. Lowercase letters not shared indicate significant differences in root access treatments within a species ($p < 0.05$), and capital letters indicate differences between species ($p < 0.05$). "NS" signifies that there are no significant differences in root access treatments within a species. The asterisk indicates significant differences between harvest types within a species ($p < 0.05$).



ries are also early successional and shade-intolerant (Burns and Honkala 1990), and thus are likely to capitalize on the increased light within the harvest gaps. Indeed, less shade-tolerant trees can invade more light-limited forests when released from belowground competition (Coomes and Grubb 2000), which may explain the positive response of cherries to root exclusion even in the selective harvest. Alleviation of root competition through interruption of root networks from harvesting and scarification could therefore be a means for encouraging the range expansion of other shade-intolerant tree species into more light-limited environments. More realistically, the implementation of 0.1 ha or larger harvest gaps may give cherry the dual benefit of alleviating both root competition and light limitation.

Black gum's success varied the least by harvest and root access treatments compared to maple or cherry. However, they still appeared to benefit from decreasing root access, growing 10 cm higher in the trenched versus the control treatments and 6 cm higher in the harvest gaps versus selective harvests. Black gum is a late-successional species with a relatively long lifespan (Abrams 2007), high drought tolerance and can occupy a wide range of habitats (Burns and Honkala 1990), which may explain why it did not have a strong preference. Black gum is also slow-growing (Orwig and Abrams 1994) and difficult to transplant (Struve 2008), illustrated by their lower survival and net growth rates that hovered around zero in our study. Many growth values were even negative, due to aboveground tissue senescing and then root sprouting in the next season. This pattern may be explained by a lack of proper mycorrhizal inoculum, novel pathogens, or inappropriate site conditions. Indeed, seedlings in assisted range expansion plantings have been shown to exhibit lower survival and growth than seedlings planted within their current range (Clark et al. 2022). Future studies are necessary to determine if black gum would acclimate to the soil conditions over time, and if inoculation with host-specific AM fungi would yield more pronounced success of black gum seedlings in this area.

Overall, our results indicate that although seedlings vary in their response to root access, AM seedling success in our study area was strongly controlled by root competition release. While greater light availability and soil temperature likely played a role in seedling success in the harvest gaps (Coomes and Grubb 2000), the differences in seedling success among root access treatment in both lower and higher light conditions suggests that nutrient competition also restricts growth even in this nutrient-rich, moist site (Berkowitz et al. 1995). Previous ectomycorrhizal-focused studies have found trenching to yield fewer fruiting bodies of mycorrhizal fungi but prolific and vigorous seedling regeneration within trenched areas (Romell 1938; Romell and Malmström 1945). As trenching does not alter light, these patterns likely arose from competition release for belowground resources such as nutrients and water (Högberg and Högberg 2022). Our results demonstrate that this pattern of higher seedling success via belowground competition release can hold in AM-dominated forests as well. Further research is necessary to determine how the balance between nutrient and light competition may shift over time in both harvest types as the canopies close and root densities increase. For example, as photosynthate declines in seedlings following canopy gap closure, continued allocation to mycorrhizal fungi may render the relationship parasitic (Johnson et al. 1997).

But if root access restricts seedling success, how do positive con-mycorrhizal feedbacks—amplification of one mycorrhizal type over another through positive feedbacks—drive AM dominance? At our site, AM seedlings have higher survival in harvest gaps formerly occupied by AM trees than in harvest gaps formerly occupied by ectomycorrhizal trees (Fitch et al. in revision). While Averill et al. (2022) hypothesized that common mycorrhizal networks were a main driver of AM dominance, we found that AM seedling success was in fact hampered when exposed to the roots and associated hyphae of neighboring AM trees. One possibility is that the rich, moist, soil of the Clement Woodlot intensified belowground competition (Berkowitz et al. 1995), and decreased the trees' needs for mycorrhizal symbionts (Johnson 1993). It is also possible that a more diverse species assemblage of AM overstory trees than our site had may have yielded a more positive response to root access. However, it seems more likely that another mechanism for AM dominance was at play like N-cycle feedbacks in these rich soils. Future research should investigate whether our results hold in a more nutrient-limited site.

