Compacting Coastal Plain soils changes midrotation loblolly pine allometry by reducing root biomass

Kim H. Ludovici

Abstract: Factorial combinations of soil compaction and organic matter removal were replicated at the Long Term Site Productivity study in the Croatan National Forest, near New Bern, North Carolina, USA. Ten years after planting, 18 preselected loblolly pine (*Pinus taeda* L.) trees were destructively harvested to quantify treatment effects on total above- and below-ground tree biomass and to detect any changes in the absolute and relative allocation patterns. Stem volume at year 10 was not affected by compaction treatments, even though the ultisols on these sites continued to have higher bulk densities than noncompacted plots. However, even when site preparation treatments were undetectable aboveground, the treatments significantly altered absolute root growth and tree biomass allocation patterns. Soil compaction decreased taproot production and significantly increased the ratio of aboveground to belowground biomass. Decreased root production will decrease carbon and nutrient stores belowground, which may impact future site productivity.

Résumé : Des combinaisons factorielles de traitements de compaction du sol et d'enlèvement de la matière organique ont été répétées dans le cadre de l'étude à long terme sur la productivité des stations dans la forêt nationale de Croatan, près de Bern en Caroline du Nord, aux États-Unis d'Amérique. Dix ans après avoir été plantés, 18 pins à encens (*Pinus taeda* L.) présélectionnés ont été récoltés pour quantifier l'effet des traitements sur les biomasses souterraine et aérienne totales et pour déceler les changements dans les profils d'allocation relative et absolue. Le volume de la tige à 10 ans n'a pas été affecté par les traitements de compaction, bien que les ultisols présents sur ces stations continuaient d'avoir une densité apparente plus élevée que dans les parcelles non compactées. Cependant, même lorsque les traitements de préparation de terrain n'avaient pas d'effets mesurables sur la partie aérienne des arbres, ils ont significativement altéré la croissance racinaire absolue et les profils d'allocation de la biomasse. La compaction du sol a causé une diminution de la croissance de la racine pivotante et significativement augmenté le rapport entre la biomasse aérienne et la biomasse souterraine. La diminution de la production de racines entraînera une diminution des réserves de carbone et de nutriments dans le sol, ce qui pourrait dans l'avenir avoir une impact sur la productivité de la station.

[Traduit par la Rédaction]

Introduction

Soil compaction and slash removal during harvest have immediate and potentially long-term effects on soil properties (Greacen and Sands 1980). Soil physical properties directly affect water and air movement through the profile and have immediate impacts on water and nitrogen availability to root systems (Rygiewiez et al. 2004). However, the extent to which root growth patterns and potential are directly affected by soil physical conditions and the duration of the effect are debatable. Soil organic matter characteristics similarly affect nutrient budgets, nutrient availability, and soil physical properties and, thus, can significantly affect root growth rate. Nutrient and water availability can also affect aboveground tree growth and vigor.

Soil compaction of fine-textured or wet soils typically affects soil physical characteristics by increasing soil bulk density; decreasing soil porosity, aeration and infiltration capacity; and increasing soil strength and, potentially, water runoff and soil erosion. Data from various sources indicate that increases in bulk density of coarse-textured soils have little or no effect on plant growth (Ares et al. 2005; Powers et al. 2005) but that comparable increases in bulk density of fine-textured soils have substantial effects on plant growth (Helms 1983; Alexander and Poff 1985; Powers et al. 2005). Other studies suggest that, even without significant differences in bulk density, important changes in macroporosity will affect water and air movement through soil, thus potentially impacting root proliferation and distribution (Aust et al. 1995).

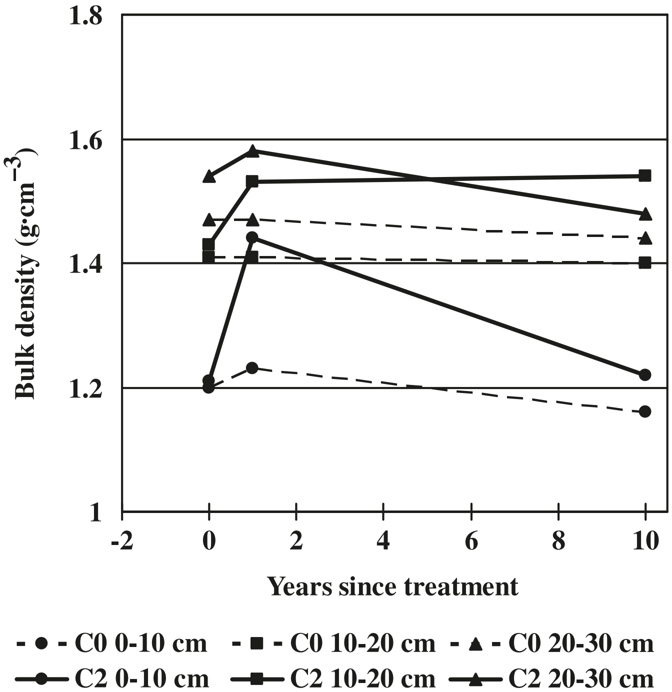
The amount of slash left on site or incorporated into the soil will moderate soil temperature and moisture, and impact nutrient storage and availability. Increases in soil temperature and moisture after canopy removal, in addition to the mixing of litter and debris with mineral soil, increase biological activity and nutrient immobilization (Eisenbies et al. 2005). Any management practice that decreases long-term nutrient storage pools on a site has the potential to impact future site productivity. Because root systems from mature loblolly pines (*Pinus taeda* L.) can persist for more than 60 years after harvest (Ludovici et al. 2002*a*), tree roots

Received 17 September 2007. Accepted 15 April 2008. Published on the NRC Research Press Web site at cjfr.nrc.ca on 30 June 2008.

