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Soil Properties in 35 y old Pine and Hardwood Plantations after Conversion from Mixed Pine-hardwood Forest

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ABSTRACT.—Past management practices have changed much of the native mixed pine-hardwood forests on upland alluvial terraces of the western Gulf Coastal Plain to either pine monocultures or hardwood (angiosperm) stands. Changes in dominant tree species can alter soil chemical, biological, and physical properties and processes, thereby changing soil attributes, and ultimately, soil functions. Restoring these forests may be slow or difficult if soil function is altered appreciably. We studied the soil properties and processes in pine or hardwood-dominated stands after 35 y since conversion from a mixed pine-hardwood stand. The pine forest floor biomass was about twice as great as that of the oak stands, the oak soils were 20–30% wetter than the pine soils throughout the sampling period, the oak soils released more CO_2 through respiration and had higher rates of N mineralization in the summer. We observed few differences between pine and oak stands in soil chemistry or microbial biomass. Since the difference in forest floor depth and soil biological activity may confer competitive advantages or disadvantages to some species, this study supports the hypothesis that pine- or hardwood-only stands create functionally different soils on these site types after 35 y.

INTRODUCTION

Native vegetation on alluvial terraces in the western Gulf Coastal Plain of the United States consists of a mix of scattered pines (primarily *Pinus taeda* L.) and various hardwood species including oaks (*Quercus alba* L., *Q. falcata* Michx., *Q. pagoda* Raf., *Q. nigra* L., *Q. phellos* L.) and others, *Liquidambar styraciflua* L and *Nyssa sylvatica* Marsh. (NatureServe, 2002). A variety of land management approaches have, in some areas, increased the pine component of these terraces through conversion to pine plantations, whereas others have eliminated the pine component and created hardwood-only areas. Because shifts in overstory tree species can cause significant changes in soil chemistry and fertility (Binkley, 1995; Binkley and Giardina, 1998), the intentional or accidental conversion of these areas from mixed-species stands to either pine or hardwood stands may alter nutrient cycling patterns and create functionally different soils. Soils with disparate functional attributes support different understory plant communities due to forest floor type and depth, soil water content and soil fertility, all of which create conditions that support species with different resource competition strategies. Changes in the overstory and understory plant communities can then lead to a divergent successional pathway (Cook, 1996) and alterations in the functional traits of the soil and biota can alter overall ecosystem functioning (Chapin *et al.*, 1997). Attempts to classify ecosystems for ecosystem management based only on current vegetation surveys may then be inaccurate (Cook, 1996) and result in ineffective management strategies.

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Studies regarding the influence of vegetation on soil properties and processes have been conducted since Dokuchaev (1879) recognized vegetation as a primary soil forming factor. Similarly, the concern that conifers may be soil ''degraders'' was first reported by Wiedemann (1923), who originally concluded the decline in Norway spruce (*Picea abies* (L.) Karst) plantation productivity over three rotations was due to the negative influence of spruce trees on soils formed under hardwood trees. Although these effects were eventually shown to be due to other factors (Powers *et al.*, 1990), the concern over ecosystem change through species conversions continues to be a topic of interest.

Little research has been conducted on species conversions and soil function in the southern United States. Lane (1975, 1990) studied the conversion of poorly stocked, high-graded *Quercus-Carya* stands to *Pinus taeda* on the South Carolina Piedmont, and Swank *et al.* (1988) studied how converting a hardwood stand to *P. strobus* affected watershed properties in the southern Appalachians, but the influence of various tree species on soil processes and these relationships to ecological functioning are still largely unknown in the uplands of the southern coastal plain. As forest management in some regions is attempting to restore specific ecosystems through ecosystem management, the need for an understanding of how previous species shifts may have changed soil function is vital.

The purpose of this study was to determine if forest floor and mineral soil properties and processes are different 35 y following the conversion of a mixed pine-oak forest to either a pine or oak forest. Specifically, our objectives were to determine (1) if stand type affects forest floor biomass and chemistry, (2) if stand type, through differential light interception, water relations and forest floor characteristics, alters surface soil climate, (3) if stand type affects soil fertility indices and (4) if stand type, through differences in forest floor characteristics and soil climate, affects soil biology and biological activity.

