

Readily available resources across sites and genotypes result in greater aboveground growth and reduced fine root production in *Pinus taeda*

Timothy J. Shively^{a,1}, Rachel Cook^a, Chris A. Maier^b, Kevin Garcia^c, Timothy J. Albaugh^d, Otávio Campoe^e, Zakiya Leggett^{a,*}

^a North Carolina State University, Department of Forestry and Environmental Resources, Raleigh, NC 27695, USA

^b Southern Research Station, US Forest Service, Research Triangle Park, NC 27709, USA

^c North Carolina State University, Department of Crop and Soil Sciences, Raleigh, NC 27695, USA

^d Virginia Tech, Department of Forest Resources and Environmental Conservation, Blacksburg, VA 24061, USA

^e Universidade Federal de Lavras, Departamento de Ciências Florestais, Lavras, MG, Brazil

ABSTRACT

Fine roots serve as the primary interface between trees and the soil, and they are dynamic in their response to environmental conditions. Among many functions, they are principle in gathering nutrients and water, and they constitute a major component of the tree. Their overall contribution to soil carbon flux is not well understood, nor is the effect of site and genotype on their dynamics, and these factors are crucial to understanding nutrient cycles and tree growth under variable conditions. This study evaluated how the fine root dynamics of loblolly pine (*Pinus taeda* L.) might be different between genotypes and on different sites. Three loblolly pine plantations were established, two in 2009 in North Carolina (NC) and Virginia (VA), and one in 2011 in Brazil (BR). Root biomass was estimated with soil cores across the three sites and between two genotypes in 2020. Seasonal and annual fine root production was measured at the NC and VA sites over the 12th growing season using ingrowth cores. The trees in BR that were two years younger were much larger than those in NC and VA and had more fine root biomass at initial sampling than those in NC, despite similar levels of fertility. Meanwhile, fine root production rates decreased with higher rates of aboveground productivity across all measured plots in NC and VA. These results indicate that (1) standing fine root biomass may be related to environmental conditions that are not easily manipulated, which could inform modeling of carbon cycles, and (2) in these intensively managed plots, sufficient resources were available to allow for increased aboveground growth despite lower rates of fine root production, which supports the employment of these intensive silvicultural practices.

1. Introduction

Loblolly pine (*Pinus taeda* L.) is the most commercially important tree species in the Southeastern United States (Schultz, 1999). Advances in silviculture and forest tree genetics continue to increase the volume of wood produced and carbon (C) sequestered per hectare (Zhao et al., 2016), in addition to relieving pressure on old-growth and other ecologically significant systems (Li et al., 1999; Pirard et al., 2016). Growing loblolly pine outside its native range can also lead to much higher rates of growth, particularly in the Southern hemisphere, though the reasons for the improved productivity remain unclear (Albaugh et al., 2018).

Fine root biomass, production, and turnover comprise about 14–25 % of loblolly pine's total C allocation (Maier et al., 2004). The term "fine root" is functional (Lukac, 2012) and refers to roots that are the primary interface between plants and soils. It is common, however, to arbitrarily

define fine roots for the purposes of study using morphological traits, such as those that are under 2 mm in diameter (Danjon et al., 2013). Compared to larger coarse roots or stems, fine roots are short lived (months to a few years), and their seasonal growth and turnover tends to vary with environmental conditions. Although our knowledge of fine roots and their contributions to nutrient cycles is largely uncertain, they are enormous contributors to soil C flux (Danjon et al., 2013).

Plasticity in the morphology and physiology of fine roots allows trees to vary C allocation patterns across a spectrum of environmental conditions (Bakker et al., 2008). Fine root biomass has generally been observed to decrease on more fertile sites (Danjon et al., 2013). In loblolly pine, addition of water and nutrients shifts belowground biomass allocation from fine to coarse and tap roots (Albaugh et al., 2004; King et al., 1999; Maier et al., 2004), though Carter et al. (2004) found that C allocation to fine roots of *P. palustris* was constant across a N availability gradient. Still, a decrease in relative allocation to fine roots due to

* Corresponding author.

E-mail addresses: tshively@vt.edu (T.J. Shively), rlcook@ncsu.edu (R. Cook), christopher.maier@usda.gov (C.A. Maier), kgarcia2@ncsu.edu (K. Garcia), talbaugh@vt.edu (T.J. Albaugh), otavio.campoe@ufla.br (O. Campoe), zakiya_leggett@ncsu.edu (Z. Leggett).

¹ Present address: Virginia Tech, School of Plant and Environmental Sciences, Blacksburg, VA 24061, USA.

increased nutrient availability has been thought to occur across all forest types (Achat et al., 2008; Gower et al., 1992; Vogt and Vogt, 1986), and increased C allocation to fine roots on nutrient limited sites is also typically paired with a decrease in foliar development (Eissenstat and Van Rees, 1994).

King et al. (2002) found, however, that production and turnover of fine roots under 1 mm diameter increased in fertilized treatments, possibly indicating higher C inputs to soils. While fine root production may increase absolutely on more productive sites, root biomass may still be higher on poor, less productive sites (Nadelhoffer et al., 1985). It is possible that although fertile sites stimulate C and N allocation to fine root growth, proportionally fewer resources are allocated to structure and protection, leading to more rapid death through senescence or predation, which results in root samples with lower biomass (Nadelhoffer, 2000). Indeed, a meta-analysis of fine root data spanning both natural and plantation forests showed that fine root production increased with soil pH, an indicator of nutrient availability, even though fine root biomass was negatively correlated with soil nitrogen (N) (Cai et al., 2019). Similarly, Li et al. (2021) showed that supplementing soil N increased fine root production and lowered measures of fine root biomass through decreased root lifespan.

To increase aboveground productivity in loblolly pine, silvicultural practices such as fertilization act primarily through increasing leaf area and biomass (e.g., Albaugh et al., 1998; Jokela and Martin, 2000; Vose and Allen, 1988; Will et al., 2002). Chen et al. (2018) linked increased leaf production to higher rates of fine root production across several studies, although fine roots increased at a slower rate than leaves at higher levels of gross productivity. Fertilization has also been shown to increase leaf biomass without altering growth efficiency (Samuelson et al., 2001), while Coyle et al. (2008) simply attributed higher aboveground productivity to enhanced overall development. Conversely, Will et al. (2002) observed increased aboveground growth increment, higher foliage biomass, and enhanced stem growth per unit of foliage for fertilized treatments, and Albaugh et al. (1998) saw greater aboveground biomass production through increased growth efficiency and partitioning shifts away from fine roots.

Our understanding of how fine root biomass, production, and turnover respond to environmental conditions is still developing. The relationship of these processes to foliar development and aboveground productivity also remains unclear. To that end, we were able to explore fine root dynamics of the same genotypes across multiple sites without a fertility gradient. The objectives of this study were to 1) quantify the effect of site and genotype on fine root biomass, 2) measure fine root production over one growing season via seasonal and annual sampling, and 3) evaluate the relationship of fine root production with aboveground growth increment and leaf biomass in loblolly pine plantations. We expected all treatments to have similar amounts of initial fine root biomass, while treatments that were more productive aboveground over the growing season would exhibit lower rates of fine root production and turnover accompanied with higher allocation to leaf biomass.

