SITE-SPECIFIC FOREST MANAGEMENT: MATCHING GENOTYPES AND SILVICULTURE TO OPTIMIZE CARBON SEQUESTRATION

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Abstract—The use of improved genotypes as well an increased understanding of the role of intensive silviculture have made southeastern pine forests some of the most productive forests in the world. The objectives of this research were to determine how two superior loblolly pine (*Pinus taeda*) genotypes, representing two distinct ideotypes, respond to manipulations of nutrient availability. Second, based on estimates of carbon (C) capture and loss, predict how treatment responses may influence net ecosystem productivity (NEP). A combination of nitrogen (N) and phosphorus fertilization and the incorporation of high C to N logging residue (LR) provided a range of nutrient availability. We found both clones increased aboveground growth in response to fertilization, but to different degrees. Additionally, there were large differences in aboveground biomass partitioning in response to LR incorporation between clones. Finally, there were significant clonal differences in soil CO_2 efflux indicating that there may be strong differences in NEP between genotype and nutrient availability.

INTRODUCTION

Southern pine plantations in the Southeastern United States are some of the most intensively managed and highly productive forested systems in the world (Allen and others 2005). Planted pine forests may create great opportunity for sequestering large amounts of carbon (C) (Johnsen and others 2001). Currently, southern pine plantations occupy more than 13 million ha and are forecast to increase 67 percent to 22 million ha by the year 2040 (Wear and Greis 2002). Intensive management of pine forests has been shown to affect net ecosystem C exchange by decreasing the time necessary for a stand to shift from a C source to a C sink (Lai and others 2002; Maier and others 2004, 2002; Sampson and others 2006). Net primary productivity (NPP) and heterotrophic respiration (R_h) are two opposing processes that contribute to net ecosystem productivity (NEP). Forest management such as nutrient additions, competition control, and site preparation most dramatically impact NEP by increasing NPP (Albaugh and others 2004, Maier and others 2004) but has also been shown to suppress the rate of soil organic matter decomposition (Fog 1988) either through reduced microbial activity (Blazier and others 2005, Gough and Seiler 2004, Homann and others 2001, Olsson and others 2005, Tyree and others 2008), decreased microbial biomass (Bååth and others 1981, Lee and Jose 2003, Thirukkumaran and Parkinson 2000, Tyree 2008), changes in microbial population composition (Bittman and others 2005, Lilleskov and others 2002), or some combination of these factors.

A typical harvesting operation in a southern pine stand can generate up to 50 t of logging debris/ha (Allen and others 2006), which historically has been gathered into large piles and burned or abandoned. These represent huge stores of organic C, which left exposed to the air will largely oxidize being released back into the atmosphere as CO_2. Forest managers routinely spread this logging debris back onto the site in an attempt to spread nutrients across a site as well as minimize disturbance from trafficking. Further, the idea has been proposed to incorporate this logging residue (LR) into the soil (see review by Johnson and Curtis 2001). Not only would this provide nutrients to successive stands, but it may additionally increase soil C sequestration as it is likely some fraction will remain as recalcitrant soil C. Agricultural studies have long shown that adding large amounts of C into the mineral soil will also impact nutrient cycling and decomposition rates of the material (Holland and Coleman 1987). Depending on the availability of organic C to decomposition and the ratio of C to N, there is both the potential to increase longer term nutrient cycling, particularly N, phosphorus (P), and sulfur. However, incorporating logging residue into the soil following harvesting may result in the acceleration of microbial decomposition of the labile C pool leading to an increase in microbial populations (Aggangan and others 1999, Ouro and others 2001) and the short-term immobilization of essential nutrients such as N (Aggangan and others 1999, Perez-Batallon and others 2001), which may result in decreased tree growth.

An exciting area of research that shows huge potential for increasing productivity of intensively managed forests is the use of superior planting stock. In fact, it has been estimated that increases in volume gains of 10 to 30 percent have been made possible as a result of selective breeding, and gains of 50 percent or more may be possible by combining the use of clones and intensive silviculture (Allen and others 2005, Martin and others 2005). With increased emphasis being placed on site-specific management there is a need to determine how specific genotypes will vary across environments (Fox 2000) as well as match specific genotypes to site conditions, e.g., resource availability.