The increasing stress on temperate forests from climate change and other disturbance regimes adds urgency to our need to implement adaptive forest management that increases tree species composition and structural complexity (Wikle et al. 2024). Forest managers also must maintain current species while also increasing the proportion of future-adapted tree species through forest assisted migration (Palik et al. 2022). However, we know little about how these practices affect mycorrhizal facilitation, root competition, and their interaction to inform the success of desired seedlings. Our research suggests that the three AM tree species are responsive to canopy-opening methods of climate-adaptive management like the harvest gaps and that one mechanism by which these gaps promote seedling success is by reducing root density. Particularly, we found competition release to facilitate the success of seedlings in areas in which they are not normally adapted (i.e., cherries in shaded regions, sugar maple in more open areas, and black gum outside their current range) despite potentially less mycorrhizal facilitation. Our results indicate that a range of AM seedlings may be successful due to, not in spite of, the inherent belowground disruption of adaptive forest management.

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Data availability

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfr-2024-0259.

References

Abrams, M.D. 1998. The Red Maple paradox: what explains the widespread expansion of red maple in eastern forests? BioScience, **48**: 355–364. doi:10.2307/1313374.

Abrams, M.D. 2007. Tales from the Blackgum, a consummate subordinate tree. BioScience, **57**: 347–359. doi:10.1641/B570409.

Assad, R., Reshi, Z.A., and Rashid, I. 2022. Seedling ectomycorrhization is central to conifer forest restoration: a case study from Kashmir Himalaya. Sci. Rep. **12**: 13321. doi:10.1038/s41598-022-17073-7.

Aubin, I., Munson, A.D., Cardou, F., Burton, P.J., Isabel, N., Pedlar, J.H., et al. 2016. Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. Environ. Rev. **24**: 164–186. doi:10.1139/er-2015-0072.

Augspurger, C.K. 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. Ecology, **94**: 41–50. doi:10.1890/12-0200.1.

Averill, C., Fortunel, C., Maynard, D.S., van den Hoogen, J., Dietze, M.C., Bhatnagar, J.M., and Crowther, T.W. 2022. Alternative stable states of the forest mycobiome are maintained through positive feedbacks. Nat. Ecol. Evol. **6**: 375–382. doi:10.1038/s41559-022-01663-9.

Bates, D., Machler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software, **67**: 1–48. doi:10.18637/jss.v067.i01.

Bennett, J.A., Maherali, H., Reinhart, K.O., Lekberg, Y., Hart, M.M., and Klironomos, J. 2017. Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. Science, **355**: 181–184. doi:10.1126/science.aai8212.

Berkowitz, A.R., Canham, C.D., and Kelly, V.R. 1995. Competition vs. facilitation of tree seedling growth and survival in early successional communities. Ecology, **76**: 1156–1168. doi:10.2307/1940923.

Bever, J.D. 2002. Negative feedback within a mutualism: host–specific growth of mycorrhizal fungi reduces plant benefit. Proc. R. Soc. London. Ser. B: Biol. Sci. **269**: 2595–2601. doi:10.1098/rspb.2002.2162.

Bonfante, P., and Genre, A. 2010. Mechanisms underlying beneficial plant–fungus interactions in mycorrhizal symbiosis. Nat. Commun. **1**: 48. doi:10.1038/ncomms1046.

Brown, A.J., Payne, C.J., White, P.S., and Peet, R.K. 2020. Shade tolerance and mycorrhizal type may influence sapling susceptibility to conspecific negative density dependence. J. Ecol. **108**: 325–336. doi:10.1111/1365-2745.13237.

Brundrett, M.C., and Tedersoo, L. 2020. Resolving the mycorrhizal status of important northern hemisphere trees. Plant Soil, **454**: 3–34. doi:10.1007/s11104-020-04627-9.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America, Volume 2: Hardwoods, Agriculture Handbook 654. U.S. Government Printing Office, Washington DC, USA.

Cale, J.A., Garrison-Johnston, M.T., Teale, S.A., and Castello, J.D. 2017. Beech bark disease in North America: over a century of research revisited. For. Ecol. Manage. **394**: 86–103. doi:10.1016/j.foreco.2017.03.031.

Chapin, F.S., Matson, P.A., and Vitousek, P.M. 2011. Principles of terrestrial ecosystem ecology. Springer, New York, NY. doi:10.1007/978-1-4419-9504-9.

Clark, P.W., D'Amato, A.W., Evans, K.S., Schaberg, P.G., and Woodall, C.W. 2022. Ecological memory and regional context influence performance of adaptation plantings in northeastern US temperate forests. J. Appl. Ecol. **59**: 314–329. doi:10.1111/1365-2664.14056.

Connell, J.H., and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. **111**: 1119–1144. doi:10.1086/283241.

Coomes, D.A., and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol. Monogr. **70**: 171–207. doi:10.1890/0012-9615(2000)070[0171:IORCIF]2.0.CO;2.