2. Materials and methods

2.1. Study sites

Loblolly pine plantations were established in three locations; the Atlantic Coastal Plain of North Carolina (NC) at Bladen Lakes State Forest in 2009 (34.8313°, -78.5873°); the Piedmont of Virginia (VA) at the Reynolds Homestead Forest Resources Research Center in 2009 (36.6423°, -80.1546°); and in Paraná, southern Brazil (BR), in 2011 (-26.1905°, -49.4963°). The NC site is within the native range of loblolly pine and represents typical planted growing conditions for the species. The VA site is just outside the native range of loblolly pine, and the site was thought to have lower growth potential due to a shorter growing season. The BR plantation is in a subtropical region where loblolly pine is commonly planted as an exotic crop tree (Vickers et al.,

2011). Climate summaries in Table 1 were retrieved from NOAA data for U.S. locations (NowData, 2010) and European Centre for Medium-Range Weather Forecasts data for Brazil (Climate-Data.org).

2.2. Experimental design

The experimental plantations were installed with a split-split plot design with three to four replications depending on the site. The primary treatment was the level of silviculture (low/operational vs high/intensive). Intensive silviculture included site preparation, fertilization with nutrient status monitoring, and competition control. The same nutrient availability was maintained across these intensive silviculture plots—foliar nutrient concentrations were sampled annually, and fertilizer applied as needed to maintain 1.35–1.40 % N along with other elements at similar optimal levels according to Albaugh et al. (2010). Site preparation and silvicultural treatments are also thoroughly explained in Yanez et al. (2017). Only NC was bedded prior to planting due to the high water table. This practice increases survival of seedlings. Split plot treatments consist of six genetic entries (one open pollinated-OP, one mass control pollinated-MCP, and four clones-C1, C2, C3, and C4) at three planting densities (Vickers et al., 2011). For this study, we focused on two genetic treatments, OP and C3, and only one silvicultural treatment (intensive silviculture planted at the highest density—1853 trees ha⁻¹ in NC and VA, or 1893 trees ha⁻¹ in BR). The two genotypes are both broad crown ideotypes but still allowed for comparison of distinctly different genetic stock.

Each plot in VA and BR consisted of 81 trees, or a rectangular planted area with nine trees planted in nine rows each, while NC plots contained 63 trees planted with nine trees in seven rows each. In all plots and all locations, the center 25 trees (five rows of five trees each) were the study area, giving all plots treated buffer rows between neighboring plots. In NC and VA, trees were planted 1.47 m apart along the row with 3.66 m separating each row, while trees in BR were spaced 2.2 m and 2.4 m apart, respectively (Albaugh et al., 2020). We sampled three plots per genotype and site combination for replication, except for OP trees in NC, for which only two plots were available due to extensive mortality in 2009–2010 (Table 2).

To study initial fine root biomass, 8.3 cm diameter soil cores were taken to 50 cm depth in NC and VA by a gas-powered soil probe mounted on an all-terrain vehicle between December 2019–January 2020, and the same diameter cores were taken by hand to the same depth in BR during October 2020. Sixteen cores per plot in NC and VA and eight cores per plot in BR were taken in each of three plots per site and genotype combination. These subsamples were averaged to produce a plot level estimate and scaled to kg ha⁻¹. Analyzing one less OP plot in NC, for the reasons described above, resulted in analysis of 17 total plots.

Core locations were randomly selected from a plot map with 40 possible spots in each plot—the possible core locations were centered either between two trees along the planting row (within row) or centered between two trees from adjacent rows (interrow). Eight within row and eight interrow locations were selected in each plot (or four and four in BR). This balance of within row and interrow cores was selected to reflect the fine root biomass across the entire plot, regardless of microsite variation or proximity to individual trees and planting beds. All cores were used to estimate initial fine root biomass, but for the purposes of subsequent ingrowth sampling in NC and VA, half were designated as “annual” cores (to be resampled once after 12 months), and the other half as “seasonal” cores (to be resampled once per season for one year). In sum, for NC and VA, four subsamples per category were taken (1. within row annual cores, 2. within row seasonal cores, 3. interrow annual cores, and 4. interrow seasonal cores). No ingrowth sampling was conducted in BR, so for initial fine root biomass, four within row and four interrow cores per plot were taken. The soil cores were then divided by depth, 0–10 cm, 10–20 cm, 20–30 cm, and 30–50 cm, and refrigerated until processed.

To measure fine root production, ingrowth cores were installed (Vogt

Table 1

Environmental data for the three pine plantation sites in North Carolina (NC), Virginia (VA), and Brazil (BR). Climate summaries for NC & VA are averages of 2009–2019 and were retrieved from NOAA data (NowData, 2010). Climate summaries for BR are averages of 2011–2019 and were retrieved from European Centre for Medium-Range Weather Forecasts data (Climate-Data.org). Soil pH and cation exchange capacity (CEC) are averages for each site.

Site	Average Annual Temperature (°C)	Average Annual Precipitation (mm)	Soil Type	Soil Texture	Soil pH	CEC (meq/100 g)	Soil Series (U. S.)
NC	16.5	1253	thermic, Typic Paleaquult	fine sandy loam	4.40	7.1	Rains
VA	13.7	1277	mesic, Typic Kanhapludult	sandy clay loam	4.44	4.1	Fairview
BR	17.2	1796	Hapludult & Inceptisol	clay loam	3.80	24.3	

Table 2

Aboveground plot characteristics after the 2020 growing season for the three pine plantation sites in North Carolina (NC), Virginia (VA), and Brazil (BR). Genotypes are a clone (C3) and open pollinated (OP) trees. 25 trees per plot were planted in 2009 in NC and VA and 2011 in BR at a spacing of 1.47 m × 3.66 m (1853 trees ha⁻¹). n = 3 for all treatments except NC OP, for which n = 2.

Site	Genotype	Mean Number of Trees per Plot	Mean Diameter at Breast Height per Tree (cm)	Mean Basal Area per Plot (m ² /ha)
NC	C3	22.3	18.7	48.6
NC	OP	19.0	20.3	47.4
VA	C3	23.3	18.8	50.4
VA	OP	20.7	19.3	47.2
BR	C3	24.3	19.0	52.9
BR	OP	23.0	20.1	56.2

and Persson, 1991) using the established core holes. Immediately after initial excavation, all holes were backfilled with sand. Ingrowth core resampling was conducted with an 8.3 cm hand auger. The same eight seasonal cores per plot in NC and VA were resampled three times (July, September, and December 2020) after approximately-six, three, and three months of incubation, respectively. Travel restrictions due to the COVID-19 pandemic precluded the first planned seasonal resampling in April 2020. Annual cores in NC and VA were resampled only once in December 2020, after 12 months of undisturbed growth.

In the lab, roots from the initial core samples were pulled from the soil with forceps as soil cores were dry sieved over a large, 0.25-inch wire mesh and, subsequently, a 2 mm soil sieve. Ingrowth cores were only sieved over the larger mesh in the field because it was much easier to identify and separate roots from the sand. Also, the sand was immediately returned each time to backfill the same core hole along with additional, new sand as needed to mitigate losses from processing, settling, and erosion.

A handmade, 2 mm ink silhouette was used to sort roots by size, and any roots larger than 2 mm diameter were discarded. Roots that varied in size along their length were cut where the diameter equaled 2 mm, and the portion greater than 2 mm diameter discarded. The fine roots were briefly rinsed and submerged in deionized water and manipulated by hand or forceps if necessary to remove as much soil and debris as possible. All samples were then oven dried at 65 °C for 48 h and weighed, which was sufficient to achieve a constant weight.