The overall objective of this research is to monitor the short-term (1 to 3 years) effects of intensive silviculture on C pools

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and fluxes, involved in C capture, biomass partitioning, and C evolution back to the atmosphere, in young loblolly pine (*Pinus taeda*). Specifically, we wanted to determine how two superior loblolly pine genotypes, which represent two distinct ideotypes, respond to manipulations of nutrient availability. Secondly, based on estimates of C capture and loss predict how treatment responses may influence NEP. We hypothesize both genotypes will respond to increased N and P by increasing NPP, but to different extents. Additionally, the incorporation of LR would decrease growth in both clones, but effect "narrow crown" ideotype to a lesser extent. Finally, differences in growth and C allocation between clones will significantly impact the rate of C evolution from these soils as well as the short-term C balance.

MATERIAL AND METHODS

Study Site

The study site was located in Berkeley County, SC, at an elevation of 24 m above mean sea level. Average annual temperature was 14.6 °C and 17.4 °C with an average daily maximum of 17.3 °C and 25.2 °C and an average daily minimum of 11.7 °C and 11.2 °C for the 2006 and 2007 year, respectively. Highest daily average temperature was 26.8 °C and 32.5 °C occurring in August 2006 and August 2007, respectively, and a low of –0.9 °C and 0.4 °C occurring in December 2006 and February 2007, respectively. Total precipitation was 90.2 cm in 2006 and 74.9 cm in 2007 spread evenly throughout the year, which was well below the average of 120 cm recorded between 1949 and 1973 (Long 1980). The dominant soil series is Ocilla (loamy, siliceous, semiactive, thermic Aquic Arenic Paleudults). Harvest of the previous 21-year-old loblolly pine stand took place in May 2004, and the site was sheared of residual material in July 2004. LR treatments were applied in October 2004, and site preparation (bedding) took place in early November 2004. Loblolly pine clones were planted in January of 2005, and data for this study was collected between January 2006 and January 2008.

Experimental Design

The study design was a split-plot, randomized complete block design replicated three times with the whole-plot treatments arranged as a full 2 by 2 factorial, which was measured repeatedly. Each 0.18-ha plot (48 x 38 m) was planted with approximately 243 container-grown, clonal loblolly pine seedlings in 9 rows at a 1.8-m spacing within rows and a 4.3-m spacing between row centers. Two levels of LR and two clones (CL32 and CL93) served as the whole-plot treatments. The two levels of LR were no LR incorporated and LR incorporated into the mineral soil (LR) at a rate of 25 Mg oven-dry weight/ha, which was concentrated onto the beds (approximately 75 Mg oven-dry weight/ha; C to N = 700). Both LR treatments also incorporated the residual forest floor of approximately 25 Mg oven-dry weight/ha. The two loblolly pine clones chosen both exhibit superior height growth but represent two distinct ideotypes. Clone 93 (CL93, "narrow crown" ideotype) has been shown to allocate more of its resources to stem growth while clone 32 (CL32, "broad crown" ideotype) allocates more resources to leaf area. Each plot was split into two 0.0013-ha measurement plots, located at opposite ends of the whole plot; each consisted of six seedlings (four measurement trees + two buffer trees) and served as the experimental unit. Each split plot received one of two fertilizer applications: no nutrient additions or N and P fertilization (F). During the 2006 growing season fertilizer was applied twice and totaled 209 kg N and 116 kg P/ha in the form of diammonium phosphate and ammonium nitrate (AN). Roughly one-third was applied on April 6 and the remaining two-thirds applied on May 8, 2006. F for the 2007 growing season was applied on March 9, 2007, at a rate of 200 kg N/ha in the form of AN.

Measurements

In January 2008, a representative tree, which most closely fit the mean tree height from each plot, was harvested to estimate biomass partitioning. The aboveground portion of each seedling was cut 10 cm above groundline. Belowground plant tissues were sampled by excavating a 1- by 1- by 0.5-m volume around the main stem. At the lab each tree was dissected into foliage, branches, main stem, tap root, and lateral roots. All samples were oven dried (>2 weeks) at a temperature of 65±5 °C then weighed gravimetrically to the nearest gram.