MATERIALS AND METHODS

SITE DESCRIPTION

The study was established within an existing 35 y old common garden experiment installed at the Forest Lake Experimental Forest in Tyler County, Texas (30°64′N, 94°8′W) by Temple-Inland Forest Products Corporation, Diboll, Texas. The general study area was distributed topographically on a second terrace of the Neches River on moderately well to somewhat poorly drained Belrose (Coarse-loamy, siliceous, superactive, thermic Oxyaquic Paleudults) and Spurger soils (Fine, smectitic, thermic Albaquultic Hapludalfs) that were intermixed throughout the study area. The climate is warm and humid, with an average annual temperature of 19.4 C and a mean monthly range of 10.0 C in Jan. to 27.2 C in Jul. The frost-free season is 241 d. Annual precipitation averages 132 cm and is well distributed throughout the year (Griffiths and Bryan, 1987).

Prior to the original study establishment, the study area was in mature, mixed pine-hardwood forest with more pine located on the better drained ridges and more hardwood on the more poorly drained flats. The original stand was harvested using conventional hand-felling and grapple skidders. Site preparation consisted of shearing and careful removal of the residual coarse woody debris without burning. The original experimental design was not known, but approximately 25 0.5-ha stands were planted to one of several tree species or combinations of species. No discernible pattern was observed, suggesting the species or species mixtures were assigned randomly to the stands. Six of these stands (three each dominated by loblolly pine or an oak species) were found that had similar physiographic positions, soils, full stocking, and no signs of insect, fire or disease outbreaks. The selected stands were all located within a 15-ha area and each stand was between 100 and 300 m from

the next closest stand. Within each stand, every tree with a diameter at breast height (dbh) greater than 5 cm was tallied by species and dbh was measured with a metal diameter tape.

FOREST FLOOR ANALYSES

Forest floor samples were collected at the beginning (May 1996) and end (Jun. 1997) of the study to determine forest floor mass and chemical composition. Twelve 0.25 m^2 forest floor samples were taken per plot at each of these two sampling periods. The entire forest floor depth, excluding all woody biomass, was collected to the mineral soil surface and included the Oi, Oe and Oa fractions. The samples taken were bulked for analysis by stand. Oven-dry weights and N and P concentrations were determined on a Scientific AC200 flow-injection spectrophotometer following wet digestion using the method of Parkinson and Allen (1975).

MINERAL SOIL ANALYSES

A 300 g composite sample was obtained for each stand by combining approximately 25 g of air-dry soil taken from six samples collected in May 1996 and six samples collected in Jun. 1997. The samples were taken of the A horizon, which was approximately 15 cm deep. Soil organic carbon was calculated using the factor of 1.724 from soil organic matter, which was determined by loss-on-ignition (Schulte and Hopkins, 1996). Soil pH was determined from a 1:2 soil:water (gravimetric) suspension with a glass electrode (Thomas, 1996). Effective cation exchange capacity (ECEC) was determined by summation of exchangeable cations (Sumner and Miller, 1996), with bases extracted with 1 *M* NH_4OAc and Al extracted with 1 *M* KCl. Soil texture was estimated in the field in each stand.

SOIL CLIMATE

Soil temperature was measured at 15 cm depth with an Orion thermocouple thermometer (Thermo Fisher Scientific, Waltham, MA) at six random points in each stand approximately monthly for 12 mo beginning in May 1996. Gravimetric water content was determined from six random samples collected approximately monthly from May 1996 to Jun. 1997. Soil bulk density was determined on two 5 cm diameter by 5 cm tall cores taken from the 5 to 10 cm depth in each stand by oven drying at 105 C to a constant weight (Grossman and Reinsch, 2002). No coarse fragments were found. Volumetric water content was calculated by multiplying gravimetric water content by bulk density.

SOIL MICROBIAL BIOMASS CARBON

Soil microbial biomass carbon (SMBC) was determined by the fumigation-extraction technique (Jenkinson and Powlson, 1976), with the carbon (C) analyzed using a total organic C analyzer (O.I. Corporation, College Station, TX). Twelve randomly located samples of the A soil horizon were taken in Aug. 1996, Jan. 1997 and Jun. 1997, respectively, and bulked by stand. The laboratory analyses were completed in duplicate. SMBC was calculated using equation 1 and adjusted for soil water content. The rate constant (k_{ec}), the fraction of SMBC extracted by K_2SO_4, was set at 0.33 (Sparling and West, 1988).

