Tree Physiology 30, 1299–1310
doi:10.1093/treephys/tpq067

Soil incorporation of logging residue affects fine-root and mycorrhizal root-tip dynamics of young loblolly pine clones

SETH G. PRITCHARD,[1,2] CHRIS A. MAIER,[3] KURT H. JOHNSEN,[3] ANDREA J. GRABMAN,[1,4] ANNE P. CHALMERS[1] and MARIANNE K. BURKE[5]

[1] *College of Charleston, Department of Biology, Charleston, SC 29401, USA*

[2] *Corresponding author (pritchards@cofc.edu)*

[3] *USDA Forest Service, Southern Research Station, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA*

[4] *Edisto Beach State Park, Edisto Island, SC 29438, USA*

[5] *USDA Forest Service, Research and Development, Science Quality Services, Washington, DC 20024, USA*

Received December 24, 2009; accepted June 27, 2010; published online July 28, 2010; handling Editor Daniel Epron

Summary Loblolly pine (*Pinus taeda* L.) plantations cover a large geographic area of the southeastern USA and supply a large proportion of the nation's wood products. Research on management strategies designed to maximize wood production while also optimizing nutrient use efficiency and soil C sequestration is needed. We used minirhizotrons to quantify the effects of incorporating logging residues into soil on fine-root standing crop, production and mortality, and mycorrhizal root tips in young loblolly pine clones of contrasting ideotypes. Clone 93 is known to allocate more C to stem growth, while clone 32 allocates less C to stems and more to leaves. The relative allocation by these clones to support fine-root turnover is unknown. Clone 32 exhibited 37% more fine-root mortality than clone 93, which was mainly the result of a greater standing crop of fine roots. Fine-root standing crop in plots amended with logging residue was initially higher than control plots, but 2.5 years after planting, standing crop in control plots had exceeded that in mulched plots. Production of mycorrhizal root tips, on the other hand, was initially higher in control than mulched plots, but during the last 9 months of the study, mycorrhizal tip production was greater in mulched than control plots, especially for clone 93. As expected, turnover rate of fine roots was greater in surface soil (0–25 cm) compared with deeper (25–50 cm) soil and for small roots (<0.4 mm diameter) compared with larger fine roots (0.4–2.0 mm diameter). Rates of fine-root turnover were similar in both clones. Organic matter additions reduced survivorship of individual roots and increased turnover rates of fine-root populations. Results indicate that management decisions should be tailored to fit the growth and allocation patterns of available clones.

Keywords: loblolly pine, fine roots, root turnover, survivorship, soil management, C sequestration.

Introduction

Periodic replacement of the finest tree roots (i.e., those <2.0 mm in diameter) demands a significant investment of carbohydrates and nutrients because of their short longevity, high metabolic rates and high N concentrations. Longevity of fine roots is reported to range from several months to a few years depending on the tree species (Coleman et al. 2000), root diameter and order (Wells et al. 2002, Guo et al. 2008*a*, 2008*b*, Pritchard and Strand 2008), depth in soil (Kern et al. 2004) and season of construction (Wells and Eissenstat 2001, Tierney et al. 2003, Guo et al. 2008*a*). Fine-root turnover may consume >30% of NPP (Santantonio and Grace 1987, Jackson et al. 1997, Reuss et al. 2003), and annual litter inputs to soil from fine roots often exceed inputs from leaves (Vogt et al. 1986, Hendrick and Pregitzer 1992, 1993, Handa et al. 2008). An additional 10–20% of the yearly carbohydrate budget for trees may be consumed in the process of establishing and maintaining mycorrhizal relationships that are mediated by first- and second-order roots (Johnson and Gehring 2007, Guo et al. 2008*a*).

It has been suggested that storage of C in soil may slow the increase in atmospheric CO_2 concentration thereby mitigating climate change. Soil C storage may prove to be particularly important because soils contain ~3× more C than is present in terrestrial vegetation and 2× more C than the atmosphere (Lal 2004). It is estimated that forest soils have already absorbed a significant proportion of anthropogenic C emissions in the USA (Ryan et al 2010). Because much of the C that flows into soil C pools is derived from turnover of root systems (Richter et al 1999), predicting the potential for forests to sequester additional C is contingent upon a better understanding of the controls of fine-root production and longevity (Iversen 2010).

Worldwide, loblolly pine is among the most important plantation tree species (Schultz 1997, Fox et al. 2007). In the southeastern USA, more than 12.1 million hectares are devoted to tree plantations, and this area is projected to double by 2040 (Wear and Creis 2002). Knowledge of how silvicultural management practices influence allocation of forest C to belowground pools in intensively managed plantations will be a particularly important component of managing forest C stocks (Jastrow et al. 2007). Currently, little is known about how specific management practices, such as incorporation of logging residue-derived mulch into soils and genotype selection, might affect fine-root and mycorrhizal production and longevity along with the biogeochemical processes that are influenced by these belowground processes.

We evaluated the effects of soil incorporation of mulch derived from logging residue on soil and plant carbon dynamics in a loblolly pine plantation (Tyree et al. 2009). Incorporation of logging residue (mulch) into the soil during site preparation has the potential to enhance soil carbon sequestration, improve soil microbiology, stimulate nutrient cycling, increase plant productivity, increase penetration of rainfall into soil and decrease erosion (Forge et al. 2008). The effects of soil mulch incorporation on tree productivity and soil processes are being studied in two loblolly pine clones that exhibit fundamentally different growth patterns. The narrow crown ideotype clone (CL93) allocates a greater proportion of biomass to stem growth, whereas the wide-crown ideotype clone (CL32) allocates significantly more carbohydrates to leaf construction. A common garden study found that, in 6-year-old trees, CL93 produced similar stem growth to CL32 with half the leaf area (Phil Dougherty, Arborgen, Inc., personal communication). In poplar, significant clonal variation in fine-root dynamics has been reported (Pregitzer et al. 1990, Dickmann et al. 1996), and clonal variation in leaf area index has also been shown to be a reliable indicator of fine-root standing crop (Al Afas et al. 2008). Such a relationship has not yet been established for loblolly pine.

The central hypothesis at this study site was that soil incorporation of logging residues during site preparation would promote tree growth and carbon storage in both tree biomass and in the soil and that the magnitude of the response will depend on the carbon allocation patterns, which are expected to differ between clones. Incorporation of logging residue mulch at this site has increased the C-to-N ratio of soil, which is likely to result in greater N immobilization. Faster tree growth coupled with N immobilization is predicted to decrease soil N availability. We hypothesized that reduced soil N availability in mulched plots would in turn increase fine-root and mycorrhizal production and increase survivorship of these structures. We further hypothesized that clones would display similar aboveground productivity in the control treatment, but because of lower leaf area and thus lower nitrogen demand, CL93 would display higher total productivity than CL32 in mulched plots. We predicted that the absolute increase in production of fine roots and mycorrhizae in mulched plots compared with controls would be more dramatic in CL32 because its higher leaf area would support greater canopy photosynthesis and total belowground C allocation.

Materials and methods

Site characteristics

The site is located on MeadWestvaco lands in Berkeley County, SC (33° N, 80° W). The soils are classified as Lynchburg/Occilla/Seagate (USDS Soil Classification System), which typically have moderate levels of organic matter and are low in phosphorous. The soils are moderately drained and have a fluctuating water table that approaches the surface. Annual rainfall is 1358 mm, and average January and July temperatures are 8 and 27 °C, respectively. In May 2004, the previous stand of loblolly pine, planted in 1984, was clear-cut harvested. There was 25 ± 10 SD Mg ha^{-1} of forest floor left on site after harvesting. The residual forest floor consisted of old litter, foliage and branch material left on site after harvesting (C:N ≈ 112). The harvested trees were chipped on site. The effluent from the chipping operation consisted of stem bark and masticated branches (C:N ≈ 700) and was the source of the mulch used in the experiment.

