BIOGEOCHEMISTRY OF THE WESTERN GULF COASTAL PLAIN AS IMPACTED BY FOREST MANAGEMENT

A Dissertation

by

JULIE A. FOOTE

Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSPHY

Chair of Committee,	Thomas W. Boutton
Committee Members,	Frank M. Hons
	D. Andrew Scott
	Mark Tjoelker
	Jason Vogel
Head of Department,	David D. Baltensperger

May 2014

Major Subject: Ecosystem Science & Management

ABSTRACT

Plantation forestry is central to supplying the global demand for forest products and sustainable production will rely on information regarding the effects of disturbance on soil biogeochemistry. The extent of ecosystem disturbance will dictate the degree to which biogeochemical processes are perturbed. To date little is known about the impact of forest harvest activities on biogeochemical cycling in the western Gulf Coastal Plain, therefore the purpose of this study was to elucidate the impact of three harvest methods (bole only, whole tree, whole tree+forest floor removal) in factorial combination with three soil compaction intensities (none, intermediate, severe) 15-years following treatment and in an archived soil time-series in a *Pinus taeda* L. forest. I evaluated soil microbial biomass (SMB), and soil organic carbon (SOC), total nitrogen (TN), and total phosphorus (TP) storage, and stable isotopes ^{15}N and ^{13}C. I used chloroform fumigation extraction, dry combustion, and lithium metaborate fusion to quantify SMB, SOC and TN, and TP, respectively, and isotope ratio mass spectrometry to analyze ^{15}N and ^{13}C.

Soil microbial biomass, TN, and TP decreased significantly in the order: bole only > whole tree > whole tree+forest floor removal; although not significant SOC followed the same pattern. Soil TN, litter and root N were generally ^{15}N enriched under the whole tree+forest floor removal treatment. Compared to control plots, harvest initially resulted in lower TN and SOC that was enriched in ^{15}N and ^{13}C, however, both C and N have been accumulating since 5-years post-treatment and have become increasingly less enriched isotopically. No evidence of a compaction or a harvest by

compaction interaction effect was found on the measured variables. Although both C and N are accumulating, there were losses initially following harvest as evidenced by isotopic enrichment. Forest harvest practices that minimize removal of above-ground biomass will likely favor soil N and P retention and maintenance of the SMB pool. Since both N and P limit productivity in the sandy soils of this region, and because SMB plays a key role in nutrient cycling, harvest practices that favor nutrient retention and SMB will ensure the productivity of future rotations.

ACKNOWLEDGEMENTS

I first wish to thank my committee members, foremost Dr. Tom Boutton for the generous invitation to work with him, what a pleasure it has been, and Dr. Andy Scott for allowing me to put holes in the Texas LTSP plots for this study. Many thanks go also to Dr. Frank Hons, Dr. Mark Tjoelker, and Dr. Jason Vogel for serving on my committee. I could not have completed my tenure at Texas A&M without support from the McMillan-Ward Memorial Endowed Graduate Fellowship.

This work could not have been carried out without the help of numerous individuals: from the USDA Forest Service, Rick Stagg and Kerry Hogg who answered my many questions regarding the experimental plots and helped me gain access to gated areas, Morris Smith for supplying me with archived soils from the LTSP study, and the folks at the Ranger District who took my daily calls checking in/out of Davy Crockett National Forest compartments 87 and 88; my motley field crew who put up with my incessant talking to, from, and in the field, Darrin Moore, Matthew Foote, and Stuart Foote; the SIBS Lab at Texas A&M, Darrin Moore and Dr. Ayumi Hyodo for elemental and isotopic analyses, Dr. Ilsa Kantola for showing me how to extract total phosphorus from soil without burning down the lab, and Ryan Mushinski for running last minute textural analyses with me; and thanks to Beau, Joe, and Keith of Groveton, Texas for pulling me out of the mud after several days of torrential rainfall in March 2012.

And finally, thanks to my family, Stuart, Nathan, and Matthew Foote, who endured this crazy and wonderful ride with me.

TABLE OF CONTENTS

Page

LIST OF FIGURES

Page

LIST OF TABLES

CHAPTER I

INTRODUCTION

Soil organic carbon (SOC) is the largest reservoir (1462-1548 Pg C; 1 Pg = 10^{15} g) in the terrestrial carbon cycle, containing almost 2X more C than the atmosphere (816 Pg C) and nearly 3X more C than terrestrial biomass (560-615 Pg C) (McKinley et al. 2011; Schlesinger and Bernhardt 2013). SOC is a dynamic component of the C-cycle and is closely linked to the atmospheric CO_2 pool via inputs from dead organic matter production (≈61.4 Pg C yr^{-1}) and losses from decomposition (≈60 Pg C yr^{-1}) (Schimel 1995; Houghton 2007). These fluxes are nearly 7X greater than fossil fuel combustion (9 Pg C yr^{-1}) (Schlesinger and Bernhardt 2013), so that even small changes in the magnitude of the SOC pool or the input/output rates associated with it could have significant impacts on the global C-cycle, the concentration of CO_2 in the atmosphere, and the climate system (Lal 2004; Pregitzer and Euskirchen 2004). Despite the obvious significance of SOC, our present concept of the global C-cycle remains limited by uncertainties in the quantitative aspects of SOC storage and dynamics.

The amount of carbon sequestered by forest ecosystems plays an important role in regulating atmospheric CO_2 concentrations (Canadell et al. 2007; Denman et al. 2007; Bonan 2008). North American forestlands cover approximately 700 million ha and currently store 103.1 Pg C, of which ⅔ is tied up in SOC and litter (FAO 2010a). It is estimated that these forest ecosystems were a net sink of 0.25 Pg C yr^{-1} from 2000-2007 (Pan et al. 2011). This carbon "sink" is a critical ecosystem service provided by forests

and its persistence or growth will be important to limiting atmospheric CO_2 increase (Bonan 2008; Canadell and Raupach 2008). However, the uncertainty regarding the magnitude of this sink is largely due to inadequate knowledge of the effects of disturbance and management practices across the continent (Birdsey et al. 2009).

Therefore, the purpose of this study is to evaluate the effects of timber harvest practices on the biogeochemistry of loblolly pine (*Pinus taeda* L.) forests in eastern Texas. In this introduction, I review the role of forestlands in biogeochemical cycles, the impact of forestry practices on soil carbon, nitrogen, and phosphorus storage and dynamics, and the influence of timber harvest on soil microbial biomass.

I.1. Role of forests on biogeochemistry in the USA and Texas

Most North American forestlands are located in the USA and Canada where approximately 15% of the total forest area is designated for production (FAO 2010b, 2010c). Recent estimates suggest that some forest management practices (e.g., fertilization, longer rotations, erosion reduction, replanting after harvest) could potentially increase C storage in forest soils by 0.025 to 0.103 Pg C yr^{-1} in the USA alone (Heath et al. 2003). Conversely, some forest management practices (e.g., short rotations, clear-cutting, whole tree harvest) could reduce forest productivity and C stores in the forest floor and soil by depleting limiting nutrients, compacting the soil, exporting large amounts of organic matter in the form of branches and leaves, and accelerating SOC decay (Currie et al. 2003; Hoover 2003; Nave et al. 2010). Thus, management effects are still poorly understood (Davis et al. 2009), and experimental studies in managed forests are required to provide ecosystem-specific guidelines that can maintain

or enhance C stores in soil and the forest floor without compromising timber production (Gough et al. 2008).

The forestlands of eastern Texas occupy 4.9 million ha (Li et al. 2011) and lie at the ecotone between forest and grassland biomes, representing the westernmost extent of the southern pine region (Siska et al. 2006). As such, these forests may be exceptionally vulnerable to changes in temperature and rainfall predicted for the future (Schmandt et al. 2009), and these climate change drivers may interact with forest management practices to influence nutrient pools and dynamics. Forestlands in eastern Texas are now dominated by commercial loblolly pine forests managed for timber production, and generated $5.7 billion in 2009 (Li et al. 2011). Despite the geographic extent, unique ecological context, and economic significance of Texas forests, little is known about the effects of forest harvest practices on biogeochemical cycling in this region, making studies in this area particularly important and timely.

Throughout the southern pine region, soils are generally nutrient limited (Haywood et al. 2003; Carter and Foster 2006; Will et al. 2006; Fox et al. 2007; Campoe et al. 2013; Johnsen et al. 2013). The removal of organic matter during forest harvest and the accompanying soil compaction ultimately may alter forest productivity through perturbations to biogeochemical cycling. Concentrations of nutrients are highest in the non-bolewood components of trees, therefore, harvest of the whole tree rather than the merchantable bole results in the export of more nutrients from a forest site (Metz and Wells 1965; Wollum and Davey 1975; Wells and Jorgensen 1979; Henderson 1995; Carter et al. 2002; Currie et al. 2003; Scott et al. 2004; Powers et al. 2005; Turner and

Lambert 2011). In addition, soil compaction that occurs during harvest operations alters soil structure and porosity, and increases bulk density and soil strength, which may result in reduced gas exchange, water infiltration, and aeration (Greacen and Sands 1980; Fisher and Binkley 2000; Powers et al. 2005; Tan et al. 2005; Ampoorter et al. 2007; Labelle and Jaeger 2011), with potential impacts on biogeochemical processes.

I.2. Forest harvest effects on soil carbon, nitrogen, and phosphorus stores

The effects of forest harvest on SOC and N have been variable based on global reviews (e.g., Johnson and Curtis 2001; Nave et al. 2010, Jerabkova et al. 2011). For example, in the meta-analysis performed by Johnson and Curtis (2001), forest harvest had no overall effect on SOC or TN. However, whole tree harvesting resulted in decreased SOC and TN, while bole only harvesting resulted in increased SOC and TN. In contrast, results from a more recent meta-analysis of forest harvesting based on an examination of 432 temperate forest sites around the world showed that SOC was reduced by an average of 8 ± 3% and forest floor C by an average of 30 ± 6% (Nave et al. 2010). In a meta-analysis focusing on N fluxes, Jerabkova et al. (2011) found that clearcut harvest in both coniferous and deciduous forests, resulted in a general trend of increased NO_3^- availability. This in turn has the potential to lead to increased N losses via leaching and denitrification; however, the coniferous forests tended to have a delayed and prolonged response to disturbance when compared to deciduous forests. While these meta-analyses provide generalized trends, the results of individual studies have likewise been variable.

In some cases, mineral soil C and N have been unaffected (Wall 2008; Zerpa et al. 2010), have decreased (Jones et al. 2011), or have increased (Vanguelova et al. 2010) with increasing harvest residue removals. Whereas Wall's (2008) observations were made over the first four growing seasons in a *Picea abies* (L.) Karst stand, the findings of Zerpa et al. (2010) were in a 10-yr old *P. taeda* stand in Alabama, USA. Jones et al. (2011) demonstrated a long-term (15-yrs) impact on soil C and N concentrations (0-10-cm) in a *Pinus radiata* stand that was attributed to the loss of the forest floor organic matter input. In contrast, Vanguelova et al. (2010) found a significant increase in both soil C and N concentrations in a whole tree versus bole only harvest in a 28-yr old *Picea sitchensis* stand in the UK that was attributed to increased mineralization in the bole only harvest.

Soil total P (TP) is thought to be a poor indicator of plant available phosphorus, however, at least one study has shown a strong positive relationship between TP and available P (Tan et al. 2008). In terrestrial ecosystems, TP is principally a result of primary mineral weathering and exists as a finite pool (Walker and Syers 1976; Vitousek et al. 2010), therefore conservative cycling of P from organic matter is likely an important source of plant P (Yanai 1992; Sanchez et al. 2006a; Cleveland and Liptzin 2007). Despite its importance to plant nutrition, rather little is known about the impact of forest harvest intensity and soil compaction on P storage. In general, losses of P from ecosystems are minimal due to biochemical and geochemical controls (Wood et al. 1984; Vitousek and Howarth 1991; Yanai 1998). Forest harvest disturbs biogeochemical P-cycling by removing organic matter that feeds into the cycle of decomposition and

mineralization, and finally plant uptake. The impact of forest harvest intensity on P has been variable, much like SOC and TN. Some studies have reported decreases in available P due to reduced microbial activity and enzyme activity, and reduced organic matter pools (Sanchez et al. 2006a; Tan et al. 2008), but others have reported no changes in P (Zerpa et al. 2010).

Routine use and more frequent entry of heavy equipment into forest stands has increased the potential for soil compaction, with potential implications for forest productivity and ecosystem carbon storage (Gomez et al. 2002; Jordan et al. 2003). The adverse effects of soil compaction on stand productivity may last for decades (Wert and Thomas 1981; Froelich et al. 1985). Soil compaction that occurs during forest harvest modifies soil structure in such a way that porosity is altered, and may lead to reduction in aeration, gas exchange, and water infiltration. In addition, bulk density and soil strength may increase (Graecen and Sands 1980; Jordan et al. 2003; Powers et al. 2005; Tan et al. 2005; Frey et al. 2009; Ampoorter et al. 2012).

It is unclear how compaction might influence SOM storage and turnover. Initially, overland flow of water may result in surface erosion that carries top soil away and would result in immediate losses of SOM. In addition, compaction of the surface soil may also result in losses of SOC and nutrients due to increased mineralization of SOM liberated by disruption of soil aggregates (Tisdall and Oades 1982). Alternatively, soil compaction of the soil may result in a greater degree of physical protection of organic matter in the surface soil by reducing pore space and gas exchange, thereby

limiting oxygen availability and SOM accessibility to decomposers (de Neve and Hofman 2000; Tan et al. 2005).

Furthermore, soil compaction may hinder growth and exploration of the soil profile by roots and mycorrhizal hyphae, potentially limiting access to water and nutrients, and reducing above- and belowground plant productivity, and organic matter inputs to the soil (Gomez et al. 2002; Jordan et al. 2003). For example, Jordan et al. (2003) found that root systems in two species of oak were severely reduced in compacted treatments, which could reduce the amount of C inputs to the soils over the long term. These findings were supported by Ludovici (2008) in a *Pinus taeda* L. stand in North Carolina, in which taproot biomass was significantly reduced in severely compacted soils.

Tree harvest and soil compaction alter biogeochemical cycles directly by influencing the amount and quality of organic matter inputs and the soil physical environment, and subsequently the soil microbial biomass (SMB) may also be impacted. SMB has been suggested as a superior metric for measuring the impact of disturbance due to its small size relative to SOC and TN pools (Powlson et al. 1987; Brookes 2001; Rodeghiero et al. 2009). For example, Tan et al. (2005) could not detect a difference in SOC and TN based on tree harvest intensity, but a significant reduction in SMB-C and –N was detectable.

I.3. Timber harvest effects on soil microbial biomass

Similar to SOC and TN, the effects of forest harvest intensity on SMB have been variable. Previous studies have found no effect of harvest intensity on SMB (Busse et al.

2006; Mariani et al. 2006; Smolander et al. 2010), which may be a consequence of resiliency of the microbial biomass to disturbance. Alternatively, others have found decreases in SMB with increasing forest harvest intensity (Hassett and Zak 2005; Tan et al. 2008), that may be attributable to losses of litter inputs and altered soil microclimate that enhances decomposition processes following harvest and eventually produces losses. Soil disturbances, such as soil compaction, occur in tandem with tree harvest, and may counteract impacts of biomass removal or exacerbate detrimental effects on SMB. Like forest harvest intensity, SMB responses to soil compaction have been variable. For example, some studies have reported higher SMB due to physical protection of microbes from predation (Jensen et al. 1996a, 1996b; Breland and Hansen 1996; Li et al. 2004; Mariani et al. 2006), but others have seen lower SMB due to decreased aeration and water conductivity (Tan et al. 2005; Frey et al. 2009). In some cases, soil compaction has had no effect on SMB (Shestak and Busse 2005; Busse et al. 2006). Because SMB is important to soil fertility, development and maintenance of soil structure, and biogeochemical cycles (Wardle 1992; Gallardo and Schlesinger 1994; Zak et al. 1994; Allen and Schlesinger 2004), monitoring fluctuations of this pool could provide early indications of changes in quality and quantity of SOM.

I.4. Stable nitrogen isotopes as indicators of ecosystem disturbance

Natural abundance of soil and plant ^{15}N has been used to examine N-cycling (Nadelhoffer and Fry 1994; Robinson 2001). Relationships between environmental factors such as mean annual precipitation and temperature and plant and soil ^{15}N abundances have been demonstrated at regional to global scales (Shearer et al. 1978;

Amundson et al. 2003; Peri et al. 2012). However, at more local scales, disturbances have been shown to influence ^{15}N abundances (Nadelhoffer and Fry 1988; Pardo et al. 2002; Choi et al. 2005; Sah and Ilvesniemi 2007) due to changes in N-cycling. For example, practices that lead to N-losses result in soil $\delta^{15}N$ values that are higher (i.e., more enriched). Because stable isotopes of N are integrators of N-processes (Robinson 2001), the impact of harvest and soil compaction may be reflected in $\delta^{15}N$ values of plant and soils due to alteration of inputs and losses associated with N-cycle processes (Nadelhoffer and Fry 1988; Pardo et al. 2002; Choi et al. 2005*;* Sah and Ilvesniemi 2007; Garten et al. 2011).

I.5. The Long-Term Soil Productivity experiment: a laboratory for forest biogeochemistry

The Long-Term Soil Productivity (LTSP) program is the world's largest coordinated research network devoted to investigating the relationship between land management and sustainable forest productivity, with 62 sites in the USA and Canada. The LTSP was initiated in 1989 to address the National Forest Management Act's concerns over possible losses in soil productivity due to soil disturbance from forest management and harvest on National Forest lands in the USA (Powers 2006). The LTSP study network is extensive, with treatments bracketing potential disturbance extremes. All sites employ a common experimental design involving three tree harvest methods (merchantable bole/stem only, whole tree, whole tree+forest floor removal) and three soil compaction intensities (none, intermediate, and severe) in factorial combination.

Under the auspices of the LTSP study, thirteen loblolly pine sites were established in the southern USA, that include the Gulf Coastal regions, to address the effects of forest harvest on productivity (Scott et al. 2004). A site was established in 1997 in the Davy Crockett National Forest near Groveton, Texas that provides a unique opportunity to examine the effects of forest management methods and associated soil disturbances on biogeochemical processes in the western Gulf Coastal Plain.

I.6. Objectives of this study

This study will evaluate the impact of tree harvest methods, soil compaction, and their interactions on forest biogeochemical processes in eastern Texas. Specific objectives are to determine the legacy of forest management practices applied 15-years earlier on the intra-annual dynamics of : 1) soil microbial biomass-C and –N; 2) soil C, N, and P storage; and 3) N-cycling dynamics. In addition, archived soil samples will be used to quantify variation in soil C and N storage from preharvest to 15-years postharvest. The results of this research will contribute new information that fills a critical gap concerning forest management practices on forest biogeochemical cycling within the western Gulf Coastal Plain.

CHAPTER II

SOIL MICROBIAL BIOMASS AND C AND N STORAGE IN US SOUTHERN PINE FORESTS: INFLUENCE OF FOREST MANAGEMENT

II.1. Synopsis

Microbial communities are integral components of the biogeochemistry, fertility, and structure of forest soils, and land management practices that alter the microbial environment may influence 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 the concerns over possible losses of soil productivity due to soil disturbance from forest management (Powers 2006). 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 microbial biomass C and N (SMB-C, -N), and soil total nitrogen (TN) and soil organic carbon (SOC) storage in a *Pinus taeda* L. forest 15-years post-treatment at the Groveton LTSP site in eastern Texas, USA. To capture seasonal variations, soils (loamy sand) were sampled five times during 2011-2012 to a maximum depth of 30-cm between living *P. taeda* stems. We quantified SMB-C and –N using the chloroform fumigation extraction method, and TN and SOC by dry combustion. SMB-C and –N in the 0-10-cm soil increment were impacted by harvest intensity and varied seasonally, and SMB-C had a

harvest by time interaction. Generally, both microbial indices decreased in the order: bole only >whole tree > whole tree+forest floor. In the 0-10-cm soil increment, TN and SOC 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. Temporal variations in SMB-C and –N, TN, and SOC were correlated with temperature, precipitation, and volumetric soil moisture. Generally there was little effect of harvest on the measured soil properties beyond the 10-cm depth. Soil compaction, and harvest x soil compaction interaction had no effect on the measured soil properties. Since N limits tree growth in the sandy soils of the western Gulf Coastal Plain, and because SMB plays a key role in N mineralization, data suggest that harvest practices that favor N retention and maintain SMB will ensure the productivity of future rotations.

II.2. Introduction

Forests in North America are considered carbon sinks (Pacala et al. 2001; Birdsey et al. 2007); however, both natural and anthropogenic disturbances can negatively impact the strength of this sink (Chen et al. 2013). 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 nutrients such as N are exported off site in the non-bolewood tissues, potentially compromising soil fertility and the productivity of subsequent forest rotations (Metz and Wells 1965; Wollum and Davey 1975; Wells and

Jorgensen 1979; Henderson 1995; Carter et al. 2002; Currie et al. 2003; Scott et al. 2004; Powers et al. 2005; Turner and Lambert 2011). The legacy of these disturbance effects on the carbon cycle of forest ecosystems may persist for more than 50 years (Chen et al. 2013). Additionally, soil compaction that occurs during forest harvest may reduce soil structure and porosity and increase bulk density, which in turn reduces aeration, gas exchange, and water infiltration (Greacen and Sands 1980; Fisher and Binkley 2000; Powers et al. 2005; Ampoorter et al. 2007; Labelle and Jaeger 2011; Berisso et al. 2012). Reductions in ecosystem carbon storage coupled with alterations in soil physical structure that often follow tree harvest events may also have adverse effects on the structure and function of soil microbial communities (Wardle 1992; Vance and Chapin 2001; Jordan et al. 2003; Frey et al. 2009).

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, Johnson and Curtis (2001) in their meta-analysis found that harvest had no overall impact on SOC and TN, but there were differences based on harvest method (i.e., bole only versus whole tree harvest), wherein SOC and TN increased in the bole only harvest and decreased in the whole tree harvest. In contrast, in a more recent meta-analysis Nave et al. (2010) found an overall decrease in forest soil C, but it was primarily related to the loss of forest floor rather than mineral soil C-losses. While individual studies have shown that forest harvest intensity (i.e., removal of more that the merchantable bole) may cause losses (Li et al. 2003; Jones et al. 2011), gains (Vanguelova et al. 2010; Grand and Lavkulich

2012), or no change (Knoepp and Swank 1997; Richter et al. 1999; Mariani et al. 2006; McLaughlin et al. 2006; Wall 2008; Zerpa et al. 2010) in SOC and TN, little is known about responses in the western Gulf Coastal Plain, USA.

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

Soil microbial communities are integral components of biogeochemical cycles, and play key roles in the development and maintenance of soil structure and fertility in forest ecosystems (Wardle 1992; Gallardo and Schlesinger 1994; Zak et al. 1994; Allen and Schlesinger 2004). 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 (Wardle 1992; Brookes 2001; Haubensak et al. 2002; Pregitzer 2003; Allen and Schlesinger 2004). Positive relationships have been demonstrated between SMB and SOC and N (Wardle 1992; Brookes 2001; Allen and Schlesinger 2004; Li et al. 2004); therefore, the removal or alteration of organic matter inputs due to harvest may diminish

the size of the SMB pool (Li et al. 2004; Tan et al. 2005; Busse et al. 2006; LeDuc and Rothstein 2007; Mummey et al. 2010). However, other studies have found little effect of harvest on SMB (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 SMB. Soil compaction may have no effect on SMB (Shestak and Busse 2005; Busse et al. 2006), lead to increases in SMB due to physical protection of microbes from predation (Jensen et al. 1996a, 1996b; Breland and Hansen 1996; Li et al. 2004; Mariani et al. 2006), or lead to decreases due to decreased aeration and water conductivity (Tan et al. 2005; Frey et al. 2009).

The purpose of this study was to determine the impact of forest harvest intensity, soil compaction and their interaction on soil microbial biomass and C and N storage in a *Pinus taeda* L. (loblolly pine) forest 15-years post-treatment. To accomplish this we quantified soil microbial biomass carbon (SMB-C), soil microbial biomass nitrogen (SMB–N), soil organic carbon (SOC), and soil total nitrogen (TN). Using experimental plots at the Long-Term Soil Productivity (LTSP) site located near Groveton, Texas, USA, three broad 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, soil compaction, and interactions; 2) lower SOC and TN under the most severe treatments will constrain nutrient availability and result in less aboveground litter and more root mass; and 3) greater losses of organic matter and soil structure changes due to compaction in the severe treatments, will result in lower SMB-C and –N.

II.3. Materials and methods

II.3.1 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 the 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 (Figure 2-1). 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).

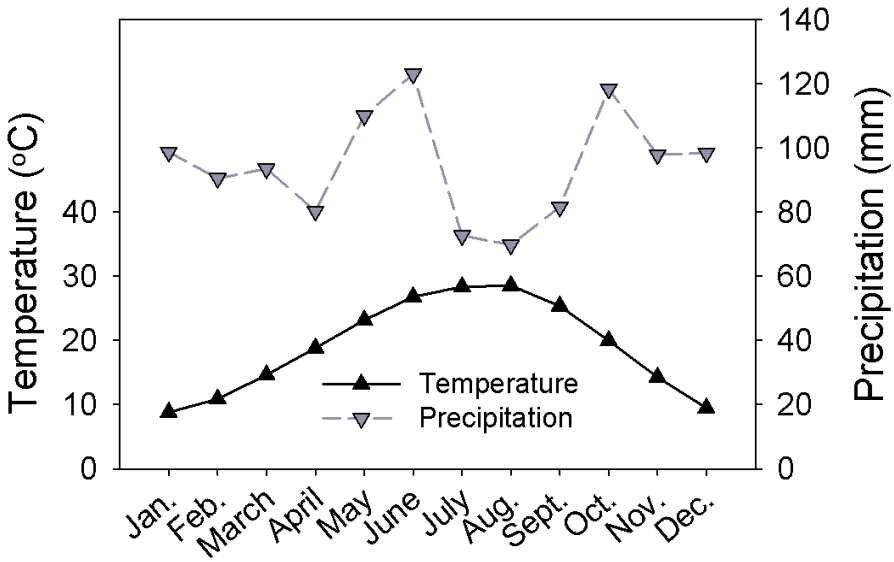

Figure 2-1. Average monthly climate conditions (1981-2010) for Crockett, Houston County, Texas (31° 18' 25.92" N, 95° 27' 3.24" W). Mean annual temperature is 19.1°C and mean annual precipitation is 1135-mm. Data from the National Oceanic and Atmospheric Administration (http://www.ncdc.noaa.gov/dailyform/DlyFORMv2).

