

Long-term effects of weed control and fertilization on the carbon and nitrogen pools of a slash and loblolly pine forest in north-central Florida

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Abstract: The effects of fertilization, weed control, and fertilization plus weed control on vegetation and soil C and N pools were examined for a loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Engelm.) forest at ages 18 and 26 years (at the end of rotation). The total C accumulated in fertilized forests without weed control was 20% (slash pine) and 40% (loblolly pine) greater than in the control forests at the end of rotation. Weed control increased pine C pools at 18 years, but by the end of rotation, weed control effectively resulted in no gain in ecosystem C. When the two treatments were combined, weed control slightly subtracted from the net C benefit produced by fertilization. This result occurred because of decreased forest floor and soil C in the weed control plots. Fertilization significantly increased stem, foliage, forest floor, and soil N pools, and N retention was 63% and 103% of the applied N in the slash and loblolly pine forests, respectively. Weed control with fertilization reduced ecosystem N retention efficiency, but weed control alone did not negatively affect ecosystem N accumulation. These results suggest that the optimal treatment for increasing C accumulation and N retention in these ecosystems is fertilization without weed control.

Résumé : Les effets de la fertilisation et du désherbage, seuls ou combinés, sur la végétation ainsi que sur les réservoirs de C et de N du sol ont été étudiés dans des forêts de pin à encens (*Pinus taeda* L.) et de pin d'Elliott (*Pinus elliottii* var. *elliottii* Engelm.) âgées de 18 et 26 ans (fin de la rotation). Le C total accumulé dans les forêts fertilisées était 20 % (pin d'Elliott) et 40 % (pin à encens) plus élevé que dans les forêts témoins à la fin de la rotation. Le désherbage a augmenté les réservoirs de C du pin à 18 ans mais n'a pas entraîné de gain de C dans l'écosystème à la fin de la rotation. Lorsque les deux traitements étaient combinés, le désherbage a légèrement réduit le bénéfice net de C obtenu avec la fertilisation. Ce résultat est survenu à cause la diminution du C dans le sol et la couverture morte dans les parcelles désherbées. La fertilisation a significativement augmenté les réservoirs de N dans la tige, le feuillage, la couverture morte et le sol et la rétention de N a atteint respectivement 63 % et 103 % de N appliqué dans les forêts de pin d'Elliott et de pin à encens. Le désherbage combiné à la fertilisation a réduit l'efficacité de rétention de N de l'écosystème mais le désherbage seul n'a pas négativement influencé l'accumulation de N dans l'écosystème. Ces résultats indiquent que le traitement optimal pour augmenter l'accumulation de C et la rétention de N dans ces écosystèmes est la fertilisation sans désherbage.

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Introduction

Forest vegetation and soils are significant repositories for C as it cycles between the terrestrial biosphere and the atmosphere. Globally, forests store approximately 1150 Pg of C in vegetation and soil, which is nearly 1.5 times greater than the current atmospheric C pool (Dixon et al. 1994). Given the large amount of C stored in forests, even small changes in this stored C could have a substantial effect on atmospheric C pools. For example, in the continental United States, forest C sequestration in vegetation biomass and soil

pools was primarily responsible for removing approximately 10% of fossil fuel CO₂ emissions between 1990 and 2004 (US Environmental Protection Agency 2005). Thus, increasing or maintaining forest C pools represents a critical option in societies' efforts to mitigate rising atmospheric CO₂.

The southeastern United States could be an attractive region for increasing CO₂ sequestration because much of the region's extensive forest coverage is under varying levels of management. Han et al. (2007) proposed that land-based C sequestration in the region could increase the capture of fossil fuel emissions from 10% to 22% with the adoption of

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improved land, primarily forest, management. Accelerated forest growth and increased C density are straightforward means to increase forest C sequestration (Pacala and Socolow 2004), and in managed southern pine stands, forestry practitioners generally accelerate the growth of stands with initial site preparation techniques, fertilization, and weed or understory control (Fox et al. 2007). Fertilization and weed control both likely improve pine growth through an increase in nutrient availability (Neary et al. 1990; Borders et al. 2004; Miller et al. 2006), while fertilization has the added benefit of relieving site level nutrient deficiencies (Miller 1981). It remains unclear, however, whether an increase in aboveground tree growth directly corresponds to an increase in ecosystem C sequestration (Richter et al. 1999; Johnson and Curtis 2001), especially given the variety of management prescriptions applied in southern pine forests (Fox et al. 2007) and the relatively few studies that have examined all ecosystem C pools (Richter and Markewitz 2001; Shan et al. 2001).

A management prescription that increases forest C sequestration would ideally also sustain or increase forest productivity for the long term. One important component of a sustainable system is the retention of nutrients, whether existing site nutrients or nutrients applied in fertilizer. For weed or understory control, previous research has suggested that complete understory control can cause a decrease in soil N in southern pine forests (Echeverría et al. 2004; Sartori et al. 2007; Rifai et al. 2010), which may eventually lead to decreased nutrient retention and stand productivity. For forest fertilization, productivity gains have been observed in subsequent rotations even without further fertilization (Comerford et al. 2002; Phelan and Allen 2008), but it is unclear how fertilization and herbicide use interact to affect long-term productivity. In the last several decades, many southern pine forests have received a combination of fertilizer and herbicide applications (McCullough et al. 2005); therefore, it is critical to understand how these treatments may interact to affect nutrient retention.

A number of studies have examined the effect of fertilization and weed control on southern pine forest C (Shan et al. 2001) and N dynamics (Will et al. 2006). However, most previous research has focused on either above- or belowground pools or stands that were several years from harvest (11–20 years old), making it difficult to infer whether the ecosystem patterns reported at earlier stages in stand development would carry over to the end of rotation. The objective of this research was to determine how fertilization, weed control, and the combined application of these management prescriptions affected the C and N dynamics of a loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Engelm.) forest in north-central Florida. For this site, researchers have reported that throughout most of stand history, aboveground biomass was increased with both fertilization and weed control (Jokela et al. 2010); however, a C and N budget has never been constructed that included both above- and belowground components. We hypothesized that a significant increase in aboveground tree growth and biomass would correspond to a significant increase in both above- and belowground components of ecosystem C and N. In addition, we hypothesized that biomass accumulation would correspond to the retention of fertilizer N. For the lo-

blolly pine forests, we also compared the aboveground vegetation and forest floor pools of C and N at two points during stand development (at age 18 and 26 years) to determine the trends in pools during the late stages of the rotation. To address this objective and hypotheses, we estimated the C and N pools in the aboveground vegetation, forest floor, roots, and soils to 1 m depth at the end of a 26-year rotation.

Site description

In 1983, researchers from the University of Florida, United States Forest Service, and forest industry established the Intensive Management Practices Assessment Center (IMPAC) to evaluate the biological growth potential of southern pine forests (Jokela and Martin 2000). An IMPAC research site was established approximately 10 km north of Gainesville, Florida (29°30'N, 82°20'W), in a recently burned and harvested slash pine forest. Mean annual precipitation is 1229 mm and mean annual temperature is 21 °C for Gainesville (National Oceanic and Atmospheric Administration 1998), and the soils at the site are classified as sandy, siliceous, hyperthermic Ultic Alaquods (Pomona fine sands; Soil Survey Staff 1999).

The IMPAC study consists of three blocks of a 2 × 2 × 2 factorial combination of species (loblolly and slash pine), fertilizer, and herbicide treatments arranged in a split-plot, randomized complete block design (Neary et al. 1990). Four treatments were randomized within each species whole plot: a control, fertilizer only (F), understory or weed control only (W), and fertilizer plus weed (FW) treatment. Trees were planted at a 1.8 m × 3.0 m spacing, with the whole plot equivalent to 820 m² and with an interior measurement plot consisting of five beds and eight trees per bed for a total 40 trees per plot (equivalent area 260 m²). Along the beds, an untreated six-tree buffer (~12 m) separated treatment plots, and across the beds, the spatial equivalent of four untreated beds (~12 m) separated adjacent plots.

Fertilizer was annually applied from stand age 0–10 and 16–18 years, with different macro- and micronutrient combinations and different application rates in each time interval (Table 1). The fertilizer was banded in a semicircle within approximately 0.5 m of each tree's base (Martin and Jokela 2004). Understory vegetation was controlled annually from ages 1 to 10 years (1983–1993) using a combination of herbicides and mechanical rotary cutters (Neary et al. 1990). Thereafter, canopy closure impeded encroachment by understory plants onto the weed control plots and herbicide application was discontinued.

Methods

The vegetation, soils, and forest floor were measured in sampling periods concentrated during the late dormant season (January to May). In 2001, or age 18 years, the loblolly pine plots were sampled from January to March for the forest floor and understory C and N concentrations and late March for loblolly pine tissues; in 2009, both pine species were sampled during the final stand harvest in early May for vegetation N concentration. In 2009, the forest floor, understory, and soils were collected between January and March for fine root and soil C and N estimates. The stands

Table 1. Fertilizer application rates and timing for the loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii* var. *elliottii*) experimental sites receiving either fertilizer only or fertilizer and weed control.

Time period	Stand age (years)	Mean annual application rate (kg·ha ⁻¹ ·year ⁻¹)										
		N	P	K	Ca	Mg	Mn	Fe	Cu	Zn	B	S
1983–1993	0–10	36.0	14.3	31.7	10.8	7.2	0.3	0.3	0.05	0.3	0.05	7.2
1998–2000	15–17	242.6	29.0	37.7	0	0	0.4	0.8	0.13	0.3	0.13	0

Table 2. Stand age of maximum stand basal area (BA), the amount of BA at its maximum, and BA at stand age 26 years for loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii* var. *elliottii*) control forests and those receiving fertilization (F), weed (W) control, and fertilization plus weed control (FW).