In July 2004, the site was stripped and sheared using a D-8 tractor with a V-shear blade. In October, two treatments were installed, a control consisting of residual forest floor only and a mulched treatment that included the residual forest floor to which 25 Mg ha^{-1} logging debris was added. All plots were double bedded using a D-8 tractor with a Savannah bedding plow to ensure adequate mixing of added mulch and mineral soil. Prior to bedding, the mulch was applied in strips to the bedding rows. The experiment consists of three blocks, designated to account for variation in the site water table, in a fully randomized design. Within each block, there are four 48 × 38 m (0.18 ha) plots consisting of nine bedded rows (~30 cm tall). Approximately 243 loblolly pine (*Pinus taeda* L.) clonal seedlings were planted in January 2005 in rows 4.3 m apart with seedlings spaced every 1.8 m. Within each block, subplots with two different clones and two soil-management treatments were implemented. The clones exhibit contrasting growth efficiencies. Once prior to planting and four times during the first year and a half of growth, competing vegetation was controlled using a combination of Arsenal and Oust.

Growth measurements

Tree height was measured monthly beginning in January of the second year of growth and continuing for the next 17 months. Ten trees were randomly selected in each treatment plot with the criteria that the height of the selected tree was within one standard deviation of the plot mean. Height was measured using a height pole.

Site water table

Ground water level was measured using PVC wells installed in the center of each treatment plot. Depth to the water table

was measured using a data logger and a submersible pressure transducer (Model WL 15, Global Water Instrumentation, Inc, Gold River, Ca). Water level measurements were recorded hourly and then averaged every 12 h.

Minirhizotron approach

Fine roots were studied with minirhizotrons. Minirhizotrons are clear plastic tubes (OD = 56 mm) that allow repeated, noninvasive measurement of root growth (Pritchard and Strand 2008). Tubes were installed in February 2005 at an angle of 45° from vertical to a vertical depth of ~50 cm. Three subsample tubes were installed into each plot for a total of 36. All statistical analyses were applied to the means of the three subsample tubes. The portion of the minirhizotron tube extending above the ground was first painted black and then painted white in order to reflect energy and to keep the tube dark. Images were collected with a BTC100× microvideo camera (Bartz Technologies, Santa Barbara, CA) once at the end of 2005 (11 November), five times in 2006 (11 January, 20 March, 18 May, 12 July and 15 October) and three times during 2007 (15 January, 23 March and 19 June). A total of ~15,000 digital images were collected.

Data were extracted from digital images using RooTracker software (Dave Tremmel, Duke University, Durham, NC). At each date, root diameters, total length of live roots, new root length production, and root length mortality were recorded. Mycorrhizal root tip production and standing crop were also recorded. Although we did not quantify percent colonization, non-mycorrhizal root tips were frequently noted. Roots were considered dead when they disappeared or upon their structural disintegration. In some cases, nonfunctional roots may have been classified as alive as long as they remained present and intact, and thus errors would be overestimations of fine-root longevity, standing crop and mortality rate.

A root turnover index was calculated as total length production during the duration of the experiment (497 days) divided by the maximum fine-root length standing crop during the experiment (Gill and Jackson 2000, Norby and Jackson 2000).

Statistical analyses

The experiment was replicated three times with the whole plots arranged as a 2 × 2 factorial (two levels of logging residue, control and mulched, in addition to two clones, CL93 and CL32). Minirhizotron images were then grouped into two depth classes representing shallow (0–25 cm) and deep (25–50 cm) soil horizons. Depth was treated as a fixed effect nested within treatments for each of the analyses performed. Data were analyzed using a linear mixed model repeated measures approach, with time as the repeated variable; clone, treatment and depth were fixed effects; and block was the random effect. We used the auto-regressive or compound symmetry covariance structure depending on which best fit with respect to Akaike's Information Criterion (AIC). In all cases, plot means were used for analyses. Where necessary, LSD tests were used to compare specific pairs. These analyses were conducted using SPSS 16.0 (SPSS for Windows, SPSS, Chicago, IL).

In order to characterize and compare root longevity, we used the Kaplan–Meier method to estimate survivorship for each treatment combination and Cox's proportional hazards model to test for the main effects of treatment, depth and diameter as well as their interactions. Log-rank and Wilcoxon's tests were further used to compare homogeneity of sur-

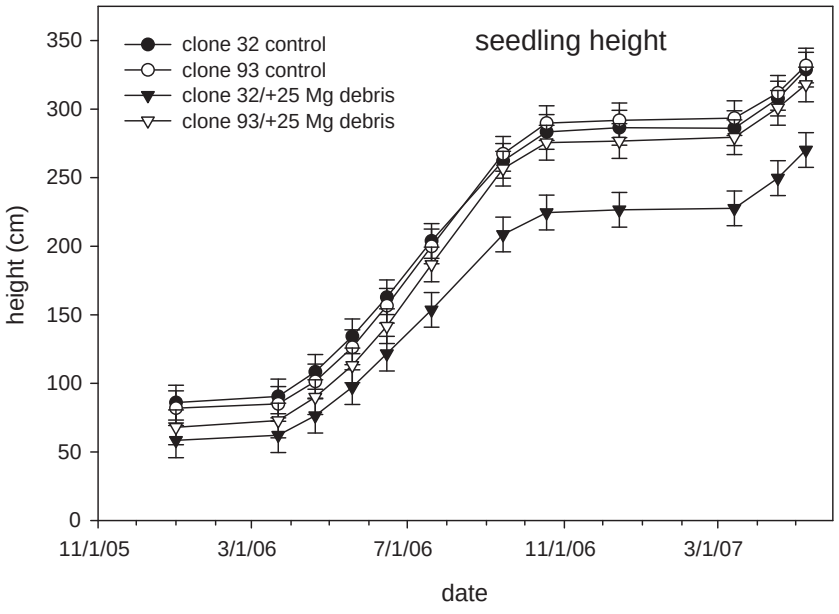

Figure 1. Early seedling height of two loblolly clones (93 and 32) grown under mulched or control conditions. Height was measured 12 times over a period of ~17 months. Error bars represent 1 SD.

vivorship curves between groups of interest identified from Cox's test. All structures that were present at the beginning of the study and those that remained at the end were considered censored. All statistical analyses of survivorship were conducted using JMP version 7.0 (SAS Institute, Cary, NC). Because of variability inherent to minirhizotron studies and because of lack of statistical power ($n = 3$), statistical trends were designated when $0.10 < P < 0.15$ and significant differences when $P < 0.10$ (Steel et al. 1997).

Results

Trees grew in height from May through October (Figure 1). Trees in the control plots were 17% taller than those in the mulched plots (+25 Mg debris) after 2.5 years of growth, but this difference was caused mainly by slower growth in CL32 in mulched plots (Table 1, Figure 1). A clone × time interaction was also observed. In general, clones did not differ in height early in the study, but by Year 2.5, CL93 was 16% taller than CL32.

The depth to the water table was greatest during May, June, July and August. During the winter months, the water table rose to the soil surface; standing water was common in the control but not the mulched plots (Figure 2). During summer, soil dried significantly, and the water table generally receded into deeper soil in control compared with mulched plots. There were no observable differences in water table depth in plots with CL93 vs CL32 (Figure 3).

Fine-root standing crop increased steadily throughout the experiment as the soil profile was colonized by young seedlings (time, $P < 0.001$; Figures 2 and 3). Fine-root production was greatest during late summer and early fall, corresponding to the rise in the water table and the decrease in the rate of stem growth. Little production was observed in winter months. Rates of fine-root mortality increased steadily from February through October of 2006 and then decreased through the winter (time, $P < 0.001$).