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 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%). Each of the 27 treatment plots was split for glyphosate herbicide treatment that was applied once per year for five years following harvest. 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 above-ground 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-m x 2-m spacing.

II.3.2 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 x 0.25-m quadrat followed by the extraction of a soil core. In March 2011, soil cores (4.8-cm diam. x 30-cm deep) were collected with a split soil corer (AMS, Inc., American Falls, ID, USA), and divided into increments of 0-10, 10-20, and 20-30-cm and pooled by split-plot. In March 2012 soils were saturated, therefore, soil cores (4.8-cm diam. x 20-cm deep) were collected and likewise divided by increment and pooled. Soil samples collected in June, September, and December 2011 were 10-cm deep x 4.8-cm diam. and likewise pooled in the field 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.

II.3.3 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 (Bouyoucos 1927; Ashworth et al. 2001).

II.3.4 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.

II.3.5 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%).

II.3.6 Microbial biomass determination

Soil microbial biomass carbon and nitrogen (SMB-C and –N) were determined on sieved soil sub-samples using the chloroform fumigation extraction (CFE) method described by Vance et al. (1987). Ten-g of each sample were fumigated at field moisture in a vacuum desiccator in the dark for 24-hours in the presence of ethanol-free chloroform. Simultaneously, a 10-g control sample was incubated in a chloroform-free vacuum desiccator. Following the incubation, each sample was extracted with 40-mL of 0.5M K_2SO_4, shaken for one hour, centrifuged at 715 x *g* for 10 minutes and filtered through pre-leached (with 0.5 M K_2SO_4) #5 Whatman filter papers, 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 the outlined in Paul et al. (1999) where:

[2-1] $MBC = (C_{fumigated} - C_{control})/k_{EC}$; and

[2-2] $MBN = (N_{fumigated} - N_{control})/k_{EN}$.

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

II.3.7 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, with each harvest/compaction combination acting as one replicate (n = 9), and season of sampling are reported. However, due to a wildfire in September 2011, replicates were reduced from nine to eight. A significance level of $\alpha \leq 0.05$ was used throughout statistical testing.

Repeated measures analysis of variance (ANOVA) was used to determine the effect of harvest on SOC, TN, SMB-C and-N, C_{mic}/C_{org}, and root biomass for the 0-10-cm depth, and litter mass over the one-year study period. Correlation analyses (Spearman's) were performed to determine relationships between SMB-C, -N, SOC, TN, litter, roots, and environmental variables examined in this study.

II.4. Results

II.4.1 Climate and soil moisture

Mean annual temperature in 2011, was 1.5°C higher than the 30-year average and total precipitation was 684-mm, approximately 40% lower than the 30-year average (Figure 2-2A). Mean temperature for the first three months of 2012 (coincidental with

the sample period) was 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.

Volumetric soil moisture was uniform throughout the upper 30-cm of the soil profile and ranged from a low of 0.03 g cm^{-3} in June 2011 to a high of 0.21 g cm^{-3} in March 2012 (Figure 2-2B) and was not affected by treatment. Soil moisture in the 0-10-cm depth had a strong positive correlation with total precipitation and a strong negative correlation with mean temperature (r = 0.68 and -0.56 respectively, both $p < 0.001$; Table 2-1).

II.4.2 Soil chemical and physical characteristics

Soil pH across the site was acidic and ranged from 3.5-4.7, 3.9-4.6, and 3.5-4.8 in the 0-10, 10-20, and 20-30-cm increments respectively (Table 2-2). Soil texture is loamy sand (Table 2-2). Sand concentration ranged from a low of 730 g kg^{-1} in the 20-30-cm increment to a high of 755 g kg^{-1} in the 0-10-cm increment. Silt concentrations ranged from a low of 176 g kg^{-1} in the 20-30-cm increment to a high of 193 g kg^{-1} in the 10-20-cm increment. Clay concentration ranged from a low of 65 g kg^{-1} in the 0-10-cm increment to a high of 94 g kg^{-1} in the 20-30-cm increment.

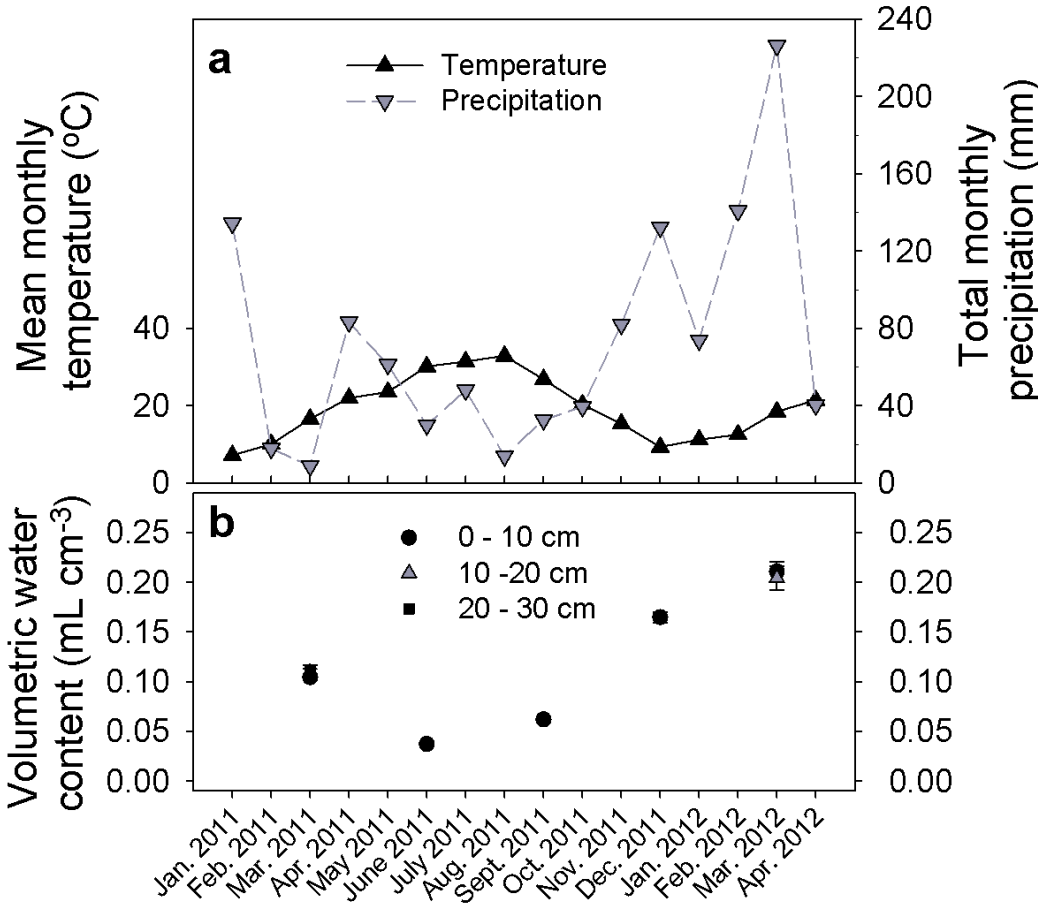

Figure 2-2. Weather conditions and soil moisture for January 2011 through April 2012. A) Crockett, Houston County, TX mean monthly temperature and total precipitation from January 2011 through April 2012, and B) mean (n = 24) volumetric soil moisture for each sample period and depth increment from 2011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

Table 2-1. Spearman's correlation coefficients among variables examined in this study.

	Precip.	Temp.	Soil moisture	Roots			Litter	SOC	TN	SOC/TN	C_{mic}/C_{org}	SMB-C	SMB-N
				Fine	Coarse	Total							
Precipitation													
Temperature	***-0.40****												
Volumetric soil moisture	***0.68****	***-0.56****											
Roots													
Fine	***-0.32****	-0.11	***-0.54****										
Coarse	-0.16	***0.19***†	***-0.23***‡	***0.23***†									
Total	***-0.23***†	0.15	***-0.34****	***0.48****	***0.96****								
Litter	***-0.37****	0.00	-0.06	-0.14	-0.11	-0.12							
SOC	0.01	***-0.21***†	***0.29***‡	0.15	0.10	0.14	0.13						
TN	-0.14	***-0.32****	***0.30****	0.01	0.06	0.07	***0.45****	***0.73****					
SOC/TN	0.17	0.13	-0.05	***0.26***‡	0.07	0.13	***-0.48****	***0.33****	***-0.36****				
C_{mic}/C_{org}	-0.04	-0.02	***-0.32****	0.15	0.08	0.10	0.03	***-0.60****	***-0.25***‡	***-0.50****			
SMB-C	***-0.11****	***-0.28***‡	-0.11	***0.45****	0.17	***0.27***‡	***0.22***†	***0.46****	***0.57****	-0.15	***0.33****		
SMB-N	-0.03	***-0.52****	0.14	***0.32****	0.00	0.09	***0.20***†	***0.44****	***0.61****	***-0.23***†	***0.23***†	***0.86***‡	

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

Table 2-2. Soil particle size distributions and pH averaged across all study plots. Based on the percentages of sand, silt, and clay the site has a soil textural classification of loamy sand.

Depth (cm)	Sand ($g\ kg^{-1}$) [a]	Silt ($g\ kg^{-1}$)	Clay ($g\ kg^{-1}$)	pH [b]
0 – 10	755 ± 7	180 ± 5	65 ± 3	4.15 ± 0.06
10 – 20	737 ± 8	193 ± 6	70 ± 5	4.23 ± 0.05
20 – 30	730 ± 12	176 ± 7	94 ± 14	4.21 ± 0.06

[a] Means ± SE (n = 24)
[b] Means ± SE (n = 27)

II.4.3 Litter and root mass

Litter mass was unaffected by increasing harvest intensity (repeated measures ANOVA, $p > 0.05$; Table 2-3), but varied significantly with time ($p < 0.05$), and was negatively correlated with precipitation (r = -0.37; Table 2-1). Litter mass was highest in March 2011 (1431-1627 g m^{-2}; Figure 2-3A), with a spike in litter mass in September 2011 (1418-1583 g m^{-2}). The lowest litter mass measurements were similar in magnitude in June 2011 and March 2012 (1292-1402 g m^{-2}; Figure 2-3A). 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 (Figure 2-3A). Fine root mass (0-10-cm) was likewise unaffected by increasing harvest intensity ($p > 0.05$; Table 2-3), and varied significantly with time ($p < 0.05$), and was negatively correlated with both precipitation (r = -0.32) and volumetric soil moisture (r = -0.54; Table 2-1). Fine root mass was highest in March and June 2011 (186-209 g m^{-2}; Figure 2-3B) and decreased over time to the lowest levels in December 2011 and March 2012 (87-105 g m^{-2}). Fine

root mass was generally lowest in the bole only treatment and highest in the whole tree harvest (Figure 2-3B). Neither coarse root nor total root mass (0-10-cm) were affected by increasing harvest intensity ($p > 0.05$; Table 2-3; Figure 2-3C, D); however, total root mass varied over time ($p < 0.05$) and was negatively correlated with precipitation (r = -0.23) and volumetric soil moisture (r = -0.34; Table 2-1). Total root mass remained stable from March 2011 - September 2011 (640-936 g m^{-2}; Figure 2-3D), but decreased to the lowest levels in December 2011 (536-598 g m^{-2}).

Table 2-3. Results of repeated measures ANOVA (p-values) testing the effects of tree harvest method, time, and their interaction on litter and root biomass, TN, SMB-N, SOC, SMB-C, and C_{mic}/C_{org}. Results for the root fractions, TN, SOC, SMB-N and –C, and C_{mic}/C_{org} are for the 0-10-cm depth.

	Harvest	Time	Harvest * Time
Biomass pools (g m^{-2})		p-value [a]	
Litter	0.0800	*<0.0001*	0.6929
Fine roots	0.8821	*<0.0001*	0.6769
Coarse roots	0.8423	0.0731	0.1130
Total roots	0.8155	*0.0017*	0.1643
SOC (g C m^{-2})	0.1828	*0.0002*	0.7579
Total N (g N m^{-2})	*0.0078*	*<0.0001*	0.5016
SMB-C (µg C g^{-1})	*0.0065*	*<0.0001*	*0.0208*
SMB-N (µg N g^{-1})	*0.0031*	*<0.0001*	0.0626
C_{mic}/C_{org}	0.8526	*<0.0001*	0.3701

[a] Italicized p-values are significant.

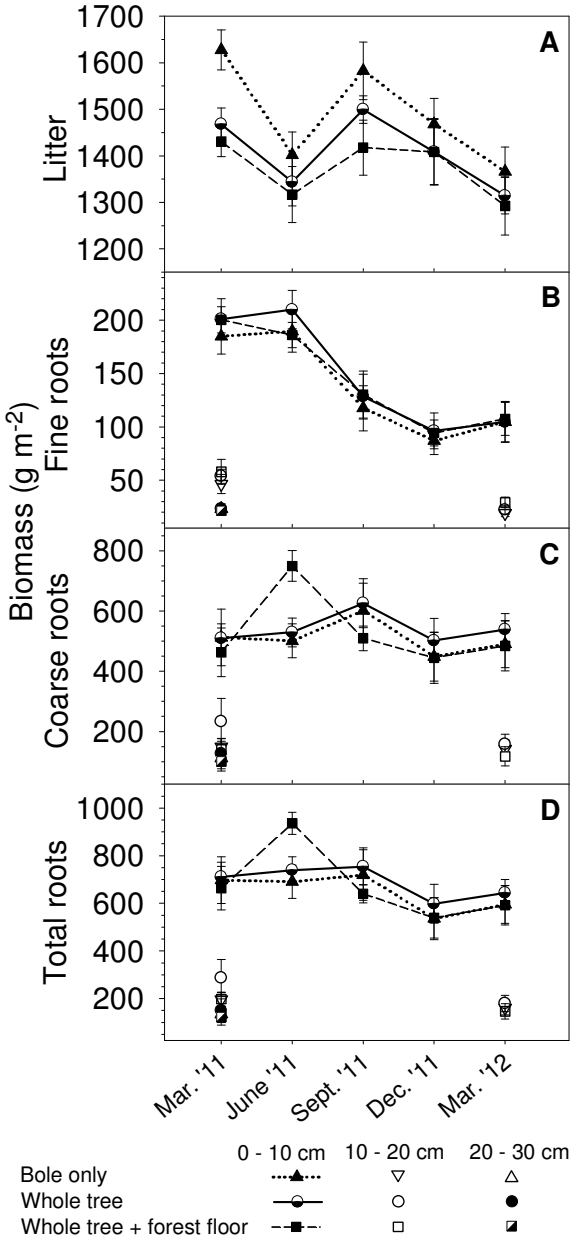

Figure 2-3. Biomass (g m^{-2}) by depth and time of sampling. A) Litter, and B-D) roots. Symbols are means ± S.E. (n = 8).

In March 2011, fine root mass was approximately 73 and 88% lower in the 10-20 and 20-30-cm increments compared to the 0-10-cm increment (Figure 2-3B). Coarse root mass was about 65 and 77% lower in the 10-20 and 20-30-cm increments compared to the 0-10-cm increment (Figure 2-3C). Total root mass in the 10-20 and 20-30-cm increments was about 67 and 81% lower than the 0-10-cm increment (Figure 2-3D). In March 2012, average decreases in root mass were slightly higher than those in March 2011. Fine root, coarse root, and total root mass were 78, 73, and 73% lower in the 10-20-cm increment compared to the 0-10-cm increment (Figure 2-3B-D).

II.4.4 Soil organic carbon and total nitrogen

Soil organic carbon content in the 0-10-cm increment was not impacted by harvest intensity ($p > 0.05$; Table 2-3; Figure 2-4A), but varied significantly over time ($p < 0.05$), and was mirrored in the soil carbon concentrations (g kg^{-1}; data not shown). Soil organic carbon content was negatively correlated with temperature ($r = -0.21$) and positively correlated with soil moisture ($r = 0.29$; Table 2-1). Average SOC was highest in March 2011 (2081±81 g C m^{-2}; Figure 2-4A) and was lowest in June 2011 (1743±55 g C m^{-2}), but recovered in September 2011 (1915±67 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 total nitrogen content was significantly reduced by increasing harvest intensity and varied over time (both $p < 0.05$; Table 2-3). N concentrations (g kg^{-1}; data not shown) were similarly affected by harvest and time. Soil TN content was negatively correlated with temperature ($r = -0.32$) and positively correlated with soil moisture ($r = 0.30$; Table 2-1). Soil TN was highest in the

bole only harvest (74-99 g N m^{-2}; Figure 2-4B) and lowest in the whole tree+forest floor treatment (61-83 g N m^{-2}). Average TN was highest in March 2011 (90±2 g N m^{-2}) and lowest in June 2011 (67±2 g N m^{-2}), and recovered in September 2011 (80±3 g N m^{-2}) and remained stable through March 2012.

Both SOC and TN decreased with depth. In March 2011, SOC in the 10-20 and 20-30-cm increments was 64 and 81% lower than the 0-10-cm increment (Figure 2-4A). Soil OC in March 2012 was approximately 64% lower in the 10-20-cm increment compared to the 0-10-cm increment (Figure 2-4A). Soil TN was approximately 54 and 68 % lower in the 10-20 and 20-30-cm increments in relation to the 0-10-cm increment in March 2011. In March 2012, soil TN was 60% lower in the 10-20-cm increment compared to the 0-10-cm (Figure 2-4B).

II.4.5 Soil microbial biomass

Both SMB-C and –N in the 0-10-cm increment were significantly impacted by harvest intensity ($p < 0.05$; Table 2-3) and varied significantly with time ($p < 0.05$). There was also a significant harvest by time interaction for SMB-C ($p < 0.05$). SMB-C was negatively correlated with both precipitation ($r = -0.11$) and temperature ($r = -0.28$) and SMB-N was negatively correlated with temperature ($r = -0.52$; Table 2-1). Bole only harvest usually had higher SMB-C (199-267 μg C g^{-1}) than the more intense harvests (165-237 μg C g^{-1}; Figure 2-4C). SMB-C on average was highest in March 2011 (238±8 μg C g^{-1}) and lowest in September 2011 (188±8 μg C g^{-1}) (Figure 2-4C). Soil microbial biomass N was generally highest in the bole only harvest (25-37 μg N g^{-1}) compared to the more intensely harvested treatments (21-33 μg N g^{-1}; Figure 2-4D).

From March 2011 to September 2011 SMB-N 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 (Figure 2-4D).

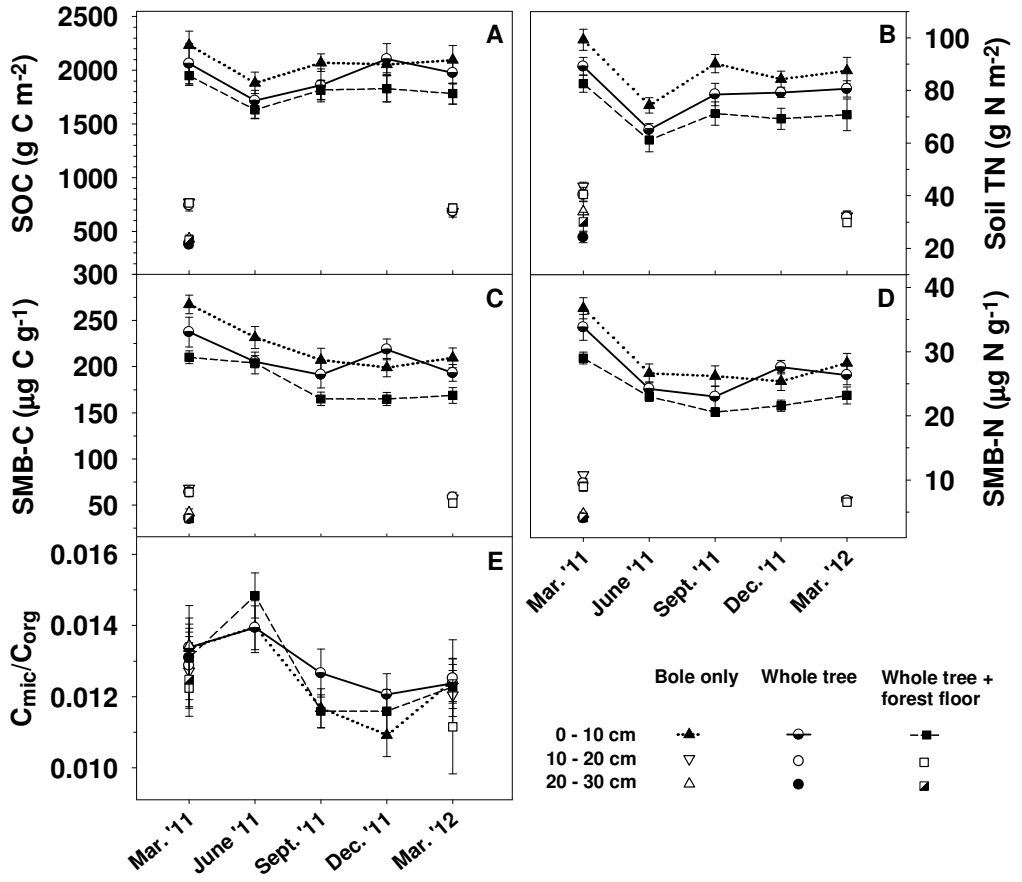

Figure 2-4. A,B) SOC and TN (g m^{-2}), C,D) SMB-C and –N (μg g^{-1}), and E) C_{mic}/C_{org} by depth and time of sampling. Symbols are means ± S.E. (n = 8). C_{mic}/C_{org} caluculated using concentrations of SMB-C and SOC.

Soil microbial biomass-C and -N decreased with soil depth. In March 2011 SMB-C in the 10-20 and 2030-cm increments was approximately 73 and 84% less than the 0-10-cm increment (Figure 2-4C), while SMB-C in March 2012 was 71% lower in the 10-20-cm increment compared to the 0-10-cm increment (Figure 2-4D). In relation to the 0-10-cm increment, SMB-N in March 2011 was 71 and 87% lower in the 10-20 and 20-30-cm increments, and in March 2012 SMB-N was 73% lower in the10-20-cm increment (Figure 2-4D).

Ratios of C_{mic}/C_{org} were unaffected by harvest treatment ($p > 0.05$; Table 2-3), but varied significantly over time ($p < 0.05$), and were negatively correlated with soil moisture ($r = -0.32$; Table 2-1). Over time C_{mic}/C_{org} decreased from highs in March and June 2011 (≈ 0.013) to a low in December 2011 (≈ 0.011; Figure 2-4E). Depth tended not to affect the ratios (Figure 2-4E).

There were significant positive correlations ($p < 0.05$) between SMB-C and –N and litter, fine root, and total root mass, and SOC, and TN (Table 2-1). SMB-C and –N were correlated more with TN ($r = 0.57$ and 0.61, respectively), than SOC ($r = 0.46$ and 0.44, respectively; Table 2-1). Of the correlations between biomass variables and SMB-C and –N, fine root biomass had a stronger relationship ($r = 0.45$ and 0.32, respectively) than did either total root biomass (SMB-C, $r = 0.27$) or litter ($r = 0.22$ and 0.20, respectively; Table 2-1).

II.5. 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 decomposition and ecosystem biogeochemistry. Our results show that increased forest harvest intensity significantly reduced soil TN and SMB-N 15-years following harvest. Litter and root mass, SMB-N, SOC, and TN varied over the course of a single year, and there was a significant harvest x time interaction for SMB-C. 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.

II.5.1 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+forest floor removal resulted in TN (61-83 g N m^{-2}) that was almost 17% lower than the bole only harvest (74-99 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 reduced soil TN persisted through time since harvest.

Soil TN has shown variable responses to harvest in other forest ecosystems throughout the world. Although Johnson and Curtis (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. 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 (Olsson et al. 1996; Jones et al. 2011). 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, repeated measures analyses across five sampling periods over one year indicate that harvest intensity had no effect on SOC in the 0-10-cm soil increment 15-years after treatment. 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 *Pinus taeda* L. in Louisiana and North Carolina (Powers et al. 2005; Sanchez et al. 2006a, 2006b). Increasing harvest intensity has been shown to decrease soil C when compared

to bole only harvests (Johnson and Curtis 2001). These results, while not statistically significant, may have longer-term implications that could ultimately influence the productivity and sustainability of subsequent rotations.

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 (Knoepp and Swank 1997; Carter et al. 2002), we did not expect to see these relatively large variations occurring over short time periods (i.e., 3-months). 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. Variations of both SOC and TN over the study period were negatively correlated with temperature and positively with soil moisture. Higher temperatures tend to enhance decomposition processes so losses were expected with increases in temperature (Campbell and Law 2005); however, because soil respiration was not measured we cannot say definitively that decomposition was higher. Of note is the finding that SMB was also smaller with higher temperatures, suggesting losses may have been due to some other factor such as loss of inputs. The positive relationships with soil moisture may have been a result of increased leaching from the litter layer, which had a negative relationship with precipitation.

II.5.2 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 (Wall

2008; Zerpa et al. 2010; Jones et al. 2011). 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 enabling higher leaf production and subsequently higher litterfall (Zerpa et al. 2010; Jones et al. 2011). 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).