Cortese, A.M., and Horton, T.R. 2024. Ectomycorrhizal tree islands in arbuscular mycorrhizal forests: hotspots of fungal inoculum important for seedling establishment of historically dominant trees. J. Ecol. **112**: 2680–2694. doi:10.1111/1365-2745.14417.

Curtis, J.T., and McIntosh, R.P. 1951. An Upland Forest continuum in the Prairie-Forest Border Region of Wisconsin. Ecology, **32**: 476–496. doi:10.2307/1931725.

Daft, M.J., and El-Giahmi, A.A. 1978. Effect of arbuscular mycorrhiza on plant growth. New Phytol. **80**: 365–372. doi:10.1111/j.1469-8137.1978.tb01570.x.

Delavaux, C.S., LaManna, J.A., Myers, J.A., Phillips, R.P., Aguilar, S., Allen, D., et al. 2023. Mycorrhizal feedbacks influence global forest structure and diversity. Commun. Biol. **6**: 1–11. doi:10.1038/s42003-023-05410-z.

Fitch, A., Goldsmith, S., D'Amato, T., Legge, E., Gannon, D., Cuprewich, S., et al. in revision. Tree mycorrhizal legacy mediates forest regeneration following timber harvesting in Northeastern forests.

Frew, A., Öpik, M., Oja, J., Vahter, T., Hiiesalu, I., and Aguilar-Trigueros, C.A. 2024. Herbivory-driven shifts in arbuscular mycorrhizal fungal community assembly: increased fungal competition and plant phosphorus benefits. New Phytol. **241**: 1891–1899. doi:10.1111/nph.19474.

Genre, A., Lanfranco, L., Perotto, S., and Bonfante, P. 2020. Unique and common traits in mycorrhizal symbioses. Nat. Rev. Microbiol. **18**: 649–660. doi:10.1038/s41579-020-0402-3.

Gerhardt, K. 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. For. Ecol. Manage. **82**: 33–48. doi:10.1016/0378-1127(95)03700-4.

Giovannetti, M., and Mosse, B. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytol. **84**: 489–500. doi:10.1111/j.1469-8137.1980.tb04556.x.

Hayman, D.S. 1974. Plant growth responses to vesiculararbuscular mycorrhiza. New Phytol. **73**: 71–80. doi:10.1111/j.1469-8137.1974.tb04607.x.

Högberg, P., and Högberg, M.N. 2022. Does successful forest regeneration require the nursing of seedlings by nurse trees through mycorrhizal interconnections? For. Ecol. Manage. **516**: 120252. doi:10.1016/j.foreco.2022.120252.

Isaac-Renton, M., Montwé, D., Hamann, A., Spiecker, H., Cherubini, P., and Treydte, K. 2018. Northern forest tree populations are physiologically maladapted to drought. Nat. Commun. **9**: 5254. doi:10.1038/s41467-018-07701-0.

Jo, I., Fei, S., Oswalt, C.M., Domke, G.M., and Phillips, R.P. 2019. Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. Sci. Adv. **5**: eaav6358. doi:10.1126/sciadv.aav6358.

Johnson, N.C. 1993. Can fertilization of soil select less mutualistic mycorrhizae? Ecol. Appl. **3**: 749–757. doi:10.2307/1942106.

Johnson, N.C., Graham, J.-H., and Smith, F.A. 1997. Functioning of mycorrhizal associations along the mutualism–parasitism continuum*. New Phytol. **135**: 575–585. doi:10.1046/j.1469-8137.1997.00729.x.

Jumpponen, A. 2001. Dark septate endophytes—are they mycorrhizal? Mycorrhiza, **11**: 207–211. doi:10.1007/s005720100112.

Jumpponen, A., and Trappe, J.M., 1998. Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. New Phytol. **140**: 295–310. doi:10.1046/j.1469-8137.1998.00265.x.

Kakouridis, A., Hagen, J., Kan, M., Mambelli, S., Feldman, L., Herman, D., et al. 2022. Routes to roots: direct evidence of water transport by arbuscular mycorrhizal fungi to host plants. New Phytol. **236**: 210–221. doi:10.1111/nph.18281.

Karst, J., Jones, M.D., and Hoeksema, J.D. 2023. Positive citation bias and overinterpreted results lead to misinformation on common mycorrhizal networks in forests. Nat. Ecol. Evol. **7**: 501–511. doi:10.1038/s41559-023-01986-1.

Ke, P., and Wan, J. 2020. Effects of soil microbes on plant competition: a perspective from modern coexistence theory. Ecol. Monogr. **90**: e01391. doi:10.1002/ecm.1391.