Table 1. Results of repeated measures analysis of variance for fine-root standing crop (std crp; m frame^{-1}), production (prod; m frame^{-1}), mortality (mort; m frame^{-1}), median diameter (diam; mm) and turnover index (720 days^{-1}), and tree height (ht). Main effects are treatment (trt) and clone (c) and depth (dpth) and the repeated measure is time (t).

	std crp	prod	mort	turn	diam	ht
trt*	NS	NS	NS	0.04	NS	0.04
c	NS	NS	0.15	NS	NS	NS
trt × c	NS	NS	NS	NS	NS	NS
dpth	NS	NS	0.03	0.008	0.15	–
dpth × trt	NS	NS	NS	NS	0.08	–
dpth × c	NS	NS	NS	NS	NS	–
dpth × trt × c	NS	NS	NS	NS	NS	–
t	<0.001	<0.001	<0.001	–	–	<0.001
t × trt	0.14	0.05	NS	–	–	NS
t × c	NS	NS	NS	–	–	<0.001
t × dpth	NS	NS	0.04	–	–	–
t × trt × c	NS	NS	NS	–	–	NS
t × dpth × c	NS	NS	NS	–	–	–

NS is nonsignificant ($P > 0.15$).

Fine-root standing crop was higher at the beginning of the study in mulched plots, but after 2.5 years, standing crop was lower in mulched than in control plots (treatment × time, $P = 0.14$). Although standing crop of fine roots was consistently higher for CL32 than CL93 (Figure 3), this effect was insignificant, and no interactions of clone with depth, treatment or time were noted.

No main effects of treatment, clone or depth were found for bimonthly fine-root production (Table 1). Production was greater in mulched plots during the summer of 2005 but was reduced compared with control plots in August and September of 2006 (time × treatment; $P = 0.05$; Figure 2).

Greater fine-root mortality was noted in shallow compared with deep soil for both clones and in both control and mulched plots but only during periods of peak root death (i.e., fall; time × depth, $P = 0.04$; data not shown). CL32 exhibited 37% more fine-root length mortality than CL93 during the experiment ($P = 0.15$). No main effect of treatment on mortality was found in spite of the observation that 28% more fine-root length mortality was noted in mulched plots than was observed in controls.

Relative fine-root length turnover rate over the course of the experiment was 1.33 (turnover$^{497\ \text{days}}$) corresponding to an estimated average longevity of 373 days (data not shown). Mean longevity of individual fine roots calculated from survivorship analysis of individual roots, estimated using a Weibul model, was 356 days, whereas median fine-root longevity was 301 days.

Turnover of fine roots was 18% faster in shallow soil compared with deep soil (Table 1; $P = 0.008$). Similarly, survivorship analysis indicated that median longevity of individual roots in deep soil was 33% greater than median longevity of roots in shallow soil. Fine-root turnover was faster in mulched plots (1.41 or 352 days) than controls (1.25 or 398 days) ($P = 0.04$). Similarly, survivorship analysis also indicated shorter median and mean fine-root longevity in mulched (277 and 324 days) compared with control plots (368 and 387 days). Cox proportional hazards tests, however, showed that the significant reduction in longevity in mulched plots was not present for CL32 in shallow soil (Figure 4a; treatment × clone × depth, $P = 0.003$). Neither relative turnover nor survivorship of individual roots differed in CL32 compared with CL93 (data not shown).

Survivorship varied with fine-root diameter (Figure 5). The smallest-diameter fine roots (<0.4 mm) had a median longevity of 277 days compared with a median longevity of 436 days for somewhat larger fine roots (0.4–2.0 mm diameter) ($P < 0.0001$). The reduction in survivorship of small compared with larger fine roots differed in mulched (estimated means for small and large were 294 and 432 days) and con-

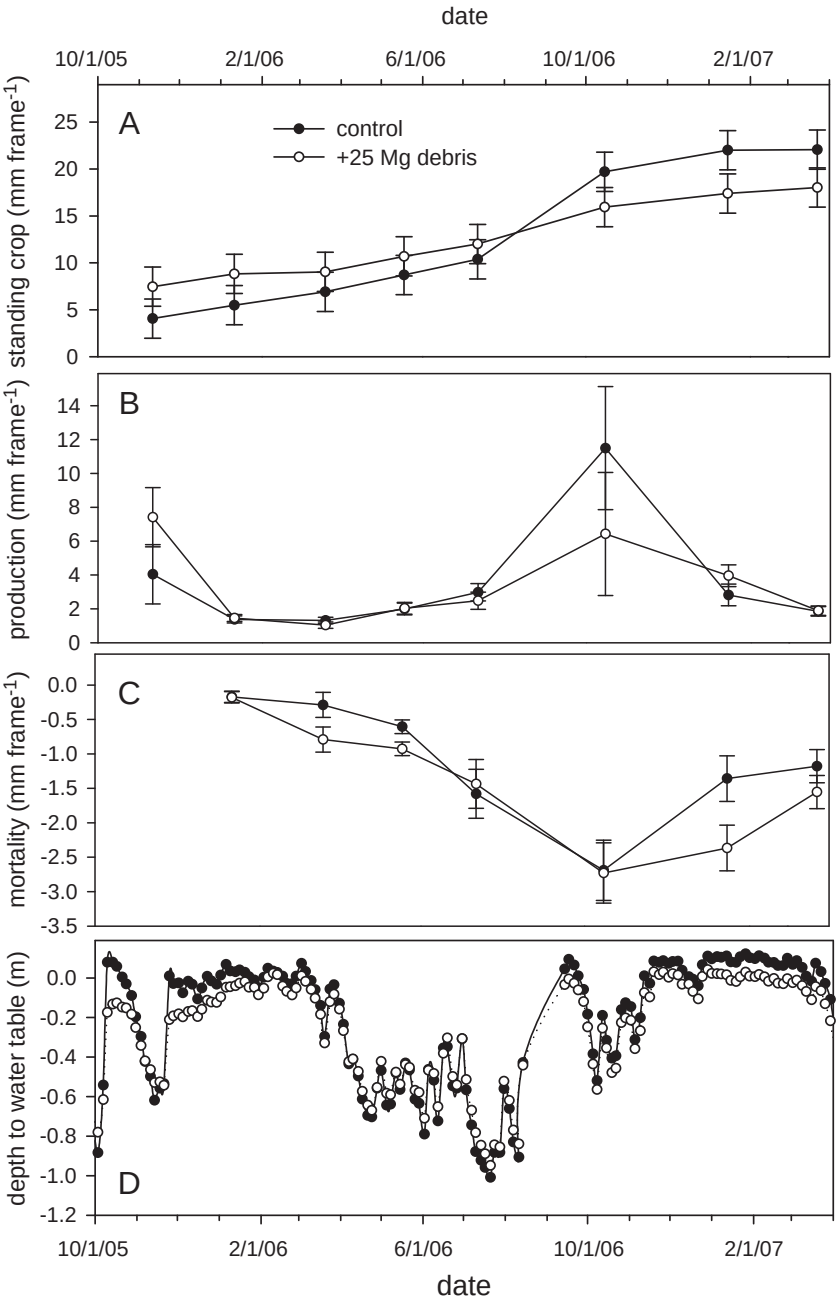

Figure 2. Fine-root standing crop (A), production (B), mortality (C) and depth to the water table (D) in mulched (i.e., +25 Mg logging debris incorporated into soil before planting) and control plots. Root data were obtained using minirhizotron cameras. Values are means of both clones (i.e., CL32 and CL93) since there were no interactions of mulching treatment with clone. Root images were collected eight times during the experimental period. Bars indicate ± 1 SD.

trol plots (means were 345 and 505 days) (Cox proportional hazards; diameter × treatment, $P = 0.0005$).