IN SITU CO_2 EFFLUX

In situ CO_2 efflux was measured at six randomly located points within each stand approximately monthly from Jun. 1996 to Jun. 1997 by the alkali trap method, using 1M NaOH as the alkali and 1M HCl as the titrant (Zibilski, 1994). A 60 mL Nalgene, wide-mouth bottle containing 10 mL of 1.0 M sodium hydroxide (NaOH) was placed on the forest floor and covered by a 15 cm diameter by 18 cm height (3.2 L) can. The can was

placed approximately 1 cm into the mineral soil in order to create a tight soil-to-can seal yet minimize root severing. Control traps consisted of placing one of the bottles with NaOH into a can sealed with a plastic lid. The traps were left on site for approximately 24 h after which the bottles were collected and tightly capped. Subsequently, CO_2 efflux was determined by titration with 1 N HCl.

IN SITU NITROGEN MINERALIZATION

Nitrogen mineralization and nitrification were determined by the sequential core technique described by Raison *et al.* (1987) and modified by Adams *et al.* (1989). At six randomly located points within each plot, two 5 cm diameter and 15 cm long soil cores (PVC tubes) were collected bimonthly. One core was immediately removed, whereas the other core remained uncovered in situ for about a month, at which point it was removed. Each soil sample was sieved at ambient water content to pass a 2 mm sieve, and the NH_4^+ and NO_3^--N extracted with 2 *M* KCl in a 5:2 solution:soil ratio. The NH_4^+ and NO_3^- concentrations in each extract were determined with a spectrophotometer.

STATISTICAL ANALYSES

The study was analyzed as a completely randomized design with two treatments (stand type) and three replications (stands) of each treatment. Repeated measures ANOVA was performed using PROC MIXED (SAS Institute, 2004) for all repeated measurements (soil climate, soil CO_2 efflux, N mineralization), and slicing was used to separate the least-squares means when significant time $\times$ stand type interactions were significant. The arcsin transformation was used to correct the non-normality of the volumetric water content data. One-way ANOVA was used for the forest floor and soil fertility analyses, and an alpha level of 0.05 was used for all analyses.

RESULTS

VEGETATION AND FOREST FLOOR

The 35 y old stands planted after the native mixed pine-hardwood stand was harvested had very different vegetative communities from one another. The pine stands were close to true monocultures, with 95% of the stand basal area in *Pinus taeda* (Table 1). In these stands, only *P. taeda* and *Liquidambar styraciflua* commonly had diameters >5 cm. The oak stands had a more mixed species composition. Although they were all dominated by the planted *Quercus* spp., many non-planted volunteer trees of other species were found within the oak stands. Twenty-one species had individuals with a dbh of at least 5 cm in the pine stands, but 30 species were tallied in the oak stands (Appendix 1). All species found in the pine stands were also found in the oak stands, but the oak stands had nine additional species; none of these additional nine species were present to any substantial degree (Table 1). The different overstory environment created a different understory as well. In the pine stands, a shrub and small tree understory was present, whereas few shrub species were present in the oak stands.

The different vegetation communities had distinctly different forest floors. The pine forest floors were relatively thick (5–10 cm) and consisted of readily recognizable Oi, Oe and Oa horizons, whereas the oak forest floors were thin (0–5 cm) and rarely had Oe horizons. The pine stands had almost twice the forest floor mass of the oak stands (Table 2). However, the oak forest floors were of much better quality with respect to N and P. The oak forest floors had 64% and 50% greater concentrations of N and P, respectively, than the pine forest floors. Although C was not measured on these forest floors, C:N ratios for the oak and pine stands would be about 60 and 90, assuming the forest floor was about 46% C

TABLE 1.—Vegetative composition of two stand types along a river terrace in eastern Texas, USA

Stand	Species	Mean basal area (m^2 ha^{-1})	Basal area range[1] (m^2 ha^{-1})	Relative dominance[2] (%)
Oak	*Quercus alba*	17.4	0–31	59
	Quercus phellos	4.2	0.4–10.7	14
	Liquidambar styraciflua	2.5	1.7–4.1	8
	Liriodendron tulipifera	1.7	0–1.9	6
	Quercus nigra	1.5	0–4.0	5
	Quercus pagoda	1.1	0.3–2.7	4
	Other species[3]	1.3		4
	Total	29.7	21.8–39.2	
Pine	*Pinus taeda*	41.4	33.5–46.1	95
	Liquidambar styraciflua	1.5	1.2–1.8	3
	Other species	0.2		2
	Total	43.7	34.9–48.6	

[1] Minimum and maximum basal area across all plots
[2] Relative dominance (% composition) was determined from basal area
[3] Appendix 1

(Ovington, 1956). Total N and P contents of the forest floor were similar between the stand types due to the relative differences in mass and nutrient concentrations, and averaged about 89 and 6 kg ha^{-1} for N and P, respectively (Table 2).