Total soil CO_2 efflux (F_S) from the soil surface was estimated using a LI-6200 portable infrared gas analyzer (LI-COR Biosciences, Lincoln, NE) with a dynamic closed soil chamber giving a total system volume of 6300 cm^3 (Selig and others 2008, Tyree and others 2008). Soil respiration measurements were taken approximately every 1 to 1.5 months starting January 2006 through December 2007 (16 sampling dates). A broken chamber hose on February 2006 and machine leaks on May and June 2006 forced us to remove all 3 sampling dates leaving 13 separate dates for the experiment. Measurements were taken at approximately the same location on each date and in the same sequential blocking order between 0800 and 1600 hours and taking between 3 to 4 hours to complete. Two subsamples were taken per measurement plot. One measurement was taken at the base of the tree and the other taken between trees to account for spatial variation on the planting bed. No measurements were taken between planting rows. Soil CO_2 evolution was measured over a 30-second period and F_S rates calculated as µmols CO_2 m^2/second.

Carbon balance was estimated by calculating NPP in Mg C/ha over two growing seasons by converting total biomass to total C content by assuming a 0.5-conversion factor. R_h was roughly estimated from our measurements of F_S. Average F_S was determined for each plot (13 sampling dates by 2 locations) and converted to metric tons of carbon per hectare over the entire study. Based on the literature, R_h was assumed to be 50 percent of F_S for this experiment (Andrews and others 1999, Hanson and others 2000, Maier and Kress 2000).

Data Analyses

Treatment differences in F_S were determined using analysis of variance with repeated measures using a MIXED model.

Covariance structures were selected using AIC, AAIC, and BIC fit statistics included in the SAS output. Treatment differences in biomass partitioning and relative C budgets were analyzed using a general linear model (GLM). Residuals and the normality curves were plotted for all analyses to confirm that the data met assumptions of equal variance and normality for all parameters measured. When data were transformed by their natural log to meet assumptions, all values were expressed as untransformed least square means and standard errors. All analyses were performed using the MIXED and GLM procedures in SAS (SAS 2006).

RESULTS AND DISCUSSION

We observed significant differences for both above- and belowground plant biomass (*P* = 0.002 and *P* = 0.08, respectively) with our nutrient manipulation treatments (fig. 1). Consistent with other researchers' findings (Albaugh and others 1998, Gough and Seiler 2004), the addition of N and P fertilizer resulted in a 101- and 65-percent increase in above- and belowground biomass, respectively, at the end of the third-growing season relative to control treatments. LR additions increased aboveground biomass by 25 percent but had no effect on belowground biomass. Interestingly, when both fertilizer and LR were added there was only a modest increase in above- and belowground biomass (29 and 18 percent, respectively) indicating that the addition of LR resulted in increased competition for nutrients by soil microbes. Data from an accompanying field study showed that microbial biomass C and microbial activity (R_h) increased with the addition of LR for these same plots (Tisdale 2008, Tyree 2008).

In contrast to our hypothesis we found no significant (*P* > 0.1) difference between genotypes in above- and belowground biomass. However, upon closer investigation we observed differences in aboveground biomass partitioning with soil amendment treatments (fig. 2). For example, plots receiving LR resulted in a 47-percent increase in foliar to stem ratio in CL32 and no change in CL93 (*P* = 0.005, fig. 2A). Plots receiving fertilizer showed the opposite trend with CL32 showing a decrease in foliar to stem ratio by 22 percent and CL93 showing a 19-percent increase (*P* = 0.06, fig. 2B).