K.H. Ludovici. USDA Forest Service, Southeastern Research Station, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA (e-mail: kludovici@fs.fed.us).

 doi:10.1139/X08-060

Fig. 1. Soil bulk density on the Long Term Site Productivity study area averaged over the three blocks and measured: before treatment installation, immediately after installation, and 10 years later. Symbols show the different depths (●, 0–10 cm; ■, 10–20 cm; ▲, 20–30 cm), and lines show differences in soil compaction level (broken, C0 (no compaction); solid, C2 (severe compaction).



have the potential to impart long-term influences on soil properties and processes. To that end, silvicultural impacts on root growth and biomass distribution should be better understood.

The purpose of this experiment is to quantify total above- and below-ground tree biomass at age 10 and determine to what extent the absolute and relative allocations shift when site quality changes because of soil compaction and organic matter removal. The specific objectives are to (*i*) quantify total tree allocation patterns and (*ii*) assess biomass partitioning for a sample of normally developing 10-year-old trees in response to soil compaction and organic matter (OM) removal treatments.

Materials and methods

Site and treatment description

In 1991, researchers with the USDA Forest Service Southern Research Station cleared a 60-year-old natural pine–hardwood stand on the Croatan National Forest in Craven County, North Carolina, and designated three 4 ha blocks (NC1, NC2, and NC3) for a Long Term Site Productivity (LTSP) study (Powers et al. 1989).[1] The site was blocked to account for soil drainage characteristics. The soil in NC1 is primarily a moderately well-drained Goldsboro soil (fine-loamy, siliceous, thermic aquic Paleudults), whereas the soils of NC2 and NC3 are somewhat poorly drained Lynchburg soils (fine-loamy, siliceous, thermic aeric Paleaqualts according to the USDA classification; Gleyic Acrisol in FAO soil unit). Additionally, the soil of NC3 is more poorly drained than that of NC2. Nine treatment plots were established in each block where three levels each of soil compaction and OM removal were applied in a 3 × 3 factorial design (Duarte 2002; Sanchez et al. 2006*a*). Precipitation and temperature data were collected from a weather station at the LTSP site. Information from the nearby Cherry Point Marine Base was used to supplement on-site climate data (www.cherrypoint.usmc.mil/weather/, accessed 2005).

Experimental LTSP treatments were imposed on 0.4 ha measurement plots using three levels of soil compaction (C0, none; C1, intermediate; C2, severe) and three levels of OM removal (OM0, stem only; OM1, whole tree; OM2, whole tree plus forest floor). Treatment plots were further split into those treated with herbicides (U–) to achieve a complete and continual competition-free condition or untreated (U+) to achieve no competition control. Plots receiving the C0 treatment were not driven on during either harvesting or site preparation. The C2 treatment was intended to be within 20% of the approximate growth-limiting bulk density (Daddow and Warrington 1983). The C1 treatment levels were designed to be near the midpoint between the C0 and C2 treatment levels.

Tree boles were removed by cranes on the C0 plots, and the increased levels of OM removal on the other C0 treatment combinations were accomplished by hand. On the C1 plots, tree boles were removed with skidders and any additional OM removal on the other C1 combination plots was done by hand. A bulldozer equipped with a shear blade removed the forest floor on the C2 plots. To facilitate severe compaction on the OM0 and OM1 plots, branches, foliage, and other forest floor material were removed prior to compaction. Mineral soil was compacted with a vibrating drum roller, without vibration on the C1 plots and with full vibration on the C2 plots. Branches, foliage, and other material removed prior to compaction were redistributed by hand on OM0 and OM1 plots. The U– plots were kept competition free using the herbicides Accord, Arsenal, and Oust. Brushsaws were used to remove volunteer pines and residual hardwoods.

Collection of soil bulk density samples were made by depth from mineral soil surface (0–10, 10–20, and 20–30 cm) using fixed volume soil rings (Blake and Hartge 1986). Pretreatment measurements included three randomly located cores per treatment plot and depth, whereas six cores per treatment plot per depth were collected to determine posttreatment soil bulk density values. All soil within that fixed volume was oven-dried and weighed. Calculations of soil bulk density used soil dry mass divided by the fixed volume.

A mixture of 1–0 half-sib loblolly pine families were hand planted at a 3 m × 3 m spacing. Every plot contained 242 seedlings such that the interior measurement plot had 80 trees, and each side of each plot was bordered by three rows of trees. Seedlings were planted after the silvicultural treat-

[1] R.F. Powers, G.A. Ruark, A.E. Tiarks, C.B. Goudey, J.F. Ragus, and W.E. Russell. 1989. Study plan for evaluating timber management impacts on long-term site productivity: a research and national forest system cooperative study. Unpublished study on file with the USDA Forest Service, Washington, D.C.