	Stand age (years)	maximum BA (m ² ·ha ⁻¹)	Maximum BA (m ² ·ha ⁻¹)	Year 25 BA (m ² ·ha ⁻¹)
Loblolly pine				
Control	25		26.1	26.1
F	16		39.7	34.9
W	20		38.7	36.2
FW	18		44.7	40.1
Slash pine				
Control	25		25.8	25.8
F	18		34.4	28.2
W	25		41.1	41.1
FW	18		40.6	33.5

were harvested in May of 2009 (age 26 years); however, the final mensurational survey was conducted in December of 2007 (age 25 years), creating an offset in time of approximately one growing season between when the aboveground pine biomass was estimated and when the pine C and N concentrations and the forest floor, understory, and soil C and N were estimated. Prior to the 25th year, all plots were measured every 1–2 years for tree diameter and height (Jokela et al. 2010).

In 2001, branch samples were acquired from the upper third of the crown of five trees and divided into foliage and branch wood. In 2009, three trees per plot were sampled for branch wood immediately after being cut during the harvest. Trees in the 2001 sampling were randomly selected across all tree size classes and, in 2009, trees in the dominant and codominant canopy classes were randomly selected for sampling. For each branch, a disk was cut at the midpoint of a mid-sized branch selected from each tree's crown. Foliage was also collected from one whorl of the three branches per tree and three trees per plot. Stem bark samples were removed with a chisel from a 5 cm × 5 cm section of the stem from six trees (in 2001) and three trees (in 2009) in each plot. In 2001, an increment borer was used to obtain stem wood samples from six loblolly pine trees per treatment plot. Understory vegetation in the F and control plots was destructively sampled from 1 m² quadrats located in four random positions in each plot. Plant tissues that were rooted outside the quadrat, but that overhung the quadrat boundaries, were not included in the sampling. Only those plants rooted in the plot were harvested. The harvested samples were divided into deciduous tree wood and leaves and saw palmetto (*Serenoa repens* (Bartr.) Small) stems, fronds, and reproductive parts. Herbaceous plants were included with deciduous foliage. Each tissue type was ground and analyzed for C and N concentration separately and recombined by proportional dry mass.

Forest floor samples were obtained using a 20.3 cm diameter cutting ring. Three sampling locations were randomly located on the bed and interbed areas (six total) of each plot. Each sample was divided into Oi (whole needles) and Oe + Oa horizons (partially decomposed needles and decomposed organic matter, respectively).

At age 26 years, soil and root C and N concentration was estimated for both the loblolly and slash pine forests. Samples were collected from within the same circle harvested for the forest floor with a 7.62 cm diameter auger. The depth intervals collected were 0–33, 33–66, and 66–100 cm. All depth intervals were composited by bed or interbed, weighed wet, and then thoroughly mixed. The soil was then subsampled based on mass so that approximately 15% of the total sample was subsequently processed. From this subsample, roots were removed and divided into <2 mm and 2–5 mm diameter size classes. Roots >5 mm diameter were discarded during this process because they were to be accounted for using an allometric approach. The remaining soil subsample was weighed wet and then dried at 65 °C. Approximately 100 g of soil was removed from the dried soil and ground in a rotary ball mill. From this sample, two samples were analyzed for C and N concentration on a CNS analyzer (NCS 2500; CE Elantech, Lakewood, New Jersey). No adjustments for rock density were made because no rocks were found during soil coring in these predominantly sandy soils.

Tissue samples were oven dried at 65 °C, weighed, and ground in a Wiley mill to pass a 1 mm screen. Concentrations of C and N were then measured (NCS 2500; CE Elantech). Preliminary analysis of the 2001 branch concentrations showed unusually high N concentrations compared with literature estimates and those from previous studies at this site (Gholz et al. 1985; Colbert et al. 1990). This was likely attributable to branch wood samples that

Table 3. Mean (\pm SE) C pools ($\text{Mg C}\cdot\text{ha}^{-1}$) of aboveground vegetation for 26-year-old loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii* var. *elliottii*) stands that received fertilization (F), weed control (W), and fertilization plus weed control (FW) treatments and the results from the ANOVA.

	Foliage	Bark	Branch	Stem	Understory	Roots			Dead tree	Forest floor		Soil depth interval (cm)		
						<2 mm	>2–5 mm	>5 mm		Oi	Oe + Oa	0–33	33–66	66–100
Vegetation, forest floor, and soil C content														
Loblolly pine														
Control	3.5 (0.1)	4.0 (0.4)	8.0 (0.2)	28.0 (1.1)	1.6 (0.3)	1.8 (0.3)	3.1 (0.3)	10.9 (0.6)	1 (1)	5 (0.2)	18 (3)	39 (5)	49 (3)	42 (12)
F	5.1 (0.3)	5.6 (1.3)	11.1 (0.3)	45.0 (1.4)	1.8 (1.4)	1.3 (0.1)	3.9 (0.3)	18.5 (0.7)	13 (4)	8 (1)	45 (10)	50 (7)	61 (3)	34 (5)
W	5.1 (0.1)	6.0 (0.4)	11.9 (0.4)	47.4 (1.9)		0.6 (0.1)	2.7 (0.3)	21.0 (0.9)	6 (1)	7 (1)	12 (3)	52 (3)	45 (7)	31 (9)
FW	5.7 (0.3)	6.9 (1.3)	12.8 (0.6)	52.9 (3.5)		0.4 (0.1)	2.8 (1.5)	23.7 (1.8)	13 (3)	9 (1)	29 (6)	53 (3)	47 (2)	29 (10)
Slash pine														
Control	3.2 (0.7)	10.4 (0.8)	5.9 (1.6)	33.5 (6.4)	2.5 (0.2)	1.5 (0.7)	2.6 (0.8)	10.8 (3.2)	6 (3)	10 (2)	28 (4)	42 (2)	56 (4)	29 (3)
F	3.4 (0.7)	11.8 (0.2)	7.2 (0.6)	42.8 (3.0)	3.4 (0.4)	1.4 (0.4)	2.2 (0.6)	21.5 (1.5)	13 (2)	10 (1)	46 (5)	46 (1)	60 (8)	37 (2)
W	5.0 (0.3)	17.1 (0.9)	10.0 (1.3)	60.0 (3.4)		0.5 (0.1)	1.3 (0.8)	28.7 (1.7)	3 (1)	11 (0.5)	22 (2)	47 (2)	54 (6)	25 (7)
FW	4.0 (0.8)	13.5 (0.6)	9.0 (1.2)	53.7 (6.6)		0.3 (0.5)	2.1 (0.7)	24.4 (3.3)	14 (2)	13 (2)	30 (5)	47 (1)	67 (4)	29 (6)
Significant ($p < 0.05$) ANOVA p values														
Source of variation														
Whole plot														
Block (df = 2)														
Species (S) (df = 1)		<0.001												
Error (df = 2)														
Split plot														
F (df = 1)	0.032			0.003				0.003	<0.001		<0.001		0.026	
W (df = 1)	<0.001	0.003	<0.001	<0.001		0.002		<0.001		0.007				0.035
F \times W (df = 1)	0.025	<0.001		0.002				0.004						
S \times F (df = 1)	<0.001	0.042		0.003				0.003						
S \times W (df = 1)		0.047		0.004				0.004						
S \times F \times W (df = 1)		0.043												
Error (df = 1)														

consisted predominately of growing tips and that had N concentrations considerably higher than from the older, woody portions of the branch that constituted most of the mass. To avoid propagating this bias to our estimates of stand-level branch N content, we used the N concentrations from the 2009 sampling for the 2001 estimates. In 2009, stem N concentrations were not collected, and as a result, 2001 values were used to estimate both loblolly and slash pine N content. Ecosystem component C and N content was estimated by multiplying dry biomass by its corresponding C and N concentrations where these were directly estimated.

To predict aboveground biomass for both species, we used a combination of allometric equations that were site specific and equations from the literature. The site-specific equations were from Jokela and Martin (2000) and were restricted to aboveground tissues (foliage, branch (bark included), stem bark, and stem wood biomass) and to the tree diameters found at the site for age 18 and 25 years. We avoided extending equations beyond the diameters of harvested trees because this can introduce a systemic overestimation of stand biomass. Treatment-specific equations were unnecessary because there were no significant difference in allometric equations (Jokela and Martin 2000). For the larger slash pine, equations from Jokela et al. (1989) were used that had been developed for mature slash pine forests in north Florida. For loblolly pine trees that were larger than the diameters of trees harvested for the Jokela and Martin (2000) equations, we used the equations of Naidu et al. (1998). For both species, the range in tree diameters for these literature equations fully encapsulated the range in tree diameters at this site.

Coarse root biomass was estimated for both species from the stem to coarse root biomass ratio (0.5) developed by Albaugh et al. (2006) for loblolly pine roots >2 mm. In their study, stem biomass explained 91% of the variance in coarse root biomass and their estimates of stem mass fully encapsulated the stem mass estimates in our study. We directly estimated the 2–5 mm fraction in the soil cores and this estimate was subtracted from the final estimate of coarse root biomass, resulting in a 5%–11% reduction in the stem to coarse root biomass ratio of Albaugh et al. (2006). The relative errors of these two approaches, and of using non-site-specific equations, are examined in the Discussion section.