MINERAL SOIL

Mineral soil fertility as evaluated by total soil C, pH and exchangeable cations and anions was not affected by 35 y of differing stand types (Table 2). Bulk density averaged 1.51 Mg m^{-3} across all stands and was not significantly different between the stand types ($P < 0.12$). The A horizon soil texture varied from sandy loam to silt loam within each stand. Whereas the stands were not paired plots, the soil texture of one stand of each stand type was coincidentally a silt loam, and the soil texture for another stand of each stand type was sandy loam. The soil texture for the remaining pine stand was sandy loam, whereas that of the remaning oak stand was loam.

TABLE 2.—Forest floor mass and nutrient content and mineral soil fertility of two stand types along a river terrace in eastern Texas, USA

Forest floor	Oak stands	Pine stands	Mineral soil	Oak stands	Pine stands
Mass (Mg ha^{-1})	9.2a[1]	18.2b	C (%)	1.4a	1.4a
N (%)	0.82a	0.50b	pH	4.8a	4.8a
P (%)	0.06a	0.04b	Ca (cmol kg^{-1})	3.1a	2.6a
N (kg ha^{-1})	73.8a	104.5a	Mg (cmol kg^{-1})	1.3a	1.3a
P (kg ha^{-1})	5.5a	7.0a	K (cmol kg^{-1})	0.2a	0.1a
			Na (cmol kg^{-1})	0.1a	0.1a
			Al (cmol kg^{-1})	2.4a	1.8a
			ECEC[2] (cmol kg^{-1})	7.0a	5.9a

[1] Means for a given measurement with different letters differ ($P = 0.05$).
[2] Effective cation exchange capacity

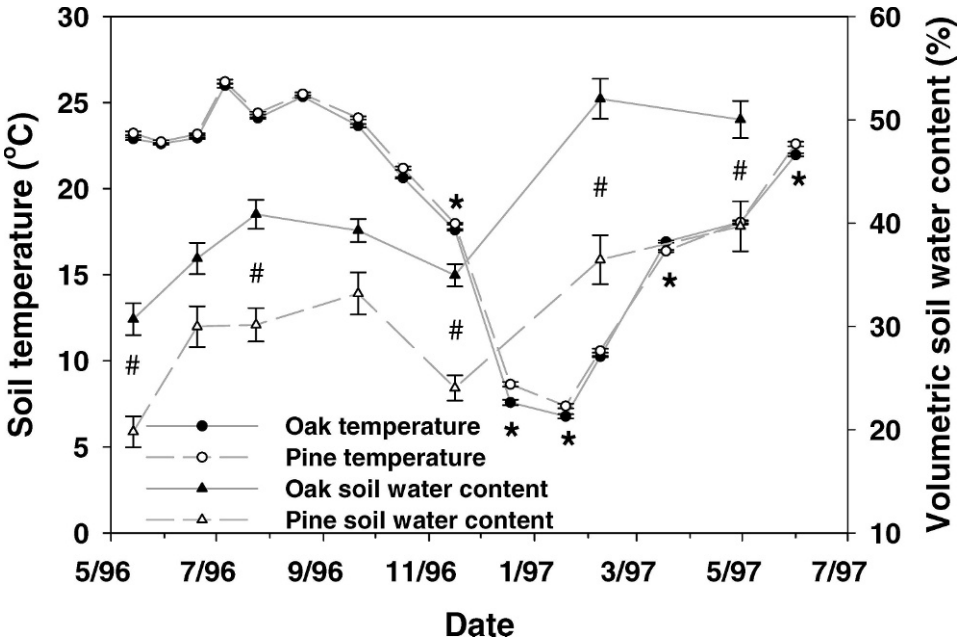

FIG. 1.—Surface (0–15 cm) soil temperature and water content for two stand types along a river terrace in eastern Texas, USA. Asterisks (*) denote a significant difference (P = 0.05) in soil temperature for an individual sampling period, whereas number signs (#) denote a significant difference in the soil water content at a given time period. Error bars represent one standard error

SOIL CLIMATE

Soil temperature followed a classical seasonal pattern for the duration of the study (Fig. 1). Overall, the pine stands maintained a higher soil temperature relative to the oak stands (P = 0.0067), but the magnitude of the difference depended upon the time of year (P = 0.0410). In general, the pine stands had warmer soil temperatures during the winter, when the oak stands had no canopy cover to slow soil cooling and when the soils were wettest (Fig. 1).