We observed a trend for a depth × treatment interaction for fine-root median diameter (Table 1, Figure 6). In general, mulched plots produced finer roots, but this was only true for the shallower soil horizon where the median diameter of fine roots was 18% smaller compared with the median diameter of fine roots in shallow soil of control plots. The variance of fine-root diameter distributions was also decreased in mulched plots compared with controls (Figure 6).

There was generally a larger standing crop of mycorrhizal root tips in control plots than mulched plots for CL32. Mulched plots generally had more mycorrhizal tips than controls for CL93, however (Figure 7; clone × treatment, $P = 0.05$). We observed a trend suggesting a treatment × time interaction for mycorrhizal tip production ($P = 0.11$). We

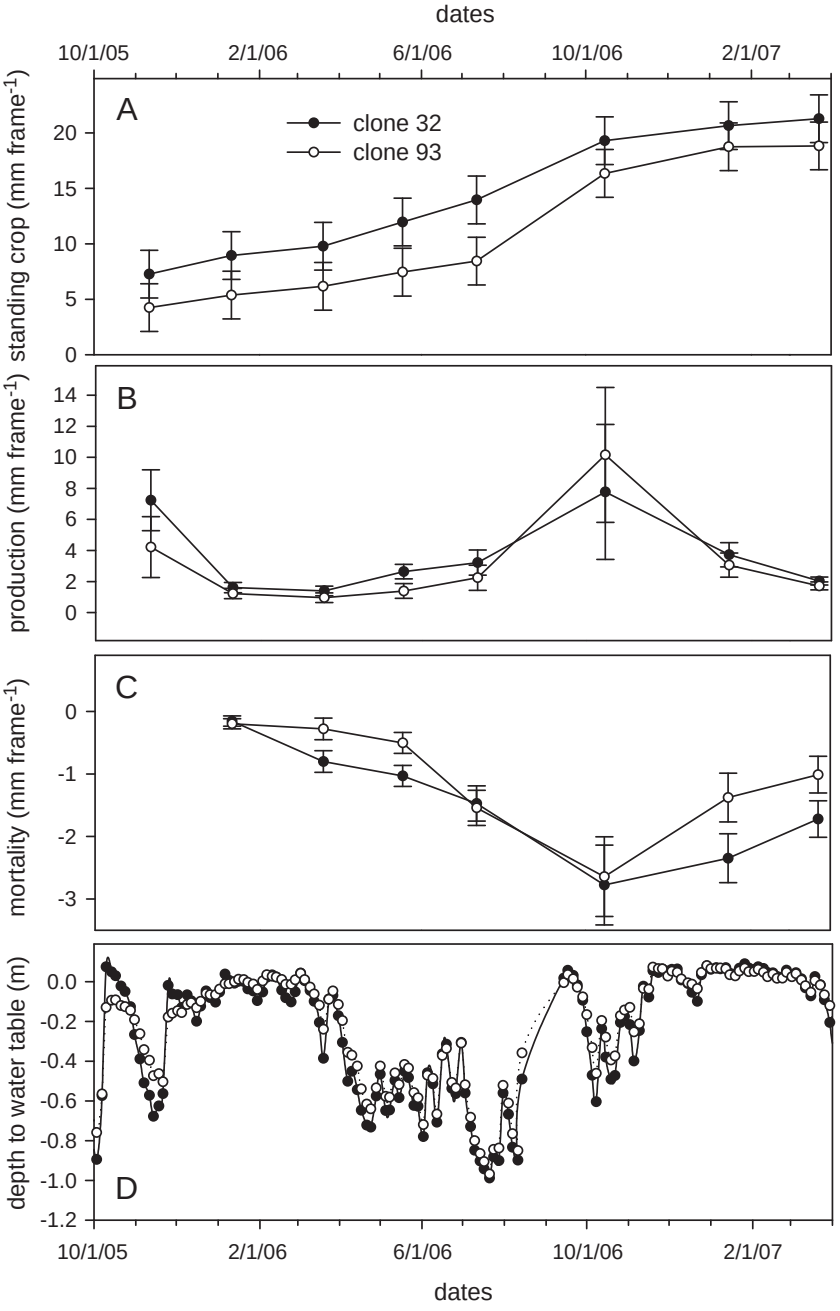

Figure 3. Fine-root standing crop (A), production (B), mortality (C) and depth to the water table (D) in plots planted with CL32 and CL93. Root data were obtained using minirhizotron cameras. Values are means of both the control and mulch treatment since there were no interactions of mulching treatment with clone. Root images were collected eight times during the experimental period. Bars indicate ± 1 SD.

therefore compared summed tip production during the early portion of our experiment (planting to 21 months) with production during the latter time period (corresponding to 21–30 months after planting). During the first 21 months following the planting of seedlings in the field, there was no difference in total mycorrhizal tip production. During the latter period, however, more mycorrhizal tips were produced in the mulched plots compared with controls (Figure 8; $P = 0.11$).

Discussion

Seasonality

Season had a greater effect on shoot growth and fine-root dynamics than either mulching treatment or genotype. Trees grew in height from May through October. Fine-root production, on the other hand, occurred mainly in early fall as the water table began to rise following the summer dry period.