Dry ash content was determined with loss on ignition in a muffle furnace at 450 °C for six hours using ground subsamples of both the initial and ingrowth sets. Dry ash procedures for initial samples taken from the native soil in NC and VA resulted in a mineral content of 17.11 % with a standard deviation of 9.09 % in NC and 12.55 % with a standard deviation of 4.30 % in VA. Mineral content for ingrowth cores was 18.13 % with a standard deviation of 3.73 % in NC and 13.45 % with a standard deviation of 5.06 % in VA for the subsequent samples taken from sandy, backfilled core holes. We reduced all sample weights by the appropriate percentage to account for mineral content of the roots and any soil particles remaining after roots were washed. Dry ash values were not available for samples from Brazil, so for this study, we applied the 12.55 % mineral content from initial VA samples. We based this

decision on the relative similarity of soil textures in the VA and BR sites, the former being a sandy clay loam and the latter a clay loam.

Used in this study for comparison with our initial fine root biomass, soil cores were taken in NC and VA from the same plots by the same methods described above in September–October 2016. However, roots were removed from the soil with an elutriator, or a device that churns water with forced air to remove mineral soil and float organic matter for retrieval, rather than by hand.

2.3. Fine root production, aboveground production, and statistical analyses

To calculate fine root production, subsample biomass totals were averaged at the plot level, scaled to kg ha⁻¹, and divided by incubation time. Seasonal production estimates were standardized to per year production rates by multiplying their respective incubation periods out to 12 months. Fine root turnover calculations were made by dividing initial fine root biomass by fine root production estimates (Bhuiyan et al., 2017), and their reciprocals were used for comparison. Ingrowth cores ease root retrieval and make production estimates more straightforward, and they are appropriate for comparing environmental conditions, even if other methods may more accurately estimate site-specific production (Vogt and Persson, 1991; Hertel and Leuschner, 2002; Osawa and Aizawa, 2012).

Leaf biomass and aboveground growth increment were calculated with data obtained from the same plots sampled in this study. Individual tree data were input to equations developed by Gonzalez-Benecke et al. in 2014 to calculate leaf biomass (FOLIAGE) as well as 2019 and 2020 total aboveground biomass (TASB, or total above stump biomass, which includes stem, branches, and leaves) in kg per tree. Leaf and tree biomass were totaled at the plot level, then scaled to a Mg ha⁻¹ basis. To determine growth increment, 2019 TASB was subtracted from 2020 TASB. The equations are:

$$FOLIAGE = e_1 \cdot (dbh^{e_2}) \cdot (e^{e_3 \cdot DBH}) \cdot (H^{e_4}) \cdot (AGE^{e_5}) \quad (1)$$

$$TASB = e_1 \cdot (dbh^{e_2}) \cdot (H^{e_3}) \cdot (AGE^{e_4}) \quad (2)$$

where dbh = diameter at breast height (cm), H = tree height (m), AGE = tree age (years), and e₁–e₄ are constant parameter estimates.

All fine root production estimates and turnover rates were analyzed using two-way analysis of variance (ANOVA) with site and genotype as main effects, including their interaction. Fine root biomass measurements from 2016 were used to compare initial fine root biomass from 2019 to 2020 in a three-way ANOVA with year, site, and genotype as main effects and all interactions included. To compare fine root biomass from initial cores taken in 2019–2020 across the three sites, two-way ANOVA was conducted with site and genotype as main effects and all interactions included, followed by a Tukey's Honestly Significant Difference (HSD) test to check pairwise comparisons. Similarly, both initial fine root biomass and fine root production were isolated by depth increment and analyzed using two-way ANOVA.

Regression was conducted by graphing each plot's basal area by its initial fine root biomass, as well as aboveground growth increment by its

fine root production estimate. Similarly, regression was conducted with two methods for foliage, using each plot's 2020 foliage biomass and using the difference between each plot's 2020 and 2019 foliage biomass. Both were plotted against their respective fine root production calculations. All statistical analyses in this study were conducted using JMP® Pro 15 with a significance level of < 0.1 .

3. Results

3.1. Initial fine root biomass was higher outside the native range

Initial fine root biomass was higher in BR than in loblolly pine's native range of NC, with no differences found between NC and VA. Fine root biomass estimates from December 2019–January 2020 in NC and VA were not significantly different from estimates derived from samples in the same plots during September–October of 2016 ($p = 0.435$). Fine root biomass in 2020 ranged from 766 kg ha^{-1} in an NC C3 plot to $2,453 \text{ kg ha}^{-1}$ in a BR C3 plot. Overall, initial fine root biomass was highest in BR with moderate evidence that it differed from NC ($p = 0.068$) and little to no evidence that it differed from VA ($p = 0.140$) (Fig. 1; Table 3). There were no differences in initial fine root biomass by genotype. By depth, there was modest evidence that BR exhibited greater fine root biomass from 10 to 20 cm ($p = 0.098$), with 358 kg ha^{-1} versus VA's 196 kg ha^{-1} in VA (Fig. 2), and there was no evidence of differences in rooting depth by genotype. At the individual plot level, initial fine root biomass showed a positive correlation with plot basal area ($r^2 = 0.313$, $p = 0.019$) (Fig. 3).

3.2. Rates of fine root production and turnover were higher in NC and for the clonal genotype

Fine root production rates were higher in the native range of NC and for C3 trees. Fine root production estimates ranged from 416 to $940 \text{ kg ha}^{-1} \text{ yr}^{-1}$ across all VA and NC plots. Both site ($p = 0.081$) and genotype ($p = 0.029$) affected fine root production, but there was no significant interaction. The NC site produced about $201 \text{ kg ha}^{-1} \text{ yr}^{-1}$ greater root biomass than VA, and the C3 genotype produced about $199 \text{ kg ha}^{-1} \text{ yr}^{-1}$ greater fine root biomass than the OP genotype (Fig. 4). There was much more fine root production at 0–10 cm than other depths ($p < 0.001$), and trees in NC produced more fine root biomass than those in VA from both 10–20 cm ($p = 0.055$) and 30–50 cm ($p = 0.003$) (Fig. 5). Genotype had some effect on fine root turnover ($p = 0.091$) where C3 plots replaced

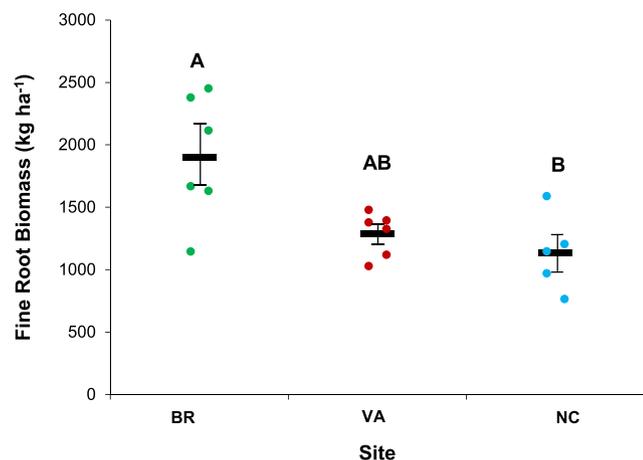


Fig. 1. Initial fine root biomass (kg ha^{-1}) from 0 to 50 cm across three sites. Soil cores were taken in October 2020 for Brazil (BR) and December 2019–January 2020 for North Carolina (NC) and Virginia (VA) to measure fine root biomass. BR had significantly more fine root biomass than NC ($p = 0.068$). Lines show mean fine root biomass by site, jittered points show plot level estimates, and error bars show standard error of the mean.