Table 1. Probability values ($p > F$) for the ANOVA analysis of the whole-tree biomass and allocation study, which included three replications of herbicide-treated compaction and organic matter removal treatment combinations.

Source	Pine height	Pine diameter	Stem volume
Compaction (C)	0.188	0.976	0.584
Organic matter removal (OM)	0.120	0.370	0.333
C × OM	0.703	0.458	0.518

Note: Pine growth measurements were made 10 seasons after site establishment at the Croatan Long Term Site Productivity study area, New Bern, North Carolina.

ments were applied, and all trees on a plot were treated in the same manner.

Growth and biomass measurements

Quantification of whole-tree biomass requires the destructive harvest of aboveground and belowground tree components and involves serious soil disturbance that could compromise the integrity of a long-term study. A decision was made to preselect trees in the innermost of the three border rows for their conformity to treatment mean height, diameter, and volume growth. A subset of six treatments was selected for this study, such that two levels of soil compaction (C, none; C2, severe) and three levels of organic matter removal (OM0, stem only; OM1, whole tree; OM2, whole tree plus forest floor) were included from each block; thus, 18 trees were destructively sampled for these analyses. To remove any effect of competition on tree growth and focus on the impacts of soil compaction and OM removal treatments, only the complete competition control plots (U–) were used in this assessment of biomass.

Tree heights were measured with a hypsometer, and diameters at breast height were measured bidirectionally with calipers before trees were directionally felled. Complete field collections of boles, branches, and foliage material were made by component for each tree, and all material was oven-dried at 70 °C to a constant mass. In addition, live branches were subsampled, such that foliage and stem tissue from the first flush of 2001 was collected from outer branches in the upper one-third of the crown, and a 5–7 cm slice of the bole, at breast height, was collected for percent moisture corrections and chemical analyses.

Root components for each tree were collected from a 2 m × 2 m × 1 m (4 m^3) volume of soil, centered on each target tree. Because fine roots may detach from larger diameter roots during rigorous extraction, they were excluded from this experiment. The entire soil volume was processed through a field sieve, and all remaining roots were collected by depth at 0–15, 15–30, 30–45 and 45–100 cm and separated into three size classes. A field sieve was used to collect all pine roots without regard to which tree they originated from.

Taproot and lateral root materials were placed into white burlap bags for transport to the laboratory. Each first-order lateral root was separated from the taproot where it initiated. Individual lateral roots were separated into 5–15 mm and >15 mm size classes. The number of first-order laterals >15 mm was recorded. Each root component was oven-dried at 70 °C to a constant mass, and dry masses were recorded to the nearest gram. Total aboveground biomass (AGB) was the sum of bole, branch, and foliage masses. Total belowground biomass (BGB) was the sum of taproot and roots >15 mm and 5–15 mm.

Statistical analyses

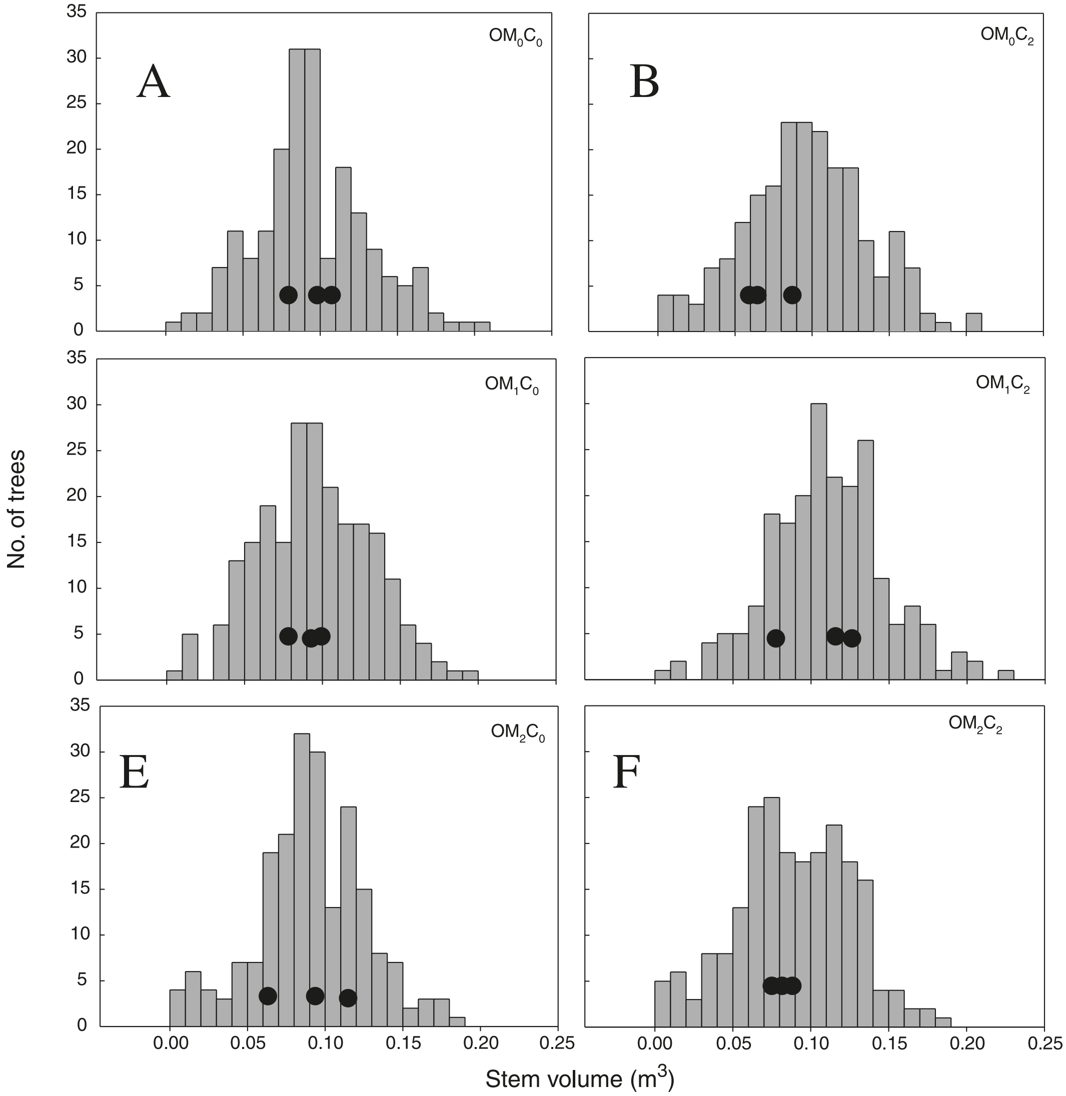
The whole-tree biomass and allocation study was designed as a 2 × 3 factorial of two soil compaction and three OM removal treatments replicated in three complete blocks. Effects of soil compaction and OM removal treatment on aboveground growth measurement, as well as absolute biomass measurements and individual component allocation, were tested using two-way analyses of variance (ANOVA) for a randomized complete-block design (Proc GLM, Statistical Analysis Systems software, version 6.12; SAS Institute Inc. 1985, Cary, N.C). Treatments were considered significant at the 0.05 level unless otherwise noted, and Duncan's mean separation tests were performed as needed.