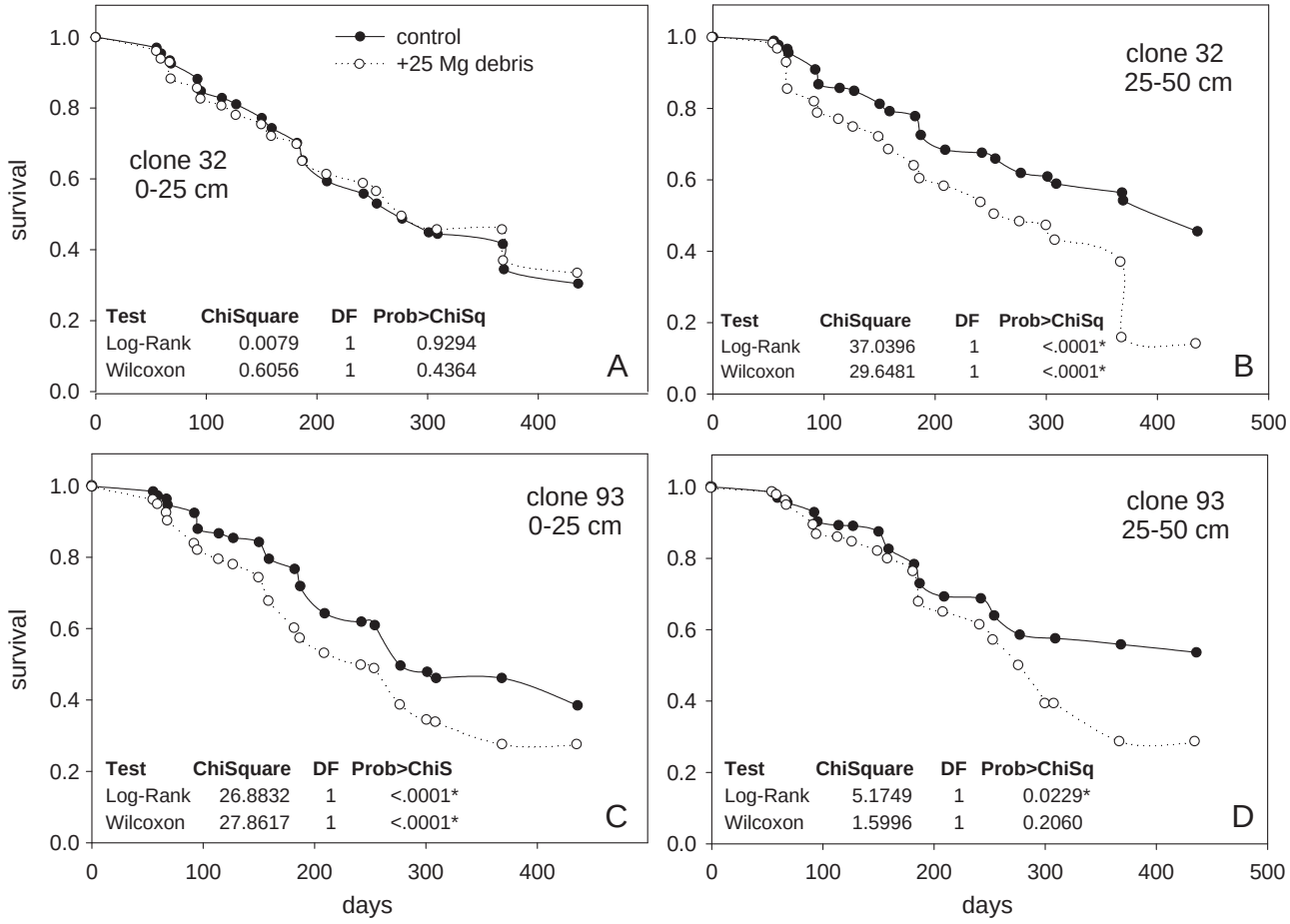

Figure 4. Kaplan–Meier estimates of survivorship probabilities for roots in mulched and control plots for CL32 in shallow soil (A), CL32 in deep soil (B), CL93 in shallow soil (C) and CL93 in deep soil (D). Results from log-rank and Wilcoxon's tests are shown.

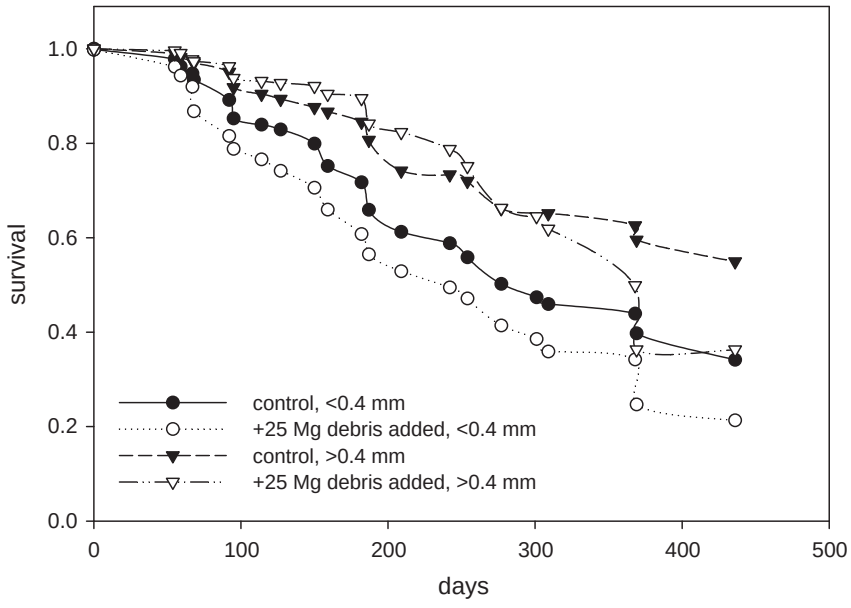

Figure 5. Kaplan–Meier estimates of survivorship probabilities for small (<0.4 mm in diameter) and larger (>0.4 mm diameter) fine roots (<2.0 mm) in both control and mulched plots (+25 Mg debris added).

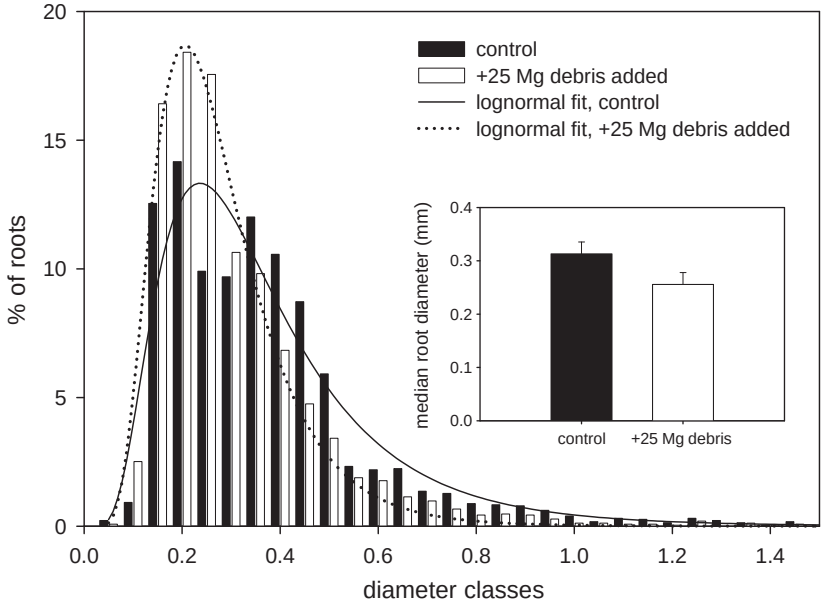

Figure 6. Histogram showing the proportion of fine roots in various size classes for control and mulched plots (+25 Mg debris added). Also shown is the median root diameter for roots in control and mulched plots (inset). This plot shows only roots produced in shallow soil (0–25 cm depth) because no difference was observed in the deeper soil horizon (25–50 cm).

During spring and summer, biomass was allocated mainly to shoot growth, and as shoot growth slowed, allocation to fine-root proliferation was favored. Asynchronous growth of fine roots and shoots, presumably caused by competition among these modules for a common pool of resources, is supported by some studies (Deans 1979, Kauchal et al. 1989) but not others (Tingey et al. 1996, Halter 1998, Pregitzer et al. 2000, King et al. 2002). The mechanistic links between fine-root demographics and shoot activity are not well understood (Anderson et al. 2003).

Fine-root survivorship

We found the average longevity of all fine roots to be 1 year. Small-diameter roots (<0.4 mm), however, lived an estimated 0.9 year compared with 1.3 years for larger diameter roots (0.4–2.0 mm). It now seems clear that longevity is controlled not by a root's diameter per se but rather by the order of a given root on a branching hierarchy (Wells et al. 2002, Guo et al. 2004, 2008*a*, 2008*b*). Diameter is a more practical predictor of longevity, however, because it is easier to measure, and it is considered robust because diameter increases with root order. The positive relationship between root diameter and longevity is well established (Wells and Eissenstat 2001, King et al. 2002, Tierney and Fahey 2002, Kern et al. 2004, Baddeley and Watson 2005, Iverson et al. 2008, Strand et al. 2008).

Longevity of fine roots also varied with soil depth. Those produced in deep soil lived 33% longer than fine roots produced in shallow soil. Increasing longevity with depth is commonly observed for fine roots of trees (Coleman et al. 2000, Kern et al. 2004) and crops (Goins and Russelle 1996, Pritchard et al. 2006), an observation usually attributed to depth-related soil gradients of water, nutrients, O_2 and/or CO_2 concentrations or microbiological activity (Coleman et al. 2000, Zak et al. 2000). Changes in longevity of fine roots with depth may also be influenced by relative proximity to resources (carbohydrates and hormones) translocated from shoots. Alternatively and unfortunately, the apparent increase in longevity of fine roots in deep soil may also simply be an artifact of the minirhizotron technique. In shallow soil, roots decompose, fragment and disappear more quickly than roots deeper in soil where decomposition is often retarded by low O_2 availability, reduced microbiological activity and low temperatures (Trumbore et al. 1995, Gill et al. 1999). It is difficult to accurately determine when fine roots have died from digital minirhizotron sequences, and therefore, roots are typically considered dead only when they begin to disintegrate or when they disappear altogether. This issue needs to be resolved.

