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Soil C and N storage and microbial biomass in US southern pine forests: Influence of forest management ☆

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ABSTRACT

Land management practices have strong potential to modify the biogeochemistry of forest soils, with implications for the long-term sustainability and productivity of forestlands. The Long-Term Soil Productivity (LTSP) program, a network of 62 sites across the USA and Canada, was initiated to address concerns over possible losses of soil productivity due to soil disturbance from forest management. Network sites employ an experimental design consisting of three harvest intensities (bole only, whole tree, whole tree + forest floor removal) in combination with three soil compaction intensities (none, intermediate, severe). Our purpose was to determine the impact of forest harvest intensity, soil compaction, and their interaction on soil organic carbon (SOC) and total nitrogen (TN) storage, and on soil microbial biomass C and N (MBC and MBN, respectively) in a *Pinus taeda* L. forest 15-years post-treatment at the Groveton LTSP site in eastern Texas, USA. Soils were sampled (0–10 cm) five times during 2011–2012, and we quantified SOC and TN by dry combustion, and MBC and MBN by chloroform fumigation extraction. SOC and TN were both higher in the bole only treatment compared to the more severe harvest treatments; however, while TN was significantly impacted by harvest and varied seasonally, SOC varied only with season. MBC and MBN were impacted by harvest intensity and varied seasonally, and SMB-N had a harvest by time interaction. Generally, both microbial indices decreased in the order: bole only >whole tree > whole tree + forest floor. Temporal variations in MBN and TN were correlated with temperature. Soil compaction and the harvest intensity × soil compaction interaction had no effect on the measured soil properties. Since N limits tree growth in forest ecosystems, and because soil microbial biomass plays a key role in N mineralization, data suggest that harvest practices that minimize removal of litter and slash will favor soil N retention, maintain the size of the soil microbial biomass pool, and maximize the potential productivity of future rotations.

1. Introduction

Forests in North America currently function as net carbon sinks (Birdsey et al., 2007; Pacala et al., 2001); however, both natural and anthropogenic disturbances can negatively impact the strength of this sink (Chen et al., 2013; Dangal et al., 2014). Forest harvest practices result in organic matter removal and may cause soil compaction, thereby enhancing the potential to impact forest productivity by altering the pool sizes of limiting nutrients and influencing rates of biogeochemical processes. When more than the merchantable bole is harvested, increasing amounts of C and nutrients such as N are exported off site in the non-bolewood tissues, potentially compromising soil fertility and the productivity of subsequent forest rotations (Carter et al., 2002; Currie et al., 2003; Henderson, 1995; Metz and Wells, 1965; Powers et al., 2005; Scott et al., 2004; Turner and Lambert, 2011; Wells and Jorgensen, 1979; Wollum and Davey, 1975). The legacy of these disturbance effects on the carbon and nitrogen cycles of forest ecosystems may persist for more than 50–100 years (Chen et al., 2013; Kellman et al., 2014). Additionally, soil compaction that occurs during forest harvest may increase bulk density and alter soil structure and porosity, which in turn decreases aeration, gas exchange, and water infiltration (Ampoorter et al., 2007; Berisso et al., 2012; Cambi et al., 2015; Fisher and Binkley, 2000; Greacen and Sands, 1980; Labelle and Jaeger, 2011; Powers et al., 2005), all of which can influence rates of biogeochemical processes in disturbed soils. Declines in ecosystem C storage coupled with alterations in soil

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physical structure that often follow tree harvest events may also have adverse effects on the size of the soil microbial biomass pool, and may also modify the structure and function of soil microbial communities (Frey et al., 2009; Jordan et al., 2003; Vance and Chapin, 2001; Wardle, 1992).

Forest harvest may result in the alteration of biogeochemical cycling within the ecosystem; however, impacts are variable due to differences in frequency, harvest method, climate, and inherent site quality (Goetz et al., 2012). For example, a meta-analysis conducted by Johnson and Curtis (2001) found that harvest had no overall impact on soil organic carbon (SOC) and soil total nitrogen (TN). However, they did note that there were significant differences between tree harvest methods. More specifically, they observed that SOC and TN were greater in bole only harvests and lower in plots where the whole trees were harvested (Johnson and Curtis, 2001). In contrast, a more recent meta-analysis by Nave et al. (2010) found an overall decrease in forest soil C in response to tree harvesting, but it was primarily related to the loss of forest floor rather than mineral soil C-losses. Despite the generalizations that emerge from these two meta-analyses, individual studies have shown that forest harvest intensity (i.e., removal of more that the merchantable bole) may cause losses (Jones et al., 2011; Kellman et al., 2014; Li et al., 2003;), gains (Grand and Lavkulich, 2012; Vanguelova et al., 2010), or no change (Jerabkova et al., 2011; Knoepp and Swank, 1997; Mariani et al., 2006; McLaughlin and Phillips, 2006; Richter et al., 1999; Scott et al., 2014; Wall, 2008; Zerpa et al., 2010) in SOC and TN.

It is unclear how soil compaction might influence SOC and TN storage and turnover. Compaction may destroy soil macroaggregates in the upper portion of the soil profile, thereby exposing soil organic matter (SOM) to decomposers and accelerating decay processes (Six et al., 2004; Tisdall and Oades, 1982). Soil compaction may also result in decreases in both root biomass and uptake of soil mineral N, increasing the potential for ecosystem N losses via leaching and denitrification (Jordan et al., 2003; Torbert and Wood, 1992). Alternatively, compaction could restrict gas exchange and reduce soil pore space, thereby limiting access of decomposers to SOM resulting in no changes (de Neve and Hofman, 2000; Cambi et al., 2015; Mariani et al., 2006; Sanchez et al., 2006b) or possibly increases in SOC and TN (Tan et al., 2005).