The LTSP study was designed as a 3 × 3 factorial, with a split plot for herbicide treatment replicated in three complete blocks. Effects of soil compaction, OM removal, and herbicide treatment on tree height, diameter, stem volume, and stand mortality were tested using the GLM procedure for a factorial split-plot design and were considered significant at the 0.05 level. It was important to include statistical analyses of the aboveground growth parameters from that larger study to add perspective to results from the subset of treatments used in this whole-tree harvest and allocation assessment.

Results and discussion

Soil compaction treatments significantly increased bulk density on the Croatan LTSP site. The machinery used to implement treatments on these sites was chosen as much for the opportunity to ensure multiple levels of soil compaction as they were to replicate common silvicultural practices. Skidders have been, and are still, used in operational harvests. Attention to soil texture, water regime, and season influence when harvesting can be accomplished and what equipment can be used. Shear blades were used for decades to remove slash and debris and increase ease of planting and site preparation treatments (Edwards 1994; Miller and Edwards 1997). For this study, soils in every block were included and delineated into three 10 cm depth increments for each combination of the two soil compaction levels and three OM removal treatments. One year posttreatment, the mean soil bulk density in the surface 10 cm was statistically different ($p = 0.002$): 1.23 $g·cm^{-3}$ and 1.48 $g·cm^{-3}$ for the C0 and C2 plots, respectively (Fig. 1). One year posttreatment, the mean soil bulk density in the 10–20 cm depth

Fig. 2. Frequency distributions of 10-year-old loblolly pine stem volume for all measurement trees grown weed free (U– plots) on the Croatan Long Term Site Productvity study area. The whole-tree biomass study included two levels of compaction and three levels of organic matter removal as factors replicated on three blocks. Stem volumes for the preselected trees that were harvested from the inner border rows are shown as circles on each bar graph.



was also statistically different (p = 0.018): 1.46 and 1.61 g·cm^{-3}, for the C0 and C2 plots, respectively (Fig. 1). The mean soil bulk density continued to be statistically different (p = 0.024) in the 10–20 cm depth even 10 years posttreatment: 1.40 and 1.54 g·cm^{-3} for the C0 and C2 plots, respectively (Fig. 1). Bulk density values from years 1 and 5 posttreatment for the Goldsboro soils in block 1 have previously been published in Page-Dumroese et al. (2006).

Soil compaction has been shown to adversely impact root penetration in deeper parts of the soil and create water stress in trees (Nambiar and Sands 1992). Tiarks and Shoulders (1982) also concluded that volume of soil or depth to available water was more important for root exploration than any soil chemical property. Differences in latent water availability between the blocks on this site, although unreplicated, may explain block source differences in growth response to soil compaction.

Tree growth and biomass production

Tree height, diameter, and stem volume of the trees included in this whole-tree biomass study were not affected by soil compaction or OM removal treatments (Table 1). Statistical analyses of the preselected trees confirmed that they measured within the 85% confidence limits for mean plot height, diameter, and stem volume and were well within the stem volume frequency distributions for their respective treatment combination (Fig. 2). This consistency supports that the preselected trees are representative of trees on the measurement plots and that the results can be related to the larger LTSP study.