Coarse woody debris and standing dead trees were estimated using the annual inventories and a modeling approach outlined by Radtke et al. (2009) for southern pine stands. The model uses the year of mortality, and then from empirically derived equations, it estimates how long a dead tree stands, how much coarse debris is produced by a tree in each year since mortality, and how quickly the stem decomposes. The modeled standing dead trees and coarse woody debris were estimated as biomass and then converted to C content by multiplying the original stem C concentrations by biomass. When a simulated decomposing tree reached 30% of its original mass, it was dropped from the “dead tree” pool and assumed to be part of the forest floor sampling. This cutoff was based on examining tree locations and determining whether the residual logs or stumps would have been sampled with the forest floor. No estimates of dead tree N content were made because N content in coarse

woody debris can vary significantly through time (Laiho and Prescott 1999).

Statistical analysis

Treatment and species effects on the C and N content and concentrations of the vegetation, forest floor, and soil components at ages 18 years (loblolly pine only) and age 26 years for slash and loblolly pine soil were determined using a split-plot analysis of variance (ANOVA, mixed model procedure) for a factorial experiment. The whole plot was species and block and block \times species (age 25 years only) were treated as random effects. Significant changes in C and N pools between the stand age 18 and 26 years were determined by estimating the 95% confidence interval for a treatment. Treatment effects were judged to be significant at $p < 0.05$. The SAS statistical package version 9.1 was used for all statistical analyses.

Results

Carbon pools

Tree basal area (BA) (square metres per hectare) was positively correlated with aboveground biomass in the 25th year of the stand (not shown), and historically, BA was at its greatest point for the F and FW control plots between ages 16 and 18 years (39.7–44.7 $\text{m}^2\cdot\text{ha}^{-1}$) for both the slash and loblolly pine forests (Table 2). For the loblolly pine W plots, BA had peaked at age 20 years (38.7 $\text{m}^2\cdot\text{ha}^{-1}$) and had declined slightly by 26 years (36.2 $\text{m}^2\cdot\text{ha}^{-1}$). In contrast, BA for the control plots and slash pine W plots continued to accrue up until the end of the rotation (25.8–41.1 $\text{m}^2\cdot\text{ha}^{-1}$) (Table 2). Indeed, at the end of rotation, the slash pine W plots had the highest BA among treatments and controls, but among all treatments and years, the 44.7 $\text{m}^2\cdot\text{ha}^{-1}$ of the 18-year-old loblolly pine FW plots was the largest recorded BA.

The C content of biomass for both pine species was consistently greatest for stems (28.0–60.0 $\text{Mg C}\cdot\text{ha}^{-1}$) followed by roots >5 mm in diameter (10.9–28.7 $\text{Mg C}\cdot\text{ha}^{-1}$) (Table 3). For slash pine, the next largest pool was bark (10.4–17.1 $\text{Mg C}\cdot\text{ha}^{-1}$) and then branches (5.9–10.0 $\text{Mg C}\cdot\text{ha}^{-1}$), with the pattern reversed for loblolly pine (Table 3). The foliage and 2–5 mm roots were the next largest pools, but the two pools varied in rank order among species and treatments. Roots <2 mm were the smallest pool (0.3–1.8 $\text{Mg C}\cdot\text{ha}^{-1}$) for both species. For most pine biomass components at both age 18 and 26 years, the F and W treatments caused an increase in C content relative to the control plots (Table 3 and 4). At age 18 years, the F and W main effects were significant for nearly all components (minus bark), but at age 26 years, the branch and bark were no longer significant for the F effect. Notably at age 26 years, the interaction terms species (S) \times F and S \times W were significant for a number of biomass components, reflecting the relatively different responses of species to treatments. In general, the response to fertilization differed among species because the F and FW treatments of slash pine supported less biomass than the fertilized loblolly plots and the W plots of slash pine supported more biomass than the weed control loblolly forests (Table 2). Only fine root (<2 mm) biomass was lower in the treated plots relative to the controls, with a significant

Table 4. Mean (\pm SE) C pools ($\text{Mg C}\cdot\text{ha}^{-1}$) of aboveground vegetation and the forest floor for the loblolly pine (*Pinus taeda*) stands at 18 years that received fertilization (F), weed control (W), and fertilization plus weed control (FW) treatments and the results from the ANOVA.

	Foliage	Bark	Branch	Stem	Understory	Roots >5 mm	Dead tree	Oi	Oe + Oa
Vegetation, forest floor, and soil C content									
Control	2.5 (0.5)	2.9 (0.8)	5.7 (1.5)	19.0 (4.8)	5.5 (0.6)	9.5 (2.4)	0.1 (0.1)	3.2 (0.7)	14.4 (2.2)
F	5.1 (0.2)	5.5 (0.3)	12.6 (0.2)	46.1 (2.0)	2.9 (0.2)	23.0 (1.0)	5.6 (3.9)	3.7 (0.7)	27.7 (1.4)
W	4.9 (0.5)	5.3 (0.4)	12.0 (1.0)	41.5 (3.2)		20.8 (1.6)	1.0 (0.1)	3.9 (1.3)	21.3 (3.6)
FW	5.5 (0.3)	6.4 (0.4)	14.5 (0.4)	50.5 (2.5)		25.5 (1.3)	4.5 (1.9)	5.5 (0.4)	31.7 (3.2)
Significant ($p < 0.05$) ANOVA p values									
Source of variation									
F (df = 1)	0.032			0.022	0.003	0.033	0.002		0.003
W (df = 1)	0.041		0.002	0.002		0.002			
F \times W (df = 1)	0.035		0.003	0.035		0.003			
Error (df = 8)									

decrease associated with the main effect of the W treatment (Table 2). The only species-level difference in C content was for bark (Table 2), which was significantly greater in slash than in loblolly pine plots because of species-level differences in total mass.

Because stand BA peaked prior to the end of the rotation for the fertilized plots (Table 2), density-related mortality occurred and corresponded to a significant increase in the estimated dead tree C content at the end of rotation (Tables 3 and 4). No significant treatment effect was observed for the Oi layer, although the C content of the Oi layer in the slash pine forest was on average 32% greater than that of the loblolly pine forest ($p = 0.08$). The C content of the forest floor Oe + Oa layer was significantly increased in the F plots at age 18 years (loblolly pine only) and 26 years (both species). At the end of rotation, this effect was partly due to the increased C concentration of the loblolly pine Oe + Oa layer (Table 3), but at age 18 years, there was no significant effect of the W or F treatment on the C concentration of any forest floor component. At age 26 years, the C content of the Oe + Oa layer was lower in the W treatment (Table 4), which was in part due to a significantly lower C concentration (Table 3).

Soil C content increased slightly going from the 0–33 cm depth interval ($39\text{--}53 \text{ Mg C}\cdot\text{ha}^{-1}$) to the 33–66 cm depth interval ($45\text{--}67 \text{ Mg C}\cdot\text{ha}^{-1}$) and then decreased in the 66–100 cm depth interval ($25\text{--}42 \text{ Mg C}\cdot\text{ha}^{-1}$) (Table 3). This trend may have occurred because the spodic or Bh horizon was found within the 33–66 cm depth interval (not shown). The response to treatment differed among soil depth intervals, with a significant F treatment main effect in the 33–66 cm depth interval reflecting an increase in soil C. For the 66–100 cm depth interval, the W main effect reflected a decrease in soil C (Table 4). These significant patterns in C content matched the trends in C concentration (Table 3), despite there being a significant negative linear relationship between C concentration and bulk density ($R^2 = 0.41$, $p < 0.001$, $n = 432$, data not shown). After summing all depth intervals, the only marginally significant result ($p = 0.14$) was for the F-only treatment, which had 12% more soil C than the control.

Nitrogen concentration and pools

The highest vegetation N concentrations were found in foliage and fine roots and understory vegetation (Tables 5 and 6). The tissues most sensitive to treatment were pine stem at age 18 years and foliage at both ages (Tables 5 and 6), with fertilization producing an average 36% increase in foliage N concentration at age 18 years (Table 5), but the magnitude of the effect decreased to 11% at age 26 years in loblolly pine (Table 6). A significant $S \times F \times W$ interaction at age 26 years highlighted the differential response of the two species' foliage to treatments (Table 6) where slash pine foliar N concentration was lowered by the W treatment relative to the control but increased for loblolly pine. For fine roots, the main effect of the W treatment was significant, reflecting an increase in N concentration. The only species difference in N concentration was observed for the bark where slash pine had a lower N concentration than loblolly pine (Table 6).

The N content of all vegetation components generally increased with fertilization at both ages in loblolly pine (Ta-

Table 5. Mean (\pm SE) N concentration ($\text{g}\cdot\text{kg}^{-1}$) of aboveground vegetation and the forest floor for 18-year-old loblolly pine (*Pinus taeda*) stands that received fertilization (F), weed control (W), and fertilization plus weed control (FW) treatments and the results from the ANOVA.

	Foliage	Stem	Bark	Understory	Oi	Oe + Oa
Vegetation and forest floor N concentration						
Control	11.0 (0.5)	0.73 (0.08)	2.4 (0.3)	6.5 (0.13)	6.4 (0.5)	11.0 (0.7)
F	14.1 (0.6)	0.80 (0.34)	2.6 (0.2)	8.4 (0.05)	6.8 (0.7)	10.1 (0.3)
W	11.3 (1.2)	0.63 (0.136)	2.5 (0.3)		5.6 (0.2)	8.3 (0.7)
FW	16.0 (0.6)	0.83 (0.12)	2.6 (0.3)		7.3 (0.4)	9.4 (0.4)
Significant ($p < 0.05$) ANOVA p values						
Source of variation						
F (df = 1)	<0.001	0.002		<0.001		
W (df = 1)		<0.001				
F \times W (df = 1)		0.003				
Error (df = 8)						

bles 7 and 8). In contrast, slash pine mortality and the resulting decrease in BA in the F and FW plots (Table 2) resulted in only a modest increase in N content for nearly all vegetation components. The exception was for the stem N content where both the F and W main effects were significant with no interactions between species and treatment. The different response of the two species to treatment was evident for foliage and branches where significant interactions occurred between S \times W (foliage) and S \times F (branches) (Table 8).