Table 3

P-values for ANOVA and Tukey's HSD of initial fine root biomass measurements. $n = 6$ for BR and VA, $n = 5$ for NC.

ANOVA		Tukey's HSD		
Variable	p-value	Site Comparison		p-value
Site	0.064	BR	NC	0.068
Genotype	0.453	BR	VA	0.140
Site \times Genotype	0.455	NC	VA	0.789

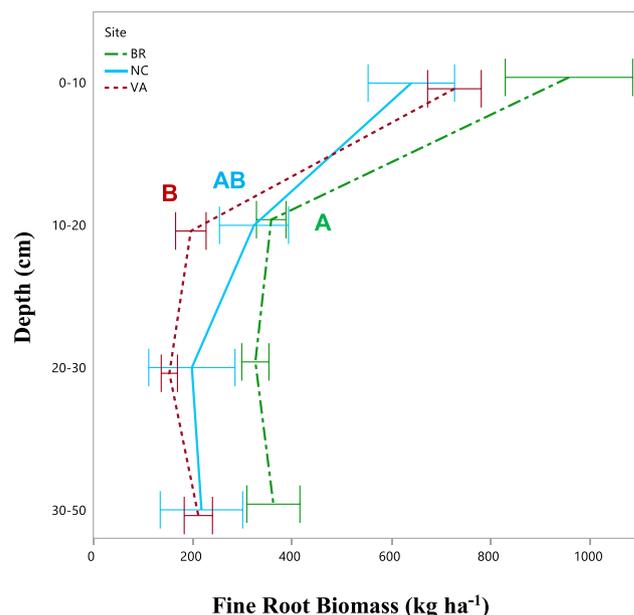


Fig. 2. Initial fine root biomass (kg ha^{-1}) by depth (cm) and site. There was significantly more fine root biomass from 0 to 10 cm than at the other depths ($p < 0.001$). At 10–20 cm only, BR demonstrated some evidence ($p = 0.098$) of more fine root biomass than in VA, indicating that, overall, rooting depth is similar among treatments. Letters indicate differences among sites at the same depth increment. Note that 30–50 cm is twice the depth of the three other increments. $n = 6$ for BR and VA, $n = 5$ for NC. Error bars show standard error of the mean.

their fine roots at a higher rate than OP plots (Table 4). Unlike initial fine root biomass, there was no correlation between fine root production and plot basal area after the 2020 growing season ($r^2 = 0.030$, $p = 0.640$).

3.3. Fine root production climaxed at similar rates between sites

Fine root production showed seasonal differences between the sites, but production rates were surprisingly similar during the peak of root production during the middle of the growing season. From January to July, NC plots produced $1173 \text{ kg ha}^{-1} \text{ yr}^{-1}$ more fine root biomass than VA plots ($p = 0.027$). From September to December, NC plots produced $199 \text{ kg ha}^{-1} \text{ yr}^{-1}$ more fine root biomass than VA ($p = 0.034$). VA experiences a shorter growing season, and in 2020, the site also experienced mild drought conditions from September–October. Interestingly NC plots had a nearly identical rate of fine root production during the January–July and July–September periods. This fine root production rate was also very similar that of VA for the July–September period. Both sites had much lower fine root production rates by December relative to their own July and September estimates (Fig. 6). There were no effects of genotype on seasonal fine root production.

3.4. Fine root production decreased as aboveground growth increased

Fine root production rates were negatively correlated with

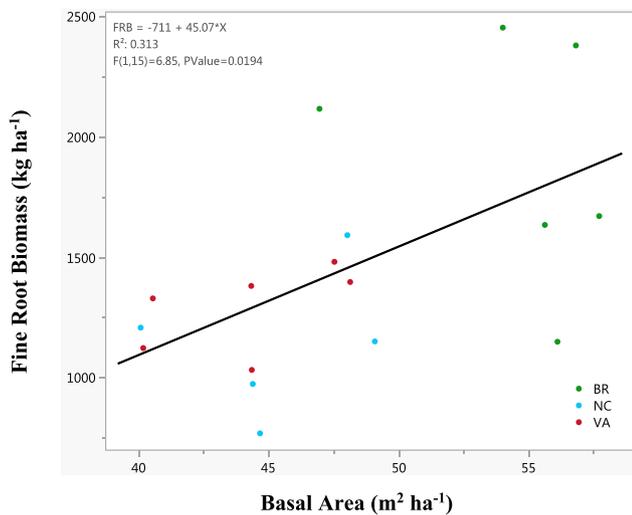


Fig. 3. Regression analysis of basal area ($\text{m}^2 \text{ha}^{-1}$) prior to the 2020 growing season by initial fine root biomass. Soil cores were taken in October 2020 for Brazil (BR) and December 2019–January 2020 for North Carolina (NC) and Virginia (VA) to measure fine root biomass. The standing crop of fine root biomass was positively correlated with plot basal area. $n = 6$ for BR and VA, $n = 5$ for NC.

aboveground growth increments. A regression of the fine root production estimates for all plots against the 2020 total above stump biomass growth increment demonstrated a negative relationship ($r^2 = 0.418$, $p = 0.032$), showing that there was a reduction in fine root production as total above stump growth increased, and this relationship was not affected by site or genotype (Fig. 7). A regression was also conducted on leaf biomass estimates versus fine root production, and no consistent relationship was found. Additionally, OP trees had a higher aboveground growth increment than C3 trees in 2020 ($p = 0.030$), though there was no effect of site.

4. Discussion

4.1. Brazil had unexpectedly high amounts of initial fine root biomass

Initial fine root biomass was higher in BR than under native conditions in NC. This was not consistent with our hypothesis—while we expected some variation in existing fine root biomass, it was surprising to see such higher amounts in BR. We believed differences among sites and/or genotypes might be observable through production and turnover estimates, not through sampling the existing fine root crop. At this stage of development, the trees in BR were two years younger, yet significantly larger than those in both VA and NC (Albaugh et al., 2018). This is despite similar fertility being maintained across all intensive silviculture plots and is consistent with a higher observed carrying capacity for loblolly pine in BR (Albaugh et al., 2018), for which greater levels of fine root biomass seem to be characteristic. Overall, our fine root biomass estimates are similar to other fine root biomass studies of North American pines (Albaugh et al., 2004; Carter et al., 2004; Litton et al., 2003; Retzlaff et al., 2001; Samuelson et al., 2004).