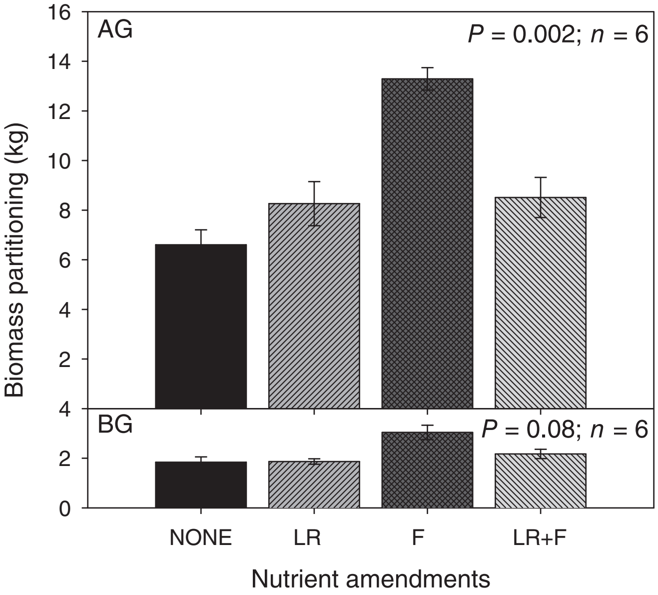

Figure 1—Mean above- (AG) and belowground (BG) biomass partitioning for logging residue (LR) and fertilization (F) nutrient manipulation treatments. Clonal loblolly pine seedlings were planted January 2005 in Berkley County, SC, and destructively harvested on January 2008.

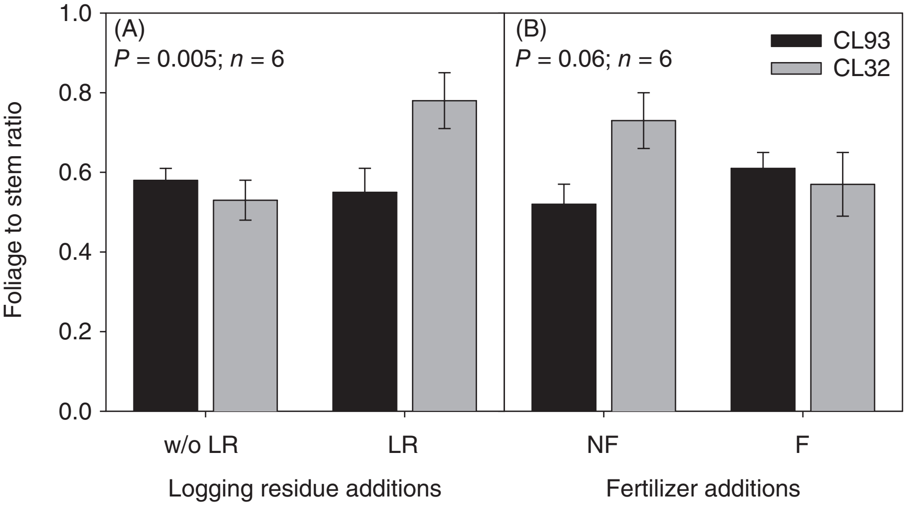

Figure 2—Mean foliage to stem ratio for (A) logging residue (LR) and (B) fertilization (F) treatments. Clonal loblolly pine seedlings were planted January 2005 in Berkley County, SC, and destructively harvested on January 2008. (w/o LR = no LR incorporated; NF = no nutrient additions.)

These data indicate that although there is no difference between genotypes in total aboveground biomass across a fertility gradient there are differences in how that aboveground tissue is distributed. Always keeping in mind that our primary objective is to produce forest products and that C sequestration will be secondary, and by planting genotypes that preferentially allocate to stem biomass we are able to optimize both these objectives.

In support of our hypothesis we observed a significant (*P* = 0.03) clone by LR by fertilizer three-way interaction when data from all 13 sampling dates were analyzed. In control treatments (none) F_S was substantially greater in CL32 than CL93 (fig. 3). This was supported by minirhizotron data from a project collaborator which showed that CL32 maintained greater fine-root (<2 mm) length then CL93.[2] Both fertilizer and LR additions resulted in a decreased F_S in CL32 (fig. 3). We found that the addition of LR in CL32 reduced stem volume and belowground biomass by 25 and 30 percent, respectively, in CL32 and not at all in CL93 (Tyree 2008). In contrast, fertilizer had only a slight increase on F_S in CL93 while LR additions resulted in a much more extreme increase in CL32. Finally, the addition of both LR and fertilizer showed no detectable difference in F_S in either genotype.