Variation in litter, and fine and total root mass over time tended to be related to environmental variables. Litter mass was negatively related to precipitation, which may indicate increased decomposition during periods of higher rainfall; however others have found decomposition of *P. taeda* needles unrelated to increased irrigation (Sanchez 2001). Fine and total root mass had stronger negative correlations with volumetric soil moisture than with temperature and precipitation. This was not unexpected considering that plants are likely to invest less energy into root production when soil moisture is available (Teskey and Hinckley 1981; Gundersen et al. 1998; Sword et al. 1998a, 1998b; Torreano and Morris 1998; Fisher and Binkley 2000; Tingey et al. 2005).

II.5.3 Harvest and time effects on SMB-C and –N, and C_{mic}/C_{org} ratios

In accordance with our hypothesis that increasing harvest intensity would adversely affect soil microbial biomass, results showed that 15-years after harvest, SMB-N was significantly and negatively impacted. In addition, SMB-C was significantly impacted by a harvest x time interaction, indicating variable responses to harvest among

the sample periods. However, there was a significant trend of lower SMB-C in the more intensely harvested treatments. Throughout this study SMB-C values in the 0-10-cm increment (165-267 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). SMB-N values (21-36 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). Harvest method had no persistent effect on the C_{mic}/C_{org} ratio, suggesting that the quality of the organic matter available to support microbial growth was comparable between treatments (Webster et al. 2001). Ratios of C_{mic}/C_{org} (0.011-0.014) fell within previously reported values for temperate/boreal coniferous forests (0.0093±0.0046) (Wardle 1992).

Soil microbial biomass is generally correlated with substrate quantity (Powlson et al. 1987; Anderson and Domsch 1989; Allen and Schlesinger 2004), however, the longevity of the effects of organic matter removals are less well known and to date variable. Harvest alone has reduced SMB-C and –N in stands <10-years old when compared to reference stands (LeDuc and Rothstein 2007; Mummey et al. 2010). Harvest intensity, on the other hand, has produced mixed results. For example, Smolander et al. (2010) found no differences in SMB-C and –N in *Picea abies* (L.) Karst Norway spruce stands >10-years old, while Busse et al. (2006) and Li et al. (2004) found no differences in SMB-C 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 SMB-N in stands >5-years old, and Hassett and Zak (2005) and Tan et al. (2008) found that harvest intensity decreased both SMB-C and –N in stands of nearly 10-years old. Hassett and Zak (2005) suggested that reduced SMB was driven by reduced litter inputs as well as modified soil microclimate and Li et al. (2004) found that SMB-N was positively related to soil C and N.

Correlation analyses indicated that stronger positive relationships existed between SMB-C and –N and fine root biomass, SOC, and TN, than existed with litter and total root mass. Additionally, SMB-C and –N 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 N, and the C_{mic}/C_{org} ratio varied significantly over the five sampling periods of this study, as did SMB-C, with a confounding harvest x time interaction. Soil microbial biomass C decreased as the soil dried, which was expected (Wardle 1992; Aponte et al. 2010); however, the relationship to soil moisture was not significant. Soil microbial biomass C and N did not increase with increasing soil moisture, which may have been a function of cooler temperatures as well as seasonal changes in plant production (e.g., less fine root mass) (Zak et al. 1994; Aponte et al. 2010) in December 2011 and saturated soils in March 2012.

Variation of C_{mic}/C_{org} over time was significant and seemed to be related to significant negative relationships with SOC and SOC:TN ratio. Although C_{mic}/C_{org} variation followed a pattern similar to that of fine root biomass there was not a significant relationship. This suggests that over the one year course of this study, C

quality decreased or there was less substrate available to the microbes and the microbial biomass is more N than C limited (Wardle 1992; Liao and Boutton 2008). Decreasing C_{mic}/C_{org} over time may have also been due to increased maintenance costs that led to less biomass being produced per unit C during the drier months (Anderson 2003).

II.5.4 Patterns with depth

Decreases in SMB-C and –N with depth have been attributed to decreases in both quantity and quality of substrates (Fierer et al. 2003; Aponte et al. 2010). Results of this study showed that both SOC and TN decreased >50% with depth, and was matched by a decrease of >70% in the SMB-C and –N. Because changes due to depth were relatively similar there was little decrease in the C_{mic}/C_{org} ratio with depth.

II.6. Conclusions

Little is known regarding the biogeochemical consequences of tree harvest methods in forest ecosystems located in the Gulf Coastal Plain of the southeastern USA. We found that forest harvest intensity in the western Gulf Coastal Plain significantly reduced soil TN, and SMB-C and –N. Moreover, these reductions have persisted for 15 years since the treatments were imposed. The persistent reduction of SMB in the most severe harvest treatments suggests that rates of key biogeochemical processes may be altered which could constrain mineralization rates of limiting nutrients and reduce the productivity of future forest rotations. Reductions in forest productivity will likely diminish their economic value and compromise the ability of these ecosystems to function as carbon sinks and mitigate the potential for future global changes.

CHAPTER III

SOIL C, N, AND P STORES CHANGE IN RESPONSE TO TREE HARVEST PRACTICES IN LOBLOLLY PINE FOREST IN SOUTHERN USA

III.1. Synopsis

Plantation forestry is central to supplying the global demand for forest products, and as such it is important to understand the impacts of harvest on soil biogeochemical cycling and nutrient storage in these plantations to ensure the productivity and sustainability of future rotations. The degree to which biogeochemical cycling is influenced is dependent on the extent to which the ecosystem is disturbed, and losses may be especially problematic in soils that are already nutrient deficient. We investigated the effect of tree harvest intensity, soil compaction, and their interactions on soil total P (TP), total N (TN), and soil organic carbon (SOC) at two soil depths (0-10- and 10-20-cm) in a *Pinus taeda* L. forest in the western Gulf Coastal Plain, USA 15-years following treatment. Treatment combinations consisted of three tree harvest methods (bole only, whole tree, whole tree+forest floor removal) in factorial combination with three soil compaction intensities (none, intermediate, severe). In the 0-10 cm depth increment, the whole tree+forest floor removal treatment reduced TP by 14% and TN by 18% compared to the bole only treatment. Although SOC was lower in the more severe harvest treatments, this difference was not significant. There was no evidence of harvest effect in the 10-20-cm soil increment, but TP, TN, and SOC were significantly lower in the deeper soil. Soil C:N and C:P ratios were unaffected by

increasing harvest intensity in both soil depths. Results of this study demonstrate the importance of maintaining forest floor materials on site following harvest in order to prevent decreases in soil stores of N and P, which are usually the two most limiting nutrients in forest production systems. Removal of the forest floor resulted in significant reductions of limiting nutrients that may ultimately lead to diminished productivity.

III.2. Introduction

Plantation forestry plays a critical role in supplying the growing global demand for forest products (FAO 2010a). The US alone removes the greatest proportion of global wood volume from its forests, and accounts for 16% of the total ≈ 3.4 billion m^3 global wood removals (FAO 2010a). In the southern US, land area devoted to pine plantations is increasing (Carter and Foster 2006), but forest production across this region is generally N and P limited (Haywood et al. 2003; Carter and Foster 2006; Will et al. 2006; Fox et al. 2007; Campoe et al. 2013; Johnsen et al. 2013). Disturbance of carbon and nutrient cycles due to the removal or redistribution of forest biomass and concurrent soil compaction during harvest activities may ultimately deplete ecosystem nutrient capital and diminish forest production capacity. As more biomass is removed (e.g., whole tree harvest, windrowing) or stand rotations are shortened, increasing amounts of nutrients are removed (Metz and Wells 1965; Switzer et al. 1978; Tew et al. 1986; Yanai 1998). Additionally, soil compaction caused by forest harvesting may alter the rates of nutrient cycling processes due to changes in the soil physical environment (Greacen and Sands 1980; Fisher and Binkley 2000; Ampoorter et al. 2007; Blazier et al. 2008; Labelle and Jaeger 2011; Berisso et al. 2012). For example, soil compaction may

alter soil-atmosphere gas exchange and change water infiltration and retention characteristics, thereby modifying the chemical and physical environment of decomposer organisms.

The impact of forest management on soil C and N storage has been shown to be variable and dependent on factors such as inherent site qualities, climate, and management intensity (e.g., Knoepp and Swank 1997; Johnson and Curtis 2001; Carter et al. 2002; Goetz et al. 2012; Johnson et al. 2003; Laiho et al. 2003; Powers et al. 2005; Kiser et al. 2009; Nave et al. 2010; Vanguelova et al. 2010; Jones et al. 2011; Grand and Lavkulich 2012). Whole tree harvesting and removal of forest harvest residues by either burning or redistribution directly impact ecosystem C and N storage by removing potential soil organic matter inputs (Kimmins 1977; Spangenberg et al. 1996; Carter et al. 2002; Li et al. 2003; Scott et al. 2004; Powers et al. 2005; Carter and Foster 2006; Wall 2008; Jones et al. 2011; Trettin et al. 2011; Wilhelm et al. 2013). Additionally, indirect losses may occur due to changes in the soil microclimate that enhance the decomposition and losses of soil nutrient capital (Londo et al. 1999; Carter et al. 2002; Gough et al. 2005). Soil compaction resulting from forest harvest operations may serve to protect soil organic matter from decomposition and result in no observable impacts (de Neve and Hofman 2000; Tan et al. 2005; Mariani et al. 2006; Sanchez et al. 2006a), or it may destroy soil aggregates thus exposing soil organic matter to microbial decomposition and potentially losses (Torbert and Wood 1992; Jordan et al. 2003).

Temperate forests have been thought to be largely N limited. However recent studies indicate that forests are likely both N and P limited (Elser et al. 2007; Fox 2007;

Kiser and Fox 2012). Despite the importance of P to plant nutrition, relatively little is known about the impact of forest management on soil P; this is especially true for the coarse-textured, acidic soils of the Gulf Coastal Plain, USA. Because P is rather immobile in acidic soils due to adsorption and precipitation with Fe and Al, relatively little is lost from the soil via leaching following harvest operations (Wood et al. 1984; Vitousek and Howarth 1991; Yanai 1998; Gravelle et al. 2009; Schlesinger and Bernhardt 2013). Instead, the greatest P losses are generally due to the removal of biomass from a site. Investigations examining the effects of forest harvest on soil total P have found no impact due to harvest (Palmer et al. 2005; Zerpa et al. 2010), and decreases in available P were due to decreased organic matter and decreased microbial and enzyme activity (Hassett and Zak 2005; Palmer et al. 2005; Sanchez et al. 2006a; Tan et al. 2008).

Despite orders of magnitude differences in soil C, N, and P abundances, soil C:N:P stoichiometry has been found to be well constrained globally across vegetation types (Cleveland and Liptzin 2007). In addition, forest foliar and litter C:N:P stoichiometry is also well controlled within forest biome types (McGroddy et al. 2004). With forest harvest practices that remove increasing amounts of biomass, or compaction that changes soil biogeochemical cycling, plant-soil nutrient feedback may become decoupled and result in altered soil C:N:P relationships. For example, as C:P and N:P ratios increase there is the expectation that P is accumulating more slowly than C and N, which may result in diminished site productivity (Cleveland and Liptzin 2007).

The purpose of this study was to determine the impact of forest harvest intensity, soil compaction, and their interaction on soil C, N, and P storage in a *Pinus taeda* L. (loblolly pine) forest 15-years post-treatment. Using the experimental plots at the Long-Term Soil Productivity site located near Groveton, Texas, USA (hereafter "Groveton LTSP") we quantified soil organic carbon (SOC), total N (TN), and total P (TP). Because of the increased removal of aboveground biomass and the changes in soil physical characteristics we hypothesized that, at mid-rotation, SOC, TN, and TP would be lowest and C:N:P ratios would be highest under the most intense forest management regimes.

III.3. Materials and methods

III.3.1 Study area

Soil samples were collected in March 2011 at the Groveton, Texas Long-Term Soil Productivity (LTSP) site (31°06' 32.48"N, 95°09' 59.15"W) located in the Davy Crockett National Forest in southeastern Texas. Mean annual temperature is 19.1° and mean annual precipitation is 1135 mm (1981-2010) that is bimodal with peaks in May-June and October. Climate data was accessed from the National Oceanic and Atmospheric Administration, data was recorded at Crockett, Houston County, TX (≈38-km northeast of the study site). Elevation across the site is 101 to 110-m with slopes between 1-3%. Soils across the study area are moderately well drained fine-loamy siliceous, thermic Oxyaquic Glossudalf in the Kurth series.

The Groveton LTSP site was established in 1997 and is a 3X3 full factorial experiment replicated three times. The main factors consist of three harvest intensities

(merchantable bole/stem only, whole tree, and whole tree+forest floor removal) and three levels of soil compaction (none, intermediate, and severe) (Powers 2006) for a total of nine treatments on 0.4-ha plots. Half of each plot received glyphosate herbicide treatment shortly after replanting and was applied once per year for five years, and the other half received no herbicide. Harvesting on the Groveton LTSP site was accomplished with a Feller buncher and skidder 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). Compaction was accomplished with the use of a 9Z pneumatic-tired roller that was loaded to 2.4 Mg m^{-1} for the moderate and 4.2 Mg m^{-1} for the severe compaction treatment, and passed over the soil a total of six times (Rick Stagg, USDA Forest Service, personal communication). Forest floor materials were removed from forest floor removal treatments by hand raking all organic matter from the plots down to the mineral soil. Containerized *P. taeda* L seedlings of ten half-sib families from US Forest Service seed orchards were hand planted on a 2-m x 2-m spacing.

III.3.2 Sample collection

Prior to sampling in March 2011, each split-plot (herbicided and non-herbicided halves) was divided into five "sub-plots"; four "sub-plots" were established at each corner and one central within the split-plot. This method was used to ensure sample points were located throughout the plots. Sample points were then randomly located within the "sub-plots" midway between two living *P. taeda* L stems interior to a three tree outer buffer. Occasionally sampling occurred within the buffer due to mortality in

some plots. At each sample point, a 0-20-cm soil core was obtained using a 4.8-cm internal diameter split corer (AMS, Inc., American Falls, ID, USA). Cores were then divided into 0-10 and 10-20-cm increments and pooled in the field by increment per split-plot. Soil samples were stored in coolers with ice in the field and maintained at 4°C in the lab until processed.

III.3.3 Soil chemical characterization

Soil samples were mixed well in the lab and an aliquot was dried at 105°C for bulk density and moisture determination. 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 soil to 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 finely ground in a TE250 ring pulverizer (Angstrom, Inc., Belleville, MI, USA) for subsequent elemental analysis. An additional sieved soil aliquot was dried at 105°C and analyzed for soil texture using the hydrometer method (Bouyoucos 1927; Ashworth et al. 2001).

III.3.4 Total phosphorus determination

Total P was determined on duplicate samples from finely ground soils from the 0-10 and 10-20-cm intervals using the lithium fusion technique (Lajtha et al. 1999). Briefly, 250-mg soil was mixed well with 750-mg lithium metaborate in a graphite crucible and heated in a muffle furnace at 1000°C for 15-minutes until white hot. The molten flux was then poured into 50-mL of 10% nitric acid and stirred for 1.5 hours until fully dissolved. Total P concentration of the extract was determined using a modified

molybdenum blue method (Murphy and Riley 1962; Dick and Tabatabai 1977). Color development was achieved by mixing 4-mL of the extract solution with ammonium molybdate reagent (20-g in 500-mL H_2O) and antimony potassium tartrate reagent (1.454-g in 500 mL H_2O). Colorimetric analysis was performed on a Spectronic 20D+ (Thermo Fisher Scientific Inc., Waltham, MA, USA) set at 720-nm transmittance (Dick and Tabatabai 1977). Concentration of total soil P was calculated based on a standard curve of potassium phosphate solution (0, 2.5, 5, 7.5, and 10 μg mL^{-1}). Phosphorus analyses were standardized using San Joaquin soil (SRM 2709a; National Institute of Standards and Technology); repeated measurements of this standard yielded a relative standard error of 677 mg P kg^{-1} ±1.3%, where RSE equals the standard error divided by the estimate of P throughout analysis multiplied by 100.

III.3.5 Carbon and nitrogen concentrations

Soil samples from the 0-10 and 10-20-cm intervals were analyzed for %C and %N 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). Repeated measurements of the acetanilide standard yielded relative standard deviations of ± 0.17 % for C and ± 0.10 % for N.

III.3.6 Statistical analyses

There were no statistically significant effects due to soil compaction, harvest x compaction interaction based on general linear models, or herbicide treatment based on *t*-tests. Findings are reported by harvest, with each harvest/compaction combination acting as one replicate (n=9). Analysis of variance (ANOVA) was used to determine if

there were differences in TP, SOC, TP, soil bulk density and moisture, and C:N, C:P, and N:P ratios based on harvest intensity. Post hoc Tukey-Kramer HSD was used to determine differences between treatments when ANOVA showed significant treatment effects. Analysis of covariance (ANCOVA) was used to determine if there were differences in SOC, TN, and TP, and C:N, C:P, and N:P ratios based on depth. A significance level of $\alpha \leq 0.05$ was used throughout statistical testing.

III.4. Results

III.4.1 Soil properties

Soil texture analyses indicated that the soil is loamy sand throughout the 0-20-cm sampling depth (Table 3-1). Clay concentrations in the two soil increments were similar and ranged from 48-154 g kg^{-1}. Silt concentrations ranged 145-283 g kg^{-1} and sand concentrations ranged from 612-791 g kg^{-1}. Overall, soil pH was acidic (Table 3-1) and ranged from 3.5-4.7 in the 0-10-cm increment and 3.7-4.6 in the 10-20-cm increment. Volumetric soil moisture at the time of sampling was uniform in the upper 20-cm of the soil column and ranged from a low of 0.08 g cm^{-3} in both soil increments to highs of 0.13 and 0.15 g cm^{-3} in the 0-10- and 10-20-cm increments, respectively (Table 3-1). Neither soil pH nor soil moisture was affected by harvest intensity ($p > 0.05$). Bulk density ranged from 0.97-1.25 g cm^{-3} at 0-10-cm, and from 1.27-1.50 g cm^{-3} at 10-20-cm.

III.4.2 Effects of harvest intensity and depth on TP, TN, and SOC

Soil total P in the 0-10-cm depth interval was 10 and 15% greater in the bole only treatment (9.08 ±0.42 g P m^{-2}) versus the whole tree (8.16 ± 0.24 g P m^{-2}) and

whole tree+forest floor removal treatment (7.69 ± 0.47 g P m^{-2}) respectively (Figure 3-1a). The effect of harvest intensity was significant (ANOVA, $p \leq 0.05$). The differences between harvest intensities in the 10-20-cm interval were not significant (Figure 3-1a). Total P was significantly greater in the 0-10-cm soil interval (16-21%) compared to the 10-20 cm depth (Figure 3-1a).

Table 3-1. Bulk density, soil particle distributions, pH, and soil moisture averaged across all study plots at the time of sampling. Based on the percentages of sand, silt, and clay the site has a soil classification of loamy sand.

Depth (cm)	Bulk density (g cm^{-3})ǂ	Soil texture (g kg^{-1})*			pHǂ	Soil moisture (g cm^{-3})ǂ
		Sand	Silt	Clay		
0 – 10	1.12±0.01	755±7	180±5	65±3	4.15±0.06	0.104±0.003
10 – 20	1.43±0.01	737±8	193±6	70±5	4.23±0.05	0.109±0.003

ǂ Means ± S.E., $n = 27$ * Means ± S.E., $n = 24$

Total nitrogen at 0-10-cm was significantly greater ($p < 0.05$) in the bole only treatment (97.6 ± 3.9 g N m^{-2}) compared to the whole tree (88.4 ± 3.1 g N m^{-2}) and whole tree+forest floor removal (81.1 ± 3.2 g N m^{-2}) treatments (Figure 3-1b). Although bole only harvest had higher TN, there was not a significant harvest effect in the 10-20-cm soil interval. There was significantly higher TN in the 0-10-cm soil interval (81-98 g N m^{-2}) compared to the 10-20-cm interval (40-43 g N m^{-2}), with the greatest difference occurring in the bole only treatment (Figure 3-1b).

Harvest intensity had no effect on SOC at either depth interval, but on average the bole only treatment (2202 ± g C m^{-2}) had slightly higher SOC than the two more

intense harvests (1911-2060 g C m^{-2}) in the 0-10-cm interval. However, this trend was not evident in the 10-20-cm increment where SOC averaged 758 ± 19.5 g C m^{-2} across all treatments (Figure 3-1c). The decrease in SOC with soil depth was significant ($p < 0.001$). The greatest depth effect was seen in the bole only harvest treatment (Figure 3-1c).

III.4.3 C:N, C:P, and N:P ratios

Soil C:N, C:P, and N:P ratios tended to increase, albeit not significantly, with increasing forest harvest intensity (Table 3-2). Depth significantly impacted all ratios ($p < 0.05$). In the 0-10-cm interval C:N ratios were 17-21% higher than the 10-20-cm ratios, with the bole only treatment exhibiting the greatest difference. Both C:P and N:P ratios were approximately 50% lower in the 10-20-cm depth increment compared to 0-10-cm.

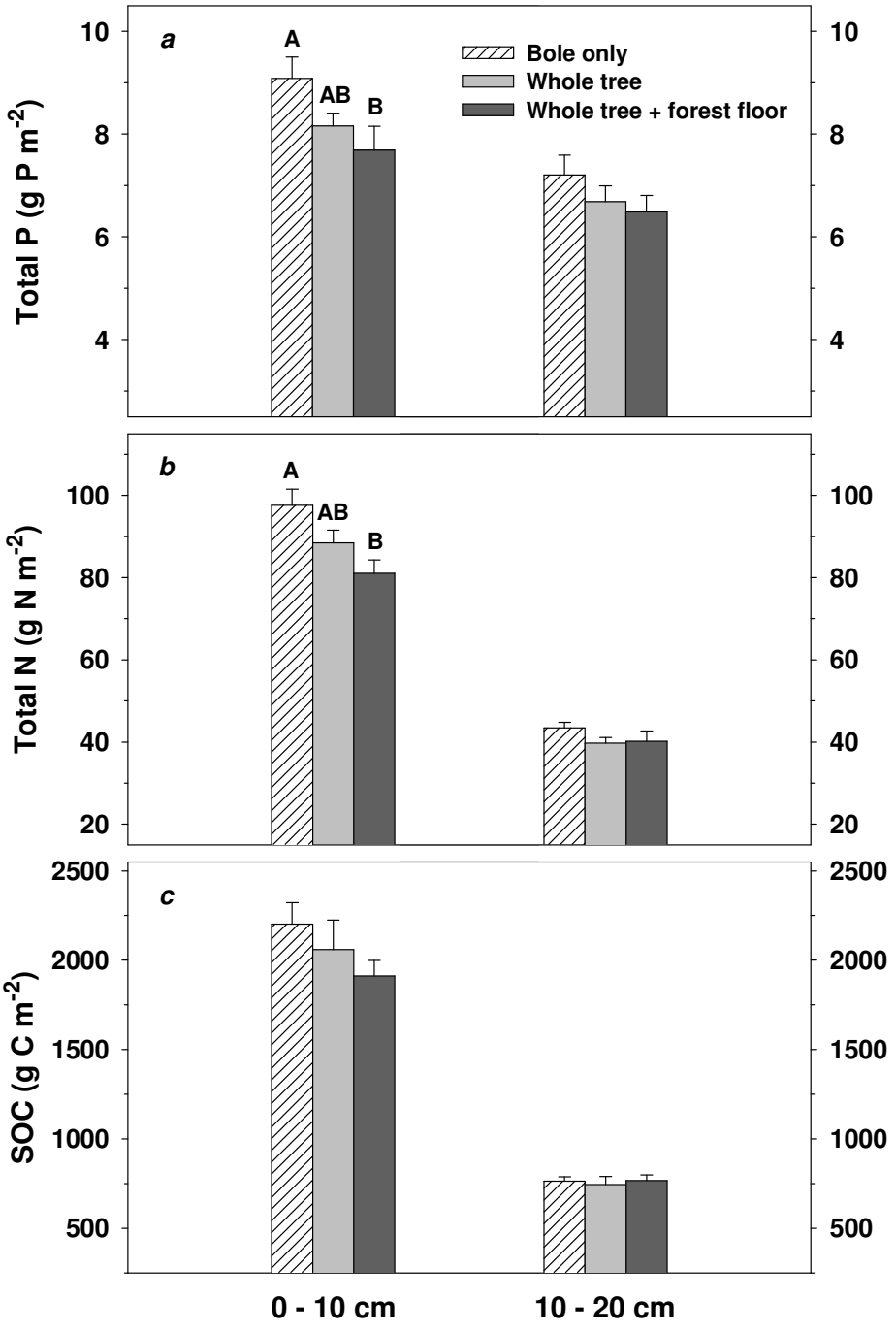

Figure 3-1. Total P (*a*), SOC (*b*), and Total N (*c*) (g m^{-2}) at 0-10- and 10-20-cm in different forest harvest treatments. Means ± S.E., $n = 9$. Bars with different letters are different in the 0-10-cm increment.

Table 3-2. Soil C:N, C:P, and N:P ratios in different forest harvest treatments.

	0 – 10-cm			10 – 20-cm		
	Bole only	Whole tree	Whole tree + forest floor	Bole only	Whole tree	Whole tree + forest floor
C:N[a]	22.5±0.7	23.0±1.2	23.6±0.5	17.8±0.9	18.9±1.3	19.7±1.1
C:P[a]	249.5±16.6	258.8±21.6	267.6±21.1	108.6±6.7	115.9±10.9	121.5±7.2
N:P[a]	11.0±0.4	11.1±0.4	11.3±0.7	6.1±0.2	6.1±0.3	6.3±0.5

[a] Means ± S.E., $n = 9$

III.5. Discussion

Forest harvest intensity and simultaneous soil compaction may modify soil conditions in such a way to alter biogeochemical cycling within the ecosystem. The results of this study supported our prediction that TP and TN would be lowest under the most intense forest harvest regime in the upper 10-cm soil increment, but the effects of harvest were not evident in the soil below this level. Although SOC decreased with increasing forest harvest in the top 10-cm of soil, it was not significant, and likewise was not evident below this level. Elemental ratios tended to increase, albeit non-significantly, with increasing forest harvest intensity. Neither soil compaction nor its interaction with forest harvest intensity affected TP, TN, or SOC or elemental ratios in this western Gulf Coastal Plain site 15-years post-treatment.