Soil water content ranged from 20 to 40% in the pine stands and 30 to 52% in the oak stands. Over the entire study period, the difference in soil water content was not significantly different (P = 0.07), but the stand type × date interaction was significant ($P < 0.04$). Analysis of the least squares means showed that the oak stand soils were significantly wetter in five of the seven time periods (Fig. 1), and on average were 11% wetter than the pine stand soils.

SOIL MICROBIAL BIOMASS

Soil microbial biomass C was not different between stand types (P = 0.6199) or between sampling periods (P = 0.2296), averaging 591 mg SMBC kg^{-1} (Table 3). Similarly, the ratio of SMBC to total soil C (x=4.2%) did not differ between stand types (P = 0.1637) and among seasons (P = 0.2305).

TABLE 3.—Seasonal soil microbial biomass C (SMBC) and the ratio of microbial to soil C for two stand types along a river terrace in eastern Texas, USA

Sampling period	SMBC (mg C g^{-1})		SMBC to soil C ratio (%)	
	Oak	Pine	Oak	Pine
Summer	587	662	4.1	4.8
Winter	532	553	3.7	4.0
Spring	585	625	4.1	4.6

SOIL CO_2 EFFLUX

Soil CO_2 efflux (Fig. 2a) varied seasonally similarly to soil temperature (Fig. 1), reaching a maximum in Sept. and a minimum in Jan. for both stand types. Overall, the oak stands had significantly higher ($P = 0.0189$) CO_2 efflux compared to the pine stands, but these differences depended upon sampling date ($P = 0.0420$). The CO_2 efflux (Fig. 2a) was similar between the stands in the cool, wet winter months but was greater in the oak stands in the warm, drier months (Fig. 1).

SOIL N MINERALIZATION

Net ammonification, nitrification, and total N mineralization did not exhibit seasonal patterns (Fig. 2b) or appear to be related to soil climate (Fig. 1). N mineralization was dominated by ammonification in both stand types, whereas nitrification was very limited in both stand types and did not differ between stand types ($P = 0.7548$). Although the overall ammonification was similar between stands ($P = 0.0673$), the stand type by sampling date was significant ($P = 0.0009$), and in the summer sampling periods of Jul.–Sept., the oak stands had over 5 times the ammonification as the pine stands.

DISCUSSION

The differences in the forest floor mass and quality were due to both differences in litterfall and decomposition rates. Although litterfall was not measured directly, we calculated it for the two stand types based on allometric equations (Harris *et al.*, 1973; Sollins *et al.*, 1973). The oak stands had about 4600 kg ha^{-1} yr^{-1} litterfall, whereas the pine stands had about 5600 kg ha^{-1} yr^{-1} litterfall at the time of this study. If we assume litterfall and forest floor mass are at steady-state, the decomposition rates (k) (Olson, 1963) based on the standing forest floor and calculated litterfall were 0.25 for the pine stands and 0.40 for the oak stands, respectively, which indicated that the pine stands have a 4 y turnover rate, whereas the oak stands have a 2.5 y turnover rate. These rates are similar to the rates reported elsewhere. Rochow (1974) found a k of 0.37 for oak stands in Missouri, and Van Lear and Goebel (1976) found a k value of 0.21 for loblolly pine.

Forest floor decomposition was faster and more complete in the oak stands due presumably to the significantly higher N and P concentrations (Table 2), assumed lower lignin concentrations (Sharpe *et al.*, 1980), and more conducive soil climate than in the pine stands. Several reviews have shown that within a given soil type and site climate, decomposition rates and limits are primarily determined by the litter quality as indexed by the lignin:N and C:N ratios (Melillo *et al.*, 1982; McClaugherty and Berg, 1987). Furthermore, the oak stands had wetter and only slightly cooler soil climates compared to the pine stands.