Soil microorganisms are integral components of biogeochemical cycles, and play key roles in the development and maintenance of soil structure and fertility in forest ecosystems (Allen and Schlesinger, 2004; Gallardo and Schlesinger, 1994; Wardle, 1992; Zak et al., 1994). Soil microbial biomass as a living and active element of the soil may serve as a bellwether of changes in soil nutrient status resulting from management practices (Allen and Schlesinger, 2004; Brookes, 2001; Haubensak et al., 2002; Pregitzer, 2003; Wardle, 1992). Positive relationships have been demonstrated between soil microbial biomass and SOC and TN (Allen and Schlesinger, 2004; Brookes, 2001; Li et al., 2004; Wardle, 1992); therefore, the removal or alteration of soil organic matter inputs due to forest harvest may diminish the size of the soil microbial biomass pool (Busse et al., 2006; LeDuc and Rothstein, 2007; Li et al., 2004; Mummey et al., 2010; Tan et al., 2005). However, other studies have found little effect of harvest on soil microbial biomass (Busse et al., 2006; Mariani et al., 2006). Soil compaction, by altering porosity, gas exchange, and water infiltration, has likewise resulted in variable impacts on soil microbial biomass. Soil compaction may have no effect on soil microbial biomass (Shestak and Busse, 2005; Busse et al., 2006), lead to increases in soil microbial biomass due to reduced pore space that limits predator access to microbes (Breland and Hansen, 1996; Jensen et al., 1996a, 1996b; Li et al., 2004; Mariani et al., 2006), or lead to decreases due to reduced aeration and water conductivity (Frey et al., 2009; Tan et al., 2005).

The Gulf Coastal Plain region of the USA currently has some of the highest rates of gross forest cover loss in the world (Hanson et al., 2010). These rates are particularly high in the southwestern-most portion of this area where gross forest cover loss exceeded 10% across large portions of this region between the years 2000–2005 (Hanson et al., 2010). Despite the importance of this land use activity, tree harvest effects on ecosystem biogeochemistry have been little studied in this region. Therefore, the purpose of this study was to determine the impact of forest harvest intensity, soil compaction and their interaction on SOC, TN, and soil microbial biomass carbon and nitrogen (MBC and MBN, respectively) in a *Pinus taeda* L. (loblolly pine) forest 15 years post-treatment at the Long-Term Soil Productivity (LTSP) site located near Groveton, Texas, USA. Three hypotheses were tested to address the impact of forest harvest and soil disturbance on C and N cycling: (1) SOC and TN will be lowest under the most severe tree harvest and soil compaction treatments; (2) lower SOC and TN under the most severe harvest treatments will constrain nutrient availability to the current rotation, resulting in less aboveground litter and more root biomass; and (3) greater losses of organic matter and soil structure changes due to compaction will result in lower MBC and MBN in the most intense harvest treatments.

2. Materials and methods

2.1. Study area

Field sampling was conducted quarterly from March 2011 through March 2012 for a total of five sample periods (March, June, September and December 2011, and March 2012) at the Long-Term Soil Productivity (LTSP) site in Davy Crockett National Forest near Groveton, TX, USA (31°06′ 32.48″N, 95°09′ 59.15″W) (hereinafter "Groveton LTSP"). The climate is subtropical with a mean annual temperature of 19.1 °C and mean annual precipitation of 1135 mm (1981–2010) that is bimodal, with peaks in May–June and October (Fig. 1). Topography is nearly flat with slopes of 1–3% and elevation ranging from 101 m to 110 m. Soils across the study area are uniform (fine-loamy siliceous, thermic Oxyaquic Glossudalf in the Kurth series) and developed in loamy coastal plain sediments of the Yegua and Whitset geological formations. The A-horizon occurs at 0–15 cm, while the E-horizon extends from 15 to 50 cm.

The Groveton LTSP treatment plots were established in 1997 in accordance with the parameters specified by the LTSP program (Powers, 2006) which consists of three harvest intensities (bole only, whole tree, and whole tree + forest floor removal) and three levels of soil compaction (none, intermediate, and severe) in

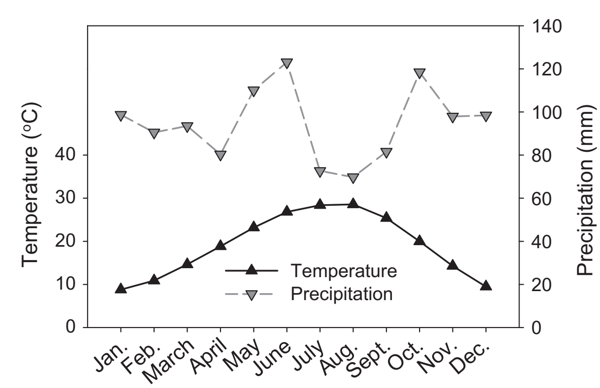

Fig. 1. Average monthly climate conditions (1981–2010) for Crockett, Houston County, Texas (31°18′25.92″N, 95°27′3.24″W). Data from the National Oceanic and Atmospheric Administration (http://www.ncdc.noaa.gov/dailyform/DlyFORMv2).

factorial combination (nine treatment combinations) replicated three times on 0.4 ha plots. At the time of harvest, stands were 55–80 years old and consisted primarily of *P. taeda* L. with scattered hardwoods (<10%). A feller buncher and skidder were used for harvesting on the compacted plots, while the non-compacted plots were hand-felled, with trees lifted off the plots with a loader (Rick Stagg, USDA Forest Service, personal communication). A 9Z pneumatic-tired roller (W.E. Grace Manufacturing Co., Dallas, TX, USA) loaded to 2.4 Mg m^{-1} and 4.2 Mg m^{-1} for the moderate and severe compaction, respectively, was towed by a farm tractor and rolled over the soil a total of six times (three passes in one direction and three passes in a second direction perpendicular to the first passes) (Rick Stagg, USDA Forest Service, personal communication). Forest floor removal was accomplished by hand raking all aboveground organic matter from the whole tree + forest floor removal treatments plots. Containerized *P. taeda* L. seedlings of 10-half sib families from US Forest Service seed orchards in Louisiana, Mississippi, and Texas were hand planted on a 2.5 m × 2.5 m spacing. Each of the 27 treatment plots was split for glyphosate herbicide treatment that was applied once per year for five years following harvest.