The results of this study indicate that there are long-lasting negative impacts on soil TP and TN as a consequence of increasing tree harvest intensity. In the 0-10-cm soil increment, soil TP was 10-15% greater in the bole only harvest versus the whole tree and

whole tree+forest floor removal treatments, below this depth, harvest impact was not evident. Total soil P consists of several fractions that differ in the degree to which they are available for plant and microbial uptake, and the degree to which they are susceptible to losses via leaching. For example, in a South Carolina pine forest, the size of the labile soil P pool remained relatively constant during 40 years of forest aggradation, while the more "slowly cycling" fractions (e.g., organic and inorganic P associated with Fe and Al oxides) became reduced in size as they buffered the uptake of labile P by the forest biomass (Richter et al. 2006). At this time we cannot say definitively which P fraction contributed to P losses. Nonetheless, similar studies have found that the removal of forest floor decreased available P in Louisiana and North Carolina due to the losses in organic matter pool that stores a substantial portion of total soil P (Sanchez et al. 2006a). In addition, a strong positive correlation has been found between available P and TP (Tan et al. 2008). While P losses at the Groveton LTSP site may be attributable to available P, we cannot rule out the possible losses of more recalcitrant P associated with Fe and Al in these acidic soils. While litter may be an important source of mineralizable P, it may not be adequate to overcome the losses of P in the most severe harvest treatment (Haywood et al. 2003).

Soil TN in the bole only treatment in 0-10-cm increment was 9-17% greater than the whole tree and whole tree+forest floor removal treatments, but beyond this depth harvest effects were not apparent. The magnitude of these differences is similar to those seen in soil TP. Although Sanchez et al. (2006a) found decreases in available P in 10-year old *P. taeda* stands in Louisiana and North Carolina, they found no overall effect of

forest harvest intensity on TN. In contrast, Jones et al. (2011) found that soil N concentrations in the upper 10-cm of the soil profile were significantly lower in treatments in which the forest floor was removed 15-years earlier in a *Pinus radiata* plantation in New Zealand. They suggested that because soil moisture was lower in the forest floor removal treatment, microbial decomposition was probably low, and the more likely scenario was that lower N was a result of reduced input until the forest floor had fully regenerated.

Similar to other studies, SOC was not significantly impacted by forest harvest intensity (Powers et al. 2005; Hoover 2011), but there was a tendency for decreasing content with increased harvest. Powers et al. (2005) attributed the lack of SOC response to root decomposition from the harvested stand and changes in bulk density. Tree harvest methods had no effect on SOC at 10-20 cm, suggesting that deeper soil carbon may be less sensitive to harvest effects in this region.

III.6. Conclusions

Forestlands across the southern USA are generally N and P limited and tree harvest accompanied by soil compaction may diminish these nutrients even further. Results of this study showed that increasing biomass removal during harvest had a significant long-lasting (*c*. 15-years) negative impact on both N and P, but compaction did not. We suggest that following harvest of the current stand, the deficit in the more intensely harvested plots may become more pronounced. In turn this may lead to diminished productivity of the subsequent rotation. The results of this study emphasize

the importance of maintaining the forest floor in place following harvest in southern forests to maintain soil fertility and future productivity.

CHAPTER IV

SOIL NITROGEN POOLS AND $\delta^{15}N$ RESPONSES TO TREE HARVEST IN THE WESTERN GULF COASTAL PLAIN 15 YEARS AFTER TREATMENT

IV.1. Synopsis

Forest harvesting increases radiation reaching the soil surface, decreases transpiration and rainfall interception, and increases the amount of precipitation reaching and infiltrating into the soil. The magnitude of these impacts varies with intensity of tree harvest method, but generally result in soil conditions that favor microbial activity and accelerate N-cycling processes potentially resulting in N losses from the ecosystem. Forest harvest that removes increasing amounts of aboveground biomass results in greater N losses, potentially limiting the productivity and sustainability of future rotations. In addition, soil compaction during tree harvest may influence the potential for N losses by altering soil structure, gas exchange, and water infiltration. To determine the impact of forest harvest intensity, soil compaction, and their interaction on N-cycling we quantified N and $\delta^{15}N$ in the litter, roots, and soil in a *Pinus taeda* L. forest in eastern Texas 15-years post-treatment. Sampling was conducted quarterly from March 2011 to March 2012 on experimental forest plots subjected to three harvest methods (bole only, whole tree, whole tree+forest floor removal) in factorial combination with three soil compaction levels (none, intermediate, severe). Litter N pool sizes were reduced by increasing harvest intensity and varied seasonally, and were highest in the bole only treatment (10-13 g N m^{-2}) and lowest in the whole tree+forest floor removal treatment

(9-10 g N m^{-2}). Soil total N in the 0-10-cm increment was also reduced by increasing harvest removal and was highest in the bole only harvest (74-99 g N m^{-2}) and lowest in the whole tree+forest floor removal treatment (61-83 g N m^{-2}). Tree harvest methods had no effect on total root N pool in the upper 10-cm of the profile; however, root N varied through time. Soil $\delta^{15}N$ was always lowest in the bole only treatment (1.21-1.96‰), and highest in the more intensely harvested treatments (1.41-2.72‰). Higher soil $\delta^{15}N$ suggests N-losses following tree harvest were greater in the more intense harvest treatments, consistent with smaller N pool sizes observed in those treatments. There was no harvest effect beyond the 10-cm depth, and neither soil compaction nor the harvest method x compaction interaction affected any response variables. Results indicate that forest harvest practices that removed the most aboveground biomass resulted in significant ecosystem N-losses that have yet to recover even 15-yrs following treatment. Since N is a limiting nutrient for tree growth in the sandy soils of the Gulf Coastal Plain, tree harvest practices that favor N-retention will help ensure the continuity of ecosystem services and sustain the productivity of forestlands in this region.

IV.2. Introduction

Forest harvesting increases the amount of solar radiation reaching the soil surface, decreases transpiration and rainfall interception, and increases the amount of precipitation reaching and infiltrating the forest floor and into the soil. The magnitude of these impacts will vary with the intensity of the tree harvest method, but generally result in warmer and wetter soils that favor microbial activity and accelerate N cycling processes that can result in leaching and gaseous N losses from the ecosystem (Bormann

and Likens 1979; Paul et al. 2003; Jerabkova et al. 2011). More intense forest harvest (i.e., removal of increasing amounts of aboveground biomass) results in greater N losses due to removal non-bolewood materials that contain higher concentrations of N, potentially limiting the productivity and sustainability of future rotations.

Major exports of N from forest stands occur when more than the merchantable bole is harvested. Studies across a broad range of forest types and bioclimatic regions indicate that when tree harvest events remove the whole tree or a combination of whole tree+forest floor, N exports range from 0.60 to 11 times higher compared to bole only harvest (Kimmins 1977; Spangenberg et al. 1996; Carter et al. 2002; Li et al. 2003; Scott et al. 2004; Powers et al. 2005; Carter and Foster 2006; Wall 2008; Jones et al. 2011; Trettin et al. 2011; Wilhelm et al. 2013). However, the response of soil total N stores to increasing harvest intensity appears to be variable and inconsistent. While some studies have reported no changes in soil total N (Olsson et al. 1996; Johnson and Todd 1998; Carter et al. 2002; Scott et al. 2004; Choi et al. 2005; McLaughlin and Phillips 2006), others have reported significant decreases (Scott et al. 2004; Choi et al. 2005; Powers et al. 2005; Sanchez et al. 2006a; Jones et al. 2011) that may persist for more than a decade in some forest soils (Sanchez et al. 2006a). Two meta-analyses found that harvest had no effect on soil total N (Johnson and Curtis 2001; Jerabkova et al. 2011). However, Johnson and Curtis (2001) found that bole only harvest increased soil N versus a decrease when the whole tree was harvested. In contrast, Jerabkova et al. (2011) found that harvest intensity did not affect post-harvest response. Although the Johnson and Curtis (2001) meta-analysis included sites from southeastern USA, there were no studies

available to represent responses in the ecologically and economically important forests of the western Gulf Coastal Plain.

Soil compaction often occurs during forest harvest, and modifies soil structure and porosity, and increases bulk density and soil strength, which may reduce aeration, gas exchange, and water infiltration (Fisher and Binkley 2000; Powers et al. 2005; Tan et al. 2005; Ampoorter et al. 2007; Labelle and Jaeger 2011), with potential implications for N cycling processes. For example, alteration in the soil atmosphere may ultimately lead to a change in N cycling by reducing N mineralization (Breland and Hansen 1996; Tan and Chang 2007) and/or nitrification (Tan et al. 2005; Tan and Chang 2007). Alternatively, compaction may have no effect on N mineralization (de Neve and Hofman 2000; Shestak and Busse 2005). A reduction in mineralization could reduce the amount of N available for plant uptake, and hence forest productivity. Furthermore, soil compaction may hinder growth and exploration of the soil profile by roots and mycorrhizal hyphae, potentially limiting access to water and nutrients, reducing above- and belowground plant productivity and organic matter inputs to the soil (Gomez et al. 2002; Ludovici 2008).

Natural $\delta^{15}N$ values of plants and soils are useful for studying N-cycle processes at spatial scales ranging from the individual organism to the globe (Nadelhoffer and Fry 1994; Hogberg 1997; Robinson 2001; Amundson et al. 2003; Craine et al. 2009; Pardo and Nadelhoffer 2010), and are sensitive to the effects of ecosystem disturbance (Bai et al. 2013). At equilibrium, soil $\delta^{15}N$ is regulated mainly by inputs (e.g., N-deposition and N-fixation) and outputs (e.g., N leaching and trace gas effluxes), but is unaffected by

internal N cycling processes that result in no net N loss such as plant uptake or microbially-mediated N-transformations (Brenner et al. 2001; Houlton et al. 2007; Bai and Houlton 2009; Houlton and Bai 2009; Koba et al. 2012). Following an ecosystem disturbance such as a forest harvest event, rates of N-transformations (e.g., nitrification, denitrification) are often accelerated (Bai et al. 2013) and can lead to N-losses via leaching and/or trace gas fluxes. Since these N-transformations also cause N isotope fractionation, disturbances often alter the $\delta^{15}N$ values of ecosystem components. $\delta^{15}N$ values of plant tissues, litter, and soils in forest ecosystems have been used to examine the consequences of fertilization, timber harvest, litter manipulations, and soil compaction on N cycle properties and processes (Nadelhoffer and Fry 1988; Johannisson and Hogberg 1994; Pardo et al. 2002; Choi et al. 2005*;* Sah and Ilvesniemi 2007; Garten et al. 2011), but few have examined ^{15}N responses on a seasonal basis (e.g., Feigen et al. 1974; Neilson et al. 1998) or seasonally in forests (e.g., Ometto et al. 2006).

The Long-Term Soil Productivity (LTSP) study is a multinational program aimed at understanding relationships between land management and sustainable forest productivity (Powers 2006). All sites within this network employ a common experimental design of three tree harvest methods (merchantable bole/stem only, whole tree, whole tree+forest floor removal) and three soil compaction intensities (none, intermediate, and severe) in factorial combination. An LTSP site was established in the Davy Crockett National Forest (herein after Groveton LTSP) in eastern Texas, USA, which represents the westernmost extent of the southern pine region (Siska et al. 2006) and lies at the ecotone between forest and grassland biomes. As such, this region may

be exceptionally vulnerable to changes in temperature and rainfall predicted for the future (Schmandt et al. 2009), and these climate change drivers may interact with forest management practices to influence nutrient pools and dynamics. Despite its unique ecological setting, little is known regarding the impacts of forest management practices on N-cycling in this region.

The purpose of this study was to determine the impact of forest harvest intensity, soil compaction intensity, and their interaction on N-cycling in a *Pinus taeda* L. (loblolly pine) forest 15-years following treatment. To accomplish this we quantified N and $\delta^{15}N$ in the litter, root, and soil compartments. Using experimental plots at the Groveton LTSP site, three broad hypotheses were tested that address the importance of forest management practices on N-cycling: 1) tree harvest, soil compaction, and their interaction will result in soil total N that is lowest in the most severe treatments; 2) lower soil N stores in the most severe treatments will be accompanied by smaller N pool sizes in the litter and root compartments; and 3) greater N losses in the most severe treatments will be reflected in higher $\delta^{15}N$ values in the litter, root, and soil compartments.

IV.3. Materials and methods

IV.3.1 Study area

Soil and forest floor samples were collected five times from March 2011 through March 2012 at the Groveton LTSP site, Texas, USA (31°06' 32.48"N, 95°09' 59.15"W). Mean annual temperature is 19.1° and mean annual precipitation is 1135 mm (1981-2010) that is bimodal with peaks in May-June and October (Figure 4-1). Climate data was recorded at Crockett, Houston County, TX (≈38-km northeast of the study site) and

subsequently obtained from the National Oceanic and Atmospheric Administration. Topography at the study site is nearly flat with slopes of 1-3% and elevation ranging from 101 m to 110 m. Soil within the study area is classified as a fine-loamy siliceous, thermic Oxyaquic Glossudalf in the Kurth series.

The Groveton LTSP site was established in 1997 as a full factorial experiment replicated three times on 0.4-ha plots. Experimental treatments consist of three harvest intensities (merchantable bole/stem only, whole tree, and whole tree+forest floor removal) and three levels of soil compaction (none, intermediate, and severe) (Powers 2006). Glyphosate was applied to one-half of each plot one time per year for five years following harvest, while the other half did not receive herbicide. Harvesting on the Groveton LTSP site was accomplished with a Feller buncher and skidder 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). Forest floor was removed by hand-raking all aboveground organic matter to the mineral soil from the whole tree+forest floor removal treatments. Moderate and severe compaction were accomplished with a 9Z pneumatic-tired roller (W.E. Grace Manufacturing Co., Dallas, TX, USA) towed by a tractor that was loaded to 2.4 Mg m^{-1} and 4.2 Mg m^{-1}, respectively (Rick Stagg, USDA Forest Service, personal communication). Each treatment plot was hand-planted with containerized *P. taeda* L. seedlings from 10-half-sib families from US Forest Service seed orchards on a 2m x 2m spacing.

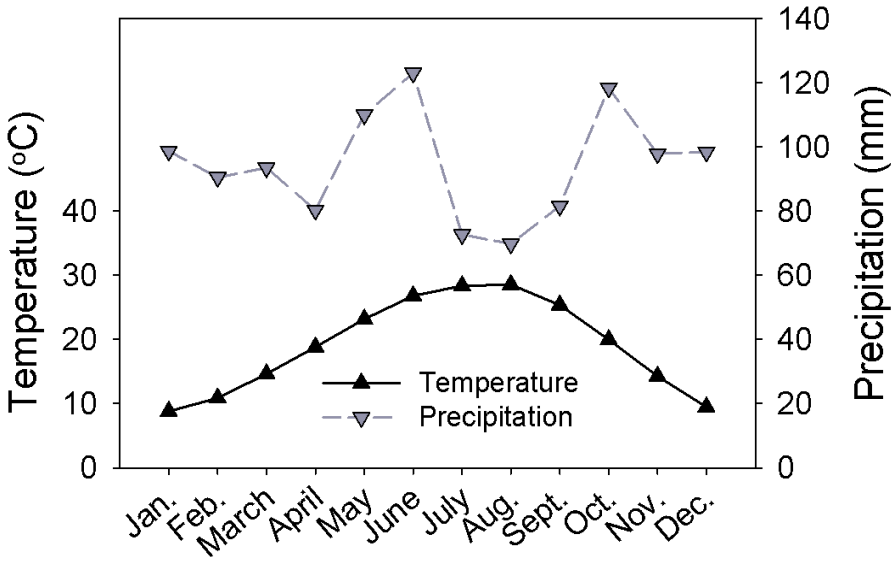

Figure 4-1. Average climate conditions (1981-2010) for Crockett, Houston County, Texas (31° 18' 25.92" N, 95° 27' 3.24" W). The mean annual temperature is 19.1°C with mean annual precipitation of 1135 mm. Data is from the National Oceanic and Atmospheric Administration (http://www.ncdc.noaa.gov/dailyform/DlyFORMv2).

IV.3.2 Sample collection

Sampling occurred in March, June, September, and December 2011, and March 2012. Prior to sampling, each split-plot was partitioned into five "sub-plots", with four based at the corners and one based centrally within the split-plot. This method was used to ensure sampling points that were located throughout the plots. Sample points were then randomly located within each "sub-plot" midway between two living *P. taeda* on the interior of a three tree outer buffer. However, due to mortality in some plots, sampling was occasionally performed within the buffer.

At each sample point, forest floor materials were collected from a 0.25 x 0.25-cm quadrat followed by the collection of a soil core. In March 2011, soil cores were collected to a depth of 30-cm with a 4.8-cm internal diameter split-corer, and divided

into 0-10, 10-20, and 20-30-cm increments and pooled in the field by split-plot. An attempt was made to collect soil cores to 30-cm in March 2012, but due to saturated soils, only the 0-10 and 10-20-cm increments could be retrieved. In June, September, and December 2011, 10-cm soil cores (4.8-cm diam.) were collected and similarly pooled in the field by split-plot. Soil samples were stored in coolers in the field and maintained at 4°C in the lab until processed.

IV.3.3 Soil chemical and physical characterization

Soil samples were mixed thoroughly 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 and gravimetric soil moisture. Volumetric water content (θ_v) was determined by multiplying gravimetric water content (θ_g; g H_2O g $soil^{-1}$) by bulk density (Jarrell et al. 1999). 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 a 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 finely ground in a TE250 ring pulverizer (Angstrom, Inc., Belleville, MI, USA) for N concentration and isotope analysis. An additional aliquot of sieved soil was dried at 105°C for texture analysis using the hydrometer method (Bouyoucos 1927; Ashworth et al. 2001).

IV.3.4 Root characterization

Roots collected during sieving were divided into a coarse and fine fraction based on diameters ≥2 mm or <2mm, respectively. Additionally, a 100-150-g aliquot of sieved

soil was used to recover fine roots using a hydropneumatic elutriation system (Gillison's Variety Fabrication, Benzonia, MI, USA) fitted with 450-µm screens. All root materials were dried at 60°C until stable mass was achieved, cut into smaller fragments, and finally ground in a ring pulverizer prior to %N and $\delta^{15}N$ analysis.

IV.3.5 Forest floor materials

Upon return to the lab, forest floor materials were dried at 60°C, sorted into woody debris and leaf matter (henceforth called 'litter"), cleaned of remaining soil particles and weighed. Litter was coarsely ground with a Thomas-Wiley Laboratory Mill (Philadelphia, PA, USA) using a 2-mm screen. The coarse mix was then finely ground in a ring pulverizer for %N and $\delta^{15}N$ analysis.

IV.3.6 Nitrogen concentration and isotopic analysis

Soil, litter, and root samples were analyzed for %N and $\delta^{15}N$ 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) interfaced with a Finnigan Delta Plus isotope ratio mass spectrometer (Thermo Fisher Scientific, Inc., Waltham, MA, USA) in continuous flow mode. N isotope values are reported in delta notation:

$$\delta^{15}N = [(R_{sample} - R_{standard})/R_{standard}] \text{ X } 1000$$

where R_{sample} is the ratio of $^{15}N/^{14}N$ in the sample and $R_{standard}$ is the ratio of $^{15}N/^{14}N$ of the international atmospheric N_2 standard (Mariotti 1983). Precision of measurements on the acetanilide working standard used during the study was standard deviation of 0.17‰ for $\delta^{15}N$ (mean = 0.48‰) and 0.15% for N-concentration (mean = 10.35%).

IV.3.7 Statistical analysis

Statistical analyses were carried out with JMP Pro (SAS Institute, Inc., Cary, NC, USA). Over the one year study period we did not see statistically significant effects due to soil compaction or the harvest by compaction interaction based on general linear models. In addition, there were no differences between herbicided and non-herbicided split-plots based on *t*-tests. Therefore, findings based only on harvest effects and time of sampling are reported, with each harvest/compaction combination treated as a replicate (n=9). However, a wildfire in September 2011 precluded the use of one replicate of each harvest intensity, resulting in an n=8. A significance level of $\alpha \leq 0.05$ was used throughout statistical testing.

Repeated measures analysis of variance (ANOVA) was used to determine the effect of harvest on N pools and their $\delta^{15}N$ values over the one-year study period for the 0-10-cm level only. Pearson correlation analysis was used to determine if relationships existed between the parameters examined during this study. Potential relationships between N cycle characteristics (i.e., pool sizes and their $\delta^{15}N$ values) based on plot means and environmental conditions (average temperature and total precipitation) for the 30-days prior to each sample date were evaluated using linear regression and multiple regression methods.

IV.4. Results

IV.4.1 Climate and soil moisture

Precipitation in 2011 was 684-mm, approximately 40% lower than the 30-year average. In contrast, precipitation in the first three months of 2012 was 441-mm,

approximately 36% higher than the 30-year average of 283-mm for the same period (Figure 4-2a). In 2011, mean annual air temperature was 1.5°C higher than the 30-year average. Mean temperature during the first three months of 2012 was 3°C higher than the 30-year average for the same period (Figure 4-2a).

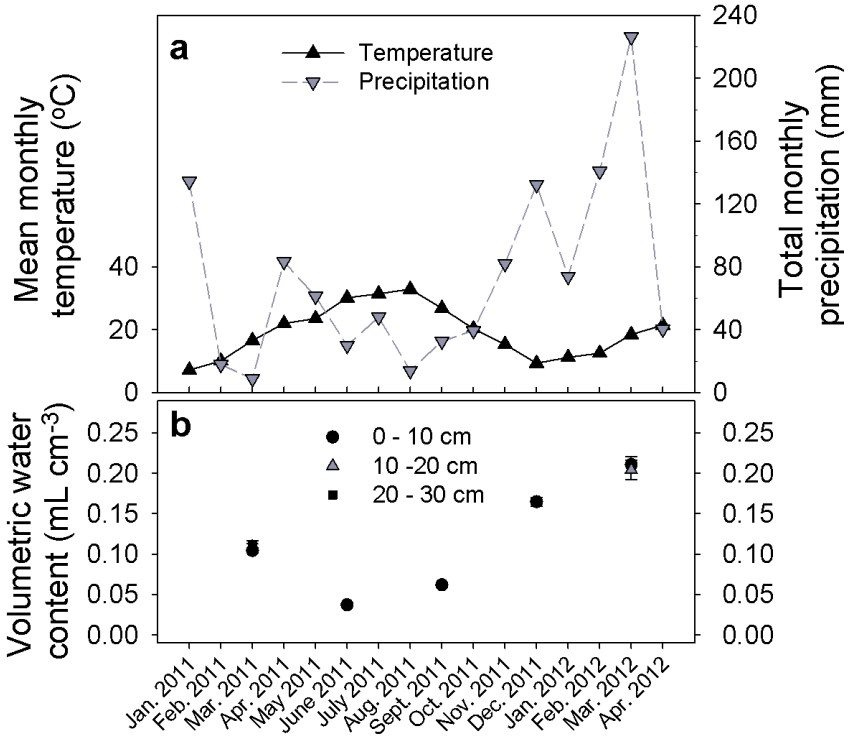

Figure 4-2. Mean monthly air temperatures and total precipitation from January 2011 through April 2012 (a), and mean volumetric water content ± S.E. (n = 24 at each depth) in 2011 and 2012 (b). Data for air temperatures and total precipitation are from the National Oceanic and Atmospheric Administration (http://www.ncdc.noaa.gov/dailyform/DlyFORMv2).

Volumetric water content ranged from a low of 0.03 mL cm^{-3} for the June 2011 sample period to a high of 0.21 mL cm^{-3} for the March 2012 sample period (Figure 4-2b)

and was not affected by harvest method and varied little with depth. Soil moisture in the 0-10-cm increment had a strong positive correlation with the total precipitation for the 30-day period prior to sampling ($r = 0.79$, $p < 0.01$) and a strong negative correlation with mean temperature for the 30-days prior to sampling ($r = -0.75$, $p < 0.01$). Together precipitation and temperature explained 80% of the variation in soil moisture in the 0-10-cm increment ($p < 0.001$, Table 4-1).

Table 4-1. Results of multiple regression analyses for prediction of soil moisture (mL cm^{-3}), N-pool sizes (g N m^{-2}), and the $\delta^{15}N_{AIR}$-values (‰) of those pools from precipitation and mean temperature during the 30-days prior to each sampling event.

	Soil moisture	Litter N	Total root N	Fine root N	Coarse root N	Soil N
R^2	0.8050	0.3025	0.4712	0.5424	0.7664	0.3375
P-value[a]	*<0.0001*	0.1152	*0.0219*	*0.0092*	*0.0002*	0.0845

	Litter $\delta^{15}N$	Fine root $\delta^{15}N$	Coarse root $\delta^{15}N$	Soil $\delta^{15}N$
R^2	0.0200	0.4436	0.5779	0.3976
P-value	0.8861	*0.0297*	*0.0057*	*0.0478*

[a] Italicized *p*-values are significant.

IV.4.2 Soil physical and chemical characteristics

Soil texture is loamy sand (Table 4-2). Sand concentration ranged from a low of 730 g kg^{-1} in the 20-30-cm increment to a high of 755 g kg^{-1} in the 0-10-cm increment. Silt concentration ranged from a low of 176 g kg^{-1} in the 20-30-cm increment and a high of 193 g kg^{-1} in the 10-20-cm increment. Clay concentration was lowest (65 g kg^{-1}) at 0-10-cm and highest (94 g kg^{-1}) in the 20-30-cm increment. Bulk density over the course of the study period was lowest in the 0-10-cm increment (0.97-1.42 g cm^{-3}), highest in

the 10-20-cm increment (1.35-1.60 g cm^{-3}), and intermediate in the 20-30-cm increment (1.28-1.51 g cm^{-3}) (Table 4-2). Overall, soil pH was acidic (Table 4-2) and ranged from 3.5-4.7 in the 0-10-cm increment, 3.9-4.6 in the 10-20-cm increment, and 3.5-4.8 in the 20-30-cm increment.