There were, however, no significant differences among fine root biomass estimates in NC and VA between 2016 and 2020, nor any effects of site and genotype, suggesting that tree size does not directly dictate levels of fine root biomass. This may also show that, belowground, the plots were fully occupied by the root system by age seven, which was around the time of crown closure (typically occurring between 6 and 8 years in high density, intensively managed loblolly pine plantations) (Campbell et al., 2013; Radtke and Burkhart, 1999). Interestingly, higher levels of initial fine root biomass were associated with greater plot basal areas, and because fertility was actively homogenized across

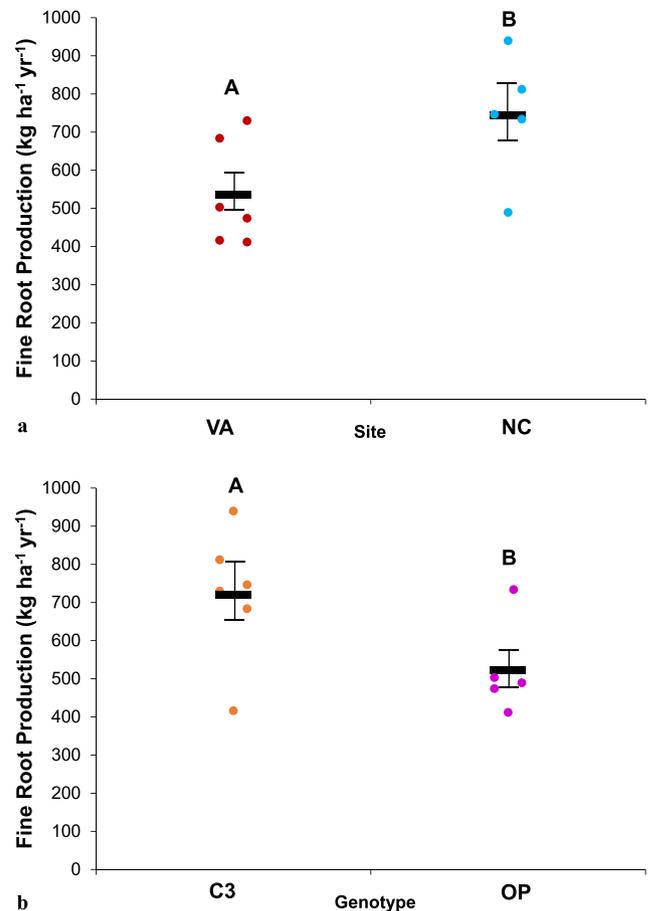


Fig. 4. Fine root production ($\text{kg ha}^{-1} \text{yr}^{-1}$) by site and by genotype. Initial cores were backfilled with sand and left for 12 months before being resampled for fine root ingrowth. (A) North Carolina (NC) had higher rates of fine root production than Virginia (VA) ($p = 0.081$), and (B) Clones (C3) had higher rates of fine root production than Open Pollinated (OP) ($p = 0.029$). $n = 6$ for VA and C3, $n = 5$ for NC and OP. Lines show mean fine root production, jittered points show individual plot level estimates, and error bars show standard error of the mean.

sites, the impacts of nutrient availability on root lifespan should have been similar among all plots. Standing fine root biomass may be more dependent on whole system characteristics or environmental conditions other than fertility and productivity, such as moisture regimes, temperature, litterfall and root decomposition rates, or even the natural ectomycorrhizal communities at each location. Indeed, precipitation has been shown to increase fine root production (Cordeiro et al., 2020) and accumulation (Zhang et al., 2019), but while temperature can increase fine root production and turnover, it may have no effect, or even decrease, standing fine root biomass depending on other conditions (Xiong et al., 2018). Although mycorrhizal associations were beyond the scope of this study, more investigation is needed into how these communities may differ across sites and how this might affect fine root dynamics.

4.2. Faster growing trees produced fewer fine roots, yet had similar foliar biomass to slower growers

This study provides evidence that aboveground growth increment is inversely related to fine root production, which supports our hypothesis. Although there was no effect of site in aboveground growth increment between NC and VA, there was a genotype effect where OP trees had a higher growth increment and lower fine root production and turnover than C3 trees over the studied year. The plot level regression of fine root

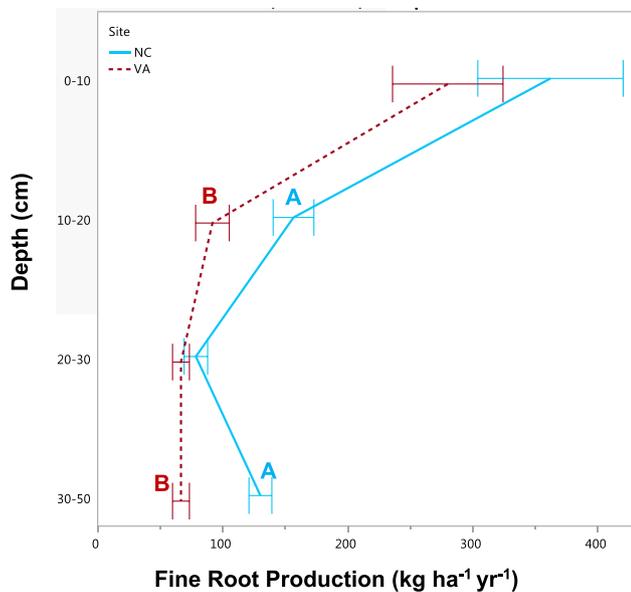


Fig. 5. Fine root production ($\text{kg ha}^{-1} \text{yr}^{-1}$) by site and depth (cm). There were higher rates of fine root production from 0 to 10 cm than any other depth ($p < 0.001$), and North Carolina (NC) produced more fine root biomass than Virginia (VA) from 10 to 20 cm ($p = 0.055$) and from 30 to 50 cm ($p = 0.003$). Letters indicate differences among sites at the same depth increment. Note that 30–50 cm is twice the depth of the three other increments. $n = 6$ for VA and $n = 5$ for NC at each depth. Error bars show standard error of the mean.

production and growth increment demonstrates the negative relationship. Both site and genotype did affect fine root production, and larger trees did not necessarily produce more fine roots—the trees in VA were larger than those in NC, and they demonstrated lower rates of fine root production. By depth, fine root production was higher in NC than VA from 10–20 cm and 30–50 cm. The NC plots were bedded prior to planting, however, so topsoil was piled in well-drained beds along the tree rows, and it is likely that fine roots are somewhat restricted by a pop pan at the VA site.

Our fine root production estimates were similar to some previous studies (Fíner and Laine, 2000; Pritchard et al., 2008), but were lower than many (Albaugh et al., 2004; Bhuiyan et al., 2017; Lee and Jose, 2003; Persson, 1980). The same is true for rates of fine root turnover which were similar to Nadelhoffer et al. (1985) and Pritchard et al. (2008), but lower than several others (Brunner et al., 2012; Guo et al., 2007; Persson, 1980). Although the literature varies slightly in methods, species, and age classes, ingrowth cores have been found to slightly underestimate fine root production when compared to other methods, and this is particularly true within the first year following core establishment (Fíner and Laine, 2000; Katayama et al., 2019). Our lower fine root production estimates relative to most other studies is consistent with this trend.

Analysis of fine root production regressed against leaf biomass yielded no consistent relationships in this study. The seasonal production of leaves and fine roots have been observed to be synchronized

(King et al., 2002). Thus, we expected negative relationships across sites and genotypes, as higher investments in one ephemeral pool (leaves) would come at the expense of another (fine roots). We hypothesized that more leaves would allow for more photosynthesis and higher growth increments. Instead, it seems that loblolly pines exhibiting higher growth rates were able to do so with fewer fine roots and no added cost of greater leaf production. The observations in this study are limited to a single growing season, however, and it is possible that tradeoffs may be reflected in allocation shifts of prior and/or subsequent years. A proportional analysis of tree level allocation patterns could elucidate the relative changes over time and how they correspond with year-to-year ephemeral and perennial tissue growth.