The 18 preselected trees were then used to evaluate AGB and BGB accumulation and allocation responses to soil compaction and OM removal treatments. Although not a significant effect, soil compaction decreased the biomass of taproots and lateral roots >15 mm and increased the biomass

Table 2. Probability values ($p > F$) for the ANOVA analysis of the whole-tree biomass measured on three replications of herbicide-treated, compaction and organic matter removal treatment combinations.

Source	Foliage	Branch	Bole	AGB	Taproot	Root >15 mm	Root 5–15 mm	BGB	Whole tree	AGB/BGB
Compaction (C)	0.528	0.446	0.602	0.544	0.074	0.132	0.667	0.073	0.352	0.028
Organic matter removal (OM)	0.893	0.701	0.720	0.913	0.961	0.520	0.900	0.724	0.989	0.182
C × OM	0.125	0.109	0.202	0.175	0.209	0.219	0.506	0.201	0.189	0.078

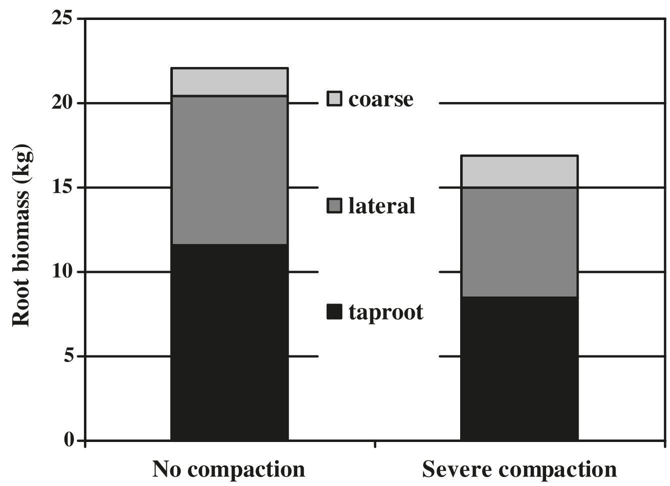
Note: Pine biomass accumulation was measured 10 growing seasons after site establishment at the Croatan Long Term Site Productivity study area, New Bern, North Carolina. AGB, total aboveground biomass; BGB, total belowground biomass.

of roots <15 mm (Table 2; Fig. 3). Because roots >15 mm (including the taproot) comprised more than 85% of the root biomass for these trees, this resulted in a decrease in total BGB (Table 3) in response to increased soil compaction. The decrease in absolute BGB changed the AGB/BGB ratio so much that it was significantly increased by the soil compaction treatment (Table 2). The 20% difference in this ratio (3.68 for C0 vs. 4.37 for C2) was largely driven by the decreased taproot biomass and was noted without a concomitant decrease in AGB.

Changes in root size distribution are important because of the different roles that roots of different diameters play. Taproots and larger diameter roots provide anchorage and storage of water nutrients and starch (Ludovici et al. 2002*b*). Smaller diameter roots conduct water, nutrients, and carbohydrates between the soil volume and the tree itself. Decreases in larger root biomass may be related to increased soil compaction because even minimal compaction can be accompanied by significant reductions in macropore volume (i.e., soil pores >50 μm in diameter). A reduction in macropore volume will be coincident with an increase in the micropore volume (<10 μm) and a decrease in total pore space. Such changes in pore size distribution are consistent with changes in the amount of roots in different size classes recorded from this harvest (Table 3). There were fewer roots in the >15 mm size class but more in the 5–15 mm size class when trees were grown on compacted plots. Smaller diameter roots can penetrate compacted soil and will create and leave behind smaller diameter channels, when compared with larger diameter roots, potentially impacting both air and water movement through a soil profile.

When trees from the entire LTSP factorial split-plot design are included in the statistical analyses, results indicate that the herbicide treatment had the overwhelming influence on planted pine growth (Table 4). Mean height, diameter, and stem volume were significantly increased when competing vegetation was controlled for the first 10 years. Pine height and diameter were not significantly impacted by soil compaction, OM removal, or their interaction (Table 4), and none of the imposed treatments significantly altered tree mortality rate by age 10. However, calculated stem volume was significantly affected by the OM removal (Table 4) but not linearly related to the intensity of the OM removal. Stem volume was greatest (1.17 m^3) on plots from which whole trees were removed but the forest floor was left intact (OM1). Stem volume was lowest on plots from which only the boles (OM0) were removed (0.92 m^3) and intermediate (1.02 m^3) on the OM2 treatment plot. Despite differences in individual stem volume, total stand volume was previously reported to be unaffected by both compaction and OM removal treatments (Sanchez et al. 2006*b*).

Fig. 3. Mean absolute biomass of root system components of loblolly pine in the no and severe compaction treatments. Means were calculated across three blocks and three organic matter removal treatments for roots grown weed free (U–) for 10 years at the Croatan Long Term Site Productivity study area.



Biomass allocation

Biomass allocation was more responsive to management treatments than was absolute biomass production. The percentage of biomass allocated to the taproot was significantly impacted by soil compaction (Table 5), even when the absolute value of biomass in the taproot was not. The percentage of total tree biomass allocated to the taproot decreased from 11.24% to 9.21% as soil compaction increased (Table 6). No other tissue allocation, aboveground nor belowground, was significantly altered by soil compaction.