2.2. Sample collection

Prior to field sampling, each of the 54 split-plots (i.e., herbicided and non-herbicided split) was divided into five "sub-plots" that were anchored at the four corners and the center of each split-plot. We used this method to ensure complete coverage of each split-plot. In the field, sample points within each "sub-plot" were randomly located interior to a three-tree outer buffer and between two living loblolly pine trees. Occasionally samples were taken within the buffer due to mortality within plots.

At each sample point, forest floor materials were collected down to the mineral soil from a 0.25 × 0.25 m quadrat followed by the extraction of a soil core. Soil cores (4.8 cm diam. × 10 cm deep) were collected with a split soil corer (AMS, Inc., American Falls, ID, USA), and pooled by split-plot. All soil samples were kept in a cooler with ice in the field and maintained at 4 °C in the lab until processed.

2.3. Soil chemical and physical characterization

Soil samples were thoroughly mixed in the lab and a 30 g aliquot of field-moist soil was dried at 105 °C until stable mass was achieved to measure bulk density, gravimetric soil moisture, and volumetric soil moisture. This aliquot was subsequently used for the determination of pH using an Accumet Basic pH meter (Denver Instrument, Arvada, CO, USA) on a 1:2 solution of soil in 0.01 M $CaCl_2$ solution (Minasny et al., 2011). The remaining soil was passed through a 2 mm sieve to remove large organic material and roots >2 mm. A 20–30 g aliquot of sieved soil was dried at 60 °C, and then finely ground in a TE250 ring pulverizer (Angstrom, Inc., Belleville, MI, USA) for C and N concentration analyses. An additional sieved soil aliquot was dried at 105 °C for texture analysis using the hydrometer method (Ashworth et al., 2001; Bouyoucos, 1927).

2.4. Litter and root quantification

Forest floor materials (i.e., all organic material above the mineral soil) were cleaned of mineral particles and sorted into woody debris (non-leaf material) and leaf matter (henceforth "litter"). Roots collected during sieving were divided into coarse and fine fractions based on diameters ⩾2 mm or <2 mm, respectively. Additionally, a 100–150 g aliquot of sieved soil was passed through a hydropneumatic elutriation system fitted with a 450 μm screen (Gillison's Variety Fabrication, Benzonia, MI, USA) to recover fine roots. All root and forest floor materials were dried at 60 °C until stable mass was achieved and then weighed.

2.5. Carbon and nitrogen concentrations

Soils were analyzed for organic C and total N concentrations in the Stable Isotopes for Biosphere Science Laboratory at Texas A&M University. Analyses were conducted on a Carlo Erba EA-1108 elemental analyzer (CE Elantech, Lakewood, NJ, USA). Precision (±SD) of acetanilide standard used during the study was 0.48% for C-concentration (mean = 71.21%) and 0.15% for N-concentration (mean = 10.35%).

2.6. Microbial biomass determination

Soil microbial biomass carbon and nitrogen (MBC and MBN) were determined on sieved soil sub-samples using the chloroform fumigation extraction (CFE) method described by Vance et al. (1987). Soil samples (10 g) were fumigated at field moisture in a vacuum desiccator in the dark for 24 h in the presence of ethanol-free chloroform. Simultaneously, a 10 g control sample was incubated in a chloroform-free vacuum desiccator. Following incubation, each sample was extracted with 40 mL of 0.5 M K_2SO_4, shaken for one hour, centrifuged at 715*g* for 10 min, filtered through #5 Whatman filter papers pre-leached with 0.5 M K_2SO_4, and frozen until analysis.

Extracts were analyzed for dissolved organic C and dissolved organic N using a Shimadzu TOC-V_{CSH} with a TNM-1 module (Shimadzu Corp., Kyoto, Japan) set for 5X dilution as described by Chen et al. (2005). Soil microbial biomass-C and -N were calculated using formulae outlined in Paul et al. (1999) where:

(1) $MBC = (C_{fumigated} - C_{control})/k_{EC}$; and
(2) $MBN = (N_{fumigated} - N_{control})/k_{EN}$.

Because extraction efficiencies for dissolved organic C and N are less than 100%, extraction coefficients for carbon (k_{EC}) of 0.45 (Allen and Schlesinger, 2004; Joergensen et al., 2011; Potthoff et al., 2009; Wu et al., 1996) and nitrogen (k_{EN}) of 0.54 (Brookes et al., 1985) were used to calculate MBC and MBN, respectively. The ratio of C_{mic}/C_{org} was computed by dividing the concentration of MBC by the concentration of SOC in the same sample.

2.7. Statistical analyses

Statistical analyses were performed with JMP Pro (SAS Institute, Inc., Cary, NC, USA). To determine if herbicided and non-herbicided split-plot data could be pooled, *t*-tests were used. No statistically significant effects were seen due to herbicide; therefore, split-plot data was pooled within each treatment plot. A general linear model was used to test the main effects of harvest and compaction, and the harvest by compaction interaction. Throughout the one-year study period we did not see statistically significant effects due to either soil compaction or the harvest by compaction interaction, therefore, findings based only on harvest effects ($N = 3$) and season of sampling are reported. A significance level of $\alpha \leqslant 0.05$ was used throughout statistical testing.