In most nutrient manipulation treatments we found that the C balance between clones did not differ except in the control and LR+F treatments (table 1). When no amendments were added (none) CL32 maintained a slightly greater C balance then CL32, but when both LR and fertilizer were applied CL93 maintained a greater C balance. We found that the C balance over the first two full growing seasons was negative

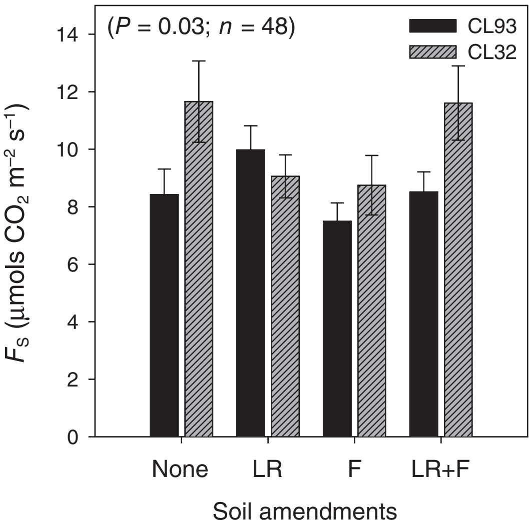

Figure 3—Total soil CO_2 efflux from the soil surface (F_S) averaged over 13 sampling dates from January 2006 through December 2007. Measurements were taken using a closed system portable infrared gas analyzer (LI-6200). (LR = logging residue; F = fertilization.)

Table 1—Average (standard error) carbon budgets for soil amendment treatment by clone. Values are estimated from January 2006 through January 2008. Positive numbers indicate a carbon sink and negative numbers indicate carbon source.

	Soil amendment added			
Response	None	LR added	F added	LR+F
	t carbon/ha			
	Clone 32 (“broad crown” ideotype)			
Net primary productivity	6.24 (0.33) b	6.47 (0.96) b	11.11 (0.57) a	6.17 (0.54) b
Heterotrophic respiration	–35.72 (1.17) a	–33.25 (6.59) a	–28.82 (2.31) a	–38.05 (5.43) a
LR incorporation	0	38	0	38
Carbon balance	–29.49 (1.00) a	11.21 (7.40) b	–17.72 (2.84) a	6.12 (5.05) b
	Clone 93 (“narrow crown” ideotype)			
Net primary productivity	5.16 (1.05) c	7.21 (1.05) bc	10.94 (0.51) a	8.25 (0.85) ab
Heterotrophic respiration	–29.54 (5.23) a	–35.80 (6.33) a	–25.22 (2.68) a	–30.16 (2.65) a
LR incorporation	0	38	0	38
Carbon balance	–24.38 (4.75) a	9.41 (6.37) b	–14.27 (3.12) a	16.09 (1.82) b

LR = logging residue; F = fertilization.

Different letters in a row indicate significant differences between soil amendment treatments using Fisher’s LSD (alpha = 0.05, *n* = 3).

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when LR was not applied. This is consistent with findings that early on these stands act as a C source due to the relatively low NPP and higher soil respiration following site disturbance and as these stands age increased NPP and decreased soil respiration increase NEP (Gough and others 2005, Sampson and others 2006). Under both clones the addition of fertilizer increases C balance relative to control treatments which is consistent with the findings of other studies (Lai and others 2002; Maier and others 2002, 2004) . Finally, the addition of LR resulted in a positive C balance early in the rotation indicating this may be a useful treatment in increasing C sequestration, but more long-term observation is needed.

CONCLUSION

In support of our findings we found that our nutrient manipulation treatments had a significant effect on plant biomass. Although there was no treatment by genotype interaction with plant biomass there were strong differences in the way aboveground biomass was partitioned between genotypes. The addition of LR resulted in a substantial increase in the foliage to stem ratio in CL32 but not CL93. Implication of this finding may be that clones can be chosen based on site nutrient availability to optimize stem production. Second, we found genetic by nutrient availability interactions in F_S, which suggests that future C models may need to account for genotypes as clonal forestry becomes more popular. Finally, NPP was the dominant factor controlling C balance. F increased NPP, therefore, increasing the C balance perhaps decreasing the time necessary for this stand to function as a C sink. Additionally, we found that incorporation of LR resulted in a positive C balance early in stand development and may be a potential treatment in increasing C sequestration. However when selecting genotypes to plant, biomass partitioning patterns need to be accounted for in addition to NPP to satisfy both timber production and C sequestration objectives.