The N content in the forest floor, or the summed Oi and Oe + Oa layers, for the two species and at the two different stand ages was between 1.8 and 4.2 times greater than the summed aboveground vegetation for each age and treatment combination (Tables 7 and 8). At age 25 years, the soil N pool was on average larger than the combined forest floor and vegetation N pools (Table 8). The F main effect for N content was significant for the Oe + Oa layer in both years, and the W and FW interaction was significant at age 26 years (Table 8). The W main effect reflected a significant N content decrease in the Oe + Oa layer. The main effect of W for the 0–33 cm soil depth interval was significant and represented an overall increase in N (Table 8). For the 33–66 cm soil depth interval, the F main effect was significant and represented an increase in soil N.

Carbon and nitrogen pools: change between years

The amount of C in the foliage and branches of loblolly pine changed between little age 18 and 26 years for the F, W, and FW plots, indicating that the canopies of treated plots were near steady state (Fig. 1). An increase in pine stem C content in the F treatment and branch C content in the control were the only significant ($p < 0.05$) changes for the overstory C content. Other pine vegetation components that increased in the control plots included stem, foliage, and bark, and by comparison, these increases were weakly significant (between $p > 0.05$ and $p < 0.07$). The dead tree C pool increased significantly for the F and W plots, the Oi layer pool of C increased for the F and FW plots, and the understory C content decreased significantly in the control plots.

The significant changes in vegetation N pools were similar to those in the C pools with the exception of FW foliar N content (Fig. 2). FW foliar N content decreased from ages

18 to 26 years primarily because of a 32% decrease in foliar N concentration (Tables 5 and 6). For the Oi and Oe + Oa layers and the understory N pools, the patterns of significant differences were identical to those of the C pools (Fig. 2)

Ecosystem C and N

Ecosystem C storage at age 26 years ranged from a low of 218 Mg C $\cdot\text{ha}^{-1}$ in the loblolly pine control to a high of 311 Mg C $\cdot\text{ha}^{-1}$ in fertilized loblolly pine without weed control. Differences in C storage among treatments were smaller for slash pine and were within the range of loblolly pine differences. The soils had the greatest percentage of ecosystem C (45%–60%) followed by vegetation biomass (31%–42%) and the forest floor (10%–22%) (Fig. 3), with the rank order in pools consistent among all treatments. In the analysis of ecosystem C, the F main effect was significant ($p < 0.001$) and the F \times W interaction was significant ($p = 0.013$). The interaction term highlighted that F alone, without weed control, brought about the largest gains in ecosystem C.

The largest pool of ecosystem N was soil (68%–80%) followed by the forest floor (7%–26%) and vegetation (4%–7%) (Fig. 4). The slash pine FW treatment had the lowest vegetation N content of any F or W treatment plot (223 kg N $\cdot\text{ha}^{-1}$), but the soil of the slash pine FW plot had the highest N content (3916 kg N ha^{-1}) of any treated or control plot. The ANOVA indicated that the F treatment had a significant effect ($p = 0.001$) on ecosystem N with no significant interaction terms.

Ecosystem N retention

The amount of fertilizer retained in an ecosystem can be approximated from the net difference in the fertilized and control plots' nutrient capital divided by the amount of fertilizer added. Summing all N pools, the loblolly and slash pine F plots accumulated 1265 and 785 kg N $\cdot\text{ha}^{-1}$ in excess of their respective control plots. The N fertilizer applied was 1098 kg N $\cdot\text{ha}^{-1}$, and therefore, the estimated percent efficiency for N retention was 115% for the loblolly pine forest and 72% for the slash pine forest. Notably, these estimates did not include coarse roots and dead trees. Although these pools were likely small relative to the rest of the ecosystem N, they were omitted from the calculations because it was

Table 6. Mean (\pm SE) N concentration ($\text{g}\cdot\text{kg}^{-1}$) for 26-year old loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii* var. *elliottii*) stands that received fertilization (F), weed control (W), and fertilization plus weed control (FW) treatments and the results from the ANOVA.

	Foliage	Bark	Branch	Understory	Roots		Forest floor		Soil depth interval (cm)		
					<2 mm	>2–5 mm	Oi	Oe + Oa	0–33	33–66	66–100
Vegetation, forest floor, and soil N concentration											
Loblolly pine											
Control	9.9 (0.32)	2.4 (0.03)	2.4 (0.15)	6.9 (1.1)	7.6 (0.92)	4.7 (0.50)	7.7 (0.32)	9.9 (0.52)	0.30 (0.05)	0.21 (0.02)	0.18 (0.02)
F	11.1 (0.32)	2.4 (0.03)	2.7 (0.12)	7.0 (1.6)	7.9 (0.78)	4.8 (0.20)	8.0 (0.33)	11.0 (0.32)	0.38 (0.06)	0.28 (0.01)	0.15 (0.02)
W	10.9 (0.21)	2.6 (0.09)	2.6 (0.15)		8.1 (0.53)	5.5 (1.10)	7.0 (0.30)	7.6 (0.62)	0.38 (0.05)	0.19 (0.02)	0.17 (0.02)
FW	10.9 (0.12)	2.4 (0.01)	2.7 (0.01)		8.7 (0.15)	5.3 (1.32)	7.7 (0.60)	10.9 (0.46)	0.37 (0.03)	0.24 (0.03)	0.14 (0.03)
Slash pine											
Control	10.2 (0.18)	2.2 (0.11)	2.6 (0.01)	6.9 (0.8)	6.6 (0.40)	5.6 (0.05)	6.2 (0.50)	9.3 (0.81)	0.35 (0.05)	0.28 (0.04)	0.14 (0.02)
F	10.3 (0.15)	2.1 (0.06)	2.7 (0.07)	7.2 (1.7)	7.1 (0.07)	5.6 (0.24)	7.3 (0.55)	11.3 (0.01)	0.35 (0.04)	0.28 (0.02)	0.16 (0.01)
W	9.8 (0.26)	2.1 (0.06)	2.9 (0.12)		7.7 (1.14)	5.2 (0.15)	5.8 (0.33)	9.2 (0.26)	0.33 (0.04)	0.26 (0.02)	0.14 (0.02)
FW	11.2 (0.59)	2.1 (0.01)	2.6 (0.20)		8.9 (0.82)	6.0 (0.63)	6.0 (0.55)	9.3 (0.61)	0.30 (0.02)	0.33 (0.01)	0.14 (0.01)
Significant ($p < 0.05$) ANOVA p values											
Source of variation											
Whole plot											
Block (df = 2)											
Species (S) (df = 1)		0.029									
Error (df = 2)											
Split plot											
F (df = 1)	0.006							<0.001		0.032	
W (df = 1)					0.053		0.042	<0.001			
F \times W (df = 1)											
S \times F (df = 1)											
S \times W (df = 1)											
S \times F \times W (df = 1)	0.009							<0.001			
Error (df = 12)											

Table 7. Mean (\pm SE) N content ($\text{kg}\cdot\text{ha}^{-1}$) of aboveground vegetation and the forest floor for 18-year-old loblolly pine (*Pinus taeda*) stands that received fertilization (F), weed control (W), and fertilization plus weed control (FW) treatments and the results from the ANOVA.

	Foliage	Bark	Branch	Stem	Understory	Oi	Oe + Oa
Vegetation and forest floor N content							
Control	58 (13)	16 (5)	30 (9)	31 (8)	78 (6)	40 (12)	347 (64)
F	137 (10)	30 (4)	70 (3)	70 (31)	54 (7)	53 (13)	627 (27)
W	119 (17)	30 (1)	66 (3)	63 (10)		40 (11)	427 (77)
FW	183 (14)	35 (1)	83 (1)	95 (9)		80 (1)	647 (52)
Significant ($p < 0.05$) ANOVA p values							
Source of variation							
F (df = 1)	<0.001	0.036	0.003	0.012			0.004
W (df = 1)	<0.001						
F \times W (df = 1)							
Error (df = 8)							

Fig. 1. Change in ecosystem C between year 18 and the end of rotation (25 years). Error bars are 95% confidence intervals and significant differences from zero are denoted by an asterisk.

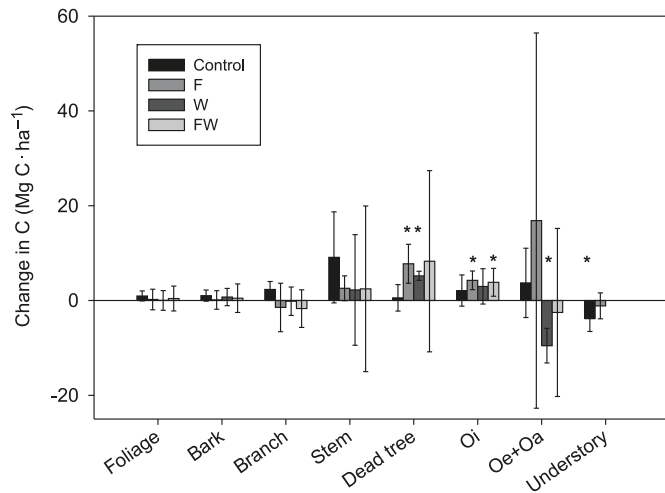


Fig. 2. Change in ecosystem N between year 18 and the end of rotation (25 years). Error bars are 95% confidence intervals and significant differences from zero are denoted by an asterisk.