Repeated measures analysis of variance (ANOVA) was used to determine the effect of harvest on SOC, TN, MBC and MBN, C_{mic}/C_{org}, and root biomass, and litter mass over the one-year study period. Correlation analyses (Pearson's) were performed to determine relationships between MBC, MBN, SOC, TN, litter, roots, and environmental variables examined in this study. Correlations with precipitation were conducted using total precipitation in the month prior to each sampling period and correlations with temperature were conducted using the mean monthly temperature in the month prior to each sampling period. For each response variable, correlations were run using the mean values for each plot for every sample period, so that each correlation analysis was based on 120 observations.

3. Results

3.1. Climate and soil moisture

Mean annual temperature in 2011 was 1.5 °C higher than the 30 year average; total precipitation was 684 mm, approximately 40% lower than the 30 year average (Fig. 2A). Mean monthly temperatures during the first three months of 2012 (coincidental with the sample period) were 3 °C higher than the 30 year average and total precipitation was 441 mm, approximately 36% higher than the 30 year average of 283 mm for the same time period.

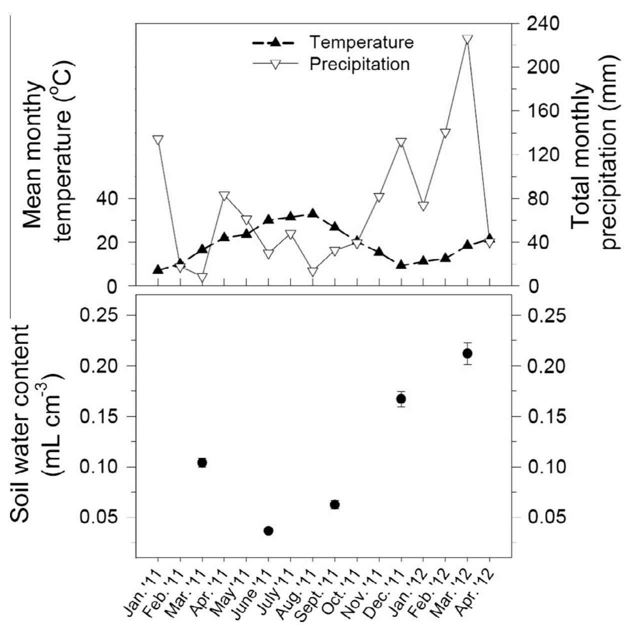

Fig. 2. Weather conditions and soil moisture for January 2011 through April 2012. (A) Crockett, Houston County, TX mean monthly temperature and total precipitation from January 2011 through April 2012, and (B) mean ± SE (n = 24–27) volumetric soil moisture for each sample period from 2011 to 2012.

Volumetric soil moisture ranged from a low of 0.03 mL cm^{-3} in June 2011 to a high of 0.21 mL cm^{-3} in March 2012 (Fig. 2B) and was not affected by treatment. Soil moisture had a strong positive correlation with total precipitation and a strong negative correlation with mean temperature (r = 0.76 and −0.71 respectively, both $p < 0.001$; Table 1).

3.2. Soil chemical and physical characteristics

Soil pH across the site was acidic and ranged from 3.5 to 4.7 (average 4.15 ± 0.06, n = 27). Soil texture is loamy sand, with sand concentration of 755 ± 7 g kg^{-1} and clay concentration of 65 ± 3 g kg^{-1} (n = 24).

3.3. Litter and root mass

Litter mass was unaffected by increasing harvest intensity (repeated measures ANOVA; $p > 0.05$; Table 2), varied significantly through time ($p = 0.05$; Table 2), and was negatively correlated with precipitation ($r = -0.53$; Table 1). Litter mass was highest in March 2011 (1471–1631 g m^{-2}; Fig. 3A), with a slightly smaller peak in September 2011 (1433–1588 g m^{-2}). The lowest litter mass measurements were similar in magnitude in June 2011 and March 2012 (1295–1404 g m^{-2}; Fig. 3A). Despite the lack of harvest effect, litter mass was generally highest in the bole only treatment and lowest in the whole tree + forest floor removal treatment (Fig. 3A).

Fine root mass was likewise unaffected by increasing harvest intensity ($p > 0.05$; Table 2), but varied significantly with time ($p < 0.05$), and was negatively correlated with both precipitation ($r = -0.39$) and volumetric soil moisture ($r = -0.56$; Table 1). Fine root mass was highest in March and June 2011 (183–204 g m^{-2}; Fig. 3B) and decreased over time to the lowest levels in December 2011 and March 2012 (88–107 g m^{-2}). Fine root mass was generally lowest in the bole only treatment and highest in the whole tree harvest (Fig. 3B). Neither coarse root nor total root mass were affected by increasing harvest intensity or time ($p > 0.05$; Table 2; Fig. 3C and D).

3.4. Soil organic carbon and total nitrogen

Soil organic carbon content was not impacted by harvest intensity ($p > 0.05$; Table 2; Fig. 4A), but varied significantly over time ($p < 0.05$). These temporal variations were not correlated with air temperature, precipitation, or soil moisture (Table 1). Average

Table 1
Pearson's correlation coefficients among variables examined in this study.

	Precip.	Temp.	Soil moisture	Roots			Litter	SOC	TN	SOC/TN	C_{mic}/C_{org}	MBC	MBN
				Fine	Coarse	Total							
Precipitation													
Temperature	−0.48*												
Volumetric soil moisture	0.76*	−0.71*											
Roots													
Fine	−0.39‡	0.04	−0.56*										
Coarse	−0.14	0.35†	−0.24	0.12									
Total	−0.27	0.34†	−0.43‡	0.48*	0.93*								
Litter	−0.53*	0.04	−0.15	−0.15	−0.17	−0.22							
SOC	−0.01	−0.25	0.24	0.23	0.02	0.10	0.06						
TN	−0.12	−0.32†	0.29	−0.04	−0.05	−0.07	0.55*	0.73*					
SOC/TN	0.13	0.11	−0.10	0.39‡	0.09	0.23	−0.67*	0.36†	−0.38*				
C_{mic}/C_{org}	−0.09	0.04	−0.35†	0.21	0.13	0.18	0.10	−0.59*	−0.29	−0.39‡			
MBC	−0.26	−0.22	−0.20	0.48*	0.12	0.28	0.35†	0.50*	0.58*	−0.12	0.32†		
MBN	−0.17	−0.53*	0.07	0.35†	−0.06	0.06	0.38†	0.44‡	0.64*	−0.26	0.24	0.84*	

* $p < 0.001$.
‡ $p < 0.01$.
† $p < 0.05$.