Kuznetsova, A., Brockhoff, P., and Christensen, R. 2017. lmerTest Package: tests in linear mixed effects models. J. Stat. Software, **82**: 1–26. doi:10.18637/jss.v082.i13.

Lang, A.K., Jevon, F.V., Vietorisz, C.R., Ayres, M.P., and Hatala Matthes, J. 2021. Fine roots and mycorrhizal fungi accelerate leaf litter decomposition in a northern hardwood forest regardless of dominant tree mycorrhizal associations. New Phytol. **230**: 316–326. doi:10.1111/nph.17155.

Leak, W.B., and Sendak, P.E. 2002. Field Note—changes in species, grade, and structure over 48 years in a managed New England Northern hardwood stand. North. J. Appl. For. **19**: 25–28. doi:10.1093/njaf/19.1.25.

Leak, W.B., and Smith, M.-L. 1996. Sixty years of management and natural disturbance in a New England forested landscape. For. Ecol. Manage. **81**: 63–73. doi:10.1016/0378-1127(95)03662-8.

Lekberg, Y., Bever, J.D., Bunn, R.A., Callaway, R.M., Hart, M.M., Kivlin, S.N., et al. 2018. Relative importance of competition and plant–soil feedback, their synergy, context dependency and implications for coexistence. Ecol. Lett. **21**: 1268–1281. doi:10.1111/ele.13093.

Length, R. 2023. emmeans: estimated marginal means, aka least-squares means.

Liang, M., Liu, X., Etienne, R.S., Huang, F., Wang, Y., and Yu, S. 2015. Arbuscular mycorrhizal fungi counteract the Janzen-Connell effect of soil pathogens. Ecology, **96**: 562–574. doi:10.1890/14-0871.1.

Mandyam, K.G., and Jumpponen, A. 2015. Mutualism–parasitism paradigm synthesized from results of root-endophyte models. Front. Microbiol. **5**. doi:10.3389/fmicb.2014.00776.

Nagel, L.M., Palik, B.J., Battaglia, M.A., D'Amato, A.W., Guldin, J.M., Swanston, C.W., et al. 2017. Adaptive silviculture for climate change: a national experiment in manager-scientist partnerships to apply an adaptation framework. J. For. **115**: 167–178. doi:10.5849/jof.16-039.

Neuendorff, J.K., Nagel, L.M., Webster, C.R., and Janowiak, M.K. 2007. Stand structure and composition in a Northern hardwood forest after 40 years of single-tree selection. North. J. Appl. For. **24**: 197–202. doi:10.1093/njaf/24.3.197.

Orwig, D.A., and Abrams, M.D. 1994. Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: gap-obligate versus gap-facultative tree species. Can. J. For. Res. **24**: 2141–2149. doi:10.1139/x94-276.

Packer, A., and Clay, K. 2003. Soil pathogens and *Prunus serotina* seedling and sapling growth near conspecific trees. Ecology, **84**: 108–119. doi:10.1890/0012-9658(2003)084[0108:SPAPSS]2.0.CO;2.

Palik, B.J., Clark, P.W., D'Amato, A.W., Swanston, C., and Nagel, L. 2022. Operationalizing forest-assisted migration in the context of climate change adaptation: examples from the eastern USA. Ecosphere, **13**: e4260. doi:10.1002/ecs2.4260.

Peters, M.P., Prasad, A.M., Matthews, S.N., and Iverson, L.R. 2020. Climate change tree atlas.

Phillips, R.P., Brzostek, E., and Midgley, M.G. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. New Phytol. **199**: 41–51. doi:10.1111/nph.12221.

Premer, M.I., and Froese, R.E. 2022. The recurring role of site challenges contemporary theories about regeneration under selection systems in northern hardwoods. Can. J. For. Res. **52**: 463–473. doi:10.1139/cjfr-2021-0179.

R Core Team. 2023. R: a language and environment for statistical computing.

Rice, A.M., Perdrial, N., Treto, V., D'Amato, A.W., Smith, G.A., and Richardson, J.B. 2024. Influence of parent material mineralogy on forest soil nutrient release rates across a nutrient richness gradient. Geoderma, **451**: 117081. doi:10.1016/j.geoderma.2024.117081.

Romell, L.-G. 1938. A trenching experiment in Spruce forest and its bearing on problems of mycotrophy. Sven. Bot. Tidskr. **32**: 89–99.

Romell, L.G., and Malmström, C. 1945. The ecology of Lichen-Pine Forest experiments (1922-42) by the late Dr. H Hesselman. Meddelanden från Statens Skogsförsöksanstalt, Stockholm, **34**: 543–625.