Table 4-2. Soil bulk density, particle size distributions, and pH by depth and averaged across all study plots. Based on the percentages of sand, silt, and clay the site has a soil classification of loamy sand.

Depth (cm)	Bulk density (g cm^{-3})[a]	Sand (g kg^{-1})[b]	Silt (g kg^{-1})	Clay (g kg^{-1})	pH[c]
0 – 10	1.18 ± 0.01	755 ± 7	180 ± 5	65 ± 3	4.15 ± 0.06
10 – 20	1.44 ± 0.01	737 ± 8	193 ± 6	70 ± 5	4.23 ± 0.05
20 – 30	1.41 ±0.01	730 ± 12	176 ± 7	94 ± 14	4.21 ± 0.06

[a] Means ± SE [n = 120 (0-10-cm); 48 (10-20-cm); 27 (20-30-cm)]
[b] Means ± SE (n = 24)
[c] Means ± SE (n = 27)

IV.4.3 Litter, soil, and root nitrogen content

Litter N pool sizes were significantly reduced by increasing harvest intensity (repeated measures ANOVA, $p < 0.001$) and varied significantly through time ($p < 0.01$, Table 4-3). Litter N was highest in the bole only treatment (9.9-12.6 g N m^{-2}) and lowest in the whole tree+forest floor removal treatment (9.0-10.2 g N m^{-2}); whole tree treatment values fell between these treatment extremes (Figure 4-3a). There was a negative relationship between precipitation and litter N with precipitation explaining

28% of the variance observed (Figure 4-4a); however, there was no relationship between 30-day average temperature and litter N (Figure 4-4b). Multiple regression of precipitation and temperature on litter N was not statistically significant (Table 4-1).

Table 4-3. Results of repeated measures ANOVA (*p*-values) testing the effects of tree harvest method, time, and their interaction on N pool sizes and their $\delta^{15}N$ values. Results for all root fractions and soil are for the 0-10-cm depth increment.

	Harvest	Time	Harvest * Time
N-pools (g m^{-2})		*p*-values [a]	
Litter	*0.0010*	*0.0036*	0.6564
Fine roots	0.7973	*< 0.0001*	0.7142
Coarse roots	0.3386	*0.0003*	0.3058
Total roots	0.6111	*< 0.0001*	0.6097
Soil	*0.0078*	*< 0.0001*	0.5016
$\delta^{15}N$ (‰)			
Litter	0.6761	0.0910	0.3155
Fine roots	*0.0248*	*< 0.0001*	0.9899
Coarse roots	0.3935	*< 0.0001*	0.4717
Soil	*0.0020*	*< 0.0001*	0.2678

[a] Italicized *p*-values are significant.

Soil total N storage in the 0-10-cm increment was also significantly impacted by increasing harvest intensity ($p < 0.01$) and time ($p < 0.001$, Table 4-3). Soil N was highest in the bole only treatment (74-99 g N m^{-2}) and lowest in the whole tree+forest floor removal treatment (61-83 g N m^{-2}, Figure 4-3k). Soil total N was approximately 54-68% lower in the 10-20 and 20-30-cm depth increments both March 2011 and 2012 across all harvest treatments (Figure 4-3 l,m). Neither total precipitation nor mean temperature during the 30-days prior to sampling could account for a significant proportion of the variation in soil N (Figure 4-4i,j). However, multiple regression using

both precipitation and temperature as predictor variables was able to account for 34% of the variation in soil N during the study period ($p < 0.1$, Table 4-1).

Fine root N-content in the 0-10-cm increment was not significantly impacted by tree harvest intensity, but varied significantly with time ($p < 0.001$, Table 4-3). Values for fine root N were highest (1.3-1.6 g N m^{-2}) during March and June 2011, and declined steadily to the lowest values in March 2012 (0.6 g N m^{-2}, Figure 4-3e). Fine root N ranged from 0.1 to 0.3 g N m^{-2} in the 10-20 and 20-30-cm depth intervals in March 2011 and 2012 (Figure 4-3f,g). There was a significant negative relationship between fine root N and the 30-day total precipitation ($r^2 = 0.47$, $p < 0.01$, Figure 4-4e). The 30-day average temperature was not related to fine root N. Together precipitation and temperature accounted for a significant proportion of variance in fine root N ($R^2 = 0.54$, $p < 0.01$, Table 4-1).

Coarse root N-content in the 0-10-cm increment was not significantly affected by harvest treatment, but varied significantly with time ($p < 0.001$, Table 4-3). Coarse root N in the 0-10-cm depth interval ranged from 1.5-2.8 g N m^{-2}, with peak values occurring in September 2011 (Figure 4-3h). Values in the 10-20 and 20-30-cm intervals were substantially lower and ranged from 0.2 to 0.7 g N m^{-2} (Figure 4-3i,j). There was a significant negative relationship between coarse root N and the 30-day total precipitation ($r^2 = 0.46$, $p < 0.01$, Figure 4-4g). There was a significant positive relationship between coarse root N and 30-day average temperature ($r^2 = 0.34$, $p < 0.05$, Figure 4-4h). Together precipitation and temperature accounted for a high proportion of the variance in coarse root N ($R^2 = 0.77$, $p < 0.001$, Table 4-1).

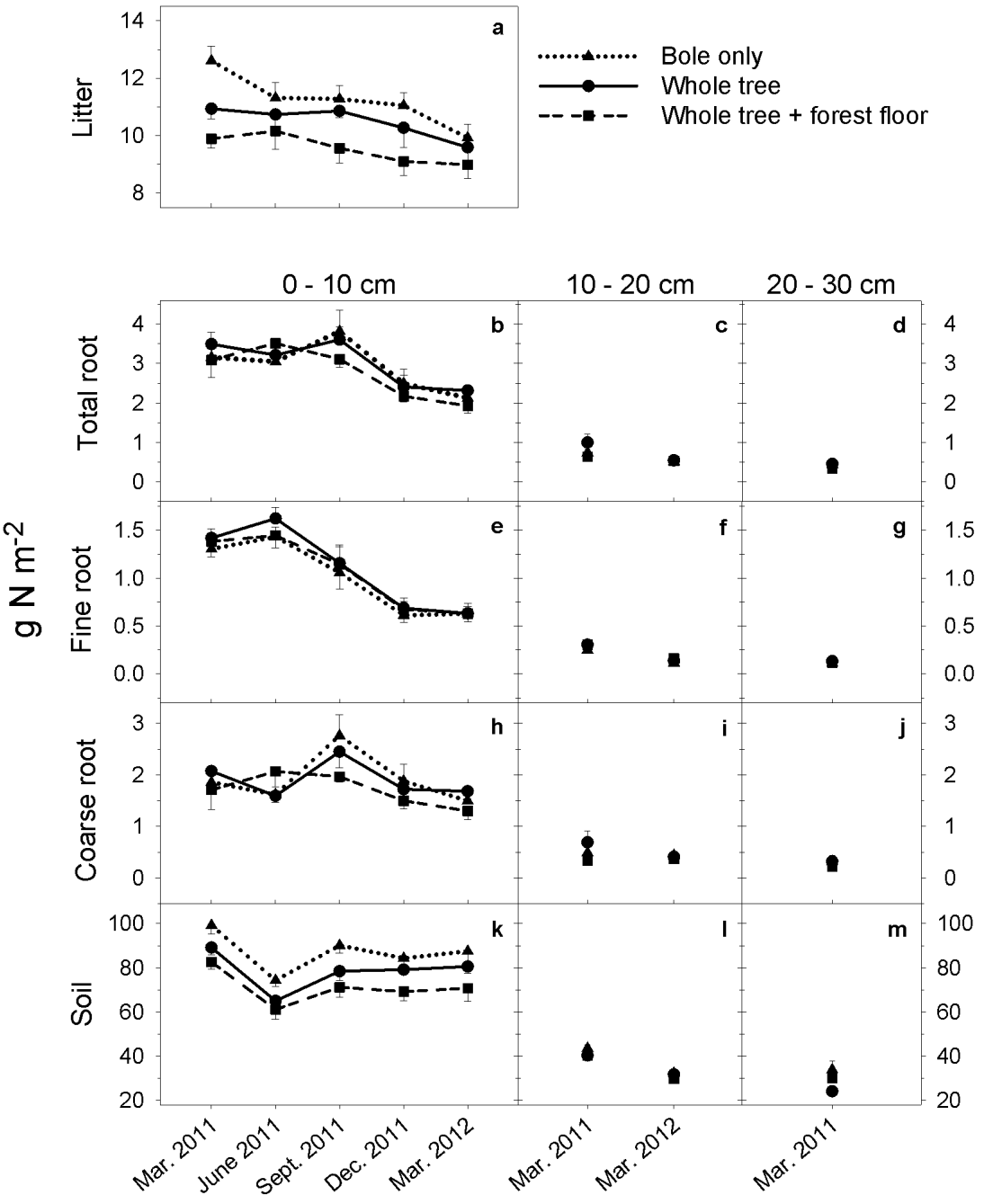

Figure 4-3. Litter (a), root (b-j), and soil (k-m) N pool (g N m^{-2}) responses to harvest intensity over time at three soil depths. Symbols are means ± S.E. (n = 8).

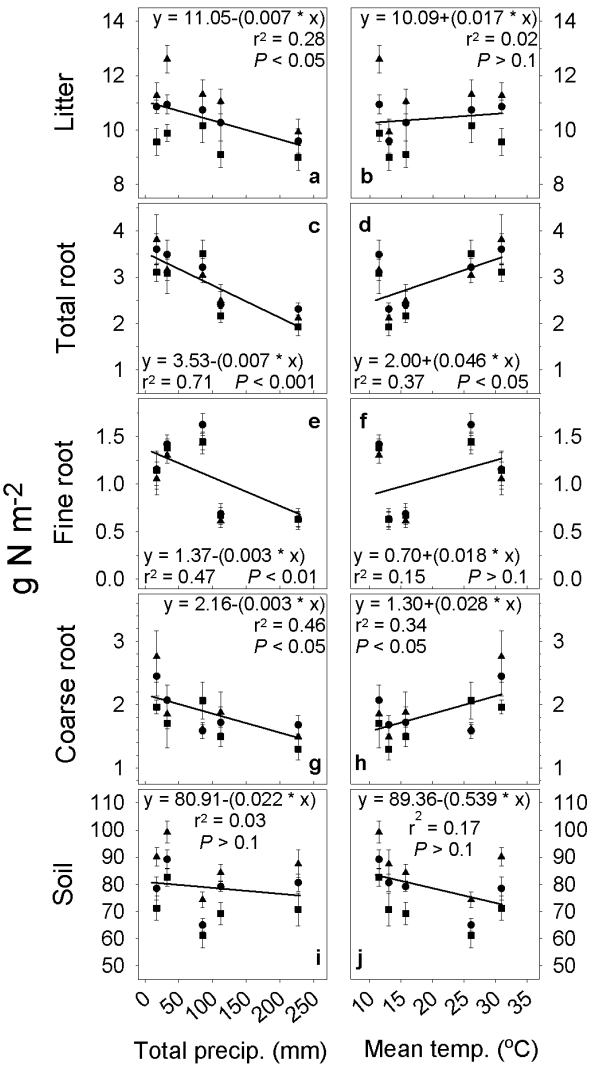

Figure 4-4. Litter (a,b), root (c-h) and soil (i,j) N pools (g N m^{-2}) in relation to total precipitation and mean temperature during the 30-days prior to each sampling event. Symbols (▲ bole only; ● whole tree; ■ whole tree+forest floor removal) are means ± S.E. (n = 8). Values for roots and soil are for the 0-10-cm depth increment.

Tree harvest method had no effect on the total root N pool (fine + coarse roots) in the upper 10-cm of the soil profile; however, this variable showed significant variation through time ($p < 0.05$, Table 4-3). Because coarse roots represented 50-76% of total

root N, the seasonal variation in total root N closely resembled that of coarse root N (Figure 4-3b). Total root N ranged from 1.9 to 3.8 g N m^{-2} in the 0-10-cm depth interval, and from 0.3 to 1.0 g N m^{-2} in the 10-20 and 20-30-cm increments (Figure 4-3c,d). There was a significant negative relationship between total root N and 30-day total precipitation (r^2 = 0.71, p < 0.001, Figure 4-4c). Conversely, there was a positive relationship between total root N and the 30-day average temperature (r^2 = 0.37, p < 0.05, Figure 4-4d). Together, precipitation and temperature accounted for a significant proportion of the variation in total root N (R^2 = 0.47, p < 0.05, Table 4-1).

IV.4.4 Litter, soil, and root $\delta^{15}N$

$\delta^{15}N$ values in the litter-root-soil system in this loblolly pine forest ranged from approximately -3.5 to 5.1‰, a range of nearly 9‰ (Figure 4-5). $\delta^{15}N$ values increased in the order: litter < coarse roots < fine roots < surface soil < deeper soil.

Litter $\delta^{15}N$ was not significantly altered by harvest method or time (Table 4-3). However, litter from the bole only treatments (-3.17 to -3.03‰) was generally more ^{15}N-depleted than the more intensely harvested treatments (-3.05 to -2.77‰, Figure 4-5a). Multiple regression of precipitation and temperature on litter $\delta^{15}N$ was not significant (Table 4-1).

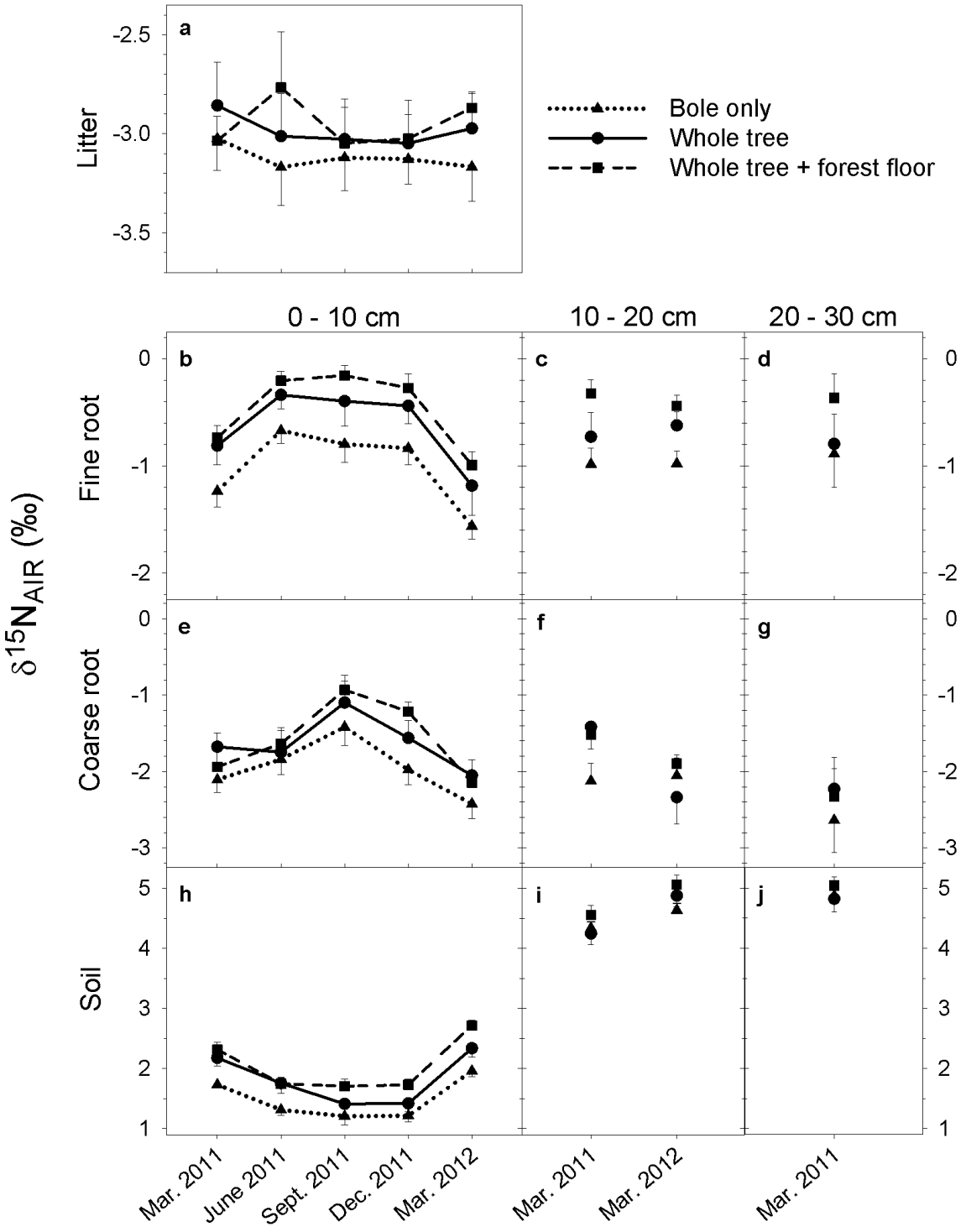

Figure 4-5. Litter (a), root (b-g), and soil (h-j) $\delta^{15}N$ responses to harvest intensity over time at three soil depths. Values are means ± SE (n = 8).

Soil $\delta^{15}N$ was significantly impacted by increasing harvest intensity ($p < 0.01$) and time ($p < 0.001$, Table 4-3). Soil $\delta^{15}N$ values in the bole only treatment were always less enriched, ranging from 1.21 to 1.96‰; in contrast, those in the more intensely harvested treatments ranged from 1.41 to 2.72‰ (Figure 4-5h). Soil $\delta^{15}N$ values became substantially higher with increasing depth in the profile, with values in the 10-20 and 20-30-cm depths ranging from 4.4 to 5.1‰ (Figure 4-5i,j). There was a positive relationship between soil $\delta^{15}N$ and 30-day total precipitation ($r^2 = 0.23$, $p < 0.1$, Figure 4-6g); in contrast, there was a significant negative relationship between soil $\delta^{15}N$ and 30-day average temperature ($r^2 = 0.35$, $p < 0.05$, Figure 4-6h). Multiple regression with precipitation and temperature accounted for 40% of the variance in soil $\delta^{15}N$ values ($p < 0.05$, Table 4-1).

$\delta^{15}N$ of fine roots in the 0-10-cm increment were significantly impacted by increasing tree harvest intensity ($p < 0.05$) and time ($p < 0.001$, Table 4-3). Fine root $\delta^{15}N$ values in the bole only treatment were always lowest (-1.56 to -0.67‰), while those in the whole tree+forest floor removal treatment were always highest (-0.99 to -0.16‰, Figure 4-5b). Fine roots at 10-20 and 20-30-cm were generally 0.25 to 0.56‰ more enriched in ^{15}N than those from the 0-10-cm increment (Figure 4-5c,d). Twenty-seven percent of the variance in fine root $\delta^{15}N$ was explained by 30-day total precipitation ($p < 0.05$, Figure 4-6c), while 38% of the variance could be explained by 30-day average temperature ($p < 0.05$, Figure 4-6d). Together precipitation and temperature accounted for 44% of the variance in root $\delta^{15}N$ ($p < 0.05$, Table 4-1).

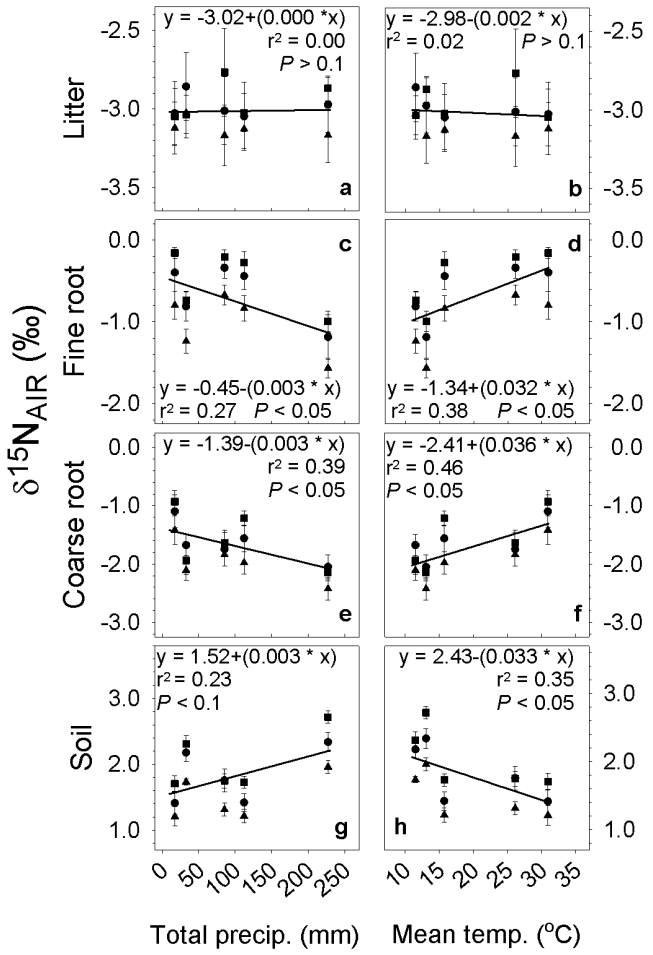

Figure 4-6. Litter (a,b), root (c-f), and soil (g,h) $\delta^{15}N_{AIR}$-values (‰) in relation to total precipitation and mean temperature during the 30-days prior to each sampling event. Symbols (▲ bole only; ● whole tree; ■ whole tree+forest floor removal) are means ± S.E. (n = 8). Values for roots and soil are for the 0-10-cm depth increment.

Coarse root $\delta^{15}N$ in the 0-10-cm increment was not affected by tree harvest intensity, but varied significantly over time ($p < 0.001$, Table 4-3). As was the case with fine roots, coarse root $\delta^{15}N$ values were always lowest in the bole only treatment (-2.42 to -1.42‰ Figure 4-5e), while those in the more intensely harvested plots were higher (-2.15 to -0.93‰, Figure 4-5e). Coarse root $\delta^{15}N$ values at the 10-20 and 20-30-cm depths

were generally similar to those in the 0-10-cm depth (Figure 4-5f,g). Thirty-nine percent of the variance in coarse root $\delta^{15}N$ was accounted for by 30-day total precipitation ($p < 0.05$, Figure 4-6e), and 46% of the variance was accounted for by the 30-day average temperature in the 0-10-cm increment ($p < 0.01$, Figure 4-6f). Multiple regression using both precipitation and temperature accounted for 58% of the variance in coarse root $\delta^{15}N$ ($p < 0.01$, Table 4-1).

IV.5. Discussion

IV.5.1 N storage in the litter, roots, and soil

Fifteen years after treatment, nitrogen storage in the litter and upper 10-cm of soil were both reduced significantly by increasing harvest intensity, but there was little or no evidence of harvest effect beyond this depth or in the root compartments (Figure 4-3). Soil total N in the upper 10-cm was up to 21% lower in the more intense harvest treatments versus the bole only. This reduction in soil N due to harvest intensity is similar in magnitude to that reported in several studies reviewed by Johnson and Curtis (2001). The litter N pool was also approximately 18% lower in the whole tree+forest floor removal treatment compared to plots where only the bole was harvested. Litter N storage at this site was slightly higher than that in a 10-year old *Pinus taeda* stand in Alabama, USA that averaged 87 kg N ha^{-1} in control and litter removed plots (Zerpa et al. 2010). Forests in general are nutrient limited and rely on continual inputs and conservative cycling to maintain nutrient stores (Sayer 2006). Due to the size of the soil and litter N pools and their importance to site productivity in this nutrient poor site, the

persistence of the N losses documented in this study (≈ 15-yrs postharvest) is quite noteworthy.

Variations in litter and root N pools over the course of this study were primarily related to temporal variations of precipitation and temperature, while soil N storage was unrelated to environmental variables (Figure 4-4). Both litter and root N pools decreased with increasing precipitation. Because this forest ecosystem is moisture limited, the observed loss of litter N during periods of higher precipitation is likely attributable to accelerated litter decay during periods of higher rainfall (Prescott et al. 2005; Scott and Messina 2010). Root production is known to be sensitive to resource availability, temperature, and rainfall (Teskey and Hinckley 1981; Sword et al. 1998a, 1998b; Torreano and Morris 1998; Fisher and Binkley 2000; Tingey et al. 2005). In this study, root production, and therefore root N pools, likely decreased during periods of higher precipitation due to increased moisture availability which would lessen the need for a more extensive and/or intensive root system (Torreano and Morris 1998). In addition, there may have been decreased air-filled pore space during periods of higher precipitation, which may have limited root growth during wetter periods (Gregory 2006). Higher temperatures were generally associated with less precipitation, suggesting that higher root N storage with increasing temperatures was a result of higher root production during periods of decreased moisture availability.

IV.5.2 $\delta^{15}N$ in litter, roots, and soil

Enrichment of ^{15}N in the litter and 0-10-cm root and soil pools was evident in the more intense forest harvest treatments compared to the bole only harvest, and was less

pronounced at 10-20-cm. However, only the $\delta^{15}N$ values from the 0-10-cm soil and fine root $\delta^{15}N$ were significantly affected (Figure 4-5). Enrichment due to increased nitrification and nitrate loss are expected following harvest (Robertson et al. 1987; Sah and Ilvesniemi 2007; Pardo et al. 2002), but because nitrate losses during the time of the current study were probably small (Johnston and Crossley 2002), ongoing N losses are likely not the driver of the long-term pattern of enrichment. The probable mechanism for enrichment of soil ^{15}N and hence the plant compartments in the most intensely harvested treatments is the pulse removal of ^{15}N-depleted biomass (i.e., branches, twigs, forest floor) at the outset of the original study in 1997 (Nadelhoffer and Fry 1988; Robinson 2001; Hogbom et al. 2002; Choi et al. 2005). However, it is also possible that the higher $\delta^{15}N$ values in the more severe harvest treatments are at least in part attributable to higher rates of N-losses due to acceleration of N-transformations (e.g., nitrification, denitrification) that enrich the residual ecosystem N. For example, more radiation would have reached the soil surface in the most severe harvest treatment where all tree biomass and the forest floor were removed, resulting in higher soil temperatures and potentially higher rates N-loss processes (e.g., nitrification/denitrification followed by leaching or gaseous losses) during the time interval between forest harvest and stand recovery.