Table 2
Results of repeated measures ANOVA (*p*-values) testing the effects of tree harvest method, time, and their interaction on litter and root biomass, TN, MBN, SOC, MBC, and C_{mic}/C_{org}.

Biomass pools (g m^{-2})	Harvest	Time	Harvest ∗ time
	p-Value[a]		
Litter	0.384	0.055	0.892
Fine roots	0.942	0.004**	0.668
Coarse roots	0.782	0.368	0.479
Total roots	0.793	0.166	0.581
SOC (g C m^{-2})	0.425	0.028*	0.100
Total N (g N m^{-2})	0.048*	0.003**	0.215
MBC (μg C g^{-1})	0.032*	0.013*	0.299
MBN (μg N g^{-1})	0.006**	0.004**	0.047*
C_{mic}/C_{org}	0.988	0.012*	0.255

[a] *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

SOC was highest in March 2011 (2058 ± 127 g C m^{-2}; Fig. 4A) and was lowest in June 2011 (1750 ± 86 g C m^{-2}), but recovered in September 2011 (1909 ± 70 g C m^{-2}) and remained stable through March 2012. Although not significant, the bole only harvest generally had higher SOC than the whole tree + forest floor removal treatment. Soil TN content was significantly lower in whole tree and whole tree + forest floor removal treatments compared to bole only, and varied over time (both $p < 0.05$; Table 2). Bole only harvest had the greatest soil TN (75–98 g N m^{-2}; Fig. 4B) while whole tree + forest floor removal treatment had the least soil TN (61–81 g N m^{-2}). Average TN was highest in March 2011 (89 ± 3 g N m^{-2}) and lowest in June 2011 (67 ± 3 g N m^{-2}), and recovered in September 2011 (80 ± 4 g N m^{-2}) and remained stable through March 2012. Soil TN content was negatively correlated with temperature ($r = -0.32$; Table 1).

3.5. Soil microbial biomass

Both MBC and MBN were significantly impacted by harvest intensity ($p < 0.05$; Table 2) and varied significantly with time ($p < 0.05$). There was also a significant harvest by time interaction for MBN ($p < 0.05$). MBN was negatively correlated with temperature ($r = -0.53$; Table 1). Generally, bole only harvest had higher MBC (197–263 μg C g^{-1}) than the more intense harvests (165–216 μg C g^{-1}; Fig. 4C). MBC on average was highest in March 2011 (239 ± 10 μg C g^{-1}) and lowest in September 2011 (188 ± 9 μg C g^{-1}) (Fig. 4C). Soil microbial biomass N was usually highest in the bole only harvest (25–37 μg N g^{-1}) compared to the more intensely harvested treatments (21–34 μg N g^{-1}; Fig. 4D). From March 2011 to September 2011 MBN declined from an average high of 33 ± 1 μg N g^{-1} to a low of 23 ± 1 μg N g^{-1} and remained stable through March 2012 (Fig. 4D).

Ratios of C_{mic}/C_{org} were unaffected by harvest treatment ($p > 0.05$; Table 2), but varied significantly over time ($p < 0.05$), and were negatively correlated with soil moisture ($r = -0.35$; Table 1). Over time C_{mic}/C_{org} decreased from highs in March 2011 and June 2011 (≈0.017) to a low in December 2011 (≈0.011; Fig. 4E).

There were significant positive correlations ($p < 0.05$) between MBC and MBN and litter, fine root mass, SOC, and TN (Table 1). MBC and MBN were correlated more strongly with TN ($r = 0.58$ and 0.64, respectively), than SOC ($r = 0.50$ and 0.44, respectively; Table 1). Of the correlations between biomass variables and MBC, there was a stronger relationship with fine root mass ($r = 0.48$) than litter mass ($r = 0.35$). In contrast, MBN had a somewhat stronger relationship with litter ($r = 0.38$) than fine root mass ($r = 0.35$; Table 1).

4. Discussion

The removal of tree biomass coupled with soil disturbance during a forest harvest event can have lasting effects on both the quality and quantity of soil organic matter as well as soil physical properties that can strongly control microbial activity and ecosystem biogeochemistry. Our results show that increased forest harvest intensity significantly reduced soil TN and MBC 15 years following harvest. Fine root mass, MBC, SOC, and TN varied over the course of a single year, and there was a significant harvest x time interaction for MBN. However, neither soil compaction nor its interaction with forest harvest intensity affected any of the response variables we measured in this western Gulf Coastal Plain site 15 years post-treatment.

4.1. Harvest and time effects on litter and root mass

Contrary to our prediction, forest harvest intensity had no effect on either aboveground litter or root mass. However, litter mass tended to be highest in the bole only harvest versus the more intense harvests, consistent with previous studies (Jones et al., 2011; Wall, 2008; Zerpa et al., 2010). Because rates of N-mineralization are positively correlated with soil total N (Booth et al., 2005), the larger pool sizes of soil TN in the bole only harvest may have enabled greater N availability in this treatment, thus facilitating greater leaf production and subsequently higher litterfall (Jones et al., 2011; Zerpa et al., 2010). In contrast, fine root mass was generally lowest in the bole only treatment, suggesting that resource availability was higher in the bole only harvest treatment. Several studies have shown that root productivity is reduced at higher soil nutrient levels (Gundersen et al., 1998; Tingey et al., 2005).