The microclimate in the oak stand soils was more conducive to microbial activity and decomposition, which was also shown in soil CO_2 efflux (Fig. 2a). Microbial activity in the

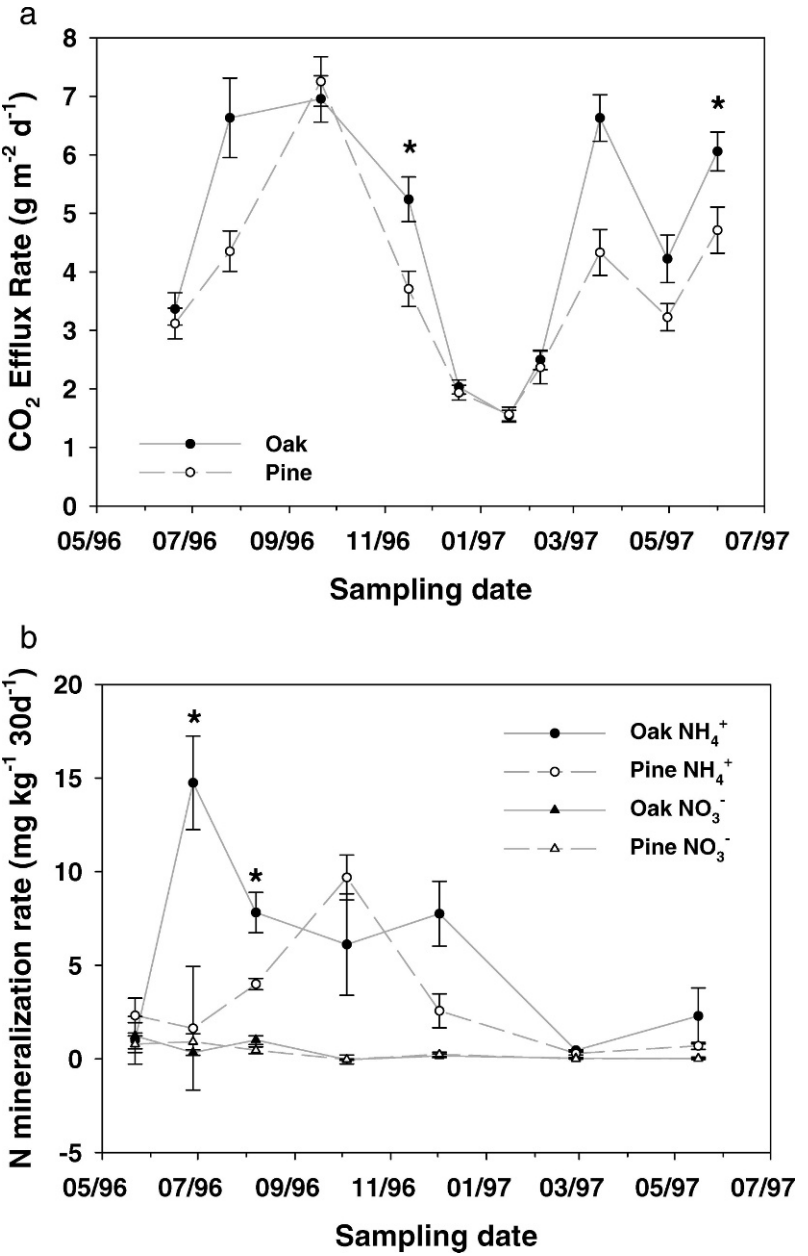

FIG. 2.—Soil CO_2 efflux (A) and surface soil (0–15 cm) nitrogen mineralization (B) from two stand types along a river terrace in eastern Texas, USA. Asterisks denote a significant difference (P = 0.05) between the means for an individual sampling period. Error bars represent one standard error

forest floor increases exponentially with increasing temperature (Edwards, 1975), and follows a $Q_{10} = 2$ (Singh and Gupta, 1977). Although the soil temperature was significantly warmer in the pine stands, the absolute difference was not great and the forest floor temperature may not have reflected the mineral soil temperature at 15 cm depth.

Soil climatic differences between the oak and pine stands were probably caused by differences in radiant heating and evapotranspiration caused by greater leaf area in the pine stands, which created warmer and drier soils compared to the oak stands. Swank *et al.* (1988) found that conversion of hardwood stands to *Pinus strobus* reduced stream outflow throughout the year and overall by about 20% due to greater leaf area, which increased evapotranspiration. However, Coile (1940) found that soil percolation was greater under loblolly pine stands than under oak stands due to greater soil mixing of the forest floor humus with the mineral soil in the pine sites. We neither measured nor observed differences in soil mixing and percolation, so we speculate that a combination of altered evapotranspiration and increased percolation may have caused the differences in seasonal water content. Differences in soil texture or bulk density between the stand types would also have affected the soil water content, but both soil texture and bulk density were similar across the stand types.