Soil and root $\delta^{15}N$ values varied temporally and were mainly related to variations in precipitation and temperature (Figure 4-6 c-h). Although not significant, higher precipitation led to ^{15}N-enrichment of soil N, suggesting increased denitrification was occurring in these highly acidic soils (Nadelhoffer and Fry 1988). In contrast, both fine

and coarse roots became ^{15}N depleted with increasing precipitation, which is consistent with global relationships of foliar $\delta^{15}N$ and MAP (Handley et al. 1999; Craine et al. 2009). The root response to increased precipitation may be driving the observed responses in soil $\delta^{15}N$, wherein roots are utilizing plant-available forms of N that are ^{15}N-depleted, thus leaving the soil comparatively enriched in ^{15}N. Increasing temperature led to lower soil $\delta^{15}N$, which is contrary to the global scale pattern of enrichment with increasing temperature (Amundson et al. 2003). In contrast, the root compartments followed the trend of enrichment with increasing temperature reported for foliar $\delta^{15}N$ (Amundson et al. 2003; Craine et al. 2009).

While ^{15}N enrichment of the soil is expected during periods of higher temperatures due to increased microbial activity, in this forest ecosystem higher temperatures were associated with decreased precipitation and drier soil, suggesting that processes may have slowed and roots were taking up more enriched N leaving the soil depleted. Alternatively, roots may have been accessing deeper soil resources that were ^{15}N-enriched, but based on the slopes of the correlations (Figure 4-6 d,f, and h), the former rather than the latter is likely occurring, especially in light of the higher N associated with the dry period.

IV.6. Conclusions

Nitrogen is a key component in forest ecosystem productivity and perturbations to N pools may result in long-lasting changes in pool sizes and dynamics. In this western Gulf Coastal Plain site, more intense forest harvest methods resulted in significant decreases in N storage in both the litter and soil pools, the largest source

pools. Higher soil $\delta^{15}N$ values in the more severe harvest treatments suggest that N losses were greater in those plots, consistent with the smaller N pool sizes observed in those treatments. Results of this study indicate that the removal of more aboveground biomass with the most intense forest harvest resulted in significant ecosystem N-losses that have yet to recover 15-years following treatment. Because future rotations will rely on site nutrient capital, and because tree growth in the sandy soils of this region is nutrient limited, forest harvest practices that minimize aboveground biomass removal are recommended to sustain productivity and ensure continuity of ecosystem services.

CHAPTER V

RECOVERY OF SOIL C AND N STORES FOLLOWING TIMBER HARVEST: A TIME SEQUENCE IN THE WESTERN GULF COASTAL PLAIN, USA

V.1. Synopsis

Worldwide forest ecosystems are the largest terrestrial carbon (C) pool, with over 40% of the C held in soils; however, disturbances have the potential to alter this sink due to changes in biogeochemical processes that ultimately affect forest productivity. The extent of disturbance may dictate the degree to which the C pool is affected and the potential of ecosystem C recovery. The purpose of this study was to determine the impact of forest harvest activities on soil organic carbon (SOC) and total nitrogen (TN) storage and to quantify accumulation rates following harvest. Soils were collected to a depth of 10-cm every five years between 5- and 15-years post-treatment from the Groveton, TX Long-Term Soil Productivity (LTSP) sites located in the western Gulf Coastal Plain USA. Treatments consisted of three harvest methods (bole only, whole tree, whole tree+forest floor removal) in factorial combination with three soil compaction levels (none, intermediate, severe) followed by planting to *Pinus taeda* L (loblolly pine), and at 15-years, unharvested plots were identified for use as controls. We quantified soil C and N by dry combustion, and used linear models to determine C and N accumulation rates. Harvest resulted in significantly lower SOC (1051-1174 g C m^{-2}) at five years and lower TN at five and 10-years (52±3-74±3 g N m^{-2}) when compared to control plots (2082±61 g C m^{-2} and 99±13 g N m^{-2}). Evidence of altered

biogeochemical cycling was apparent in the enrichment of ^{13}C and ^{15}N in the SOC and TN, respectively. However, accumulation rates of 86-103 g C m^{-2} yr^{-1} and 3-4 g N m^{-2} yr^{-1} resulted in nearly complete recovery of both SOC and TN by 15-years post-harvest. Soil compaction and the harvest by soil compaction interaction had no effect on the measured soil variables. Results of this study suggest that, overall, harvest may not have a long-term negative impact on SOC and TN storage in the western Gulf Coastal Plain. However, lower accumulation rates in the most intensely harvested treatments may impact the productivity of subsequent rotations.

V.2. Introduction

Globally forest ecosystems are the largest terrestrial carbon (C) pool and store 861±66 Pg C, with 44% located in the soil to a depth of one meter (Pan et al. 2011). Forests worldwide are a net C sink taking up 1.1±0.8 Pg C $year^{-1}$ (Pan et al. 2011). The United States alone accounts for uptake of 0.25 Pg C $year^{-1}$ (Pan et al. 2011), with the southeastern region considered the largest sink. In addition, forests in the southeastern US are projected to continue acting as sinks through the end of the century (Song et al. 2013). However, the ability of forests to serve as C sinks is impacted by disturbance and will depend on the time since disturbance (Pregitzer and Euskirchen 2004) and severity of disturbance and site specific factors (Goetz et al. 2012).

Carbon accumulation in soils is closely linked to nitrogen (N) availability (Kiser et al. 2009) and forest harvest may impact C accumulation by removing increasing amounts of nutrient rich biomass (e.g., leaves, branches). The effects of forest management on C and N are still not well understood and variances have been attributed

to climate, inherent site characteristics, disturbance type and frequency, and previous land use history (Richter et al. 1999; Johnson and Curtis 2001; Goetz et al. 2002; Guo and Gifford 2002; Nave et al. 2010). Several studies have found that as forests age, accumulation of C is generally in the biomass, with little to no overall accumulation in the mineral soil (Richter et al. 1999; Schlesinger and Lichter 2001). However, in the course of 40-years Richter et al. (1999) did find significant accumulation in the 0-7.5-cm mineral soil, and Kelly and Mays (2005) likewise saw C accumulations after 26-years that they suggested was a function of understory growth and the possibility that the forest was still aggrading. Because of the close linkages of C and N cycles, a disturbance to one cycle will likely disrupt the other.

Natural abundances of isotopes of C and N have been used to examine the impact of disturbances, land use change, and vegetation shifts on biogeochemical cycling (Chang and Handley 2000; Billings and Richter 2006; Bai et al. 2009) and are integrators of C and N cycling within ecosystems (Robinson 2001; Ehleringer et al. 2000; Billings and Richter 2006). Isotopic signatures in the soil therefore rely upon the isotopic character of inputs and outputs and the input/output balance, as well as discrimination events during transformations. Following disturbance there is a tendency for both TN and SOC to become more enriched. Total N may become more enriched due to altered N-transformation rates (e.g., denitrification, nitrification) and accelerated gaseous N-losses and/or leaching losses (Bai et al. 2013). Enrichment of SOC may be a function of removal of depleted organic materials (e.g., roots, litter) (Nadelhoffer and Fry 1988) and/or kinetic fractionation during decomposition in which ^{12}C is

preferentially respired leaving the soil enriched (Diochon and Kellman 2009). As time progresses isotopic depletion of SOC and TN may occur due to the incorporation of isotopically depleted litter and root biomass (Nadelhoffer and Fry 1988).

To understand the impact of forest harvest activities on soil C and N storage over time we used archived soil samples (5-and 10-years post-treatment) and more recently collected samples (15-years) from the Groveton, Texas Long-Term Soil Productivity (LTSP) site (herein after "Groveton LTSP"). Experimental units in the LTSP network, spanning the US and Canada, were designed to understand the relationships between forestry practices and sustainable forest productivity (Powers 2006). The network uses a factorial combination of three tree harvest intensities (bole only, whole tree, whole tree+forest floor removal) and three soil compaction intensities.

The Groveton LTSP site was established in the Davy Crockett National Forest in eastern Texas, USA, and represents the westernmost extent of the southern pine region (Siska et al. 2006) lying at the ecotone between forest and grassland biomes. As such, this region may be extraordinarily susceptible to changes in rainfall and temperature predicted for the future (Schmandt et al. 2009), and these climate change drivers may interact with forest management practices to influence C and N storage and accumulation. Despite its unique ecological context, little is known about the long-term impact of forestry practices on C and N storage and accumulation in the soils in this region. Therefore, the objectives of this study are to 1) determine the impact of forest harvest activities on soil C and N storage over time compared to untreated control plots, and 2) quantify accumulation rates of C and N.

V.3. Materials and methods

V.3.1 Study area and sample collection

The study site is located at the Long-Term Soil Productivity (LTSP) site in the Davy Crockett National Forest near Groveton, TX, USA (31°06' 32.48"N, 95°09' 59.15"W). 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 (Figure 5-1). Climate data was recorded at Crockett, Houston County, TX (≈38-km northeast of the study site) and subsequently obtained from the National Oceanic and Atmospheric Administration. Topography of the site 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).

The Groveton LTSP treatment plots were established in 1997 in accordance with the parameters specified by the LTSP program 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) (Powers 2006) replicated three times and replicate blocks designated TX1, TX2, TX3. Organic materials from forest floor removal treatment plots were raked off of the plots by hand. Glyphosate was applied once per year for five years to control understory growth on one-half of each 0.4-ha treatment plots and the other half received no herbicide treatment. On compacted plots, a feller-buncher and skidder were used for harvesting and 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). Containerized *Pinus taeda* L (loblolly pine) seedlings of 10-half sib families from USDA Forest Service seed orchards in Texas, Louisiana, and Mississippi were hand planted on a 2-m x 2-m spacing.

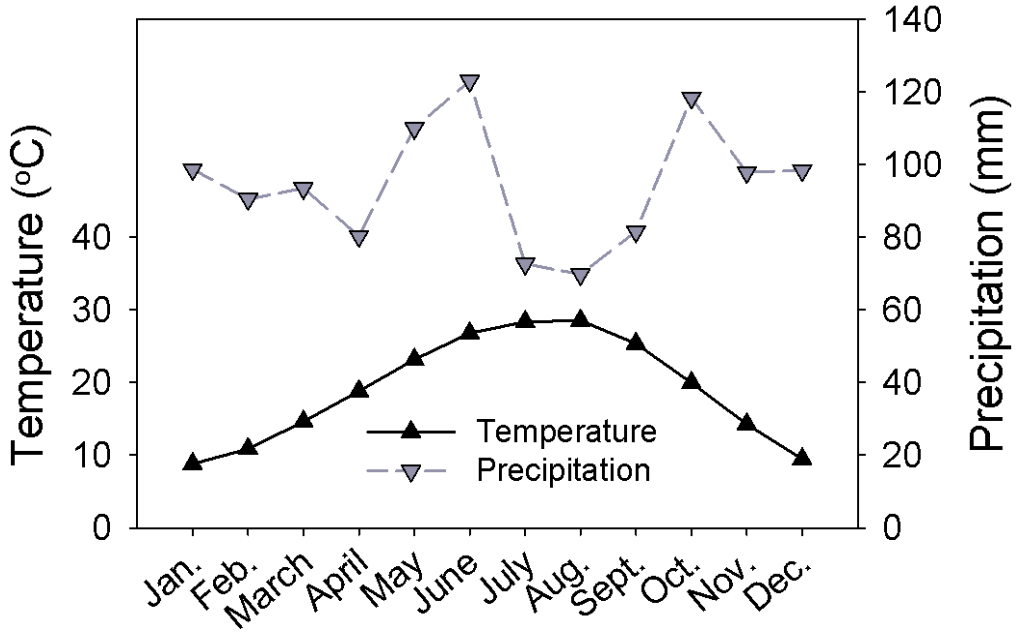

Figure 5-1. Mean monthly temperature and precipitation (1981-2010) for Crockett, Houston County, Texas (31° 18' 25.92" N, 95° 27' 3.24" W). The mean annual temperature is 19.1°C with mean annual precipitation of 1135 mm. Data from the National Oceanic and Atmospheric Administration, (http://www.ncdc.noaa.gov/dailyform/DlyFORMv2).

Soil sampling occurred at 5-, 10-, and 15-years after timber harvest treatments were implemented. Because pre-treatment soils were unavailable for the plots subjected

to timber harvest, three unharvested plots on the same soil type with tree ages ranging from 50-80 years were established in the surrounding "old-growth" forest and designated as controls. Archived soil samples from 5- and 10-years postharvest were obtained from the USDA Forest Service. At stand age 5-years old, 10-samples per split-plot were extracted, at 10-years old 10-samples per split-plot were extracted from TX1, and 5-samples per split-plot from TX2 and TX3. At stand age 15-years old, 5-samples were taken per split plot, and 5-samples were taken from each control plot. For each time period soil samples from the 0-10-cm increment were pooled by split plot and homogenized thoroughly.

V.3.2 Soil processing, physical and chemical analyses

The soil samples from both control and experimental plots that were taken 15-years after the treatments were installed were used for soil chemical and physical analyses. An aliquot of the bulked soil was dried at 105°C until stable mass was reached for bulk density determination, and subsequently used for pH determination using an Accumet Basic pH meter (Denver Instrument, Arvada, CO, USA) on a 1:2 solution of soil in a 0.01 M $CaCl_2$ solution (Minasny et al. 2011). An additional aliquot of soil was sieved through a 2-mm mesh and dried at 105°C for texture analysis using the hydrometer method (Bouyoucos 1927; Ashworth et al. 2001).

V.3.3 Carbon and nitrogen concentrations, and isotopic analyses

Samples from all time periods were thoroughly mixed and sieved to remove organic materials and roots > 2-mm. All soils were dried and finely ground in a TE 250

ring pulverizer (Angstrom, Inc., Belleville, MI, USA) for C and N concentration and isotope analyses.

Soil samples were analyzed for C and N concentrations, $\delta^{13}C$, and $\delta^{15}N$ 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) interfaced with a Finnigan Delta Plus isotope ratio mass spectrometer (Thermo Fisher Scientific, Inc., Waltham, MA, USA) in continuous flow mode. Carbon and N isotope values are reported in delta notation:

$$\delta^{xx}E = [(R_{sample} - R_{standard})/R_{standard}] \text{ X } 1000$$

where *E* is the element, R_{sample} is the ratio of either $^{13}C/^{12}C$ or $^{15}N/^{14}N$ in the sample, and $R_{standard}$ is the ratio of $^{13}C/^{12}C$ of the international standard V-PDB or $^{15}N/^{14}N$ of the international atmospheric N_2 standard (Mariotti 1983). Precision of measurements on the acetanilide working standard used during the study was 0.48% for C-concentration (mean = 71.21%) and 0.15% for N-concentration (mean = 10.35%). Precision for $\delta^{13}C$ was 0.10‰ (mean = -30.2‰) and precision for $\delta^{15}N$ was 0.17‰ (mean = 0.48‰). Soil C and N densities (g m^{-2}) were computed as the product of the elemental concentration, soil bulk density, and soil depth (Ellert and Bettany 1995).

V.3.4 Statistical analyses

Statistical analyses were performed with JMP Pro (SAS Institute, Inc., Cary, NC, USA). Based on general linear models and *t*-tests, we did not see statistically significant effects due to either soil compaction or the harvest by compaction interaction, and herbicide treatments, respectively. Therefore, findings based only on harvest effects are

reported with each harvest/compaction combination acting as one replicate. Analysis of variance (ANOVA) was used to determine if there were differences in SOC, TN, $\delta^{13}C$, and $\delta^{15}N$ between the control plots and harvest levels during each sample period. Tukey's HSD was used when differences were significant. Soil organic carbon and TN were regressed against date of sampling to determine if slopes were significantly different from zero and to determine accumulation rates using the equation in the form of $y = mx + b$. A significance level of $\alpha \leq 0.05$ was used throughout statistical testing.

V.4. Results

V.4.1 Soil physical and chemical characteristics

Overall soil pH was acidic (4.01-4.27) and soil texture was loamy sand (Table 5-1). Bulk density in the control plots averaged 1.22±0.02 g cm^{-3} and was highest 5-years post-treatment (1.27±0.01 g cm^{-3}) with the lowest mean at 15-years post-treatment (1.12±0.01 g cm^{-3}) (Table 5-1).

V.4.2 Soil organic carbon and total nitrogen content

Soil organic carbon content was significantly higher in the control plots (2082±61 g C m^{-2}, $p < 0.05$) when compared to each harvest method at 5-years post-harvest (1051 to 1174 g C m^{-2}) and by 15-years harvest effect was no longer evident when compared to the control plots (1911 to 2202 g C m^{-2}; Figure 5-2A). Carbon content was consistently highest in the bole only treatment when compared to the whole tree and whole tree+forest floor removal treatments (Figure 5-2A). Carbon accumulation rates in all treatments were significant ($p < 0.001$) with the lowest rate

occurring in the whole tree+forest floor removal (86 g C m^{-2} yr^{-1}) and highest in the bole only treatment (103 g C m^{-2} yr^{-1}; Table 5-2).

Table 5-1. Bulk density (g cm^{-3}), pH and soil texture.

	Control[a]	Post harvest		
		5-years[d]	10-years[d]	15-years
Bole only[a]				
Bulk density (g cm^{-3})	1.22 ± 0.02	1.25 ± 0.02	1.17 ± 0.03	1.08 ± 0.02
pH				4.27 ± 0.05
Whole tree[a]				
Bulk density (g cm^{-3})		1.26 ± 0.02	1.15 ± 0.02	1.12 ± 0.03
pH				4.17 ± 0.12
Whole tree+forest floor[b]				
Bulk density (g cm^{-3})		1.33 ± 0.02	1.25 ± 0.02	1.17 ± 0.02
pH				4.01 ± 0.09
Soil texture[c]				
Sand (g kg^{-1})				755 ± 7
Silt (g kg^{-1})				180 ± 5
Clay (g kg^{-1})				65 ± 3

[a] Mean ± SE (control n = 3; all others n = 9)
[b] Mean ± SE (5- and 10-years n = 7; 15-years n = 9)
[c] Mean ± SE (n = 24)
[d] Data courtesy of Dr. D. Andrew Scott, USDA Forest Service

Control plots had significantly higher TN content (99±13 g N m^{-2}, $p < 0.05$) than any of the harvest methods at 5- and 10-years following treatment (52±3 to 74±3 g N m^{-2}), and by 15-years post-treatment there were no differences (Figure 5-2B). Total nitrogen was highest in the bole only treatment over the course of the sample periods (Figure 5-2B). Accumulation rates under all harvest methods were significant ($p <$

0.001) with nitrogen accumulating slightly more rapidly in the bole only harvested plots versus the two more intensive harvests (4 g N m^{-2} yr^{-1} versus 3 g N m^{-2} yr^{-1}; Table 5-2).

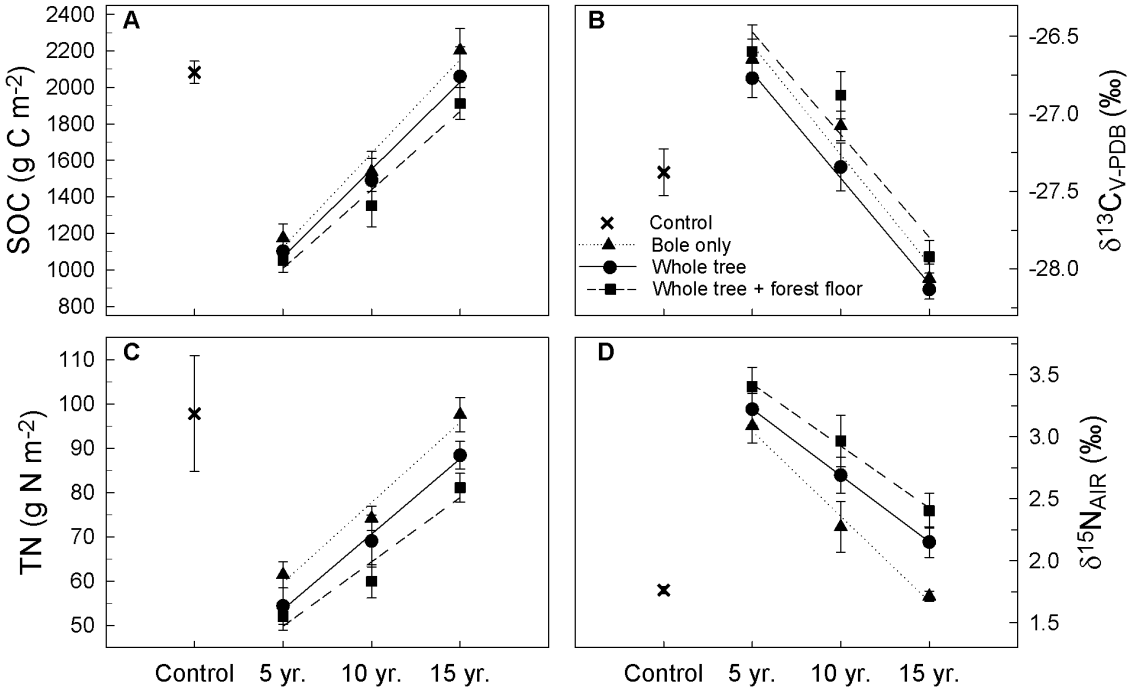

Figure 5-2. A) SOC (g C m^{-2}); B) TN (g N m^{-2}); C) $\delta^{13}C$ and D) $\delta^{15}N$ (‰) of control, 5-, 10- and 15-year post-harvest soils to 10-cm. Control means ± SE (n = 3); 5- and 10-year means ± SE (n = 9 bole only and whole tree, n = 7 whole tree+forest floor); and 15-year means ± SE (n = 9).

V.4.3 $\delta^{13}C$ and $\delta^{15}N$

The mean $\delta^{13}C$ of SOC in the control plots (-27.4±0.15‰) was significantly lower than the values in all harvest methods at 5-years (-26.8±0.12 to -26.6±0.13‰) and was significantly higher than all harvest methods at 15-years (-28.1±0.06 to -27.9± 0.11‰; Figure 5-2C). The whole tree harvest tended to have the most depleted SOC and the whole tree+forest floor was the least depleted. Mean soil $\delta^{15}N$ in the control plots

(1.76±0.03‰) was significantly lower than those in all of the harvest treatments at 5- and 10-years, and the whole tree+forest floor removal treatment 15-years following harvest (2.27±0.20 to 3.40±0.16‰; Figure 5-2D). The whole tree+forest floor removal treatment tended to have the most enriched TN (2.40±0.14 to 3.40±0.16‰; Figure 5-2D) compared to the other harvest methods.

Table 5-2. Linear regression of SOC and TN by harvest method against time.

	SOC			
	Equation (y = b+mx)	R^2 Adj.	*p*-value	Accumulation (g C m^{-2} yr^{-1})
Bole only	610 + 103x	0.65	<0.001	103
Whole tree	592 + 96x	0.54	< 0.001	96
Whole tree+forest floor	578 + 86x	0.67	< 0.001	86
	TN			
	Equation (y = b+mx)	R^2 Adj.	*p*-value	Accumulation (g N m^{-2} yr^{-1})
Bole only	42 + 4x	0.69	< 0.001	4
Whole tree	37 + 3x	0.52	< 0.001	3
Whole tree+forest floor	35 + 3x	0.62	< 0.001	3

V.5. Discussion

Worldwide, forest soils store 44% of ecosystem carbon; however, disturbances caused by forestry operations may diminish this pool due to alterations of input and output. Results of this study showed that forest harvest, regardless of intensity, negatively impacted SOC and TN stores initially when compared to an undisturbed stand, but generally recovered after 15-years. Evidence of the disturbance and recovery

are borne out in the isotopic signatures of the SOC and TN over time. Neither soil compaction nor the soil compaction by harvest interaction had an effect on the variables examined.

Unlike previous studies of LTSP sites (Powers et al. 2005), the Groveton site had significant initial reductions in SOC and TN content (g m^{-2}) at five years. Based on isotope values we suggest that two interacting mechanisms produced the result shown in our study: 1) reduced inputs from both aboveground litter and roots, and 2) decomposition of residual soil organic matter that led to the initial enrichment of both SOC and TN.

Plant materials are commonly more depleted in the heavier isotopes when compared to soils (i.e., δ-values are more negative) (Nadelhoffer and Fry 1988; Fry 1991; Amundson et al. 2003) and following harvest when the input of both roots and above-ground litter are eliminated, soils will likely become more enriched. Because root input in this study was likely diminished equally across all harvest treatments, higher $\delta^{13}C$ and $\delta^{15}N$-values seen in the whole-tree+forest floor removal treatments versus the bole only harvest were probably a function of the removal of more above-ground input. Reduced inputs in turn may have led to mineralization of remaining SOM and subsequent losses of SOC, whereas N was likely lost due to soil conditions that accelerated nitrification/denitrification associated losses (Bormann and Likens 1979; Paul et al. 2003; Jerabkova et al. 2011). Both loss mechanisms would result in the enrichment of remaining SOC and TN, respectively (Diochon and Kellman 2009).