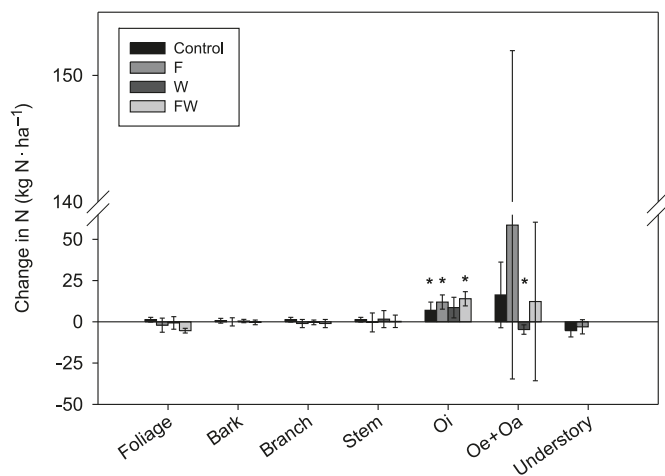


Fig. 3. Carbon content in the soil, forest floor, and vegetation biomass of a loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii* var. *elliottii*) forest.

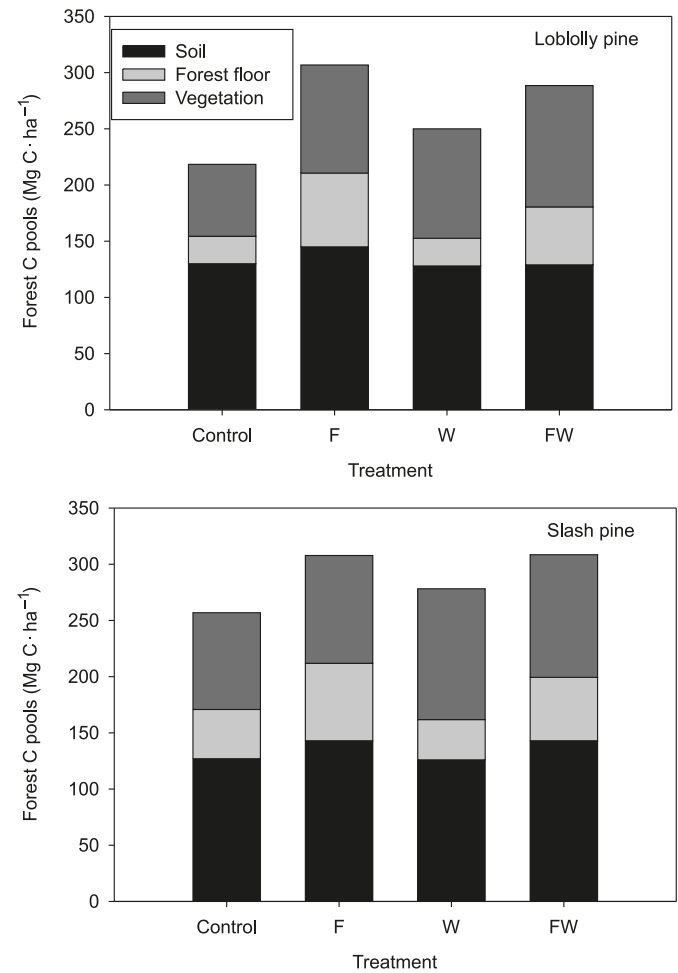
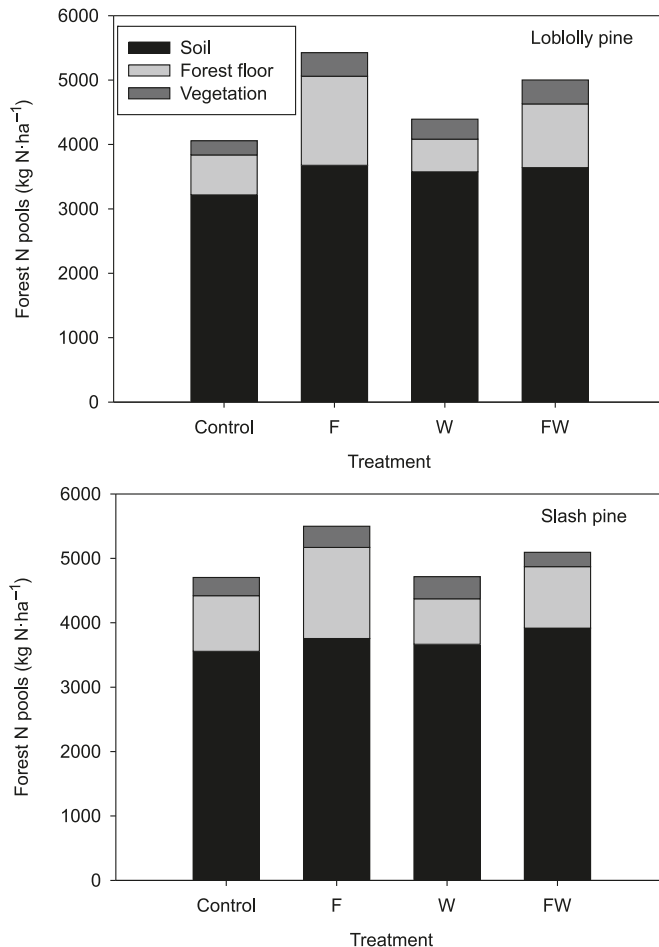


Table 8. Mean (\pm SE) N content ($\text{kg}\cdot\text{ha}^{-1}$) for 26-yearold loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii* var. *elliottii*) stands that received fertilization (F), weed control (W), and fertilization plus weed control (FW) treatments and the results from the ANOVA.

	Foliage	Bark	Branch	Stem	Understory	Roots		Forest floor		Soil depth interval (cm)		
						<2 mm	2–5 mm	Oi	Oe + Oa	0–33	33–66	66–100
Vegetation, forest floor, and soil N content												
Loblolly pine												
Control	71 (15)	26 (5)	43 (12)	46 (11)	23 (1)	26 (8)	31 (9)	110 (2)	510 (79)	1097 (131)	1137 (61)	983 (194)
F	115 (8)	25 (5)	64 (7)	75 (33)	27 (4)	21 (4)	38 (6)	173 (24)	1210 (24)	1347 (10)	1480 (90)	850 (95)
W	112 (8)	28 (1)	66 (1)	65 (11)		10 (1)	29 (7)	127 (23)	380 (80)	1623 (290)	1033 (107)	920 (112)
FW	131 (2)	34 (3)	74 (6)	98 (3)		8 (1)	27 (3)	220 (10)	770 (125)	1600 (260)	1250 (201)	790 (217)
Slash pine												
Control	65 (2)	45 (2)	32 (1)	54 (4)	37 (8)	20 (3)	30 (5)	163 (27)	700 (123)	1280 (200)	1477 (97)	800 (51)
F	67 (6)	50 (7)	42 (3)	77 (35)	48 (16)	21 (1)	25 (5)	173 (27)	1240 (76)	1310 (96)	1543 (188)	903 (64)
W	103 (4)	73 (3)	61 (2)	84 (18)		8 (2)	14 (3)	157 (3)	550 (31)	1483 (200)	1413 (90)	770 (151)
FW	90 (11)	58 (9)	48 (3)	105 (19)		5 (2)	22 (16)	237 (35)	718 (118)	1323 (91)	1783 (75)	810 (69)
Significant ($p < 0.05$) ANOVA p values												
Source of variation												
Whole plot												
Block (df = 2)												
Species (S) (df = 1)		0.028										
Error (df = 2)												
Split plot												
F (df = 1)	<0.001		<0.001	0.041				<0.001	<0.001		0.006	
W (df = 1)	0.017	<0.001	0.018	0.047		<0.001			<0.001	0.006		
F \times W (df = 1)	0.031		0.028						0.043			
S \times F (df = 1)												
S \times W (df = 1)	0.002											
S \times F \times W (df = 1)												
Error (df = 12)												

Fig. 4. Nitrogen content in the soil, forest floor, and vegetation biomass of a loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii* var. *elliottii*) forest.



difficult to assign reasonable N concentrations. If only those N pools that responded significantly to fertilization were summed (foliage, stem, forest floor, and 33–66 cm soil), then the efficiency decreased to 103% and 62% for the loblolly and slash pine forests, respectively. For the FW plots, the N retention was calculated based on the N content of the W plots. For the N pools significantly affected by fertilization, the FW treatment plots retained between 62% and 53% of the added N for the loblolly and slash pine forests, respectively. The lower N retention was calculated for fertilized slash pine forests because the slash pine control plots had 27% greater background N content in the forest floor and surface soil than the loblolly pine control plots and was not the result of lower accumulation in the F plots of the two species (5451 kg N·ha⁻¹ for loblolly pine versus 5425 kg N·ha⁻¹ for slash pine).

Discussion

Fertilization and weed control dramatically increased pine growth rates and biomass accumulation at this site (Jokela et al. 2010); however, in the treated plots, pine net primary productivity generally peaked at about age 6 years (Martin and Jokela 2004) and stand BA and biomass have been near steady state or slightly declining since ages 16–20 years in

most plots (Table 2) (Jokela et al. 2010). Thus, it was unclear whether the gains in C that had presumably occurred with increased pine growth were maintained to the end of rotation. We found that fertilization alone resulted in an increase in ecosystem C relative to controls plots of 20% (slash pine) to 40% (loblolly pine). When both weed control and fertilization were applied to a stand, C accumulation decreased relative to the fertilizer-only plots between 3% and 8% in the slash and loblolly pine forests, respectively (Fig. 3). This decrease in the FW relative to the F treatments occurred primarily because of a decrease in the C found in the forest floor and mineral soils. Although weed control did increase some aboveground pine C pools at age 18 and 26 years, the total increase in ecosystem C that occurred with silviculture was only significant in the fertilized forests.