Root longevity reported here (~1 year) exceeds a previous report for 8-year-old loblolly pine trees in which roots <1.0 mm in diameter lived 0.5 years and fine roots 1–2 mm in diameter lived 0.8 years (King et al. 2002). Our estimate, however, was less than the average longevity of fine roots of 21-year-old loblolly pine trees (1.6 years) (Pritchard et al. 2008). Longevity estimates of fine roots depend not only on soil environmental conditions but also upon the methods used to obtain the estimates, including minirhizotron experiment duration, and these results should therefore be accepted with caution (Pritchard and Strand 2008, Strand et al. 2008). In relatively short-term experiments on very young seedlings, as is the case for the current study, relative differences between experimental treatments should be emphasized,

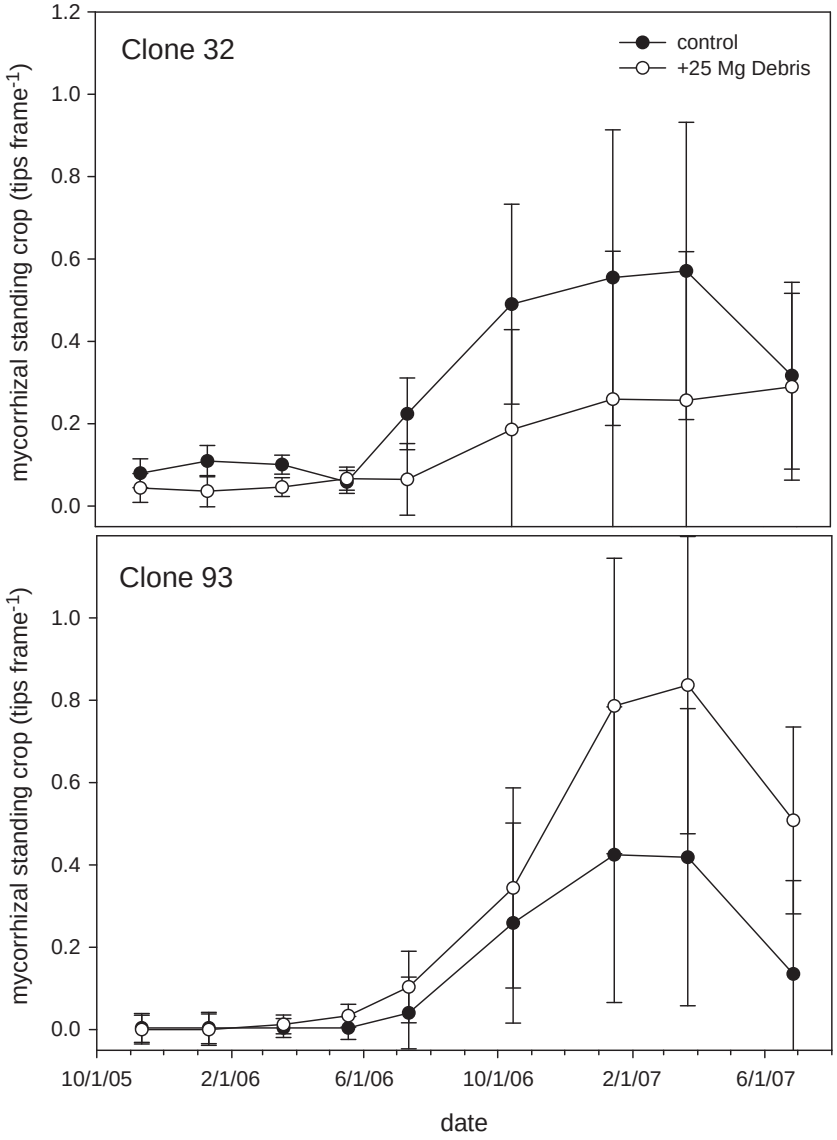

Figure 7. Standing crop of mycorrhizal root tips for CL32 and CL93 for control and mulched plots (+25 Mg debris added) from the time of planting in winter 2005 though summer of 2007. Root images were collected eight times during the experimental period.

while absolute values should be considered carefully alongside data from the literature.

Shoot and root responses to mulching

Although fine-root length standing crop was greater in mulched plots compared with controls very early in the study, by the end of the experiment (i.e., 2.5 years after planting), fine-root length was greater in control plots. This observation is explained by the increase in mortality, higher fine-root turnover index and nearly 20% decrease in estimated mean root lifespan found in mulched plots relative to controls. Accelerated turnover is likely explained by the decrease in median fine-root diameters and an increase in the proportion of roots belonging to the finest diameter classes. As discussed above, the positive relationship between fine-root diameter and longevity is well established. Furthermore, not only was the fine-root pool finer, but the survivorship of these roots also decreased relative to the same size roots in control plots (Figure 5). The observation that mycorrhizal root tip production in mulched plots exceeded production in control plots by the end of the experiment may indicate a shift in allocation from fine roots to symbionts. Since mycorrhizal colonization occurs mainly on the finest first- and second-order roots, the decrease in fine-root diameters is consistent with the increase in mycorrhizal colonization.

A shift in size distributions and longevity of fine roots and a surge in mycorrhizal colonization at the end of the experiment in experimental plots may also be linked to changes in soil properties brought about through mulching such as microbiology, hydrology, temperature, bulk density or nutrient availability. For example, extended periods of inundation,

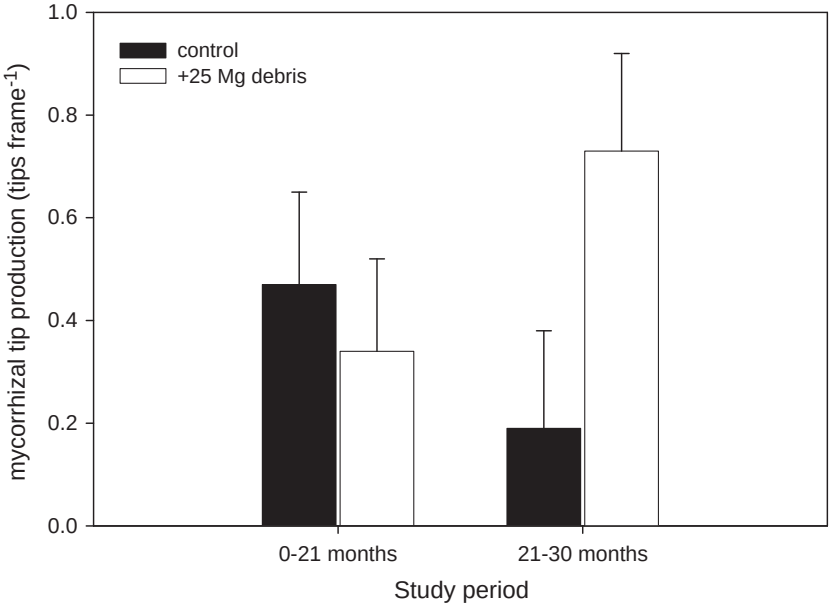

Figure 8. Pairwise comparisons of cumulative mycorrhizal tip production for control and mulched plots (+25 Mg debris added) from planting through 21 months and from 21 months after planting to the end of the study (30 months after planting).

shown previously to increase fine-root longevity (Burke and Chambers 2003), were more common in control than mulched plots. Second, mulching also decreased soil bulk density (Maier et al., unpublished data), which may have favored more extensive proliferation of very fine roots rather than growth of larger, structural roots.