Effects of OM removal were also significant when evaluated as percent allocation (Table 5), rather than an absolute amount. Averaged across soil compaction levels, percent allocation to the bole was greatest in the OM1 (65%) compared with the OM0 (60%) or OM2 treatments (61%) (Table 6). Conversely, mean percent allocation to roots <15 mm in diameter was significantly less in OM1 (8.72%) compared with OM0 (11.32%) or OM2 (10.39%) treatments (Table 6). No other aboveground or belowground tissue-allocation patterns were significantly altered by OM removal treatments (Table 5).

Few studies have included the whole-tree responses as Tateno et al. (2004) have and report that percentages of belowground net primary productivity to total net primary productivity increased as soil nitrogen availability decreased. Another study included multiple species on a sandy site (Coyle and Coleman 2005). There, the allometric relationships between woody perennial tissues rarely differed among

Table 3. Aboveground/belowground biomass ratio (AGB/BGB) and biomass (kg/tree) for the whole-tree biomass study, by tree component, for both main effect treatments of compaction and organic matter removal.

	Compaction		Organic matter removal		
	None	Severe	Bole only	Whole tree	Whole tree+ ff
AGB/BGB	3.68 (16)	4.37 (18)	3.67 (21)	4.37 (8)	4.02 (25)
Tree component (%)					
Aboveground	80.25 (25)	74.81 (23)	75.59 (26)	80.06 (23)	76.94 (26)
Foliage	5.36 (26)	4.95 (28)	5.22 (31)	4.94 (26)	5.29 (27)
Branch	12.79 (38)	11.35 (29)	12.59 (36)	10.97 (30)	12.66 (37)
Bole	62.10 (24)	58.51 (24)	57.78 (26)	64.15 (22)	58.99 (25)
Belowground	22.46 (31)	17.31 (22)	20.92 (28)	18.42 (24)	20.32 (40)
Stump and taproot	11.57 (33)	8.50 (30)	10.06 (30)	9.75 (24)	10.29 (52)
Other roots	10.89 (32)	8.81 (18)	10.86 (29)	8.67 (29)	10.03 (29)
Roots >15 mm	8.84 (42)	6.53 (35)	8.69 (37)	6.65 (42)	7.71 (50)
Roots 5–15 mm	1.69 (23)	1.84 (48)	1.71 (17)	1.70 (17)	1.88 (61)

Note: Values are means with coefficients of variation (%) given in parentheses. Pine biomass accumulation was measured 10 growing seasons after site establishment at the Croatan Long Term Site Productivity study area, New Bern, North Carolina (*n* = 18 trees). ff, forest floor.

Table 4. Probability values ($p > F$) for the ANOVA analysis of the Croatan Long Term Site Productivity study area, on the effects of compaction, organic matter removal, and herbicide treatments on pine growth.

Source	Pine height	Pine diameter	Stem volume	Mortality
Block	0.141	0.049	0.026	0.205
Compaction (C)	0.103	0.417	0.508	0.657
Orgainic matter removal (OM)	0.138	0.234	0.032	0.224
C × OM	0.576	0.431	0.428	0.486
Herbicide (U–)	0.0001	0.0001	0.0001	0.179
C × U–	0.726	0.152	0.481	0.698
OM × U–	0.113	0.013	0.007	0.134
C × OM × U–	0.293	0.006	0.045	0.723

Note: Pine growth measurements were made 10 growing seasons after site establishment at the Croatan Long Term Site Productivity study area, New Bern, North Carolina.

Table 5. Probability values ($p > F$) for the ANOVA analysis on the effects of compaction and organic matter removal on percent allocation of pine biomass during 10 growing seasons following site preparation and establishment at the Croatan Long Term Site Productivity study area, New Bern, North Carolina.

Source	Foliage	Branch	Bole	Taproot	Roots >15 mm	Roots 5–15 mm
Compaction (C)	0.784	0.864	0.122	0.033	0.276	0.397
Organic matter removal (OM)	0.605	0.211	0.029	0.898	0.182	0.041
C × OM	0.109	0.026	0.812	0.053	0.318	0.582

treatments. Improved resource availability caused large increases in growth and, consequently, accelerated development but had little effect on belowground allocation that was not explained by development. This suggests that resource availability controls growth rate (Morris et al. 1993; Ludovici and Morris 1996) but not biomass allocation pattern, and there must be some other factor causing biomass allocation shifts.

Interaction between the soil compaction and OM removal treatments resulted in significant ($p = 0.026$) impacts on percent allocation to branches (Table 6). There was a decrease in percent allocation to branches with increasing OM removal on the C0 plots (14.39%, 11.16%, and 11.00% from OM0, OM1, and OM2, respectively) but an increase on the C2 plots (11.19%, 10.93%, and 14.91% from OM0, OM1, and OM2, respectively). The interaction between OM removal and soil compaction treatments yielded nearly significant ($p = 0.053$) (Table 6) increases in taproot allocation with increased OM removal on no-compaction sites (10.27%, 10.64%, and 12.82% from OM0, OM1, and OM2, respectively) and a decrease in allocation to the taproot with increased OM removal on the compacted plots (10.66%, 9.32%, and 7.64% from OM0, OM1, and OM2, respectively).

Conclusions

Results from this work demonstrate that loblolly pine root systems respond to silvicultural treatments even when stem growth through 10 years apparently does not. This is in agreement with the results on 1-year-old loblolly pine seed-

Table 6. Mean values with coefficients of variation (%) given in parentheses for 10 year tree growth and biomass allocation at the Croatan Long Term Site Productivity study area by soil compaction and organic matter removal treatment combinations.