Ruiz-Lozano, J.M. 2003. Arbuscular mycorrhizal symbiosis and alleviation of osmotic stress. New perspectives for molecular studies. Mycorrhiza, **13**: 309–317. doi:10.1007/s00572-003-0237-6.

Rustad, L.E., and Campbell, J.L. 2012. A novel ice storm manipulation experiment in a northern hardwood forest. Can. J. For. Res. **42**: 1810–1818. doi:10.1139/x2012-120.

Schimel, J.P., and Bennett, J. 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology, **85**: 591–602. doi:10.1890/03-8002.

Simard, S.W. 2009. Mycorrhizal networks and complex systems: contributions of soil ecology science to managing climate change effects in forested ecosystems. Can. J. Soil. Sci. **89**: 369–382. doi:10.4141/cjss08078.

Simard, S.W., Perry, D.A., Smith, J.E., and Molina, R. 1997. Effects of soil trenching on occurrence of ectomycorrhizas on *Pseudotsuga menziesii* seedlings grown in mature forests of *Betula papyrifera* and *Pseudotsuga menziesii*. New Phytol. **136**: 327–340. doi:10.1046/j.1469-8137.1997.00731.x.

Smith, H.C., and Miller, G.W. 1987. Managing Appalachian hardwood stands using four regeneration practice—34-year results. North. J. Appl. For. **4**: 180–185. doi:10.1093/njaf/4.4.180.

Smith, S.E., and Read, D.(Eds.), 2008. Mycorrhizal Symbiosis. 3rd ed. Academic Press, London. doi:10.1016/B978-012370526-6.50021-0.

Struve, D.K. 2008. Growing blackgum whips in ground beds increases survival and growth following transplanting to field. J. Environ. Hortic. **26**: 105–108. doi:10.24266/0738-2898-26.2.105.

Tourville, J.C., Zarfos, M.R., Lawrence, G.B., McDonnell, T.C., Sullivan, T.J., and Dovčiak, M. 2023. Soil biotic and abiotic thresholds in sugar maple and American beech seedling establishment in forests of the northeastern United States. Plant Soil, **491**: 387–400. doi:10.1007/s11104-023-06123-2.

Trotter, R.T., III, and Shields, K.S. 2009. Variation in winter survival of the invasive hemlock woolly adelgid (Hemiptera: Adelgidae) across the eastern United States. Environ. Entomol. **38**: 577–587. doi:10.1603/022.038.0309.

Van Der Heijden, M.G.A., and Horton, T.R. 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. J. Ecol. **97**: 1139–1150. doi:10.1111/j.1365-2745.2009.01570.x.

van der Heijden, M.G.A., Martin, F.M., Selosse, M.-A., and Sanders, I.R. 2015. Mycorrhizal ecology and evolution: the past, the present, and the future. New Phytol. **205**: 1406–1423. doi:10.1111/nph.13288.

Van Nuland, M.E., Ke, P.-J., Wan, J., and Peay, K.G. 2023. Mycorrhizal nutrient acquisition strategies shape tree competition and coexistence dynamics. J. Ecol. **111**: 564–577. doi:10.1111/1365-2745.14040.

Vierheilig, H., Coughlan, A.P., Wyss, U., and Piché, Y. 1998. Ink and Vinegar, a Simple Staining Technique for Arbuscular-Mycorrhizal Fungi. Appl. Environ. Microbiol. **64**: 5004–5007. doi:10.1128/AEM.64.12.5004-5007.1998.

Warton, D.I., and Hui, F.K.C. 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology, **92**: 3–10. doi:10.1890/10-0340.1.

Wikle, J.L., and D'Amato, A.W. 2023. Stand spatial structure outcomes of forest adaptation treatments in northern hardwood forests in North America. Can. J. For. Res. **53**: 721–734. doi:10.1139/cjfr-2022-0274.

Wikle, J.L., D'Amato, A.W., Palik, B.J., Woodall, C.W., Evans, K.S., and Nagel, L.M. 2024. Structural outcomes of climate adaptation treatments in two contrasting northern temperate forests. For. Ecol. Manage. **562**: 121932. doi:10.1016/j.foreco.2024.121932.

Youngquist, M.B., Eggert, S.L., D'Amato, A.W., Palik, B.J., and Slesak, R.A. 2017. Potential effects of foundation species loss on wetland communities: a case study of black ash wetlands threatened by emerald ash borer. Wetlands, **37**: 787–799. doi:10.1007/s13157-017-0908-2.