Effects of mulching on soil N may have affected root dynamics in the current study (Nadelhoffer 2000). Incorporation of mulch, characterized by a C:N of ~700, significantly decreased the rates of N mineralization and N availability (Tisdale 2008) probably because of increased microbial immobilization of nutrients. It is therefore possible that a finer, more dynamic fine-root pool in mulched plots, coupled with an increase in mycorrhizal production, represent plastic responses to maximize tree function in the face of reduced nutrient availability (Eissenstat 1992). Producing a larger proportion of very small roots, which have a higher potential for resource uptake (Eissenstat 1992), represents a mechanism for increasing uptake capacity while decreasing standing crop mass in need of maintenance. Furthermore, faster turnover might indicate more intense mining of a given volume of soil for a more dilute pool of plant-available nutrients. An increase in leaf-level photosynthesis in mulched plots suggests that these seedlings were able to overcome soil N limitations to some extent, and it is likely that the increase in mycorrhizal symbionts, in addition to an increase in photosynthetic nitrogen use efficiency, was responsible for this response (Tyree et al. 2009).

Alternatively, mulching appeared to stimulate fine-root proliferation early in the experiment immediately after planting, perhaps before nutrient demand by very small seedlings began to exceed nutrient availability in the soil. But this early crop of fine roots might have died back, perhaps because nutrient immobilization created an environment where insufficient N was available to support the current standing crop. The increase in mycorrhizal tips toward the end of the experiment also supports this view.

In an experiment on older loblolly pine trees (21 years), we found that turnover was negatively related to N availability, while median fine-root diameter was positively related to soil [N], which supports the current results (Pritchard et al., unpublished manuscript). On the other hand, others have suggested that root longevity should increase, and turnover should decrease, with decreasing N availability (Nadelhoffer 2000, Rasse 2002). Experimental results to date are equivocal. Whether the uncertainty concerning fine-root responses to soil [N] are based on biological complexity or methodological shortfalls remains unknown.

Faster turnover of fine roots in mulched plots and increased mycorrhizal colonization may suggest a greater rate of C flow into soil, which, in addition to the mulch itself, may represent a mechanism for increasing soil C storage during early seedling development in forest plantations. On the other hand, the finest, most ephemeral roots typically contain higher concentrations of N relative to somewhat coarser fine roots and therefore are presumably better substrates for herbivores and decomposers (i.e., they are more labile; Guo et al. 2008*b*). Furthermore, it is also important to note that early seedling shoot growth was negatively impacted by mulching (for CL32), suggesting that the rate of C accumulation aboveground may be negatively influenced by mulching. Clearly, longer duration experiments that involve simultaneous quantification of canopy and root dynamics, along with analyses of decomposition and soil C changes, will be required to inform management decisions regarding soil C storage strategies.

Clonal differences in shoot growth and fine-root processes

The two clones selected for this experiment were chosen because they have contrasting patterns of biomass allocation. CL32 allocates significantly more biomass to leaf construction, whereas CL93 allocates more biomass to stem growth (i.e., produces a similar mass of stem while maintaining one-half of the leaf area). Tyree (2008) found that CL32 had more foliar biomass than CL93, indicating a greater ability to acquire N from soil. Our results generally agree with this since we observed a non-significant 28% increase in fine-root production coupled with a statistical trend indicating higher fine-root mortality (+37%) in CL32. Evidently, CL32 requires a higher standing crop of fine roots in order to maintain a greater leaf area. This result is consistent with a report on poplar clones in which fine-root surface area was positively correlated with leaf area (Al Afas et al. 2008).

Although we found few significant genotype × environment interactions, we did note that the negative effect of mulching on early seedling height growth was greatest in CL32. Similarly, mycorrhizal colonization was reduced for CL32 in mulched plots compared with controls. CL93 had a significantly higher standing crop of mycorrhizal tips in mulched plots than in control plots. Interestingly, whereas fine roots generally turned over faster in mulched plots, we found that mulching had no effect on the longevity of fine roots of CL32 in shallow soil. These results may suggest that CL32 did not exhibit the same plasticity to adapt to limited N under mulched conditions compared with CL93 and that this resulted in a negative effect of mulch on shoot growth and mycorrhizal tip standing crop.

Conclusion

We have shown that incorporating logging residue into soil increased fine-root turnover rate of loblolly pine clones and increased mycorrhizal colonization, particularly for CL93. Shifts in fine-root biology also occurred that likely compensated, to some extent, for the immobilization of soil N in mulched plots for CL93 but not for CL32. These results indicate that management decisions should be tailored to fit the life history strategies and plasticity of available clones. Furthermore, mulching may decrease the depth of the water table during especially wet periods, thereby decreasing the proportion of time roots spend exposed to anoxic soil conditions, at least in seasonally flooded stands such as this one.

Acknowledgments

The authors thank the USDA Forest Service, Agenda 2020 for funding this research and MeadWestvaco for preparing, maintaining and providing access to the study site.

References

Al Afas, N., N. Marron, C. Zavalloni and R. Ceulemans. 2008. Growth and production of a short-rotation coppice culture of poplar—IV: Fine root characteristics of five poplar clones. Biomass Bioenergy 32:494–502.

Anderson, L.J., L.H. Comas, A.N. Lakso and D.M. Eissenstat. 2003. Multiple risk factors in root survivorship: a 4-year study in concord grape. New Phytol. 158:489–501.

Baddeley, J.A. and C.A. Watson. 2005. Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. Plant Soil 276:15–22.

Burke, M.K and J.L. Chambers. 2003. Root dynamics in bottomland hardwood forests of the Southeastern United States Coastal Plain. Plant Soil 250:141–153.

Coleman, M.D., R.E. Dickson and J.G. Isebrands. 2000. Contrasting fine-root production, survival and soil CO_2 efflux in pine and poplar plantations. Plant Soil 225:129–139.

Deans, J.D. 1979. Fluctuations of the soil environment and fine root growth in a young Sitka spruce plantation. Plant Soil 52:195–208.

Dickmann, D.I., P.V. Nguyen and K.S. Pregitzer. 1996. Effects of irrigation and coppicing on above-ground growth, physiology, and fine root dynamics of two field-grown hybrid poplar clones. For. Ecol. Manage. 80:163–174.

Eissenstat, D. M. 1992. Costs and benefits of constructing roots of small diameter. J. Plant Nutrition 15:763–782.

Forge, R.A., E.J. Hogue, G. Neilsen and D. Neilsen. 2008. Organic mulches alter nematode communities, root growth and fluxes of phosphorus in the root zone of apple. Appl. Soil Ecol. 39:15–22.

Fox, T.R., E.J. Jokela and H.L. Allen. 2007. The development of pine plantation silviculture in the southern United States. J. For. Res. 105:337–347.

Gill, R., I.C. Burke, D.G. Milchunas and W.K. Lauenroth. 1999. Relationship between root biomass and soil organic matter pools in the shortgrass steppe of Eastern Colorado. Ecosystems 2: 226–236.

Gill, R.A. and R.B. Jackson. 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytol. 147:13–31.

Goins, G.D. and M.P. Russelle. 1996. Fine root demography in alfalfa (*Medicago sativa* L.). Plant Soil 185:281–291.

Guo, D.L., R.J. Mitchell and J.J. Hendricks. 2004. Fine root branch orders respond differently to carbon source–sink manipulations in a longleaf pine forest. Oecologia 140:450–457.

Guo, D.L., H. Li, R.J. Mitchell, W. Han, J.J. Hendricks, T.J. Fahey and R.L. Hendrick. 2008*a*. Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotrons and carbon isotope methods. New Phytol. 177: 443–456.

Guo, D., R.J. Mitchell, J.M. Withington, P.-P. Fan and J.J. Hendricks. 2008*b*. Endogenous and exogenous controls of root life span, mortality and nitrogen flux in a longleaf pine forest: root branch order predominates. J. Ecol. 96:737–745.