By measuring ecosystem C pools at two different ages, we were able to determine the trajectory of the different pools in response to treatment and their relative importance over time. At age 18 years, we found that loblolly pine biomass responded to fertilization to a greater degree than the forest floor, but at age 26 years, the pools that contributed the most to net C gain in the fertilized forests were the forest floor and dead tree pool (47%) followed by vegetation biomass (36%). Forest floor pools were particularly dynamic through time, with the W treatment causing a decrease in the Oe + Oa layer between ages 18 and 25 years. Gholz and Fisher (1982) reported that past the age of 24 years in managed slash pine stands, the forest floor increased in mass even as vegetation biomass remained at steady state; however, these stands did not receive fertilizer or weed control treatments. In comparison, our results suggest that forest floor dynamics are sensitive to understory or weed control and that as stands age, the forest floor becomes more important to C balance as a pool that can be either lost or gained in response to silvicultural treatment.

The mineral soil layers were sensitive to both the weed control and fertilization treatment. In many regions, mineral soils respond very little to forest management (Jandl et al. 2007); however, previous research has indicated that southern pine forests can lose soil C with understory treatments or weed control (Carter et al. 2002; Echeverría et al. 2004; Sartori et al. 2007; Rifai et al. 2010), which has been attributed to decreased fine root growth and turnover (Albaugh et al. 1998; Shan et al. 2001). Similarly, with weed control, we observed a significant C decrease in the deepest soil layer (66–100 cm) and an overall decrease in fine root mass of nearly 60%. Fine roots were a very small component of vegetation biomass (Table 7), but their rapid mortality and turnover can add significant amounts of C to the deeper soil horizons (Haile et al. 2010) and create the soil structure that then moderates soil organic matter decomposition (Sarkhot et al. 2008).

Forest fertilization has been shown to increase mineral soil C in other ecosystems (Johnson and Curtis 2001; McFarlane et al. 2009; Nave et al. 2010), but our observation of increased mineral soil C with fertilization is unique relative to many other studies that have examined southern pine forests (Harding and Jokela 1994; Echeverría et al. 2004; Leggett and Kelting 2006; Sartori et al. 2007). Our results may differ from previous studies because we examined forests at the end of the rotation, whereas other than Harding

and Jokela (1994), most studies have focused on forests 18 years or younger. A difference of only 8 years may seem too short a time period to result in changes in mineral soil C, but radiocarbon measures of soil C (Richter et al. 1999) and studies of silviculture effects on soil C early in stand history (Sarkhot et al. 2007) have indicated substantial C changes within this time frame for southern pine forests. Notably, Rifai et al. (2010) reported significantly increased soil C in a 20-year-old fertilized forest. Alternatively, previous research at this site has consistently indicated greater soil C in fertilized plots at different periods of stand history (Polglase et al. 1992b; Grierson et al. 1998), suggesting that some unique aspect of the site or treatment regime may have increased soil C. An important factor may have been the relationship between background fertility and soil C response to fertilization. In this regard, McFarlane et al. (2009) compared Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) forests of varying background fertility and found that soil C at the lowest fertility site increased with fertilization but that soil C at the moderate and high fertility sites were unchanged. The Spodosols (Pomona series) examined in this study are nutrient poor relative to other Florida soils that support southern pines (Harding and Jokela 1994).

An uncertainty in our biomass estimates was the use of non-site-specific allometric equations to estimate above-ground biomass for trees larger than those harvested at the site. In general, allometric relationships for stem biomass are highly constrained across tree species and sites (Jenkins et al. 2003); therefore, we only assessed potential bias for the branch and foliage biomass. For trees that overlapped in diameter, on average 36% and 9% more branch and foliage biomass would be estimated with the site-specific equations, respectively, than with the equations for slash pine (Jokela et al. 1989) and loblolly pine (Naidu et al. 1998). We cannot say for certain, but we believe that these biases reflect that the 16-year-old trees harvested for site-specific equations had only begun to senesce larger branches due to intertree competition, and likely the literature equations that included older, larger trees were more accurate for the large trees at the site. Exchanging equations had no effect on the statistical contrasts of both elements in the foliage and branch pools, which together represented between 3% and 8% of ecosystem C and N.

The estimates of coarse root biomass were also made using a ratio derived for sites other than those measured here and only for loblolly pine (Albaugh et al. 2006), but we applied the ratio to the slash pine plots because of the similarity in the two species. It is difficult to assess the potential error of this choice because at present, there are no published allometric equations for slash pine coarse roots. Previous researchers have used the equation of Santantonio et al. (1977) developed for all conifers to estimate coarse root biomass for this species (Gholz and Fisher 1982; Shan et al. 2001). These researchers estimated a stem to coarse root biomass ratio of between 0.77 and 0.74 for slash pine, considerably more than the ratio of 0.5 found by Albaugh et al. (2006) for loblolly pine. One aspect of the Albaugh et al. (2006) sampling methodology that could have caused this result is that they explored deeper into the horizon than many other researchers, an approach that has proven critical in identifying highly variable stem to coarse root biomass

ratios (cf. King et al. 2007). Given the paucity of literature on coarse root biomass and the inherent variability in the measurements, it is difficult to assess whether treatment differences could have occurred that would have affected our comparisons, although Retzlaff et al. (2001) reported that the effect of fertilization on loblolly pine coarse roots was only a function of tree size and not shifts in allometric ratios. Using a ratio of 0.5 or 0.77 would translate to a 3%–5% change in the ecosystem C estimates.

The N content of pine aboveground biomass was generally increased by both treatments relative to the control (Table 8), and for weed control, we believe that the N content increase reflected past N availability. Other studies have examined weed control effects on N availability early in stand history and have reported net N mineralization increasing (Vitousek et al. 1992), remaining unchanged (Gurlevik et al. 2004; Meason et al. 2004; Sartori et al. 2007), or decreasing with weed control (Polglase et al. 1992a; Will et al. 2006). In our study, loblolly pine stem and slash pine foliage N concentrations were decreased significantly in the weed control plots relative to the control plots, suggesting lower overall N availability at the time of our measurements. This observation, in conjunction with greater biomass N content, suggests that the weed control treatment relieved a deficiency in N earlier in stand history than our measurement period (Dalla-Tea and Jokela 1994). Alternative, complementary explanations are that weed control relieved the limitation of another element, resulting in N dilution at the tissue level but an increase in total N content, or that understory removal relieved interspecies competition for water, thereby allowing pine to take up greater amounts of N (Samuelson et al. 2004). We cannot disentangle these possible explanations from our results but note them as potential hypotheses for future studies.

At the end of the rotation, forest floor N was decreased by weed control and increased by the fertilization treatment. Fertilization likely increased N in the forest floor and soil because the added N was immobilized by soil microbes or was perhaps abiotically fixed (Johnson 2006). For the weed control treatments, the forest floor N was 113–156 kg N·ha⁻¹ (loblolly and slash pine) lower than in the control plots at the end of rotation. In contrast, for a 13-year-old loblolly forest, Will et al. (2006) reported no difference in forest floor N, and in our study, when the loblolly stands were 18 years old, the forest floor N was slightly lower in the control than in the weed controls plots. However, from 18 to 26 years, 233 kg N·ha⁻¹ accumulated in the control plots, while the weed control plots only accumulated 30 kg N·ha⁻¹. In the control plots, this reflects an accumulation rate of 26 kg N·ha⁻¹·year⁻¹, which is more than double the 11 kg N·ha⁻¹·year⁻¹ rate estimated by Gholz et al. (1985) for a chronosequence of Florida slash pine forests. One reason for this difference may be that our study site was twice affected by tropical storms at age 21 years, which caused reductions in overstory leaf area (T.A. Martin, unpublished data). In response to this disturbance, the understory in the control and fertilized plots may have responded to the increased light and contributed more to forest floor buildup than what would have normally occurred.

In certain intervals within the soil profile, soil N was increased by both fertilization and weed control. The increase

in surface (0–33 cm) soil N with weed control was unusual relative to other studies in loblolly pine forests (Echeverría et al. 2004; Sartori et al. 2007; Rifai et al. 2010), although Polglase et al. (1992b) reported a significant soil N increase in the furrows of the weed control plots at this same site. Some of the increased N could have been redistributed from deeper in the soil profile because for both the 33–66 and 66–100 cm intervals, the soil N in weed control plots was nominally less than in the controls. Alternatively, the early fast biomass accrual in the weed control plots could have resulted in greater capture of atmospheric N inputs, or retention of background N levels, relative to the control plots. With the treated stands tending to stagnate in terms of biomass accumulation over the last several years of the rotation (Table 2), N that was previously found in the forest floor may have begun accumulating in the soil profile rather than being taken up and recycled through the canopy.

Nitrogen retention efficiency ranged from 62% to 103% for the fertilized-only slash and loblolly forests, respectively. For the loblolly forests, previous studies have also estimated relatively high fertilizer N retention efficiencies of 89% (Will et al. 2006) and 76% (Albaugh et al. 2006). Because we were unsure how to assign N concentrations to coarse roots and the dead trees, our estimates excluded these N pools, but based on the C pools, it is likely that these pools would have differed from the controls and further increased the estimates of ecosystem N retention. Nitrogen retention efficiencies in excess of 100% are fairly common in fertilization studies and are reported both in studies using the ^{15}N isotope labeling approach and in those using the treatment-minus-control method described here (Schlesinger 2009). Why this occurs is unclear, but accumulating errors in measurements and (or) the alteration of N cycling within the fertilized plots are plausible explanations. For the species differences, the lower N retention efficiency of slash pine relative to loblolly pine reflected greater N contents in the slash pine control forest floor and soil rather than lower accumulated N in the fertilized plots (Fig. 4). Rather than edaphic differences in the control plots, we believe that this reflects that the inherently lower leaf area of slash pine relative to loblolly pine is accentuated under low nutrient availability (Peduzzi et al. 2010). This attribute of slash pine, and the apparent feedback that occurs between the understory and forest floor N retention, may explain the greater forest floor N accumulations in the control plots of slash pine relative to loblolly pine.