ACKNOWLEDGMENTS

We thank U.S. Forest Service, Agenda 2020, for funding this research and their technical support. MeadWestvaco for their monumental effort in preparing, maintaining, and providing access to the study site. Special thanks to John Peterson, Jeremy Stovall, Ben Templeton, and the U.S. Forest Service for their help in the destructive harvest. Finally, the authors would like to thank John Peterson, Ben Templeton, and Dr. David Jones for their help taking soil respiration measurements.

LITERATURE CITED

Aggangan, R.T.; O'Connell, A.M.; McGrath, J.F.; Dell, B. 1999. The effects of *Eucalyptus globulus* Labill. leaf letter on C and N mineralization in soils from pasture and native forest. Soil Biology & Biochemistry. 31(11): 1481–1487.

Albaugh, T.J.; Allen, H.L.; Dougherty, P.M.; Johnsen, K.H. 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. Forest Ecology and Management. 192(1): 3–19.

Albaugh, T.J.; Allen, H.L.; Dougherty, P.M. [and others]. 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. Forest Science. 44(2): 317–328.

Allen, H.L.; Fox, T.R.; Campbell, R.G. 2005. What is ahead for intensive pine plantation silviculture in the South? Southern Journal of Applied Forestry. 29(2): 62–69.

Allen, H.L.; Fox, T.R.; Maier, C.A.; McKeand, S. 2006. Site carbon sequestration and intensive pine plantation management. Critical processes and properties regulating carbon cycling in southern forests. Asheville, NC: Southern Forest Research Partnerssship, Inc.; U.S. Department of Agriculture Forest Service, Southern Research Station. [Number of pages unknown].

Andrews, J.A.; Harrison, K.G.; Matamala, R.; Schlesinger, W.H. 1999. Separation of root respiration from total soil respiration using carbon-13 labeling during free-air carbon dioxide enrichment (FACE). Soil Science Society of America Journal. 63(5): 1429–1435.

Bååth, E.; Lundgren, B.; Soderstrom, B. 1981. Effects of nitrogen-fertilization on the activity and biomass of fungi and bacteria in a podzolic soil. Zentralblatt Fur Bakteriologie Mikrobiologie Und Hygiene I Abteilung Originale C-Allgemeine Angewandte Und Okologische Mikrobiologie. 2(1): 90–98.

Bittman, S.; Forge, T.A.; Kowalenko, C.G. 2005. Responses of the bacterial and fungal biomass in a grassland soil to multi-year applications of dairy manure slurry and fertilizer. Soil Biology & Biochemistry. 37(4): 613–623.

Blazier, M.A.; Hennessey, T.C.; Deng, S.P. 2005. Effects of fertilization and vegetation control on microbial biomass carbon and dehydrogenase activity in a juvenile loblolly pine plantation. Forest Science. 51(5): 449–459.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic-matter. Biological Reviews of the Cambridge Philosophical Society. 63(3): 433–462.

Fox, T.R. 2000. Sustained productivity in intensively managed forest plantations. Forest Ecology and Management. 138(1-3): 187–202.

Gough, C.M.; Seiler, J.R. 2004. Belowground carbon dynamics in loblolly pine (*Pinus taeda*) immediately following diammonium phosphate fertilization. Tree Physiology. 24(7): 845–851.

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

Hanson, P.J.; Edwards, N.T.; Garten, C.T.; Andrews, J.A. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry. 48(1): 115–146.

Holland, E.A.; Coleman, D.C. 1987. Litter placement effects on microbial and organic-matter dynamics in an agroecosystem. Ecology. 68(2): 425–433.

Homann, P.S.; Caldwell, B.A.; Chappell, H.N. [and others]. 2001. Douglas-fir soil C and N properties a decade after termination of urea fertilization. Canadian Journal of Forest Research. 31(12): 2225–2236.

Johnsen, K.H.; Wear, D.; Oren, R. [and others]. 2001. Carbon sequestration and southern pine forests. Journal of Forestry. 99: 14–21.

Johnson, D.W.; Curtis, P.S. 2001. Effects of forest management on soil C and N storage: meta analysis. Forest Ecology and Management. 140(2-3): 227–238.