Halter, R. 1998. Root growth of *Eucalyptus pauciflora* Sieber ex Sprengel ssp. *pauciflora* on Mount Sirling, southeastern Australia. Northwest Science 72:274–282.

Handa, I.T., F. Hagedorn and S. Hättenschwiler. 2008. No stimulation in root production in response to 4 years of in situ CO_2 enrichment at the Swiss treeline. Funct. Ecol. 22:348–358.

Hendrick, R.L. and K.S. Pregitzer. 1992. The demography of fine roots in a northern hardwood forest. Ecology 73:1094–1104.

Hendrick, R.L. and K.S. Pregitzer. 1993. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. Can. J. For. Res. 23:2507–2520.

Iversen, C.M. 2010. Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems. New Phytol. 186:346–357.

Iversen, C.M., J. Ledford and R.J. Norby. 2008. CO_2 enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. New Phytol. 179:837–847.

Jackson, R.B., H.A. Mooney and E.D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proc. Natl Acad. Sci. USA 94:7362–7366.

Jastrow, J.D., J.E. Amonette and V.L. Bailey. 2007. Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. Clim. Change 80:5–23.

Johnson, N.C. and C.A. Gehring. 2007. Mycorrhizas: symbiotic mediators of rhizosphere and ecosystem processes. *In* The Rhizosphere. Eds. Z.G. Cardon and J.L. Whitbeck. Elsevier, Burlington, MA, pp 73–100.

Kauchal, P., J.M. Guehl and G. Aussenac. 1989. Differential growth response to atmospheric carbon dioxide enrichment in seedlings of *Cedrus atlantica* and *Pinus nigra* ssp. Laricio var Corsicana. Can. J. For. Res. 19:1351–1358.

Kern, C.C., A.L. Friend, J.M-F. Johnson and M.D. Coleman. 2004. Fine root dynamics in a developing *Populus deltoides* plantation. Tree Physiol. 24:651–660.

King, J.S., T.J. Albaugh, H.L. Allen, M. Buford, B.R. Strain and P. Dougherty. 2002. Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. New Phytol. 154:389–398.

Lal, R. 2004. Soil carbon sequestration to mitigate climate change. Geoderma 123:1–22.

Nadelhoffer, K.J. 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. New Phytol. 147: 131–139.

Norby, R.J. and R.B. Jackson. 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytol. 147:3–12.

Pregitzer, K.S., D.I. Dickmann, R. Hendrick and P.V. Nguyen. 1990. Whole-tree carbon and nitrogen partitioning in young hybrid poplars. Tree Physiol. 7:79–93.

Pregitzer, K.S., J.S. King, A.J. Burton and S.J. Brown. 2000. Response of tree fine roots to temperature. New Phytol. 147:105–115.

Pritchard, S.G. and A. E. Strand. 2008. Can you believe what you see? Reconciling minirhizotron and isotopic estimates of fine root longevity. New Phytol. 177:285–287.

Pritchard, S.G., S.A. Prior, H.H. Rogers, M.A. Davis, G.B. Runion and T.W. Popham. 2006. The effects of elevated atmospheric CO_2 concentration on root dynamics of sorghum grown under sustainable and conventional agricultural management systems. Agric. Ecosyst. Environ. 113:175–183.

Pritchard, S.G., A.E. Strand, M.L. McCormack, M.A. Davis, A.C. Finzi, R.B. Jackson, R. Matamala, H.H. Rogers and R. Oren. 2008. Fine root dynamics in a loblolly pine forest are influenced by Free-Air-CO_2-Enrichment (FACE): a six year minirhizotron study. Global Change Biol. 14:588–602.

Rasse, D.P. 2002. Nitrogen deposition and atmospheric CO_2 interactions on fine root dynamics in temperate forests: a theoretical model analysis. Global Change Biol. 8:486–503.

Reuss, R.W., R.L. Hendrick, A.J. Burton, K.S. Pregitzer, B. Sveinbjornsson, M.E. Allen and G.E. Maurer. 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol. Monogr. 73:643–662.

Richter, D.D., D. Markewitz, S.E. Trumbore and C.G. Wells. 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. Nature 400:56–58.

Ryan, M.G., M.E. Harmon, R.A. Birdsey, C.P. Giardina, L.S. Heath, R.A. Houghton, R.B. Jackson, D.C. McKinley, J.F. Morrision, B.C. Murray, D.E. Pataki and K.E. Skog. 2010. A synthesis of the science on forests and carbon for U.S. Forests. Issues Ecol. 13: 1–15.

Santantonio, D. and J.C. Grace. 1987. Estimating fine-root production and turnover from biomass and decomposition data- a compartment flow model. Can. J. For. Res. 17:900–908.

Schultz, R.P. 1997. Loblolly pine: the ecology and culture of loblolly pine (*Pinus taeda* L.). Agric. Handbook 713, For. Service. USDA, Washington, DC, 503 p.

Steel, R.G.D., J.H. Torrie and D.A. Dickey. 1997. Principles and procedures of statistics: a biometrical approach 3rd edn. McGraw-Hill, New York.

Strand, A.E., S.G. Pritchard, M.L. McCormack, M.A. Davis and R. Oren. 2008. Irreconcilable differences: fine root lifespans and soil carbon persistence. Science 319:456–458.

Tierney, G.L. and T.J. Fahey. 2002. Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. Can. J. For. Res. 32:1692–1697.

Tierney, G.L., T.J. Fahey, P.M. Groffman, J.P. Hardy, R.D. Fitzhugh, C.T. Driscoll and J.B. Yavitt. 2003. Environmental control of fine root dynamics in a northern hardwood forest. Global Change Biol. 9:670–679.

Tingey, D.T., M.G. Johnson, D.L. Phillips, D.W. Johnson and J.T. Ball. 1996. Effects of elevated CO_2 and nitrogen on the synchrony of shoot and root growth in ponderosa pine. Tree Physiol. 16:905–914.

Tisdale, J.L. 2008. Quantifying the effects of organic residues on soil nitrogen and phosphorus availability. MS Thesis, Department of Forestry, North Carolina State University, Raleigh, NC, 73 p.

Trumbore, S.E., E.A. Davidson, P.B. de Camargo, D.C. Neptsad and L.A. Martinelli. 1995. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochem. Cycles 9:515–528.

Tyree, M.C. 2008. Genetics by nutrient availability interactions on short-term carbon pools and fluxes in young *Pinus taeda* plantations. Ph.D Dissertion, Forestry, Virginia Tech, Blacksburg, 272 p.

Tyree, M.C., J.R. Seiler, C.A. Maier and K.H. Johnsen. 2009. *Pinus taeda* clones and soil nutrient availability: effects of soil organic matter incorporation and fertilization on biomass partitioning and leaf physiology. Tree Physiol. 29:1117–1131.

Vogt, K.A., C.C. Grier and D.J. Vogt. 1986. Production, turnover, and nutrient dynamics of above- and below-ground detritus of world forests. Adv. Ecol. Res. 15:303–377.

Wear, D.N. and J.G. Creis. 2002. In: USDA (Eds.), Southern forest resource assessment: summary of findings. For. Serv. pp 299–328.

Wells, C.E. and D.M. Eissenstat. 2001. Marked differences in survivorship among apple roots of different diameters. Ecology 82: 882–893.

Wells, C.E., D.M. Glenn and D.M. Eissentat. 2002. Changes in the risk of fine root mortality with age: a case study in peach, *Prunus persica* (Rosaceae). Am. J. Bot. 89:79–87.

Zak, D.R., K.S. Pregitzer, J.S. King and W.E. Holmes. 2000. Elevated atmospheric CO_2, fine roots and the response of soil microorganisms: a review and hypothesis. New Phytol. 147:201–222.