Water content affects microbial activity and decomposition in the forest floor similarly to how it affects microbial activity in mineral soil. In soil, microbial activity is highest at a water content intermediate between saturated and dry and declines in a linear fashion as water potential or aeration decreases (Skopp *et al.*, 1990). Londo *et al.* (1999) were able to fit a negative quadratic model to soil respiration rates and soil water content in a bottomland hardwood forest on the same river terrace as our study. Since the mostly intact forest floor surface layer may dry out more quickly than the soil, dry conditions may limit surface litter decomposition more than fragmented litter and humus (Waring and Schlesinger, 1985). On these sites, the pine litter was much thicker than the oak litter, and the surface litter in the pine stands was generally observed to be drier than that at the soil surface. The surface litter in the pine sites was observed to be dry even when the soil and lower litter were wet throughout the study. The oak litter was thinner and appeared to be relatively moist during all but the driest sampling period. Although the forest floors were both visually and quantitatively quite different in the Oi and Oe horizons, the Oa horizons were much more similar in appearance and were intermixed with the surface mineral soil in both stand types.

The differences in forest floor quantity and quality, between these two stand types, did not combine to affect mineral soil organic matter, pH, extractable cations (Table 2) or microbial biomass C. Certain conifers, especially *Picea* and to a lesser extent the hard yellow pines, have historically been called soil acidifiers, whereas hardwood trees tend to increase basic cations in the surface soil (Gast, 1937). Podzolization is the downward movement of cations and organic matter through a soil profile (Buol *et al.*, 2003). Podzolization can occur under both hardwood trees and conifers, but is more widely found under conifers due to the relatively high quantity and strength of organic acids produced from decomposing conifer forest floors and the relatively lower uptake of cations by conifers compared to hardwoods (Wilson and Grigal, 1995). Hardwood trees are generally thought to explore deeper soils for base cations and redistribute these nutrients to the surface soil layers in their litterfall, but actual data only partly support this hypothesis. Challinor (1968) found that after 30 y, soil Ca in the surface 13 cm below *Quercus rubra* was similar to soils under *Picea abies* (L.) Karst, *Pinus resinosa* and *P. strobus*. Within the surface 2.5 cm, however, the soils under oak had 59% greater Ca than the soils under the pines and 14% less Ca than the soil under spruce. In contrast, Lane (1975) found no difference in soil Ca or K in the

surface 15 cm 7 y after converting a hardwood stand to a loblolly pine plantation. In the current study, the relatively short-term (compared to soil development time-scale) occupation of two stand types and the inclusion of both stand types in the previous site vegetation kept any differential acidification processes from modifying extractable cations and anions in the top 15 cm. Unfortunately in both Lane's (1975) study and our study, cations were not analyzed on the forest floor or by incremental depths to determine if future changes in soil cations could be expected with continued oak vs. pine management.

The lack of a change in soil C was not surprising due to the relatively small ecosystem change (tree species) and short time period relative to the large background pool of soil C. Forest soil organic C generally changes in relatively short periods of time only in response to relatively large ecosystem perturbations, such as complete deforestation or afforestation (Lal, 2005), whereas treatments that maintain similar canopy cover generally do not alter soil C quickly (Thornley and Cannell, 2000). Finzi *et al.* (1998) found, similarly to this study, that mineral soil C content was not different beneath any of six different tree species (five hardwood and one conifer) in the 0–7.5 cm depth and only higher under one hardwood species (sugar maple, *Acer saccharum* Marsh.) compared to three of the other species in the 7.5 to 15 cm depth.

The lack of a response of the soil microbial community to the different forest floors was surprising. We expected that even though the total soil organic C was not different between the stand types, the greater forest floor biomass in the pine stands would provide substrate for a larger microbial community in the mineral soil. Apparently, the decomposition of the forest floors of both stand types provided similar amounts of active soil C to the mineral soil or the contribution of rhizosphere C to the mineral soil equalized any difference in forest floor input.