4.3. Seasonal fine root production was largely dictated by environmental conditions

Genotype did not affect fine root production in any season, but site did affect it from January to July and from September to December. The increased fine root production in NC versus VA during both periods is likely due, at least in part, to milder winter conditions and a longer growing season at the NC site, along with mild drought conditions in VA from September–October. Interestingly, when standardized to annual production rates, fine root production in NC was nearly identical from January–July and from July–September, and VA's fine root production from July–September was very similar to NC's over the same period. This common rate of fine root production could be indicative of a maximum for which, even during the most active periods of root production and given no limiting nutrients, these trees only allocated a certain amount of their resources to this specific pool of tissue. It may be that there are diminishing returns beyond this production rate due to the costs of respiration and maintenance, or perhaps resources are being used for other compartments.

4.4. Conclusion

This study provides evidence that a higher aboveground growth increment in loblolly pine is paired with lower rates of fine root production and slower turnover. We did not find evidence, however, that this is due to a direct tradeoff with resource allocation to leaves—this suggests that sufficient resources were available in these intensively managed plots for both lower rates of fine root production and increased aboveground growth. Larger trees in Brazil had greater standing fine root biomass than those in the native range of North Carolina, and overall, increased standing fine root biomass was related to higher basal areas, though fine root production and turnover were not.

CRediT authorship contribution statement

Timothy J. Shively: Conceptualization, Formal analysis, Investigation, Writing – original draft. **Rachel Cook:** Conceptualization, Writing – review & editing, Visualization, Supervision, Funding acquisition. **Chris A. Maier:** Writing – review & editing, Formal analysis, Validation. **Kevin Garcia:** Writing – review & editing, Validation. **Timothy J. Albaugh:** Writing – review & editing, Formal analysis, Data curation,

Table 4

P-values from ANOVA conducted for fine root turnover rates. Fine root turnover was calculated by dividing initial fine root biomass by annual rates of fine root production. The right side of the table shows turnover rates (years^{-1}) and the time (yr) with standard error (SE) it would take for the entire fine root network to turnover, or replace itself, one time.

ANOVA				
Effect	P-value	Site or Genotype	Fine Root Turnover Means (yr^{-1})	Time to Complete Turnover (yr) (SE)
Site	0.129	VA	0.39	2.56 (0.32)
Genotype	0.091	NC	0.63	1.59 (0.25)
Site × Genotype	0.984	C3	0.56	1.79 (0.34)
		OP	0.40	2.50 (0.30)

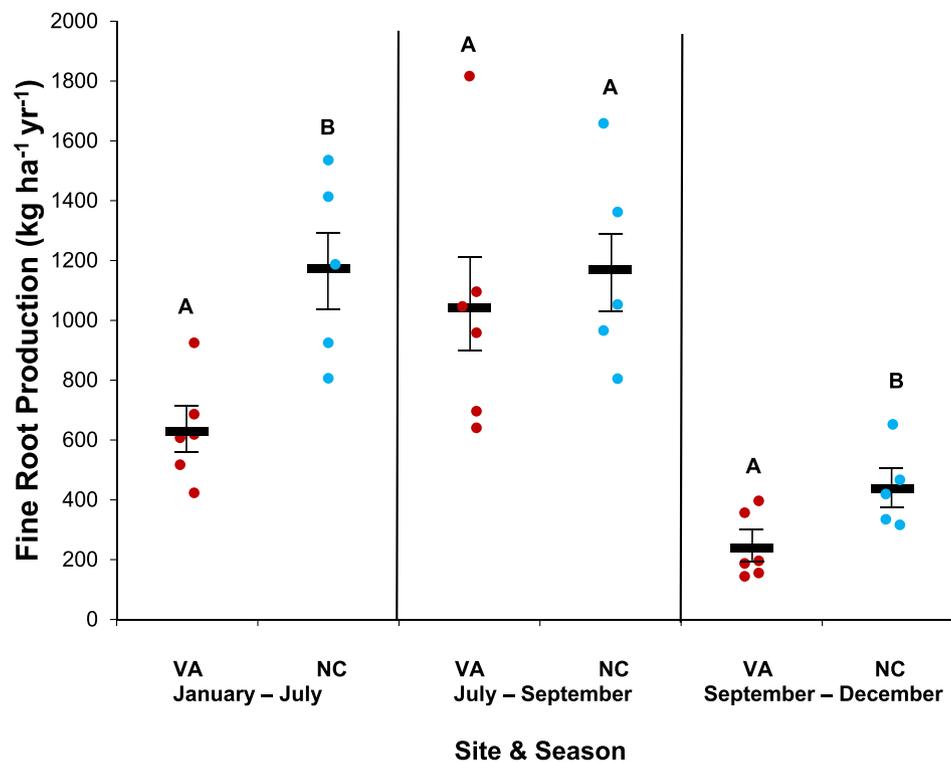


Fig. 6. Seasonal fine root production estimates ($\text{kg ha}^{-1} \text{yr}^{-1}$), by site. Letters represent differences in fine root production between sites for a particular season. North Carolina (NC) had higher rates of fine root production than Virginia (VA) in spring and early summer as well as fall. Lines show mean fine root production, jittered points show individual plot level estimates, and error bars show standard error of the mean. $n = 6$ for VA and $n = 5$ for NC.

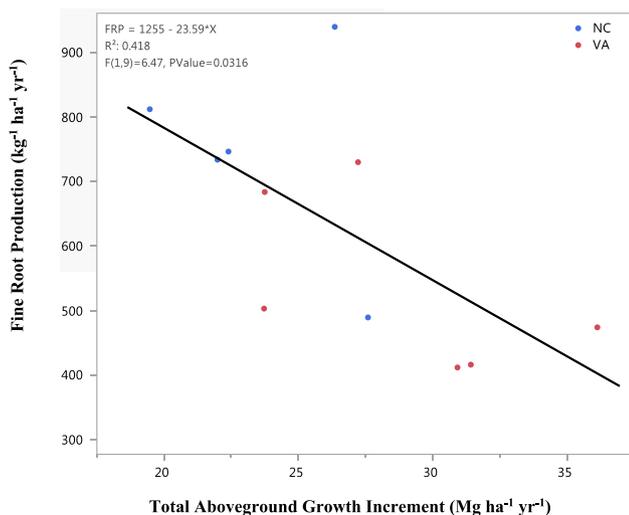


Fig. 7. Regression analysis of the aboveground growth increment vs fine root production of each plot in which ingrowth cores were installed. Individual points represent each plot's growth increment in total above stump biomass by its fine root production estimate for a single year.

Resources. **Otávio Campoe:** Investigation, Data curation. **Zakiya Leggett:** Writing – review & editing, Conceptualization, Methodology, Validation, Supervision, Resources.

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.

Data availability

Data will be made available on request.

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References

- Achat, D.L., Bakker, M.R., Trichet, P., 2008. Rooting patterns and fine root biomass of *Pinus pinaster* assessed by trench wall and core methods. *J. Forest Res.* 13 (3), 165–175. <https://doi.org/10.1007/s10310-008-0071-y>.
- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., King, J.S., 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *Forest Sci.* 44 (2), 317–328. <https://doi.org/10.1093/forestscience/44.2.317>.
- Albaugh, J.M., Blevins, L., Allen, H.L., Albaugh, T.J., Fox, T.R., Stape, J.L., Rubilar, R.A., 2010. Characterization of foliar macro- and micronutrient concentrations and ratios in loblolly pine plantations in the southeastern United States. *South. J. Appl. For.* 34 (2), 53–64. <https://doi.org/10.1093/sjaf/34.2.53>.