Seasonal variation in litter and fine root mass was related to environmental variables. Litter mass was negatively related to precipitation during the previous month, which may reflect increased decomposition during periods of higher rainfall; however, others have found decomposition of *P. taeda* needles unrelated to wetter conditions (Sanchez, 2001). Fine root mass had a stronger negative correlation with volumetric soil moisture than with precipitation. This was not unexpected considering that plants are likely to invest less energy in root production when soil moisture is available (Gundersen et al., 1998; Fisher and Binkley, 2000; Sword et al., 1998a, 1998b; Teskey and Hinkley, 1981; Tingey et al., 2005; Torreano and Morris, 1998).

4.2. Harvest and time effects on TN and SOC

In line with our expectation, TN was significantly and negatively impacted by intensified levels of biomass removal during tree harvest. On average, whole tree harvest (61–96 g N m^{-2}) and whole tree + forest floor removal (61–81 g N m^{-2}) resulted in TN that was 10% and 18% lower, respectively, than the bole only harvest (75–98 g N m^{-2}). Total N content throughout the study approximated the range (75.4–85.3 g N m^{-2}) reported in the uncompacted bole only harvest treatments at 10 years at the Louisiana and North Carolina LTSP installations (Sanchez et al., 2006a). Results from the current study are also consistent with previous findings obtained 5 years post-harvest at this site, wherein whole tree + forest floor removal resulted in approximately 19% lower TN concentration compared to the bole only harvest (Scott et al., 2004), suggesting that diminished soil TN has persisted through time since harvest in the most intensely harvested plots.

Soil TN has shown variable responses to harvest in other forest ecosystems throughout the world. Although Johnson and Curtis

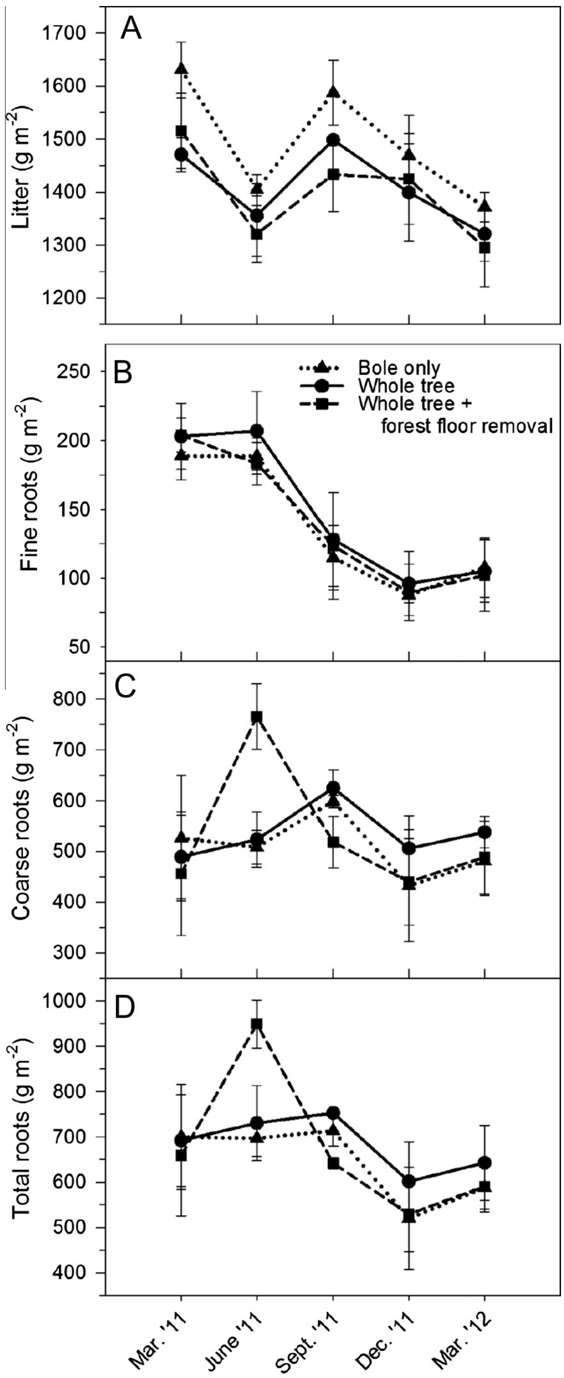

Fig. 3. Biomass (g m^{-2}) by time of sampling. (A) Litter; and (B–D) roots. Symbols are means ± SE ($n = 3$).

(2001) found little overall effect of forest harvest on TN, they showed that whole tree harvest slightly diminished N and bole only harvest significantly increased N when compared to controls. Additionally, conifer species tended to have significant increases in soil TN following bole only harvest (Johnson and Curtis, 2001). While we cannot say that bole only harvest increased TN per se, we can say that intensified forest harvest led to lower TN which has been reported in other studies (Jones et al., 2011; Kellman et al., 2014; Olsson et al., 1996). For example, in a *Pinus radiata* forest in New Zealand 15-years post-treatment, Jones et al. (2011) found that whole tree + forest floor removal led to a significant decrease in TN concentrations (≈18%) when compared to preharvest, but bole only harvest led to a non-significant increase (≈9%). Although we are unable to suggest definitively a mechanism for the TN loss observed in our most severe harvest treatments, we hypothesize that our results may diverge from the results synthesized by Johnson and Curtis (2001) due to (a) the sandy soil texture at our site which affords little physical protection for soil organic matter (e.g., von Lutzow et al., 2007), and (b) the high mean annual temperatures that prevail at the southwestern limit of the forest biome in the USA that would favor rapid decay of organic matter.