Recovery of SOC was probably due to increased above- and belowground inputs as a result of increased productivity as the stands aged and is reflected in the depletion of ^{13}C in the SOC. Rates of SOC accumulation were between 86-103 g C m^{-2} yr^{-1} which are higher than those reported elsewhere (e.g., Richter et al. 1999; Post and Kwon 2000; Luxmoore et al. 2008), but similar in magnitude (110 g C m^{-2} yr^{-1} over 20-years) to those reported from in a humid tropical forest (Fonseca et al. 2011). Carbon accumulation rate in a re-establishing forest in South Carolina was reported as 4 g C m^{-2} yr^{-1} that was attributed to the upper 7.5-cm of the mineral soil (Richter et al. 1999), with the low rate of accumulation attributed to rapid cycling of C. Post and Kwon (2000) found on average 33 g C m^{-2} yr^{-1} was being accumulated in soils following forest or grassland establishment. In addition, a simulation performed by Luxmoore et al. (2008) found that soil C in a loblolly pine stand increased ≈1600 g C m^{-2} over the course of 25-years, which would equate to an accumulation rate of 64 g C m^{-2} yr^{-1} if the accrual was linear. Depletion of ^{13}C beyond that of the control plots, suggests that equilibrium has not yet been reached in the treatment plots.

Nitrogen in the treatment plots accumulated at rates of 3-4 g N m^{-2} yr^{-1}. Because these plots were not fertilized during establishment or thereafter, and there was no evidence of leguminous plants, either atmospheric deposition, free-living N-fixation, nutrient uplift, or a combination of these factors may be responsible for the observed accumulation rates. Average atmospheric deposition of inorganic N (NO_3^- + NH_4^+) between 1997-2011 was ≈0.35 g N m^{-2} yr^{-1} (National Atmospheric Deposition Program, National Trends Network, http://nadp.isws.illinois.edu), accounting for little of the

observed accumulation. In addition, free-living N-fixation may have likewise accounted for very little of the N-accumulation seen in this study. Reed et al. (2011) reported free-living N fixation rates of 0.001-1.2 g N m^{-2} yr^{-1} in temperate forests, which, when summed with the average atmospheric deposition, would account for about one-half of the N-accumulation rates seen at the Groveton LTSP site. Nutrient uplift of limiting nutrients has been suggested as an additional mode of augmenting surface soil nutrients (Jobbagy and Jackson 2001). Although we cannot say with certainty that uplift occurred, it is a possible explanation for the increase of TN over time.

V.6. Conclusions

The effects of forest harvest activities on soil organic C and total N has been variable across studies. In this study there was significantly less SOC and TN in the upper 10-cm of soil at 5-years post-harvest compared to control plots. Enrichment of stable isotopes of C and N confirmed that losses occurred following harvest and was likely due to two mechanisms, diminished input from isotopically depleted roots and above-ground litter inputs, and microbial activity that led to mineralization of residual soil organic matter that culminated in additional ^{13}C and ^{15}N enrichment. Although losses were significant, accumulation of both C and N after 15-years has resulted in soil stores that are nearing control plots levels. Collectively, these results show that this western Gulf Coastal Plain forest has been able to recover important soil nutrients following harvest activities by mid-rotation. However, under the most extreme harvest (whole tree+forest floor removal), both SOC and TN are still far from control plot levels,

suggesting that this harvest method may not be sustainable in the loamy sand soils of this region.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Forests across the globe provide many ecosystem services, one of which is the uptake of carbon from the atmosphere. However, demand for forest products and subsequent forest harvest activities have the potential to alter biogeochemical processes in forestlands and may in turn alter forests' ability to act as C sinks by reducing productivity. The removal of biomass and compaction of soils during harvest may perturb nutrient cycles by changing input and output of the system, but because studies examining the effects of harvesting have been variable, generalizations across diverse forest biomes is ill-advised. In addition, there is little in the literature regarding the impact of harvest operations in the western Gulf Coastal Plain, USA. Therefore, the objective of this study was to determine the impact of forest harvest practices on biogeochemical cycling in a *Pinus taeda* L. (loblolly pine) forest in east Texas. This study used the Groveton Long-Term Soil Productivity (LTSP) experimental site to examine the effect of tree harvest method and compaction on biogeochemical processes quarterly over the course of one year (5 sample periods) 15-years after plot establishment and planting of *P. taeda*.

The LTSP experimental program is a network of over 60 core sites in the USA and Canada that examines the effect of forest harvest activities on soil productivity. At the outset of the program two factors were identified as those most directly affected by forest management: site organic matter and soil porosity (Powers 2006). In other words,

the volume of above-ground biomass removed during harvest and soil compaction due to the entry of harvest machinery on plots. Consequently, sites within the network employ a factorial experiment consisting of three harvest methods (bole only, whole tree, whole tree+forest floor) in combination with three soil compaction levels (none, intermediate, severe) with each 0.4-ha plot split for herbicide.

At 15-years post-treatment both total nitrogen (TN) and total phosphorus (TP) were significantly lower in the most intensely harvested plots in the upper 10-cm of the soil profile. Soil microbial biomass-N and –C (SMB-N and –C) were also negatively impacted by increasing harvest intensity. Although soil organic carbon (SOC) was generally lowest in the most intensely harvested plots, the impact was not significant. Over the one year sample period TN, SOC, SMB-N and –C varied significantly with time. Post-harvest re-accumulation of both C and N was evident over the time period from 5- to 15-years. Over the course of this study there was no evidence of a compaction, compaction by harvest interaction effect or any treatment effect beyond the 10-cm depth.

Consistently lower soil TN under the most intense harvest treatment (61-83 g N m^{-2}) compared to the bole only harvest (74-99 g N m^{-2}) was likely a legacy effect of the harvest 15-years ago rather than contemporary losses. Two lines of evidence support this contention. First, examination of archived soils showed that N is accumulating at about the same rate (3-4 g N m^{-2} yr^{-1}) in the upper 10-cm of soil under all harvest treatments, and second, in the most intensely harvested treatments TN remains more enriched (1.41-2.72‰) compared to the bole only harvest (1.21-1.96‰) despite similar

accumulation rates. Nitrogen is considered a limiting nutrient, and as such is generally conservatively cycled within ecosystems, so that losses are minimal in an undisturbed system. However, a disturbance such as harvest, removes potential sources of nutrients in the biomass that is depleted of ^{15}N compared to the soil. In addition, decreased plant uptake paired with soil conditions that enhance microbial processes and N-transformation rates following harvest may lead to further soil ^{15}N enrichment due to N losses.

Total P was quantified at one point in time during this study and was significantly lower under the whole tree+forest floor removal treatment (≈8 g P m^{-2}) compared to the bole only harvest (9 g P m^{-2}). Several fractions of P exist in the soil, and vary in their availability for plant uptake and degree to which they are prone to leaching losses. It is unknown which fraction was lost from the soil at the Groveton LTSP site, but like N, P is a limiting nutrient that is tightly cycled in forested ecosystems, and losses due to leaching are likely low after vegetation establishes. This result suggests, once again, that the observed pattern of lower TP in the most intensely harvested treatments was due to a legacy effect of harvest activity 15-years ago rather than on-going losses.

Fifteen years following treatment, SMB-N and -C were lower in the whole tree+forest floor treatment (21-29 μg N g^{-1} and 165-210 μg C g^{-1}, respectively) versus the bole only harvest (25-37 μg N g^{-1} and 199-267 μg C g^{-1}, respectively). These results are noteworthy simply because 15-years have elapsed since disturbance; however, it is not unexpected in light of nutrient levels seen in these treatments. When substrates are

diminished, as seen in the more intensely harvested treatments, there is the probability that SMB will likewise be lower, and vice versa. Because SMB is central to nutrient cycling in forested ecosystems, the reduction of SMB may well have a negative impact on productivity.

In contrast, SOC was not significantly impacted by forest harvest intensity 15-years post-treatment. However, SOC tended to be highest in the bole only harvest (2054-2232 g C m^{-2}) versus the whole tree+forest floor removal treatment (1631-1949 g C m^{-2}). Interestingly, at 15-years, differences between the two end-member harvests were more pronounced than at 5-years post-harvest, which is likely due to a higher C-accumulation rate in the bole only harvest (103 g C m^{-2} yr^{-1}) versus the whole tree+forest floor removal (86 g C m^{-2} yr^{-1}). Lower accumulation rates in the whole tree+forest floor removal treatments may be attributed to lower N and P as well as lower soil microbial biomass which may be affecting productivity in these plots.

Quarterly sampling at 15-years showed that TN, SOC, SMB-N and –C varied with time, but the relationship of bole only > whole tree > whole tree+forest floor removal was generally maintained throughout. Due to the size of the TN and SOC pools the magnitude of fluctuation over the year was unexpected and was negatively related to temperature and positively to precipitation. These results were not unexpected in that higher temperatures generally result in accelerated decomposition and losses. However, precipitation was associated with cooler temperatures that may have led to slowed decomposition as evidenced by smaller SMB pools and subsequent increases of SOC and TN.

Collectively, these results suggest that bole only harvest is more conducive to soil nutrient storage and cycling. The soils in this forest ecosystem are currently acting as a sink for C as seen in the soil accumulation, but the duration of this sink is unknown. Due to the fluctuations that occurred over the course of one year of sampling, a one point in time sample may be inadequate to tease out soil processes with any degree of certainty. Results of this study will contribute fundamental knowledge regarding the impacts of forest management on biogeochemical cycles and may be of use to stakeholders such as state, federal, and private forestland owners who wish to manage forests in a sustainable manner. In addition, knowledge from this study may be helpful to those modeling regional biogeochemical cycles influencing an ecosystem's ability to serve as a carbon sink.

REFERENCES

Allen, A.S., Schlesinger, W.H., 2004. Nutrient limitations to soil microbial biomass and activity in loblolly pine forests. Soil Biology & Biochemistry 36, 581-589.

Ampoorter, E., Goris, R., Cornelis, W.M., Verheyen, K., 2007. Impact of mechanized logging on compaction status of sandy forest soils. Forest Ecology and Management 241, 162-174.

Ampoorter, E., de Schrijver, A., van Nevel, L., Hermy, M., Verheyen, K., 2012. Impact of mechanized harvesting on compaction of sandy and clayey forest soils: results of a meta-analysis. Annals of Forest Science 69, 533-542.

Amundson, R., Austin, A.T., Schuur, E.A.G., Yoo, K., Matzek, V., Kendall, C., Uebersax, A., Brenner, D., Baisden, W.T., 2003. Global patterns of the isotopic composition of soil and plant nitrogen. Global Biogeochemical Cycles 17(1), 1031, doi:10.1029/2002GB001903.

Anderson, T-H., Domsch, K.H., 1989. Ratios of microbial biomass carbon to total organic carbon in arable soils. Soil Biology & Biochemistry 21 (4), 471-479.

Anderson, T-H., 2003. Microbial eco-physiological indicators to assess soil quality. Agriculture, Ecosystems & Environment 98, 285-293.

Aponte, C., Maranon, T., Garcia, L.V., 2010. Microbial C, N and P in soils of Mediterranean oak forests: influence of season, canopy cover and soil depth. Biogeochemistry 101, 77-92.

Ashworth, J., Keyes, D., Kirk, R., Lessard,R., 2001. Standard procedure in the hydrometer method for particle size analysis. Communications in Soil Science and Plant Analysis 32(5-6), 633-642.

Bai, E., Houlton, B.Z., 2009. Coupled isotopic and process-based modeling of gaseous nitrogen losses from tropical rain forests. Global Biogeochemical Cycles 23, GB2011. doi: 10.1029/2008GB003361

Bai, E., Boutton, T.W., Liu, F., Wu, X.B., Archer, S.R., 2013. ^{15}N isoscapes in a subtropical savanna parkland: spatial-temporal perspectives. Ecosphere 4(1), 4. http://dx.doi.org/10.1890/ES12-00187.1.

Berisso, F.E., Schjonning, P., Keller, T., Lamande, M., Etana, A., de Jonge, L.W., Iversen, B.V., Arvidsson, J., Forkman, J., 2012. Persistent effect of subsoil compaction on pore size distribution and gas transport in a loamy soil. Soil & Tillage Research 122, 42-51.

Billings, S.A., Richter, D.D., 2006. Changes in stable isotopic signatures of soil nitrogen and carbon during 40 years of forest development. Oecologia 148, 325-333.

Birdsey, R.A., Jenkins, J.C., Johnston, M., Huber-Sannwald, E., Amero, B., de Jong, B., Barra, J.D.E., French, N., Garcia-Oliva, F., Harmon, M., Heath, L.S., Jaramillo, V.J., Johnsen, K., Law, B.E., Marin-Spiotta, E., Masera, O., Neilson, R., Pan, Y., Pregitzer, K.S., 2007. North American Forests. In: King, A.W., L. Dilling, G.P. Zimmerman, D.M. Fairman, R.A. Houghton, G. Marland, A.Z. Rose, and T.J. Wilbanks (Eds.), The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, NC, pp. 117-126.

Birdsey, R., Bates, N., Behrenfeld, M., Davis, K., Doney, S.C., Feely, R., Heath, L., Kasischke, E., Kheshgi, H., Law, B., Lee, C., McGuire, A.D., Raymond, P., Tucker, C.J., 2009. Carbon cycle observations: gaps threaten climate mitigation policies. Eos, Transactions of the American Geophysical Union 90(34), 292.

Blazier, M.A., Patterson, W.B., Hotard, S.L., 2008. Straw harvesting, fertilization, and fertilizer type alter soil microbiological and physical properties in a loblolly pine plantation in the mid-south USA. Biology and Fertility of Soils 45, 145-153.

Bonan G., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444-1449.

Booth, M.S., Stark, J.M., Rastetter, E.., 2005. Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. Ecological Monographs 75, 139-157.

Bormann, F.H., Likens, G.E., 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, NY.

Bouyoucos, G.J., 1927. The hydrometer as a new method for the mechanical analysis of soils. Soil Science 23, 343-353.

Breland, T.A., Hansen, S., 1996. Nitrogen mineralization and microbial biomass as affected by soil compaction. Soil Biology & Biochemistry 28, 655-663.

Brenner, D.L., Amundson, R., Baisden, W.T., Kendall, C., Harden, J., 2001. Soil N and ^{15}N variation with time in a California annual grassland ecosystem. Geochimica et Cosmochimica Acta 65(22), 4171-7186.

Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biology & Biochemistry 17(6), 837-842.

Brookes, P., 2001. The soil microbial biomass: concept, measurement and applications in soil ecosystem research. Microbes and Environments 16 (3), 131-140.

Busse, M.D., Beattie, S.E., Powers, R.F., Sanchez, F.G., Tiarks, A.E., 2006. Microbial community responses in forest mineral soil to compaction, organic matter removal, and vegetation control. Canadian Journal of Forest Research 36, 577-588.

Campbell, J.L., Law, B.E., 2005. Forest soil respiration across three climatically distinct chronosequences in Oregon. Biogeochemistry 73(1), 109-125.

Campoe, O.C., Stape, J.L., Albaugh, T.J., Allen H.L., Fox, T.R., Rubilar, R., Binkley, D., 2013. Fertilization and irrigation effects on tree level aboveground net primary production, light interception and light use efficiency in a loblolly pine plantation. Forest Ecology and Management 288, 43-48.

Canadell, J.G., Le Quere, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T., Ciais, P., Conway, T.J., Gillett, N.P., Houghton, R.A., Marland, G., 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences (USA) 104, 18866–18870.

Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. Science 320, 1456-1457.

Carter, M.C., Dean, T.J., Zhou, M., Messina, M.G., Wang, Z., 2002. Short-term changes in soil C, N, and biota following harvesting and regeneration of loblolly pine (*Pinus taeda* L.). Forest Ecology and Management 164, 67-88.

Carter, M.C., Foster, C.D., 2006. Milestones and millstones: a retrospective on 50 years of research to improve productivity in loblolly pine plantations. Forest Ecology and Management 227, 137-144.

Chang, S.X., Handley, L.L., 2000. Site history affects soil and plant ^{15}N natural abundances ($\delta^{15}N$) in forest of northern Vancouver Island, British Columbia. Functional Ecology 14, 273-280.

Chen, C.R., Xu, Z.H., Keay, P., Zhang, S.L., 2005. Total soluble nitrogen in forest soils as determined by persulfate oxidation and by high temperature catalytic oxidation. Australian Journal of Soil Research 43, 515-523.

Chen, G., Tian, H., Huang, C., Prior, S.A., Pan, S., 2013. Integrating a process-based ecosystem model with Landsat imagery to assess impacts of forest disturbance on terrestrial carbon dynamics: Case studies in Alabama and Mississippi. Journal of Geophysical Research: Biogeosciences 118, 1208-1224

Choi, W-J., Chang, S.X., Curran, M.P., Ro, H-M., Kamaluddin, M., Zwiazek, J.J., 2005. Foliar $\delta^{13}C$ and $\delta^{15}N$ response of lodgepole pine and Douglas-fir seedlings to soil compaction and forest floor removal. Forest Science 51, 546-555.

Cleveland, C.C., Liptzin, D., 2007. C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochemistry 85, 235-252.

Craine, J.M., Elmore, A.J., Aidar, M.P.M., Bustamante, M., Dawson, T.E., Hobbie, E.A., Kahmen, A., Mack, M.C., McLauchlan, K.K., Michelsen, A., Nardoto, G.B., Pardo, L.H., Penuelas, J., Reich, P.B., Schuur, E.A.G., Stock, W.D., Templer, P.H., Virginia, R.A., Welker, J.M., Wright, I.J., 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. New Phytologist 183(4), 980-992.

Currie, W.S., Yanai, R.D., Piatek, K.B., Prescott, C.E., Goodale, C.L., 2003. Processes affecting carbon storage in the forest floor and in downed woody debris. In: Kimble, J.M., Heath, L.S., Birdsey, R.A., Lal, R. (Eds.), The Potential of US Forest Soils to Sequester Carbon and Mitigate the Greenhouse Effect. CRC Press, Boca Raton, FL, pp. 135-157.

Davis, S.C., Hessl, A.E., Scott, C.J., Adams, M.B., Thomas, R.B., 2009. Forest carbon sequestration changes in response to timber harvest. Forest Ecology and Management 258, 2101-2109.

de Neve, S., Hofman, G., 2000. Influence of soil compaction on carbon and nitrogen mineralization of soil organic matter and crop residues. Biology and Fertility of Soils 30, 544-549.

Denman, K.L., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P.M., Dickinson, R.E., Hauglustaine, D., Heinze, C., Holland, E., Jacob, D., Lohmann, U., Ramachandran, S., da Silva Dias, P.L., Wofsy, S.C., Zhang, X., 2007. Couplings between changes in the climate system and biogeochemistry. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

Dick, W.A., Tabatabai, M.A., 1977. An alkaline oxidation method for determination of total phosphorus in soils. Soil Science Society of America Journal 41, 511-514.

Diochon, A.C., Kellman, L., 2009. Physical fractionation of soil organic matter: destabilization of deep soil carbon following harvesting of a temperate coniferous forest. Journal of Geophysical Research 114, G01016, doi:10.1029/2008JG000844.

Ehleringer, J.R., Buchmann, N., Flanagan, L.B., 2000. Carbon isotope ratios in belowground carbon cycle processes. Ecological Applications 10(2), 412-422.

Ellert, B.H., Bettany, J.R., 1995. Calculation of organic matter and nutrients stored in soils under contrasting management regimes. Canadian Journal of Soil Science 75, 529-538.

Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10, 1135-1142.

Feigen, A., Kohl, D.H., Shearer, G., Commoner, B., 1974. Variation in the natural nitrogen-15 abundance in nitrate mineralized during incubation of several Illinois soils. Soil Science Society of America Proceedings 38, 90-95.

Fierer, N., Schimel, J.P., Holden, P.A., 2003. Variations in microbial community composition through two soil depth profiles. Soil Biology & Biochemistry 35, 167-176.

Fisher R.F., Binkley, D., 2000. Ecology and Management of Forest Soils (3rd ed.) John Wiley & Sons, Inc., New York, NY.

Fonseca, W., Benayas, J.M.R., Alice, F.E., 2011. Carbon accumulation in the biomass and soil of different aged secondary forests in the humid tropics of Costa Rica. Forest Ecology and Management 262, 1400-1408.

Food and Agriculture Organization, 2010a. Global Forest Resources Assessment 2010. FAO Forestry Paper 163. Food and Agriculture Organization of the United Nations, Rome, Italy.

Food and Agriculture Organization, 2010b. Global Forest Resources Assessment 2010, Country Report Canada. Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy.

Food and Agriculture Organization, 2010c. Global Forest Resources Assessment 2010, Country Report United States of America. Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy.

Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A., 2007. Tree nutrition and forest fertilization of pine plantations in the southern United States. Southern Journal of Applied Forestry 31(1), 5-11.

Frey, B., Kremer, J., Rudt, A., Sciacca, S., Matthies, D., Luscher, P., 2009. Compaction of forest soils with heavy logging machinery affects soil bacterial community structure. European Journal of Soil Biology 45, 312-320.

Froehlich, H.A., Miles, D.W.R., Robbins, R.W., 1985. Soil bulk density recovery on compacted skid trails in central Idaho. Soil Science Society of America Journal 49, 1015-1017.

Fry, B., 1991. Stable isotopes diagrams of freshwater food webs. Ecology 72(6), 2293-2297

Gallardo, A., Schlesinger, W.H., 1994. Factors limiting microbial biomass in the mineral soil and forest floor of a warm-temperate forest. Soil Biology & Biochemistry 26(10), 1409-1415.

Garten, C.T., Jr., Iversen, C.M., Norby, R.J., 2011. Litterfall ^{15}N abundance indicates declining soil nitrogen availability in a free-air CO_2 enrichment experiment. Ecology 92, 133-139.

Goetz, S.J., Bond-Lamberty, B., Law, B.E., Hicke, J.A., Huang, C., Houghton, R.A., McNulty, S., O'Halloran, T., Harmon, M., Meddens, A.J.H., Pfeifer, E.M., Mildrexler, D., Kasischke, E.S., 2012. Observations and assessment of forest carbon dynamics following disturbance in North America. Journal of Geophysical Research 117, G02022, doi:10.1029/2011JG001733.

Gomez, A., Powers, R.F., Singer, M.J., Horwath, W.R., 2002. Soil compaction effects on growth of young ponderosa pine following litter removal in California's Sierra Nevada. Soil Science Society of America Journal 66, 1334-1343.

Gough, C.M., Seiler, J.R., Wiseman, P.E., Maier, C.A., 2005. Soil CO_2 efflux in loblolly pine (*Pinus taeda* L.) plantation on the Virginia Piedmont and South Carolina Coastal Plain over a rotation-length chronosequence. Biogeochemistry 73 (1), 127-147.

Gough, C.M., Vogel, C.S., Schmid, H.P., Curtis, P.S., 2008. Controls on annual forest carbon storage: lessons from the past and predictions for the future. BioScience 58, 609-622.

Grand, S., Lavkulich, L.M., 2012. Effects of forest harvest on soil carbon and related variables in Canadian spodosols. Soil Science Society of America Journal 76, 1816-1827.

Gravelle, J.A., Ice, G., Link, T.E., Cook, D.L., 2009. Nutrient concentration dynamics in an inland Pacific Northwest watershed before and after timber harvest. Forest Ecology and Management 257, 1663-1675.

Greacen, E.L., Sands, R., 1980. Compaction of forest soils. A review. Australian Journal of Soil Research 18, 163-189.

Gregory, P.J., 2006. Plant Roots: Growth, Activity and Interactions with Soils. Blackwell Publishing, Oxford, UK.

Gundersen, P., Emmett, B.A., Kjonaas, O.J., Koopmans, C.J., Tietema, A., 1998. Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. Forest Ecology and Management 101, 37-55.

Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. Global Change Biology 8, 345-360.

Handley, L.L., Austin, A.T., Robinson, D., Scrimgeour, C.M., Raven, J.A., Heaton, T.H.E., Schmidt, S., Stewart, G.R., 1999. The ^{15}N natural abundance ($\delta^{15}N$) of ecosystem values reflects measures of water availability. Australian Journal of Plant Physiology 26, 185-199.

Hassett, J.E., Zak, D.R., 2005. Aspen harvest intensity decreases microbial biomass, extracellular enzyme activity, and soil nitrogen cycling. Soil Science Society of America Journal 69, 227-235.

Haubensak, K.A, Hart, S.C., Stark, J.M., 2002. Influences of chloroform exposure time and soil water content on C and N release in forest soils. Soil Biology & Biochemistry 34, 1549-1562.

Haywood, J.D., Goelz, J.C., Sayer, M.A.S., Tiarks, A.E., 2003. Influence of fertilization, weed control, and pine litter on loblolly pine growth and productivity and understory plant development through 12 growing seasons. Canadian Journal of Forest Research 33, 1974-1982.

Heath, L.S., Kimble, J.M., Birdsey, R.A., Lal, R., 2003. The potential of US forest soils to sequester carbon. In: Kimble, J.M., Heath, L., Birdsey, R., Lal, R. (Eds.), The Potential of U.S. Forest Soils to Sequester Carbon and Mitigate the Greenhouse Effect. CRC Press, Boca Raton, FL, pp. 211-238.

Henderson, G.S., 1995. Soil organic matter: a link between forest management and productivity. In: McFee, W.W., Kelly, J.M. (Eds.), Carbon Forms and Functions in Forest Soils. Soil Science Society of America, Inc., Madison, WI, pp. 419-435.

Hogberg, P., 1997. ^{15}N natural abundance in soil-plant systems. New Phytologist 137, 179-203.

Hogbom, L., Nilsson, U., Orlander, G., 2002. Nitrate dynamics after clear felling monitored by *in vivo* nitrate reductase activity (NRA) and natural ^{15}N abundance of *Deschampsia flexuosa* (L.) Trin. Forest Ecology and Management 160, 273-280.

Hoover, C.M., 2003. Soil carbon sequestration and forest management: Challenges and opportunities. In: Kimble, J.M., Heath, L., Birdsey, R., Lal, R. (Eds.), The Potential of U.S. Forest Soils to Sequester Carbon and Mitigate the Greenhouse Effect. CRC Press, Boca Raton, FL, pp. 211-238.