- Albaugh, T.J., Lee Allen, H., Dougherty, P.M., Johnsen, K.H., 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *For. Ecol. Manage.* 192 (1), 3–19. <https://doi.org/10.1016/j.foreco.2004.01.002>.
- Albaugh, T.J., Fox, T.R., Maier, C.A., Campoe, O.C., Rubilar, R.A., Cook, R.L., Raymond, J.E., Alvares, C.A., Stape, J.L., 2018. A common garden experiment examining light use efficiency and heat sum to explain growth differences in native and exotic *Pinus taeda*. *For. Ecol. Manage.* 425, 35–44. <https://doi.org/10.1016/j.foreco.2018.05.033>.
- Albaugh, T.J., Maier, C.A., Campoe, O.C., Yáñez, M.A., Carbaugh, E.D., Carter, D.R., Cook, R.L., Rubilar, R.A., Fox, T.R., 2020. Crown architecture, crown leaf area distribution, and individual tree growth efficiency vary across site, genetic entry, and planting density. *Trees* 34 (1), 73–88. <https://doi.org/10.1007/s00468-019-01898-3>.
- Bakker, M.R., Jolicœur, E., Trichet, P., Augusto, L., Plassard, C., Guinberteau, J., Loustau, D., 2008. Adaptation of fine roots to annual fertilization and irrigation in a 13-year-old *Pinus pinaster* stand. *Tree Physiol.* 29, 229–238. <https://doi.org/10.1093/treephys/tpn020>.
- Bhuiyan, R., Minkinen, K., Helmsaari, H.-S., Ojanen, P., Penttilä, T., Laiho, R., 2017. Estimating fine-root production by tree species and understorey functional groups in two contrasting peatland forests. *Plant Soil* 412 (1–2), 299–316. <https://doi.org/10.1007/s11104-016-3070-3>.
- Brunner, I., Bakker, M.R., Björk, R.G., Hirano, Y., Lukac, M., Aranda, X., Børja, I., Eldhuset, T.D., Helmsaari, H.S., Jourdan, C., Konópka, B., López, B.C., Miguel Pérez, C., Persson, H., Ostonen, I., 2012. Fine-root turnover rates of European forests revisited: An analysis of data from sequential coring and ingrowth cores. *Plant Soil* 362 (1–2), 357–372. <https://doi.org/10.1007/s11104-012-1313-5>.
- Cai, H., Li, F., Jin, G., 2019. Fine root biomass, production and turnover rates in plantations versus natural forests: effects of stand characteristics and soil properties. *Plant Soil* 436 (1–2), 463–474. <https://doi.org/10.1007/s11104-019-03948-8>.
- Campbell, T.N., Jones, P.D., Ezell, A.W., Demarais, S., 2013. Growth and competition response in intensively established loblolly pine plantations at crown closure. *J. Forest.* 111 (5), 313–318. <https://doi.org/10.5849/jof.12-045>.
- Carter, D.C., Hendricks, J.J., Mitchell, R.J., Pecot, S.D., 2004. Fine root carbon allocation and rates in longleaf pine forests. *Forest Sci.* 50 (2), 177–187. <https://doi.org/10.1093/forests/50.2.177>.
- Chen, G., Hobbie, S.E., Reich, P.B., Yang, Y., Robinson, D., Thrall, P., 2018. Allometry of fine roots in forest ecosystems. *Ecol. Lett.* 22 (2), 322–331. <https://doi.org/10.1111/ele.13193>.
- Climate-Data. <https://en.climate-data.org/search/?q=río+negrinho> (accessed 16 March 2021).
- Cordeiro, A.L., Norby, R.J., Andersen, K.M., Valverde-Barrantes, O., Fuchsluger, L., Oblitas, E., Hartley, I.P., Iversen, C.M., Gonçalves, N.B., Takeshi, B., Lapola, D.M., Quesada, C.A., 2020. Fine-root dynamics vary with soil depth and precipitation in a low-nutrient tropical forest in the Central Amazonia. *Plant-Environ. Interact.* 1 (1), 3–16. <https://doi.org/10.1002/pei3.10010>.
- Coyle, D.R., Coleman, M.D., Aubrey, D.P., 2008. Above- and below-ground biomass accumulation, production, and distribution of sweetgum and loblolly pine grown with irrigation and fertilization. *Can. J. For. Res.* 38 (6), 1335–1348. <https://doi.org/10.1139/X07-231>.
- Danjon, F., Stokes, A., Bakker, M.R., 2013. *Root Systems of Woody Plants. Plant Roots: The Hidden Half*, 4th ed. CRC Press. pp. 29–1–29–26.
- Eissenstat, D.M., Van Rees, K.C.J., 1994. The growth and function of pine roots. *Ecol. Bull.* 43, 76–91. <https://www.jstor.org/stable/20113133>.
- Finer, L., Laine, J., 2000. The ingrowth bag method in measuring root production on peatland sites. *Scand. J. For. Res.* 15 (1), 75–80. <https://doi.org/10.1080/02827580050160493>.
- Gonzalez-Benecke, C.A., Gezan, S.A., Albaugh, T.J., Allen, H.L., Burkhart, H.E., Fox, T.R., Jokela, E.J., Maier, C.A., Martin, T.A., Rubilar, R.A., Samuelson, L.J., 2014. Local and general above-stump biomass functions for loblolly pine and slash pine trees. *For. Ecol. Manage.* 334, 254–276. <https://doi.org/10.1016/j.foreco.2014.09.002>.
- Gower, S.T., Vogt, K.A., Grier, C.C., 1992. Carbon dynamics of rocky mountain douglas-fir: Influence of water and nutrient availability. *Ecol. Monogr.* 62 (1), 43–65. <https://doi.org/10.2307/2937170>.
- Guo, L.B., Wang, M., Gifford, R.M., 2007. The change of soil carbon stocks and fine root dynamics after land use change from a native pasture to a pine plantation. *Plant Soil* 299 (1–2), 251–262. <https://doi.org/10.1007/s11104-007-9381-7>.
- Hertel, D., Leuschner, C., 2002. A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus-Quercus* mixed forest. *Plant Soil* 239, 237–251. <https://doi.org/10.1023/A:1015030320845>.
- Jokela, E.J., Martin, T.A., 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. *Can. J. For. Res.* 30 (10), 1511–1524. <https://doi.org/10.1139/x00-082>.
- Katayama, A., Kho, L.K., Makita, N., Kume, T., Matsumoto, K., Ohashi, M., 2019. Estimating fine root production from ingrowth cores and decomposed roots in a Bornean tropical rainforest. *Forests* 10 (36), 1–13. <https://doi.org/10.3390/f10010036>.
- King, J.S., Albaugh, T.J., Allen, H.L., Kress, L.W., 1999. Stand-level allometry in *Pinus taeda* as affected by irrigation and fertilization. *Tree Physiol.* 19 (12), 769–778. <https://doi.org/10.1093/treephys/19.12.769>.
- King, J.S., Albaugh, T.J., Allen, H.L., Buford, M., Strain, B.R., Dougherty, P., 2002. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. *New Phytol.* 154, 389–398. <https://doi.org/10.1046/j.1469-8137.2002.00393.x>.
- Lee, K.-H., Jose, S., 2003. Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. *For. Ecol. Manage.* 185 (3), 263–273. [https://doi.org/10.1016/S0378-1127\(03\)00164-6](https://doi.org/10.1016/S0378-1127(03)00164-6).