Lai, C.T.; Katul, G.; Butnor, J. [and others]. 2002. Modeling the limits on the response of net carbon exchange to fertilization in a south-eastern pine forest. Plant Cell and Environment. 25(9): 1095–1119.

Lee, K.H.; Jose, S. 2003. Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. Forest Ecology and Management. 185(3): 263–273.

Lilleskov, E.A.; Fahey, T.J.; Horton, T.R.; Lovett, G.M. 2002. Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. Ecology. 83(1): 104–115.

Long, B.M. 1980. Soil survey of Berkeley County, South Carolina. [Place of publication unknown]: U.S. Department of Agriculture, Soil Conservation Service and Forest Service. 94 p. In cooperation with: South Carolina Land Resources Conservation Commission and South Carolina Agricultural Experiment Station.

Maier, C.A.; Albaugh, T.J.; Allen, H.L.; Dougherty, P.M. 2004. Respiratory carbon use and carbon storage in mid-rotation loblolly pine (*Pinus taeda* L.) plantations: the effect of site resources on the stand carbon balance. Global Change Biology. 10(8): 1335–1350.

Maier, C.A.; Johnsen, K.H.; Butnor, J. [and others]. 2002. Branch growth and gas exchange in 13-year-old loblolly pine (*Pinus taeda*) trees in response to elevated carbon dioxide concentration and fertilization. Tree Physiology. 22(15-16): 1093–1106.

Maier, C.A.; Kress, L.W. 2000. Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. Canadian Journal of Forest Research. 30(3): 347–359.

Martin, T.A.; Dougherty, P.M.; McKeand, S.E. 2005. Strategies and case studies for incorporating ecophysiology into southern pine tree improvement programs. Southern Journal of Applied Forestry. 29(2): 70–79.

Olsson, P.; Linder, S.; Giesler, R.; Hogberg, P. 2005. Fertilization of boreal forest reduces both autotrophic and heterotrophic soil respiration. Global Change Biology. 11(10): 1745–1753.

Ouro, G.; Perez-Batallon, P.; Merino, A. 2001. Effects of silvicultural practices on nutrient status in a *Pinus radiata* plantation: nutrient export by tree removal and nutrient dynamics in decomposing logging residues. Annals of Forest Science. 58(4): 411–422.

Perez-Batallon, P.; Ouro, G.; Macias, F.; Merino, A. 2001. Initial mineralization of organic matter in a forest plantation soil following different logging residue management techniques. Annals of Forest Science. 58(8): 807–818.

Sampson, D.A.; Waring, R.H.; Maier, C.A. [and others]. 2006. Fertilization effects on forest carbon storage and exchange and net primary production; a new hybrid process model for stand management. Forest Ecology and Management. 221: 91–109.

SAS. 2006. SAS online. Version 9. Cary, NC: SAS Institute Inc.

Selig, M.F.; Seiler, J.R.; Tyree, M.C. 2008. Soil carbon and CO_2 efflux as influenced by the thinning of loblolly pine (*Pinus taeda* L.) plantations on the Piedmont of Virginia. Forest Science. 54(1): 58–66.

Thirukkumaran, C.M.; Parkinson, D. 2000. Microbial respiration, biomass, metabolic quotient and litter decomposition in a lodgepole pine forest floor amended with nitrogen and phosphorous fertilizers. Soil Biology & Biochemistry. 32(1): 59–66.

Tisdale, J.L. 2008. Quantifying the effects of organic residues on soil nitrogen and phosphorus availability. Raleigh, NC: North Carolina State University, Department of Forestry. [Number of pages unknown]. M.S. thesis.

Tyree, M.C. 2008. Genetics by nutrient availability interactions on short-term carbon pools and fluxes in young *Pinus taeda* plantations. Blacksburg, VA: Virginia Tech. [Number of pages unknown]. Ph.D. dissertation.

Tyree, M.C.; Seiler, J.R.; Fox, T.R. 2008. The effects of fertilization on soil respiration in two-year-old *Pinus taeda* L. clones. Forest Science. 54(1): 21–30.

Wear, D.N.; Greis, J.G. 2002. Southern forest resource assessment: summary report. Gen. Tech. Rep. SRS-54. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 103 p.