	No compaction			Severe compaction		
	Bole only	Whole tree	Whole tree + ff	Bole only	Whole tree	Whole tree + ff
Growth						
Height (m)	11.45 (3)	11.87 (5)	11.18 (9)	10.99 (15)	12.84 (9)	11.53 (3)
DBH (cm)	17.43 (6)	16.93 (7)	17.47 (16)	14.67 (7)	17.73 (8)	16.33 (3)
Volume (m^3)	1.09 (6)	1.07 (8)	1.07 (19)	0.74 (20)	1.27 (14)	0.97 (4)
Tree component (%)						
Aboveground	78.30 (15)	80.65 (30)	75.91 (35)	78.12 (27)	81.95 (14)	82.85 (20)
Foliage	5.74 (10)	5.15 (31)	4.85 (33)	5.00 (33)	4.93 (24)	6.12 (27)
Branch	14.39 (10)	11.16 (45)	11.00 (53)	11.19 (30)	10.93 (19)	14.91 (28)
Bole	58.18 (19)	64.34 (28)	60.06 (32)	61.93 (26)	66.08 (15)	61.82 (18)
Belowground	21.70 (15)	19.35 (38)	24.09 (36)	21.88 (34)	18.05 (10)	17.15 (17)
Stump and taproot	10.27 (17)	10.64 (32)	12.82 (42)	10.66 (41)	9.32 (19)	7.64 (28)
Other roots	11.43 (17)	8.71 (45)	11.27 (29)	11.22 (28)	8.73 (14)	9.51 (14)
Roots >15 mm	9.47 (19)	6.61 (67)	9.36 (41)	8.34 (44)	6.86 (18)	6.25 (51)
Roots 5–15 mm	1.59 (13)	1.95 (26)	1.44 (33)	2.04 (23)	1.55 (1)	2.51 (72)

Note: ff, forest floor; DBH, diameter at breast height.

lings in a similar compaction study. Seedling top masses were similar among treatments, even though root volume was significantly reduced with soil compaction (Page-Dumroese et al. 1998). Results from this study also suggest that direct physical constraints to root growth and development under conditions of adequate water and nutrients are the most likely cause of shifting allocation from belowground.

Pine root biomass comprises 20%–30% of the total mass of large trees mass and leaves substantial amounts of nutrients in the soil after harvest. It follows that forest management activities that decrease biomass allocation to pine roots will decrease nutrient pools in the soil. Because tree root systems persist for decades after harvest (Ludovici et al. 2002*a*), roots are a major component of forest carbon budgets, and decreases in root biomass could have long-term impacts on site quality. It is important to consider the long-term implications of soil compaction and organic matter removal on potential root growth and long-term site productivity. This work supports the hypothesis that intensive soil disturbances may decrease long-term site productivity by decreasing tree root biomass the associated nutrient storage capacity without significantly reducing short-term aboveground productivity.

Acknowledgements

Thanks are extended to the USDA Forest Service, including Dr. Greg Ruark, Dr. Marilyn Buford, and Dr. Felipe Sanchez, for support of this research through the LTSP program. Robert Eaton, Tom Christensen, and Karen Sarsony of the USDA Forest Service, Southern Research Station, deserve special recognition for their tireless work in the field and laboratory. Thank you also to Dr. Mary Ann Sword-Thayer, Dr. Tom Terry, Dr. Ken Stolte, and two anonymous referees for their thoughtful presubmission reviews. Special appreciation is extended to Dr. Bob Powers and Dr. Stan Zarnoch for their insights on statistical analysis and interpretation of these data.

References

Alexander, E.B., and Poff, R. 1985. Soil disturbance and compaction in wildlife management. USDA Forest Service, Pacific Southwest Region, Vallejo, Calif. Earth Resour. Monogr. 8.

Ares, A., Terry, T.A., Miller, R.E., Anderson, H.W., and Flaming, B.L. 2005. Ground-based forest harvesting effects on soil physical properties and Douglas-fir growth. Soil Sci. Soc. Am. J. **69**: 1822–1832. doi:10.2136/sssaj2004.0331.

Aust, W.M., Tippett, M.D., Burger, J.A., and McKee, W.H. 1995. Compaction and rutting during harvesting affect better drained soils more than poorly drained soils on wet pine flats. South. J. Appl. For. **19**: 72–77.

Blake, G.R., and Hartge, K.H. 1986. Bulk density. *In* Methods of soil analysis. Part 1. *Edited by* A. Klute. American Society of Agronomy, Madison, Wis. Agronomy 9(1). pp. 363–375.

Coyle, D.R., and Coleman, M.D. 2005. Forest production responses to irrigation and fertilization are not explained by shifts in allocation. For. Ecol. Manage. **208**: 137–152. doi:10.1016/j.foreco.2004.11.022.

Daddow, R.L., and Warrington, G.E. 1983. Growth-limiting soil bulk densities as influenced by soil texture. USDA Forest Service, Watershed Systems Development Group, Washington, D.C. WSDG Rep. WSDG-TN-00005.