The reduced N retention efficiency of the FW plots relative to the F plots was the result of their significantly lower N pools in the understory biomass, fine roots, and the forest floor. These results suggest that FW treatments lost a greater fraction of the applied N through volatilization or leaching than did the F treatments. Nitrogen is more likely to be lost from forests when foliage N concentrations exceed 1.4% (Gundersen et al. 2006), and after 3 years of intensive fertilization, the loblolly FW forests had a foliar N concentration of 1.6% at age 18 years. This concentration was higher than any other that was measured over stand rotation (Dalla-Tea and Jokela 1994; Martin and Jokela 2004) and may have indicated a period of N loss for the FW forests. In addition, the pine biomass was apparently near steady state and had reached steady state earlier in stand history for the FW than

for the F forests (Table 2); thus, it is possible that reduced vegetation demand for N at this later point in stand development was allowing some N to leave the FW forests. One mechanism for this process may be that the soils of southern pine forests receiving understory control are generally warmer and wetter than plots with an intact understory (Gurlevik et al. 2004), which may have stimulated N mineralization in the forest floor or the volatilization of applied fertilizer (Kissel et al. 2004).

Species-level effects for both C and N pools were most prevalent in the interaction terms for aboveground vegetation. These effects highlighted a notable difference between the two species: slash pine mortality increased significantly with fertilization relative to loblolly pine (Jokela et al. 2010). This mortality muted some of the C and N accumulation in aboveground components and may reflect slash pine's greater sensitivity than loblolly pine to pitch canker (*Gibberella circinata* Nirenberg & O'Donnell 1998) infection (Dwinell and Barrowsbroaddus 1979) and density-related competition. Similar to Colbert et al. (1990), the only other statistically significant difference between the two species was the greater bark C content, and lesser N concentration, in slash pine relative to loblolly pine. Generally, the statistical analyses provided few species differences in C or N pools as main effects, which may have reflected that species was the whole-plot error in the analysis. However, the many significant interactions between treatments and species do suggest that further research is needed to understand how species differences may affect C accumulation and nutrient retention.

Conclusions

Silvicultural treatments that increased southern pine biomass had mixed results for ecosystem C and N accumulation and N retention. Fertilization increased C storage in these ecosystems, while weed control had no effect alone, or a negative effect on C storage when combined with fertilization. This influence of weed control would have not been found at age 18 years and without an analysis that included all components of ecosystem C. Notably, weed control reduced forest floor C and decreased it through time in a manner that differed from the observations of continuous increase (Gholz et al. 1985) or steady-state conditions (Richter and Markewitz 2001) that have been previously reported for southern pine forests having received no weed control or fertilizer additions. Weed control also reduced ecosystem N retention efficiency of applied fertilizer, but there was no evidence that weed control would result in a significant loss in background levels of N beyond what was removed during harvest. A significant finding of this research is that the understory plays a role in ecosystem C and N dynamics through its effects on the forest floor and soils that is proportionately much larger than its pools of C or N.

Extending our results to operational conditions is difficult because a more extensive set of plots are needed, and studies are needed in forests managed using silvicultural techniques that are closer to "typical" for southern pines. The experiment that we describe here was designed to test the physiological limits of pine growth, and therefore, the treatment levels were more intensive than would be found under

most operational conditions. Indeed, the level of weed control resulted in effectively no understory coverage, and the fertilization treatments that occurred between ages 16 and 18 years were well beyond stand needs and did not increase stand growth (Martin and Jokela 2004). This suggests that the observed C benefits, and perhaps even greater N retention, could be achieved with lower levels of fertilization. It is also likely that lower levels of weed control can be employed with fertilization in a manner that results in higher rates of N retention and C accumulation.

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References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., and King, J.S. 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. *For. Sci.* **44**(2): 317–328.
- Albaugh, T.J., Allen, H.L., and Kress, L.W. 2006. Root and stem partitioning of *Pinus taeda*. *Trees Struct. Funct.* **20**(2): 176–185. doi:10.1007/s00468-005-0024-4.
- Borders, B.E., Will, R.E., Markewitz, D., Clark, A., Hendrick, R., Teskey, R.O., and Zhang, Y. 2004. Effect of complete competition control and annual fertilization on stem growth and canopy relations for a chronosequence of loblolly pine plantations in the lower coastal plain of Georgia. *For. Ecol. Manag.* **192**(1): 21–37. doi:10.1016/j.foreco.2004.01.003.
- Carter, M.C., Dean, T.J., Zhou, M.Y., Messina, M.G., and Wang, Z.Y. 2002. Short-term changes in soil C, N, and biota following harvesting and regeneration of loblolly pine (*Pinus taeda* L.). *For. Ecol. Manag.* **164**(1–3): 67–88. doi:10.1016/S0378-1127(01)00590-4.
- Colbert, S.R., Jokela, E.J., and Neary, D.G. 1990. Effects of annual fertilization and sustained weed control on dry-matter partitioning, leaf area, and growth efficiency of juvenile loblolly and slash pine. *For. Sci.* **36**(4): 995–1014.
- Comerford, N.B., McLeod, M., and Skinner, M. 2002. Phosphorus form and bioavailability in the pine rotation following fertilization — P fertilization influences P form and potential bioavailability to pine in the subsequent rotation. *For. Ecol. Manag.* **169**(3): 203–211. doi:10.1016/S0378-1127(01)00680-6.
- Dalla-Tea, F., and Jokela, E.J. 1994. Needlefall returns and resorption rates of nutrients in young intensively managed slash and loblolly pine stands. *For. Sci.* **40**(4): 650–662.
- Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexler, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. *Science*, **263**(5144): 185–190. doi:10.1126/science.263.5144.185.
- Dwinell, L.D., and Barrowsbroaddus, J. 1979. Susceptibility of half-sib families of slash and loblolly pine to the pitch canker fungus, *Fusarium moniliforme* var. *subglutinans*. *Phytopathology*, **69**(5): 527.
- Echeverría, M.E., Markewitz, D., Morris, L.A., and Hendrick, R.L. 2004. Soil organic matter fractions under managed pine plantations of the southeastern USA. *Soil Sci. Soc. Am. J.* **68**(3): 950–958. doi:10.2136/sssaj2004.0950.
- Fox, T.R., Jokela, E.J., and Allen, H.L. 2007. The development of pine plantation silviculture in the southern United States. *J. For.* **105**(7): 337–347.
- Gholz, H.L., and Fisher, R.F. 1982. Organic matter production and distribution in slash pine (*Pinus elliottii*) plantations. *Ecology*, **63**(6): 1827–1839. doi:10.2307/1940124.
- Gholz, H.L., Fisher, R.F., and Prichett, W.L. 1985. Nutrient dynamics in slash pine plantation ecosystems. *Ecology*, **66**(3): 647–659. doi:10.2307/1940526.
- Grierson, P.F., Comerford, N.B., and Jokela, E.J. 1998. Phosphorus mineralization kinetics and response of microbial phosphorus to drying and rewetting in a Florida Spodosol. *Soil Biol. Biochem.* **30**(10–11): 1323–1331. doi:10.1016/S0038-0717(98)00002-9.
- Gundersen, P., Schmidt, I.K., and Raulund-Rasmussen, K. 2006. Leaching of nitrate from temperate forests — effects of air pollution and forest management. *Environ. Rev.* **14**(1): 1–57. doi:10.1139/a05-015.
- Gurlevik, N., Kelting, D.L., and Allen, H.L. 2004. Nitrogen mineralization following vegetation control and fertilization in a 14-year-old loblolly pine plantation. *Soil Sci. Soc. Am. J.* **68**(1): 272–281. doi:10.2136/sssaj2004.0272.
- Haile, S.G., Nair, V.D., and Nair, P.K.R. 2010. Contribution of trees to carbon storage in soils of silvopastoral systems in Florida, USA. *Glob. Change Biol.* **16**(1): 427–438. doi:10.1111/j.1365-2486.2009.01981.x.
- Han, F.X.X., Plodinec, M.J., Su, Y., Monts, D.L., and Li, Z.P. 2007. Terrestrial carbon pools in southeast and south-central United States. *Clim. Change*, **84**(2): 191–202. doi:10.1007/s10584-007-9244-5.
- Harding, R.B., and Jokela, E.J. 1994. Long-term effects of forest fertilization on site organic matter and nutrients. *Soil Sci. Soc. Am. J.* **58**(1): 216–221. doi:10.2136/sssaj1994.03615995005800010032x.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkinen, K., and Byrne, K.A. 2007. How strongly can forest management influence soil carbon sequestration? *Geoderma*, **137**(3–4): 253–268. doi:10.1016/j.geoderma.2006.09.003.
- Jenkins, J.C., Chojnacky, D.C., Heath, L.S., and Birdsey, R. 2003. National-scale biomass estimators for United States tree species. *For. Sci.* **49**: 12–35.
- Johnson, D.W. 2006. Progressive N limitation in forests: review and implications for long-term responses to elevated CO₂. *Ecology*, **87**(1): 64–75. doi:10.1890/04-1781.
- Johnson, D.W., and Curtis, P.S. 2001. Effects of forest management on soil C and N storage: meta analysis. *For. Ecol. Manag.* **140**(2–3): 227–238. doi:10.1016/S0378-1127(00)00282-6.
- Jokela, E.J., and Martin, T.A. 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. *Can. J. For. Res.* **30**(10): 1511–1524. doi:10.1139/cjfr-30-10-1511.
- Jokela, E.J., Harding, R.B., and Nowak, C.A. 1989. Long-term effects of fertilization on stem form, growth relations, and yield estimates of slash pine. *For. Sci.* **35**(3): 832–842.
- Jokela, E.J., Martin, T.A., and Vogel, J.G. 2010. Twenty-five years of intensive forest management with southern pines: important lessons learned. *J. For.* **108**(7): 338–347.
- King, J.S., Giardina, C.P., Pregitzer, K.S., and Friend, A.L. 2007. Biomass partitioning in red pine (*Pinus resinosa*) along a chronosequence in the Upper Peninsula of Michigan. *Can. J. For. Res.* **37**(1): 93–102. doi:10.1139/X06-217.
- Kissel, D.E., Cabrera, M.L., Vaio, N., Craig, J.R., Rema, J.A., and Morris, L.A. 2004. Rainfall timing and ammonia loss from urea in a loblolly pine plantation. *Soil Sci. Soc. Am. J.* **68**(5): 1744–1750. doi:10.2136/sssaj2004.1744.