Contrary to our prediction, harvest intensity had no effect on SOC 15 years after treatment. However, there was a general trend of highest SOC occurring in the bole only harvest treatment and lowest SOC in the whole tree + forest floor removal treatment. In this study, intra-annual variation in the SOC content at the Groveton LTSP site ranged from 1600 to 2200 g C m^{-2} which was within the range of values (1600–4400 g C m^{-2}) found at five and 10 years at other LTSP sites with *P. taeda* L. in Louisiana and North Carolina (Powers et al., 2005; Sanchez et al., 2006a, 2006b).

Both SOC and TN varied significantly with time over the course of this study. While others have found large interannual fluctuations of SOC and TN concentrations (Carter et al., 2002; Knoepp and Swank, 1997), we did not expect to see these relatively large variations occurring over short time periods (i.e., 3-months). Changes in SOC during this one-year study were not related to environmental variables. Post and Kwon (2000) suggested that short-term shifts in SOC may be due to the dynamic nature of the light-fraction of organic carbon, and may change in response to seasonal litter inputs such as those that occurred in June and September 2011. Variation of TN over the study period was negatively correlated with temperature. Higher temperatures will favor more rapid decomposition and N-transformation rates, increasing the potential for N-losses via leaching and trace gas emissions.

4.3. Harvest and time effects on MBC and MBN, and C_{mic}/C_{org} ratios

In accordance with our hypothesis that increasing harvest intensity would reduce the size of the soil microbial biomass pool, results showed that MBC was significantly and negatively impacted 15 years after harvest. Throughout this study MBC values (164–268 µg C g^{-1}) were similar to the average (216 µg C g^{-1}) reported for an LTSP loblolly plantation site in North Carolina (Busse et al., 2006), and also fell within the range reported for temperate/boreal coniferous forests (736 ± 661 µg C g^{-1}) (Wardle, 1992). Harvest method had no persistent effect on the C_{mic}/C_{org} ratio, with values (0.011–0.015) that fell within the range of values previously reported for temperate/boreal coniferous forests (0.0093 ± 0.0046) (Wardle, 1992).

In addition, MBN was significantly impacted by a harvest × time interaction, indicating variable responses to harvest among the sample periods. However, there was a significant trend of lower MBN in the more intensely harvested treatments. MBN values (21–37 µg N g^{-1}) fell at the lower range reported for combined temperate angiosperm and temperate/boreal coniferous forests (93 ± 65 µg N g^{-1}) (Wardle, 1992).

Soil microbial biomass is generally correlated with substrate quantity (Allen and Schlesinger, 2004; Anderson and Domsch, 1989; Powlson et al., 1987). However, few studies have addressed the direction, magnitude, and duration of soil microbial biomass responses following forest harvest events that alter organic matter inputs to the soil. In coniferous forests, tree harvest reduced soil microbial biomass in stands <10 years old when compared to reference stands (LeDuc and Rothstein, 2007; Mummey et al., 2010). In contrast, Smolander et al. (2010) found no differences in MBC and MBN in *Picea abies* (L.) Karst Norway spruce stands >10 years old. Forest harvest intensity (i.e., extent of organic matter removal) has also produced mixed results. For example, Busse et al. (2006)