Duarte, N. 2002. Effects of compaction and organic matter removal on nitrogen form and availability in a *Pinus taeda* (loblolly pine) stand in the Coastal Plain of North Carolina. Doctoral thesis, North Carolina State University, Raleigh, N.C.

Edwards, M.B. 1994. Ten-year effect of six-site preparation treatments on Piedmont loblolly pine survival and growth. USDA Forest Service Southeast. For. Exp. Stn. Res. Pap. SE-288.

Eisenbies, M.H., Burger, J.A., Aust, W.M., and Patterson, S.C. 2005. Soil physical distribution and logging residue effects on changes in soil productivity in five-year-old pine plantations. Soil Sci. Soc. Am. J. **69**: 1833–1843. doi:10.2136/sssaj2004.0334.

Greacen, E.L., and Sands, R. 1980. Compaction of forest soils, a review. Aust. J. Soil Res. **18**: 163–189. doi:10.1071/SR9800163.

Helms, J.A. 1983. Soil compaction and stand growth—final report to the USDA Forest Service. Ueristy of California, Berkeley, Calif.

Ludovici, K.H., and Morris, L.A. 1996. Responses of loblolly pine, sweetgum and crabgrass roots to localized increases in nitrogen in two watering regimes. Tree Physiol. **16**: 933–939. PMID: 14871786.

Ludovici, K.H., Zarnoch, S.J., and Richter, D.D. 2002*a*. Modeling in-situ pine root decomposition using data from a 60-year chronosequence. Can. J. For. Res. **32**: 1675–1684. doi:10.1139/x02-073.

Ludovici, K.H., Allen, H.L., Albaugh, R.J., and Dougherty, P.M. 2002*b*. The influence of nutrient and water availability on carbohydrate storage in loblolly pine. For. Ecol. Manage. **159**: 261–270. doi:10.1016/S0378-1127(01)00439-X.

Miller, J.H., and Edwards, M.B. 1997. Forest site preparation effects on Georgia Piedmont soils over a 10-year period. *In* Proceedings, Fifty Years of Weed Science: Foundation for the Future 50th Annual Meeting, 20–22 Jan. 1997, Houston, Tex. Southern Weed Science Society, Mississippi State University, Mississippi State, Miss. p. 112.

Morris, L.A., Moss, S.A., and Garbett, W.S. 1993. Competitive interference between selected herbaceous and woody plants and *Pinus taeda* L. during two growing seasons following planting. For. Sci. **39**: 166–187.

Nambiar, E.K.S., and Sands, R. 1992. Effects of compaction and simulated root channels in the subsoil on root development, water uptake and growth of radiate pine. Tree Physiol. **10**: 297–306. PMID:14969986.

Page-Dumroese, D.S., Harvey, A.E., Jurgensen, M.F., and Amaranthus, M.P. 1998. Impacts of soil compaction and tree stump removal on soil properties and outplanted seedlings in northern Idaho, USA. Can. J. Soil Sci. **78**: 29–34.

Page-Dumroese, D.S., Jurgensen, M.F., Tiarks, A.E., Ponder, F., Jr., Sanchez, F.G., Fleming, R.L., Kranabetter, J.M., Powers, R.F., Stone, D.M., Elioff, J.D., and Scott, D.A. 2006. Soil physical property changes at the North American Long-Term Soil Productivity study sites: 1 and 5 years after compaction. Can. J. For. Res. **36**: 551–564. doi:10.1139/x05-273.

Powers, R.F., Scott, D.A., Sanchez, F.G., Voldseth, R.A., Page-Dumroese, D., Elioff, J.D., and Stone, D.M. 2005. The North American long-term soil productivity experiment: findings from the first decade of research. For. Ecol. Manage. **220**: 31–50. doi:10.1016/j.foreco.2005.08.003.

Rygiewiez, P.T., Zabowski, D., and Skinner, M.F. 2004. Site disturbance effects on a clay soil under *Pinus radiata*—root biomass, mycorrhizal colonization, ^{15}ammonium uptake, and foliar nutrient levels. N.Z. J. For. Sci. **34**: 238–254.

Sanchez, F.G., Tiarks, A.E., Kranabetter, J.M., Page-Dumroese, D.S., Powers, R.F., Sanborn, P.T., and Chapman, W.K. 2006*a*. Effects of organic matter removal and soil compaction on fifth-year mineral soil carbon and nitrogen contents for sites across the United States and Canada. Can. J. For. Res. **36**: 565–576. doi:10.1139/x05-259.

Sanchez, F.G., Scott, D.A., and Ludovici, K.H. 2006*b*. Negligible effects of severe organic matter removal and soil compaction on loblolly pine growth over 10 years. For. Ecol. Manage. **227**: 145–154. doi:10.1016/j.foreco.2006.02.015.

SAS Institute Inc. 1985. SAS/STAT^{TM} guide for personal computers, version 6 edition. SAS Institute Inc., Cary, N.C.

Tateno, R., Hishi, T., and Takeda, H. 2004. Above- and below-ground biomass and net primary production in a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. For. Ecol. Manage. **193**: 297–306. doi:10.1016/j.foreco.2003.11.011.

Tiarks, A.E., and Shoulders, E. 1982. Effects of shallow water tables on height growth and phosphorus uptake by loblolly and slash pines. USDA For. Serv. South. For. Exp. Stn. Res. Note RN-SO-285.