Hoover, C.M., 2011. Management impacts on forest floor and soil organic carbon in northern temperate forests of the US. Carbon Balance and Management 6, 17-24.

Houghton, R.A., 2007. Balancing the global carbon budget. Annual Review of Earth & Planetary Science 35, 313-347.

Houlton, B.Z., Bai, E., 2009. Imprint of denitrifying bacteria on the global terrestrial biosphere. Proceedings of the National Academy of Sciences 106, 21713–21716.

Houlton, B.Z., Sigman, D.M., Schuur, E.A., Hedin, L.O., 2007. A climate-driven switch in plant nitrogen acquisition within tropical forest communities. Proceedings of the National Academy of Sciences 104, 8902–8906.

Jarrell, W.M., Armstrong, D.E., Grigal, D.F., Kelly, E.F., Monger, H.C., Wedin, D.A., 1999. Soil water and temperature status. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), Standard Soil Methods for Long-Term Ecological Research. Oxford University Press, New York, NY, pp. 55-73.

Jensen, L.S., McQueen, D.J., Ross, D.J., Tate, K.R., 1996a. Effects of soil compaction of N-mineralization and microbial-C and –N. II. Laboratory simulation. Soil & Tillage Research 38, 189-202.

Jensen, L.S., McQueen, D.J., Shepherd, T.G., 1996b. Effects of soil compaction on N-mineralization and microbial-C and –N. I. Field measurements. Soil & Tillage Research 38, 175-188.

Jerabkova, L., Prescott, C.E., Titus, B.D., Hope, G.D., Walters, M.B., 2011. A meta-analysis of the effects of clearcut and variable-retention harvesting on soil nitrogen fluxes in boreal and temperate forests. Canadian Journal of Forest Research 41, 1852-1870.

Jobbagy, E.G., Jackson, R.B., 2001. The distribution of soil nutrients with depth: global patterns and the imprints of plants. Biogeochemistry 53(1), 51-77.

Joergensen, R.G., Wu, J., Brookes, P.C., 2011. Measuring soil microbial biomass using an automated procedure. Soil Biology & Biochemistry 43, 873-876.

Johannisson, C., Hogberg, P., 1994. ^{15}N abundance of soils and plants along an experimentally induced forest nitrogen supply gradient. Oecologia 97(3), 322-325

Johnsen, K.H., Samuelson, L.J., Sanchez, F.G., Eaton, R.J., 2013. Soil carbon and nitrogen content and stabilization in mid-rotation, intensively managed sweetgum and loblolly pine stands. Forest Ecology and Management 302, 144-153.

Johnson, D.W., Todd, D.E., Jr., 1998. Harvesting effects on long-term changes in nutrient pools of mixed oak forest. Soil Science Society of America Journal 62, 1725-1735.

Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N: meta analysis. Forest Ecology and Management 140, 227-238.

Johnson, D.W., Todd, D.E., Jr., Tolbert, V.R., 2003. Changes in ecosystem carbon and nitrogen in a loblolly pine plantation over the first 18 years. Soil Science Society of America Journal 67, 1594-1601.

Johnston, J.M, Crossley, D.A.,Jr., 2002. Forest ecosystem recovery in the southeast US: soil ecology as an essential component of ecosystem management. Forest Ecology and Management 155, 187-203.

Jones, H.S., Beets, P.N., Kimberley, M.O., Garrett, L.G., 2011. Harvest residue management and fertilisation effects on soil carbon and nitrogen in a 15-year-old *Pinus radiata* plantation forest. Forest Ecology and Management 262, 339-347.

Jordan, D., Ponder, F., Jr., Hubbard, V.C., 2003. Effects of soil compaction, forest leaf litter, and nitrogen fertilizer on two oak species and microbial activity. Applied Soil Ecology 23, 33-41.

Kelly, J.M., Mays, P.A., 2005. Soil carbon changes after 26 years in a Cumberland Plateau hardwood forest. Soil Science Society of America Journal 69, 691-694.

Kimmins, J.P., 1977. Evaluation of the consequences for future tree productivity of the loss of nutrients in whole-tree harvesting. Forest Ecology and Management 1, 169-183.

Kiser, L.C., Kelly, J.M., Mays, P.A., 2009. Changes in forest soil carbon and nitrogen after a thirty-year interval. Soil Science Society of America Journal 73, 647-653.

Kiser, L.C., Fox, T.R., 2012. Soil accumulation of nitrogen and phosphorus following annual fertilization of loblolly pine and sweetgum on sandy sites. Soil Science Society of America Journal 76, 2278-2288.

Knoepp, J.D., Swank, W.T., 1997. Forest management effects on surface soil carbon and nitrogen. Soil Science Society of America Journal 61, 928-935.

Koba, K., Fang, Y., Mo, J., Zhang, W., Lu, X., Liu, L., Zhang, T., Takebayashi, Y., Toyoda, S., Yoshida, N., Suzuki, K., Yoh, M., Senoo, K., 2012. The ^{15}N natural abundance of the N lost from an N-saturated subtropical forest in southern China. Journal of Geophysical Research 117(2), G02015. doi:http://dx.doi.org/10.1029/2010JG001615.

Labelle, E.R., Jaeger, D., 2011. Soil compaction caused by cut-to-length forest operations and possible short-term natural rehabilitation of soil density. Soil Science Society of America Journal 75, 2314-2329.

Laiho, R., Sanchez, F., Tiarks, A., Dougherty, P.M., Trettin, C.C., 2003. Impacts of intensive forestry on early rotation trends in site carbon pools in the southeastern US. Forest Ecology and Management 174, 177-189.

Lajtha, K., Driscoll, C.T., Jarrell, W.M., Elliott, E.T., 1999. Soil phosphorus characterization and total element analysis. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), Standard Soil Methods for Long-Term Ecological Research. Oxford University Press, New York, NY, pp. 115-142.

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

LeDuc, S.D., Rothstein, D.E., 2007. Initial recovery of soil carbon and nitrogen pools and dynamics following disturbance in jack pine forests: a comparison of wildfire and clearcut harvesting. Soil Biology & Biochemistry 39, 2865-2876.

Li, Q., Allen, H.L., Wilson, C.A., 2003. Nitrogen mineralization dynamics following the establishment of a loblolly plantation. Canadian Journal of Forest Research 33, 364-374.

Li, Q., Allen H.L., Wollum, A.G.,II, 2004. Microbial biomass and bacterial functional diversity in forest soils: effects of organic matter removal, compaction, and vegetation control. Soil Biology & Biochemistry 36, 571-579.

Li, Y., Edgar, C.B., Carraway, A.B., 2011. Economic Impact of the Texas Forest Sector, 2009. Texas Forest Service, Forest Resource Development and Sustainable Forestry, College Station, TX.

Liao, J.D., Boutton, T.W., 2008. Soil microbial biomass response to woody plant invasion of grassland. Soil Biology & Biochemistry 40, 1207-1216.

Londo, A.J., Messina, M.G., Schoenholtz, S.H., 1999. Forest harvesting effects on soil temperature, moisture, and respiration in a bottomland hardwood forest. Soil Science Society of America Journal 63, 637-644.

Ludovici, K.H., 2008. Compacting Coastal Plain soils changes midrotation loblolly pine allometry by reducing root biomass. Canadian Journal of Forest Research 38, 2169-2176.

Luxmoore, R.J., Tharp, M.L., Post, W.M., 2008. Simulated biomass and soil carbon of loblolly pine and cottonwood plantations across a thermal gradient in southeastern United States. Forest Ecology and Management 254, 291-299.

Mariani, L., Chang, S.X., Kabzems, R., 2006. Effects of tree harvesting, forest floor removal, and compaction on soil microbial biomass, microbial respiration, and N availability in a boreal aspen forest in British Columbia. Soil Biology & Biochemistry 38, 1734-1744.

Mariotti, A., 1983. Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. Nature 303, 685-687.

McGroddy, M.E., Daufresne, T., Hedin, L.O., 2004. Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. Ecology 85(9), 2390-2401.

McKinley, D.C., Ryan, M.G., Birdsey, R.A., Giardina, C.P., Harmon, M.E., Heath, L.S., Houghton, R.A., Jackson, R.B., Morrison, J.F., Murray, B.C., Pataki, D.E., Skog, K.E., 2011. A synthesis of current knowledge on forest and carbon storage in the United States. Ecological Applications 21(6), 1902-1924.

McLaughlin, J.W., Phillips, S.A., 2006. Soil carbon, nitrogen, and base cation cycling 17 years after whole-tree harvesting in a low-elevation red spruce (*Picea rubens*)-balsam fir (*Abies balsamea*) forested watershed in central Maine, USA. Forest Ecology and Management 222, 234-253.

Metz, L.J., Wells, C.G., 1965. Weight and nutrient content of the aboveground parts of some loblolly pines. Research Paper SE-17. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 21 p.

Minasny, B., McBratney, A.B., Brough, D.M., Jacquier, D., 2011. Models relating soil pH measurements in water and calcium chloride that incorporate electrolyte concentration. European Journal of Soil Science 62(5), 728-732.

Mummey, D.L., Clarke, J.T., Cole, C.A., O'Connor, B.G., Gannon, J.E., Ramsey, P.W., 2010. Spatial analysis reveals differences in soil microbial community interactions between adjacent coniferous forest and clearcut ecosystems. Soil Biology & Biochemistry 42, 1138-1147.

Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27, 31-36.

Nadelhoffer, K.J., Fry, B., 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Science Society of America Journal 52, 1633-1640.

Nadelhoffer, K.J., Fry, B., 1994. Nitrogen isotope studies in forest ecosystems. In: Lajtha, K., Michener R.H. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Scientific Publications, Oxford, UK, pp. 22-44.

Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2010. Harvest impacts on soil carbon storage in temperate forests. Forest Ecology and Management 259, 857-866.

Neilson, R., Hamilton, D., Wishart, J., Marriott, C.A., Boag, B., Handley, L.L., Scrimgeour, C.M., McNicol, J.W., Robinson, D., 1998. Stable isotope natural abundances of soil, plants and soil invertebrates in an upland pasture. Soil Biology and Biochemistry 30(13), 1773-1782.

Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J., Rosen, K., 1996. Carbon and nitrogen in coniferous forest soils after clear-felling and harvest of different intensity. Forest Ecology and Management 82, 19-32.

Ometto, J.P.H.B., Ehleringer, J.R., Domingues, T.F., Berry, J.A., Ishida, F.Y., Mazzi, E., Higuchi, N., Flanagan, L.B., Nardoto, G.B., Martinelli, L.A., 2006. The stable carbon and nitrogen isotopic composition of vegetation in tropical forests of the Amazon Basin, Brazil. Biogeochemistry 79, 251-274.

Pacala, S.W., Hurtt, G.C., Baker, D., Peylin, P., Houghton, R.A., Birdsey, R.A., Heath, L., Sundquist, E.T., Stallard, R.F., Ciais, P., Moorcroft, P., Caspersen, J.P., Shevliakova, E., Moore, B., Kohlmaier, G., Holland, E., Gloor, M., Harmon, M.E., Fan, S.M., Sarmiento, J.L., Goodale, C.L., Schimel, D., Field, C.B., 2001. Consistent land- and atmosphere-based U.S. carbon sink estimates. Science 292, 2316-2320.

Palmer, D.J., Lowe, D.J., Payn, T.W., Hock, B.K., McLay, C.D.A., Kimberley, M.O., 2005. Soil and foliar phosphorus as indicators of sustainability for *Pinus radiata* plantation forestry in New Zealand. Forest Ecology and Management 220, 140-154.

Pan, Y., Birdsey, R.A., Fang, J., Hougthon, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988-993.

Pardo, L.H., Hemond, H.F., Montoya, J.P., Fahey, T.J., Siccama, T.G., 2002. Response of the natural abundance of ^{15}N in forest soils and foliage to high nitrate loss following clear-cutting. Canadian Journal of Forest Research 32, 1126-1136.

Pardo, L.H., Nadelhoffer, K.J., 2010. Using nitrogen isotope ratios to assess terrestrial ecosystems at regional and global scales. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (Eds.), Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping. Springer, New York, NY, pp. 221-249.

Paul, E.A., Harris, D., Klug, M.J., Ruess, R.W., 1999. The determination of microbial biomass. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), Standard Soil Methods for Long-Term Ecological Research. Oxford University Press, New York, NY, pp. 291-317.

Paul, K.I., Polglase, P.J., O'Connell, A.M., Carlyle, J.C., Smethhurst, P.J., Khanna, P.K., 2003. Defining the relation between soil water content and net nitrogen mineralization. European Journal of Soil Science 54, 39-47.

Peri, P.L., Ladd, B., Pepper, D.A., Bonser, S.P., Laffan, S.W., Amelung, W., 2012. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope composition in plant and soil in Southern Patagonia's native forests. Global Change Biology 18, 311-321.

Post, W.M., Kwon, K.C., 2000. Soil carbon sequestration and land-use change: processes and potential. Global Change Biology 6, 317-327.

Potthoff, M., Jackson, L.E., Sokolow, S., Joergensen, R.G., 2009. Below and aboveground responses to lupines and litter mulch in a California grassland restored with native bunchgrasses. Applied Soil Ecology 42, 124-133.

Powers, R.F., Scott, D.A., Sanchez, F.G., Voldseth, R.A., Page-Dumroese, D., Elioff, J.D., Stone, D.M., 2005. The North American long-term soil productivity experiment: findings from the first decade of research. Forest Ecology and Management 220, 31-50.

Powers, R.F., 2006. Long-term soil productivity: genesis of the concept and principles behind the program. Canadian Journal of Forest Research 36, 519-528.

Powlson, D.S., Brookes, P.C., Christensen, B.T., 1987. Measurement of soil microbial biomass provides an early indication of changes in total soil organic matter due to straw incorporation. Soil Biology & Biochemistry 19(2), 159-164.

Pregitzer, K.S., 2003. Carbon cycling in forest ecosystems with an emphasis on belowground processes. In: Kimble, J.M., Heath, L.S., Birdsey, R.A., Lal, R. (Eds.), The Potential of US Forest Soils to Sequester Carbon and Mitigate the Greenhouse Effect. CRC Press, Boca Raton, FL, pp. 93-107.

Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biology 10, 2052-2077.

Prescott, C.E., 2005. Do rates of litter decomposition tell us anything we really need to know? Forest Ecology and Management 220, 66-74.

Reed, S.C., Cleveland, C.C., Townsend, A.R., 2011. Functional ecology of free-living nitrogen fixation: a contemporary perspective. Annual Review of Ecology, Evolution, and Systematics 42, 489-512.

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

Richter, D.D., Allen, H.L., Li, J., Markewitz, D., Raikes, J., 2006. Bioavailability of slowly cycling soil phosphorus: major restructuring of soil P fractions over four decades in aggrading forest. Oecologia 150, 259-271.

Robertson, G.P., Vitousek, P.M., Matson, P.A., Tiedje, J.M., 1987. Denitrification in a clearcut loblolly pine (*Pinus taeda* L.) plantation in the southeastern US. Plant and Soil 97, 119-129.

Robinson, D., 2001. $\delta^{15}N$ as an integrator of the nitrogen cycle. *TRENDS* in Ecology and Evolution 16, 153-162.

Rodeghiero, M., Heinemeyer, A., Schrumpf, M., Bellamy, P., 2009. Determination of carbon stocks and changes. In: Kutsch, W.L., Bahn, M., Heinemeyer, A. (Eds.), Soil Carbon Dynamics: An Integrated Methodology. Cambridge University Press, Cambridge, United Kingdom, pp. 49-75.

Sah, S.P., Ilvesniemi, H., 2007. Interspecific variation and impact of clear-cutting on natural ^{15}N abundance and N concentration in the needle-to-soil continuum of a boreal conifer forest. Plant, Soil and Environment 53, 329-339.

Sanchez, F.G., 2001. Loblolly pine needle decomposition and nutrient dynamics as affected by irrigation, fertilization, and substrate quality. Forest Ecology and Management 152, 85-96.

Sanchez, F.G., Scott, D.A., Ludovici, K.H., 2006a. Negligible effects of severe organic matter removal and soil compaction on loblolly pine growth over 10 years. Forest Ecology and Management 227, 145-154.

Sanchez, F.G., Tiarks, A.E., Kranabetter, J.M., Page-Dumroese, D.S., Powers, R.F., Sanborn, P.T., Chapman, W.K., 2006b. 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. Canadian Journal of Forest Research 36, 565-576.

Sayer, E.J., 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biological Reviews 81, 1-31.

Schimel, D.S., 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1, 77-91.

Schlesinger, W.H., Lichter, J., 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. Nature 411, 466-469.

Schlesinger, W.H., Bernhardt, E.S., 2013. Biogeochemistry: An Analysis of Global. Change (3rd ed.). Academic Press, Waltham, MA.

Schmandt, J., Clarkson, J., North, G.R., (Eds.), 2009. The Impact of Global Warming on Texas (2nd ed.). University of Texas Press, Austin, TX.

Scott, D.A., Tiarks, A.E., Sanchez, F.G., Elliott-Smith, M, Stagg, R., 2004. Forest soil productivity on the southern Long-term Soil Productivity sites at age 5. In: Connor, K.F. (Ed.), Proceedings of the 12th Biennial Southern Silvicultural Research Conference, Gen, Tech. Rpt. SRS – 71, Asheville, N.C.: USDA Forest Service, Southern Research Station.

Scott, D.A., Messina, M.G., 2010. Soil properties in 35 y old pine and hardwood plantations after conversion from mixed pine-hardwood forest. The American Midland Naturalist 163(1), 197-211.

Shearer, G., Kohl, D.H., Chien, S-E., 1978. The nitrogen-15 abundance in a wide variety of soils. Soil Science Society of America Journal 42, 899-902.

Shestak, C.J., Busse, M.D., 2005. Compaction alters physical but not biological indices of soil health. Soil Science Society of America Journal 69, 236-246.

Siska, P., Bryant, V.M., Hung, I.K., 2006. Geospatial analysis of southern pine biome and pollen distribution patterns in southeastern United States. Geograficky Casopis 58(4), 239-258.

Six, J., Bossuyt, H., Degryze, S., Denef, K., 2004. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. Soil Tillage & Research 79, 7-31.

Smolander, A., Kitunen, V., Tamminen, P., Kukkola, M., 2010. Removal of logging residue in Norway spruce thinning stands: long-term changes in organic layer properties. Soil Biology & Biochemistry 42, 1222-1228.

Song, X., Tian, H., Xu, X., Hui, D., Chen, G., Sommers, G., Marzen, L., Liu, M., 2013. Projecting terrestrial carbon sequestration of the southeastern United States in the 21st century. Ecosphere 4(7), 88. http://dx.doi.org/10.1890/ES12-00398.1.

Spangenberg, A., Grimm, U., Sepeda da Silva, J.R., Folster, H., 1996. Nutrient store and export rates of *Eucalyptus urograndis* plantations in eastern Amazonia (Jari). Forest Ecology and Management 80, 225-234.

Switzer, G.L., Nelson, L.E., Hinesley, L.E., 1978. Effects of utilization on nutrient regimes and site productivity. In: McMillan, C.W. (Ed.), Complete Tree Utilization of Southern Pine, April 1978, New Orleans. Forest Products Research Society, Madison, WI.

Sword, M.A, Chambers, J.L., Gravatt, D.A., Haywood, J.D., Barnett, J.P., 1998a. Ecophysiological response of managed loblolly pine to changes in stand environment. In: Mickler, R.A., Fox, S. (Eds.), The Productivity and Sustainability of Southern Ecosystems in a Changing Environment. Springer-Verlag, New York, NY, pp. 185-206.

Sword, M.A., Haywood, J.D., Andries, C.D., 1998b. Seasonal lateral root growth of juvenile loblolly pine after thinning and fertilization on a Gulf Coastal Plain site. In: Waldrop, T.A. (Ed.), Proceedings of the Ninth Biennial Southern Silvicultural Research Conference, Gen. Tech Rpt. SRS-20, Asheville, N.C.: USDA Forest Service, Southern Research Station.

Tan, X., Chang, S.X., Kabzems, R., 2005. Effects of soil compaction and forest floor removal on soil microbial properties and N transformations in a boreal forest long-term soil productivity study. Forest Ecology and Management 217, 158-170.

Tan, X., Chang, S.X., 2007. Soil compaction and forest litter amendment affect carbon and net nitrogen mineralization in a boreal forest soil. Soil Tillage and Research 93, 77-86.

Tan, X., Chang, S.X., Kabzems, R., 2008. Soil compaction and forest floor removal reduced microbial biomass and enzyme activities in a boreal aspen forest soil. Biology and Fertility of Soils 44, 471-479.

Teskey, R.O., Hinckley, T.M., 1981. Influence of temperature and water potential on root growth of white oak. Physiologia Plantarum 52, 363-369.

Tew, D.T., Morris, L.A., Allen, H.L., Wells, C.G., 1986. Estimates of nutrient removal, displacement and loss resulting from harvest and site preparation of a *Pinus taeda* plantation in the piedmont of North Carolina. Forest Ecology and Management 15, 257-267.

Tingey, D.T., Phillips, D.L., Johnson, M.G., Rygiewicz, P.T., Beedlow, P.A., Hogsett, W.E., 2005. Estimates of Douglas-fir fine root production and mortality from minirhizotrons. Forest Ecology and Management 204, 359-370.

Tisdall, J.M., Oades, J.M., 1982. Organic matter and water-stable aggregates in soils. Journal of Soil Science 33, 141-163.

Torbert, H.A., Wood, C.W., 1992. Effects of soil compaction and water-filled pore space on soil microbial activity and N losses. Communications in Soil Science and Plant Analysis 23(11&12), 1321-1331.

Torreano, S.J., Morris, L.A., 1998. Loblolly pine root growth and distribution under water stress. Soil Science Society of America Journal 62, 818-827.

Trettin, C.C., Jurgensen, M.F., Gale, M.R., McLaughlin, J.W., 2011. Recovery of carbon and nutrient pools in a northern forested wetland 11 years after harvesting and site preparation. Forest Ecology and Management 262, 1826-1833.

Turner, J., Lambert, M.J., 2011. Analysis of nutrient depletion in a radiata pine plantation. Forest Ecology and Management 262, 1327-1336.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biology & Biochemistry 19, 703-707.

Vance, E.D., Chapin, F.S., III, 2001. Substrate limitations to microbial activity in taiga forest floors. Soil Biology & Biochemistry 33, 173-188.

Vanguelova, E., Pitman, R., Luiro, J., Helmisaari, H-S., 2010. Long term effects of whole tree harvesting on soil carbon and nutrient sustainability in the UK. Biogeochemistry 101, 43-59.

Vitousek, P.M., Howarth, R.W., 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13, 87-115.

Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecological Applications 20(1), 5-15.

von Lutzow, M., Kogel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., Marschner, B., 2007. SOM fractionation methods: relevance to functional pools and to stabilization mechanisms. Soil Biology & Biochemistry 39, 2183-2207.

Walker, T.W., Syers, J.K., 1976. The fate of phosphorus during pedogenesis. Geoderma 15, 1–19.

Wall, A., 2008. Effect of removal of logging residue on nutrient leaching and nutrient pools in the soil after clearcutting in a Norway spruce stand. Forest Ecology and Management 256, 1372-1383.

Wardle, D.A., 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biological Reviews 67, 321-358.

Webster, E.A., Hopkins, D.W., Chudek, J.A., Haslam, S.F.I., Simek, M., Picek, T., 2001. The relationship between microbial carbon and the resource quality of soil carbon. Journal of Environmental Quality 30,147–150.

Wells, C.G., Jorgensen, J.R., 1979. Effect of intense harvesting on nutrient supply and sustained productivity. In: Proceedings: Impact of Intensive Harvesting on Forest Nutrient Cycling. State University of New York, Syracuse, NY, pp. 212-230.

Wert, S., Thomas, B.R., 1981. Effects of skid roads on diameter, height, and volume growth in Douglas-fir. Soil Science Society of America Journal 45, 629–632.

Wilhelm, K., Rathsack, B., Bockheim, J., 2013. Effects of timber harvest on macronutrient cycling in oak-dominated stands on sandy soils of northwest Wisconsin. Forest Ecology and Management 291, 1-12.

Will, R.E., Markewitz, D., Hendrick, R.L., Meason, D.F., Crocker, T.R., Borders, B.E., 2006. Nitrogen and phosphorus dynamics for 13-year-old loblolly pine stands receiving complete competition control and annual N fertilizer. Forest Ecology and Management 227, 155-168.

Wollum, A.G., II, Davey, C.B., 1975. Nitrogen accumulation, transformation, and transport in forest soils. In: Bernier, B., Winget, C.H. (Eds.), Forest Soils and Forest Land Management. Les Presses de L' Universite Laval, Quebec, Canada, pp. 67-106.

Wood, T., Bormann, F.H., Voigt, G.K., 1984. Phosphorus cycling in a northern hardwood forest: biological and chemical control. Science 223, 391-393.

Wu, J., Brookes, P.C., Jenkinson, D.S., 1996. Evidence for the use of a control in the fumigation-incubation method for measuring microbial biomass carbon in soil. Soil Biology & Biochemistry 28 (4/5), 511-518.

Yanai, R.D., 1992. Phosphorus budget of a 70-year-old northern hardwood forest. Biogeochemistry 17(1), 1-22.

Yanai, R. D., 1998. The effect of whole-tree harvest on phosphorus cycling in a northern hardwood forest. Forest Ecology and Management 104, 281-295.

Zak, D.R., Tilman, D., Parmenter, R.R., Rice, C.W., Fisher, F.M., Vose, J., Milchunas, D., Martin, C.W., 1994. Plant production and soil microorganisms in late-successional ecosystems: a continental-scale study. Ecology 75(8), 2333-2347.

Zerpa, J.L., Allen, H.L., Campbell, R.G., Phelan, J., Duzan, H., 2010. Influence of variable organic matter retention on nutrient availability in a 10-year-old loblolly pine plantation. Forest Ecology and Management 259, 1480-1489.