- Laiho, R., and Prescott, C.E. 1999. The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests. *Can. J. For. Res.* **29**(10): 1592–1603. doi:10.1139/cjfr-29-10-1592.
- Leggett, Z.H., and Kelting, D.L. 2006. Fertilization effects on carbon pools in loblolly pine plantations on two upland sites. *Soil Sci. Soc. Am. J.* **70**(1): 279–286. doi:10.2136/sssaj2003.0232.
- Martin, T.A., and Jokela, E.J. 2004. Developmental patterns and nutrition impact radiation use efficiency components in southern pine stands. *Ecol. Appl.* **14**(6): 1839–1854. doi:10.1890/03-5262.
- McCullough, S.D., Straka, T.J., and Dubois, M.R. 2005. Identifying intensively managed pine plantation acreage in the South. *South. J. Appl. For.* **29**(3): 163–166.
- McFarlane, K.J., Schoenholtz, S.H., and Powers, R.F. 2009. Plantation management intensity affects belowground carbon and nitrogen storage in northern California. *Soil Sci. Soc. Am. J.* **73**(3): 1020–1032. doi:10.2136/sssaj2008.0158.
- Meason, D., Markewitz, D., and Will, R. 2004. Annual fertilization and interspecific competition control: effects on *in situ* forest floor nitrogen fluxes of different-aged *Pinus taeda* stands in southeast Georgia, USA. *Can. J. For. Res.* **34**(9): 1802–1818. doi:10.1139/x04-053.
- Miller, H.G. 1981. Forest fertilization: some guiding concepts. *Forestry*, **54**(2): 157–167. doi:10.1093/forestry/54.2.157.
- Miller, J.H., Allen, H.L., Zutter, B.R., Zedaker, S.M., and Newbold, R.A. 2006. Soil and pine foliage nutrient responses 15 years after competing vegetation control and their correlation with growth for 13 loblolly pine plantations in the southern United States. *Can. J. For. Res.* **36**(10): 2412–2425. doi:10.1139/X06-164.
- Naidu, S.L., DeLucia, E.H., and Thomas, R.B. 1998. Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Can. J. For. Res.* **28**(8): 1116–1124. doi:10.1139/cjfr-28-8-1116.
- National Oceanic and Atmospheric Administration. 1998. Climatological data, Florida. National Climate Center, Environmental Data Service, National Oceanic and Atmospheric Administration, Asheville, N.C.
- Nave, L.E., Vance, E.D., Swanston, C.W., and Curtis, P.S. 2010. Harvest impacts on soil carbon storage in temperate forests. *For. Ecol. Manag.* **259**(5): 857–866. doi:10.1016/j.foreco.2009.12.009.
- Neary, D.G., Rockwood, D.L., Comerford, N.B., Swindel, B.F., and Cooksey, T.E. 1990. Importance of weed control, fertilization, irrigation, and genetics in slash and loblolly pine early growth on poorly drained Spodosols. *For. Ecol. Manag.* **30**(1–4): 271–281. doi:10.1016/0378-1127(90)90142-X.
- Pacala, S., and Socolow, R. 2004. Stabilization wedges: Solving the climate problem for the next 50 years with current technologies. *Science*, **305**(5686): 968–972. doi:10.1126/science.1100103.
- Peduzzi, A., Allen, H.L., and Wynne, R.H. 2010. Leaf area of overstory and understory in pine plantations in the flatwoods. *South. J. Appl. For.* **34**(7): 154–160.
- Phelan, J. (B.), and Allen, H.L. 2008. Have repeated applications of nitrogen and phosphorus to a loblolly pine plantation changed stand productivity and soil nutrient supply? *Can. J. For. Res.* **38**(3): 637–644. doi:10.1139/X07-131.
- Polglase, P.J., Jokela, E.J., and Comerford, N.B. 1992a. Nitrogen and phosphorus release from decomposing needles of southern pine plantations. *Soil Sci. Soc. Am. J.* **56**(3): 914–920. doi:10.2136/sssaj1992.03615995005600030039x.
- Polglase, P.J., Jokela, E.J., and Comerford, N.B. 1992b. Phosphorus, nitrogen, and carbon fractions in litter and soil of southern pine plantations. *Soil Sci. Soc. Am. J.* **56**(2): 566–572. doi:10.2136/sssaj1992.03615995005600020036x.
- Radtke, P.J., Amateis, R.L., Prisley, S.P., Copenheaver, C.A., Chojnacky, D.C., Pittman, J.R., and Burkhart, H.E. 2009. Modeling production and decay of coarse woody debris in loblolly pine plantations. *For. Ecol. Manag.* **257**(3): 790–799. doi:10.1016/j.foreco.2008.10.001.
- Retzlaff, W.A., Handest, J.A., O'Malley, D.M., McKeand, S.E., and Topa, M.A. 2001. Whole tree biomass and carbon allocation of juvenile trees of loblolly pine (*Pinus taeda* L.): influence of genetics and fertilization. *Can. J. For. Res.* **31**(6): 960–970. doi:10.1139/cjfr-31-6-960.
- Richter, D.D., and Markewitz, D. 2001. Understanding soil change. Cambridge University Press, New York.
- Richter, D.D., Markewitz, D., Trumbore, S.E., and Wells, C.G. 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. *Nature*, **400**(6739): 56–58. doi:10.1038/21867.
- Rifai, S.W., Markewitz, D., and Borders, B. 2010. Twenty years of intensive fertilization and competing vegetation suppression in loblolly pine plantations: impacts on soil C, N, and microbial biomass. *Soil Biol. Biochem.* **42**(5): 713–723. doi:10.1016/j.soilbio.2010.01.004.
- Samuelson, L.J., Johnsen, K., and Stokes, T. 2004. Production, allocation, and stemwood growth efficiency of *Pinus taeda* L. stands in response to 6 years of intensive management. *For. Ecol. Manag.* **192**(1): 59–70. doi:10.1016/j.foreco.2004.01.005.
- Santantonio, D., Hermann, R.K., and Overton, W.S. 1977. Root biomass studies in forest ecosystems. *Pedobiologia (Jena)*, **17**: 1–31.
- Sarkhot, D., Comerford, N.B., Jokela, E.J., and Reeves, J.B., III. 2007. Effects of forest management intensity on carbon and nitrogen content in different soil size fractions of a north Florida Spodosol. *Plant Soil*, **294**(1–2): 291–303. doi:10.1007/s11104-007-9255-z.
- Sarkhot, D.V., Jokela, E.J., and Comerford, N.B. 2008. Surface soil carbon size–density fractions altered by loblolly pine families and forest management intensity for a Spodosol in the southeastern US. *Plant Soil*, **307**(1–2): 99–111. doi:10.1007/s11104-008-9587-3.
- Sartori, F., Markewitz, D., and Borders, B.E. 2007. Soil carbon storage and nitrogen and phosphorus availability in loblolly pine plantations over 4 to 16 years of herbicide and fertilizer treatments. *Biogeochemistry*, **84**(1): 13–30. doi:10.1007/s10533-007-9072-8.
- Schlesinger, W.H. 2009. On the fate of anthropogenic nitrogen. *Proc. Natl. Acad. Sci. U.S.A.* **106**(1): 203–208. doi:10.1073/pnas.0810193105.
- Shan, J.P., Morris, L.A., and Hendrick, R.L. 2001. The effects of management on soil and plant carbon sequestration in slash pine plantations. *J. Appl. Ecol.* **38**(5): 932–941. doi:10.1046/j.1365-2664.2001.00648.x.
- Soil Survey Staff. 1999. Soil taxonomy a basic system of soil classification for making and interpreting soil surveys. U.S. Dep. Agric. Agric. Handb. 436.
- US Environmental Protection Agency. 2005. Greenhouse gas mitigation potential in U.S. forestry and agriculture. EPA 430-R-05-006. Office of Atmospheric Programs, Washington, D.C.
- Vitousek, P.M., Andariese, S.W., Matson, P.A., Morris, L., and Sanford, R.L. 1992. Effects of harvest intensity, site preparation, and herbicide use on soil nitrogen transformations in a young loblolly pine plantation. *For. Ecol. Manag.* **49**(3–4): 277–292. doi:10.1016/0378-1127(92)90141-U.
- Will, R.E., Markewitz, D., Hendrick, R.L., Meason, D.F., Crocker,

T.R., and Borders, B.E. 2006. Nitrogen and phosphorus dynamics for 13-year-old loblolly pine stands receiving complete

competition control and annual N fertilizer. *For. Ecol. Manag.* **227**(1–2): 155–168. doi:10.1016/j.foreco.2006.02.027.