- Li, B., McKeand, S., Weir, R., 1999. Tree improvement and sustainable forestry—Impact of two cycles of loblolly pine breeding in the U.S.A. *Forest Genetics* 6 (4), 229–234.
- Li, X., Zhang, C., Zhang, B., Wu, D., Shi, Y., Zhang, W., Ye, Q., Yan, J., Fu, J., Fang, C., Ha, D., Fu, S., 2021. Canopy and understorey nitrogen addition have different effects on fine root dynamics in a temperate forest: implications for soil carbon storage. *New Phytol.* 231 (4), 1377–1386. <https://doi.org/10.1111/nph.17460>.
- Litton, C.M., Ryan, M.G., Tinker, D.B., Knight, D.H., 2003. Belowground and aboveground biomass in young postfire lodgepole pine forests of contrasting tree density. *Can. J. For. Res.* 33 (2), 351–363. <https://doi.org/10.1139/X02-181>.
- Lukac, M., 2012. *Fine Root Turnover*. In: Mancuso, S. (Ed.), *Measuring Roots: An Updated Approach*. Springer, pp. 363–373.
- Maier, C.A., Albaugh, T.J., Allen, H.L., Dougherty, P.M., 2004. Respiratory carbon use and carbon storage in mid-rotation loblolly pine (*Pinus taeda* L.) plantations: The effect of site resources on the stand carbon balance. *Glob. Change Biol.* 10, 1335–1350. <https://doi.org/10.1111/j.1365-2486.2004.00809.x>.
- Nadelhoffer, K.J., 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytol.* 147 (1), 131–139. <https://doi.org/10.1046/j.1469-8137.2000.00677.x>.
- Nadelhoffer, K.J., Aber, J.D., Melillo, J.M., 1985. Fine roots, net primary production, and soil nitrogen availability: A new hypothesis. *Ecology* 66 (4), 1377–1390. <https://doi.org/10.2307/1939190>.
- NOWData, 2010. NOAA. <https://w2.weather.gov/climate/xmacis.php?wfo=ilm> (accessed 16 March 2021).
- Osawa, A., Aizawa, R., 2012. A new approach to estimate fine root production, mortality, and decomposition using litter bag experiments and soil core techniques. *Plant Soil* 355 (1–2), 167–181. <https://doi.org/10.1007/s11104-011-1090-6>.
- Persson, H., 1980. Spatial distribution of fine-root growth, mortality and decomposition in a young Scots pine stand in Central Sweden. *Oikos* 34 (1), 77–87. <https://doi.org/10.2307/3544552>.
- Pirard, R., Dal Secco, L., Warman, R., 2016. Do timber plantations contribute to forest conservation? *Environ. Sci. Policy* 57, 122–130. <https://doi.org/10.1016/j.envsci.2015.12.010>.
- Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., Finzi, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., Oren, R., 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO₂-enrichment: A six-year-minirhizotron study. *Glob. Change Biol.* 14, 588–602. <https://doi.org/10.1111/j.1365-2486.2007.01523.x>.
- Radtke, P.J., Burkhart, H.E., 1999. Basal area growth and crown closure in a loblolly pine spacing trial. *Forest Sci.* 45 (1), 35–44. <https://doi.org/10.1093/forests/45.1.35>.
- Retzlaff, W.A., Handest, J.A., O'Malley, D.M., McKeand, S.E., Topa, M.A., 2001. Whole-tree biomass and carbon allocation of juvenile trees of loblolly pine (*Pinus taeda*): Influence of genetics and fertilization. *Can. J. For. Res.* 31, 960–970. <https://doi.org/10.1139/cjfr-31-6-960>.
- Samuelson, L.J., Johnsen, K., Stokes, T., 2004. Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to 6 years of intensive management. *For. Ecol. Manage.* 192 (1), 59–70. <https://doi.org/10.1016/j.foreco.2004.01.005>.
- Samuelson, L., Stokes, T., Coosey, T., McLemore III, P., 2001. Production efficiency of loblolly pine and sweetgum in response to four years of intensive management. *Tree Physiol.* 21 (6), 369–376. <https://doi.org/10.1093/treephys/21.6.369>.
- Schultz, R.P., 1999. Loblolly – the pine for the twenty-first century. *New Forest.* 17, 71–88. <https://doi.org/10.1023/A:1006533212151>.
- Vickers, L.A., Fox, T.R., Stape, J.L., Albaugh, T.J., 2011. Silviculture of varietal loblolly pine plantations: Second year impacts of spacing and silvicultural treatments on varieties with different crown ideotypes. In: *Proceedings of the 16th Biennial Southern Silvicultural Research Conference*, pp. 363–367. https://www.srs.fs.fed.us/pubs/gtr/gtr_srs156/gtr_srs156_363.pdf.
- Vogt, K.A., Persson, H., 1991. Measuring growth and development of roots. In: Lassoie, J.P., Hinkley, T.M. (Eds.), *Techniques and Approaches in Forest Tree Ecophysiology*. CRC Press, Inc, pp. 477–501.
- Vogt, K.A., Vogt, D.J., 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Adv. Ecol. Res.* 15, 303–366. [https://doi.org/10.1016/S0065-2504\(08\)60122-1](https://doi.org/10.1016/S0065-2504(08)60122-1).
- Vose, J.M., Allen, H.L., 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. *Forest Sci.* 34 (3), 547–563. <https://doi.org/10.1093/forests/34.3.547>.
- Will, R.E., Munger, G.T., Xiang, Y., Borders, B.E., 2002. Effects of annual fertilization and complete competition control on current annual increment, foliar development and growth efficiency of different aged *Pinus taeda* stands. *Can. J. For. Res.* 32 (10), 1728–1741. https://www.proquest.com/citedby/MSTAR_230523590/4B5667D9645145BCPQ?accountid=14826.
- Xiong, D., Yang, Z., Chen, G., Liu, X., Lin, W., Huang, J., Bowles, F.P., Lin, C., Xie, J., Li, Y., Yang, Y., 2018. Interactive effects of warming and nitrogen addition on fine root dynamics of a young subtropical plantation. *Soil Biol. Biochem.* 123, 180–189.

- Yanez, M.A., Fox, T.R., Seiler, J.R., 2017. Silvicultural intensity and site effects on stand uniformity of loblolly pine varieties and families. *Forest Sci.* 63 (6), 606–613. <https://doi.org/10.5849/FS-2016-036R2>.
- Zhang, X., Xing, Y., Yan, G., Han, S., Wang, Q., Lupwayi, N., 2019. Effects of precipitation change on fine root morphology and dynamics at a global scale: a meta-analysis. *Can. J. Soil Sci.* 99 (1), 1–11. <https://doi.org/10.1139/cjss-2018-0114>.
- Zhao, D., Kane, M., Fox, T.R., Albaugh, T.J., Allen, H.L., Rubilar, R., 2016. Maximum response of loblolly pine plantations to silvicultural management in the southern United States. *Forest. Ecol. Manage.* 375, 105–111. <https://doi.org/10.1016/j.foreco.2016.05.035>.