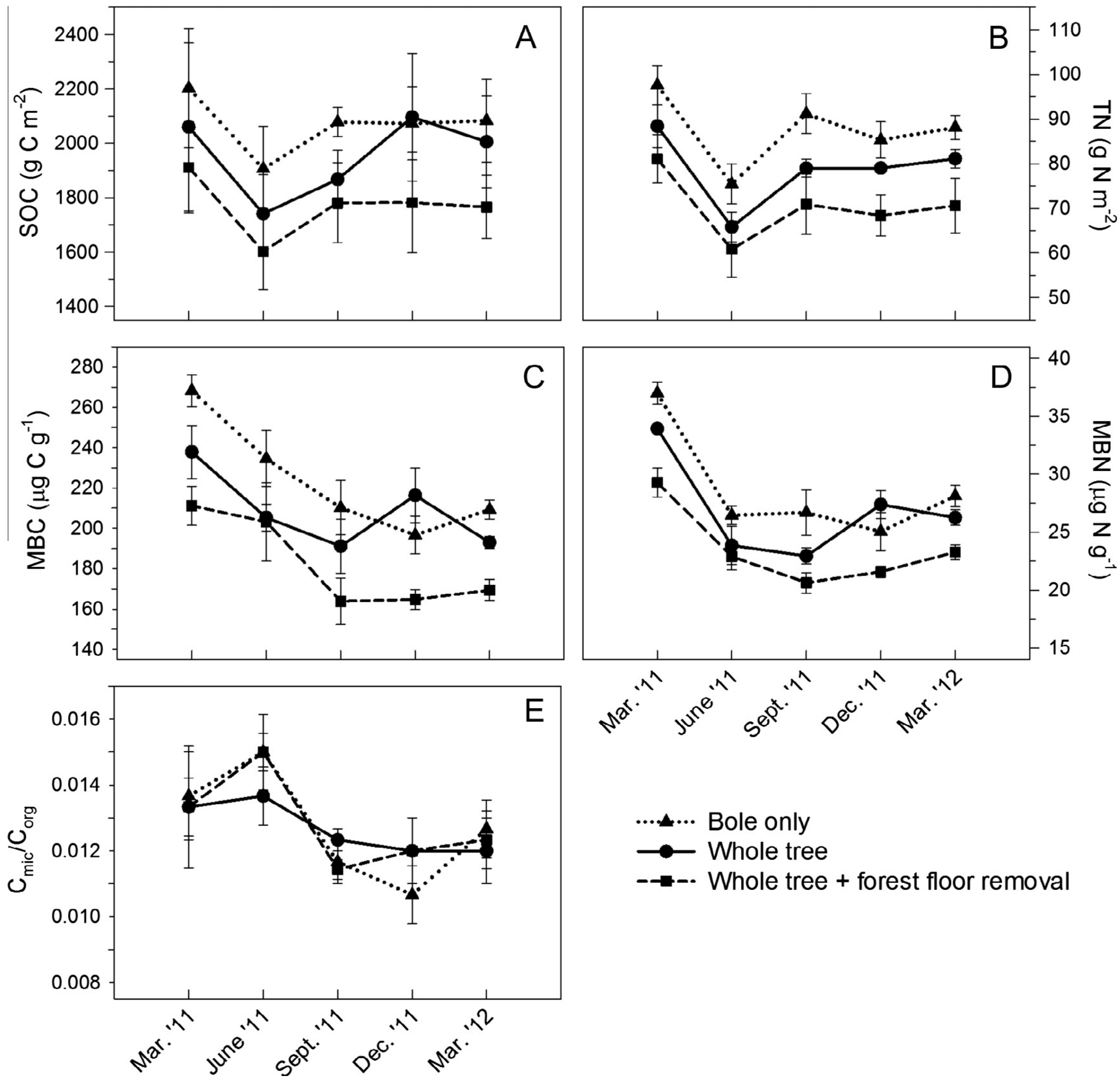

Fig. 4. (A and B) SOC and TN (g m^{-2}); (C and D) MBC and MBN (μg g^{-1}); and (E) C_{mic}/C_{org} by time of sampling. Symbols are means ± SE (n = 3). C_{mic}/C_{org} calculated using concentrations of MBC and SOC.

and Li et al. (2004) found no differences in MBC based on harvest intensity in *P. taeda* stands >5 years old in North Carolina. However, in those same *P. taeda* stands, Li et al. (2004) found that harvest intensity decreased MBN in stands >5 years old. Similarly, Hassett and Zak (2005) and Tan et al. (2008) found that harvest intensity decreased both MBC and MBN in aspen stands of nearly 10 years old. Hassett and Zak (2005) suggested that reduced soil microbial biomass was driven by reduced litter inputs as well as modified soil microclimate, and Li et al. (2004) found that MBN was positively related to soil C and N. We found that MBC and MBN were more strongly related to TN than to SOC, suggesting that in this system N may be more important than C as a limitation to microbial biomass.

Microbial biomass C, and the C_{mic}/C_{org} ratio varied significantly over the five sampling periods of this study, while MBN varied in response to a significant harvest x time interaction. Soil microbial biomass C was highest at the beginning of the study in March 2011, and then decreased during the following summer as the soil dried, consistent with other studies (Aponte et al., 2010; Wardle, 1992). MBC and MBN remained low during winter 2011 and the following spring, likely in response to the cooler temperatures and smaller fine root pool sizes that prevailed during that time. In addition, very high soil moisture during March 2012 may have slowed the recovery of the soil microbial biomass during that spring season.

The C_{mic}/C_{org} ratio varied significantly over time, with higher values during March–June 2011 compared to the September 2011–March 2012 interval. Over the course of the entire study, C_{mic}/C_{org} ratio was correlated negatively with SOC and the SOC:TN ratio. Since C_{mic}/C_{org} is higher when SOC pool size is lower, the microbial biomass is probably not carbon-limited. And, C_{mic}/C_{org} is higher when the C/N ratio of the soil organic matter is lower. Taken together, these observations suggest that the soil microbial biomass pool in this study area is probably N-limited (Liao and Boutton, 2008; Wardle, 1992).

4.4. Potential implications for forest productivity

Given that soil TN, MBC, and MBN were significantly lower in the more severe harvest treatments, is there any evidence that these differences in key indices of soil fertility have affected tree productivity at this site? At 5 years following the implementation of treatments at the Groveton LTSP site, stand volumes were 6.88 m^3 ha^{-1} in the bole only, 5.13 m^3 ha^{-1} in the whole tree, and 2.42 m^3 ha^{-1} in the whole tree + forest floor removal plots

(Scott et al., 2004). All treatments were significantly different from each other at that time. At 15 years following the implementation of treatments, stand volumes (±SE) were 163.8 ± 10.2 $m^3 ha^{-1}$ in the bole only, 156.3 ± 11.6 $m^3 ha^{-1}$ in the whole tree, and 143.7 ± 8.6 $m^3 ha^{-1}$ in the whole tree + forest floor removal plots (Scott et al., 2014). Although stand volumes were 5–14% higher in the bole only treatment, these differences were not significant at 15 years post-treatment. We postulate that during the first 5 years of regrowth, loblolly pine root systems may have been largely confined to the uppermost portion of the soil profile where soil N and microbial biomass were most impacted by the previous harvest, thereby limiting tree productivity in the more severe harvest treatments. By 15 years postharvest, root systems are likely to be more extensive and more deeply distributed, potentially providing trees with access to nutrient stores that may not have been diminished by the previous harvest event, thereby alleviating harvest effects. It will be important to reevaluate these potential treatment effects towards the end of the rotation period to assess their longer-term impact on forest productivity.

5. Conclusions

The forest ecosystems of the southeastern USA are among the most important timber producing regions in North America, making it important to understand the impacts of tree harvesting on the biogeochemistry of this region. We found that forest harvest practices that removed more than the tree bole significantly reduced soil TN, and MBC and MBN in loblolly pine forests of the western Gulf Coastal Plain region. Moreover, these reductions were still evident 15 years after the treatments were imposed. Although recent stand volumes show little response to the intensity of harvest, the persistent reduction of soil TN and soil microbial biomass pool sizes in the most severe harvest treatments suggests that rates of key biogeochemical processes may be altered. This in turn could constrain mineralization rates of limiting nutrients and reduce the productivity of subsequent rotations. Our results suggest that harvest practices in the southeastern USA that maximize retention of aboveground biomass and litter will minimize soil N losses, which should help sustain the long-term productivity, carbon sink strength, and the economic value of forestlands in this region.

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