Several authors have proposed that soil organic matter development processes could be indicated by changes in the microbial biomass and the ratio of microbial C to soil C (Anderson and Domsch, 1986, 1989; Bosatta and Ågren, 1994), and Bauhus *et al.* (1998) proposed that the ratio could be used to elucidate the relative effect of tree species on soil microbial and organic matter processes. In our study, neither SMBC nor SMBC-to soil C varied between the stand types. Bauhus *et al.* (1998) and Scheu and Parkinson (1995) found that SMBC and SMBC to soil C were lower under conifers than under hardwood trees, but Sparling *et al.* (1994) found no indicators of soil organic matter change under exotic *P. radiata* plantations compared to the native *Nothofagus* forest.

Bauhus *et al.* (1998) also found that tree species significantly changed the ratio of microbial C to total organic C in the forest floor although the forest floor biomass was not changed. It is likely that although the microbial patterns in the mineral soil of this study were not different, the large differences in forest floor biomass and quality would have been observed in the forest floor microbial community. If so, these differences would account for the greater rates of soil respiration in the oak stands compared to the pine stands, although Scheu and Parkinson (1995) found less C in the forest floor microbial biomass of the conifer forest and a correspondingly lower rate of soil respiration.

The higher soil CO_2 efflux in the oak stands indicated higher rates of biological activity in the oak forests. Soil CO_2 efflux is comprised of both autotrophic (plant root) and heterotrophic (decomposers) respiration. The pine stands had 47% higher basal area than the oak stands, indicating that the root contribution to CO_2 efflux would be higher in the pine stands if patterns of belowground: aboveground allometry are similar between the stand types. Loblolly pine plantation and natural oak-hickory stands in Tennessee had root:shoot ratios of 0.28 and 0.27, respectively (DeAngelis *et al.*, 1997), suggesting that the

pine stands in this study should have had considerably higher root biomass than the oak stands. The opposite was true for soil biological activity, *i.e.*, CO_2 efflux was greater in the oak stands (Fig. 2a), indicating that heterotrophic biological activity was greater in the oak stands. Since the soil microbial biomass did not reflect this greater activity, it is likely that the forest floor microbial biomass was more active in the oak stands.

Although the oak stands had significantly more N mineralization than the pine stands, the high variability and non-seasonal patterns in both stand types makes clear interpretations difficult. Because N mineralization was greater under the oak stands during only two sampling periods, few general comments can be made regarding the impact of stand type on N dynamics. The lack of nitrification in either stand was expected. Although some loss of NO_3^- could have occurred through leaching since the in situ cores were left uncovered or through denitrification during particularly wet periods, many acidic forested soils do not exhibit high rates of nitrification except after disturbance when mineralization rates far exceed those of immobilization (Paul and Clark, 1996). Because the soils under oak approached and at times exceeded saturation and were frequently wetter than the soils under pine (Fig. 1) the soils under oak had a greater potential for denitrification than the pine sites. Although the oak forest floor was a better quality substrate than the pine forest floor, the greatest differences in CO_2 efflux rates and N mineralization rates between stand types generally occurred during sampling periods that corresponded to the same times as the greatest differences in soil water content between the stand types (Fig. 1), such as in Jul.–Aug. 1996 and Nov. 1996–Feb. 1997.

CONCLUSIONS

Soil properties and processes were different between the oak and pine stand types after 35 y of development following the harvest of the natural mixed pine-hardwood stand. Forest floor biomass was twice as great in the pine stands as in the oak stands, but the total N and P contained in the forest floor was similar due to the 50–65% higher P and N concentration in the oak stand forest floor. In addition, the surface soil under oak stands was about 10% (v/v) wetter than the soil under pine throughout most of the study, while the soil under pine was occasionally and only slightly warmer than the soil under the oak stands. Biological activity in the soil as measured by in situ CO_2 efflux and N mineralization was inconsistently higher in the oak stands, apparently in response to the higher quality litter and wetter soil conditions. Mineral soil fertility, however, had not shown any influence of stand type through 35 y. This study supports the hypothesis that converting a mixed pine-oak stand to either pine or hardwood-only stands changes soil attributes. Whether the change in these soil attributes contributes substantially to any specific soil function, such as sustained productivity or ability to be restored to mixed pine-hardwood ecosystems, remains to be seen as these stands develop over time.

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APPENDIX 1.—Woody species found in six stands of two stand types along a river terrace in eastern Texas, USA

Common name	Scientific name	Occurrence	
		Pine stands	Oak stands
American elm	*Ulmus americana* L.	Yes	Yes
American holly	*Ilex opaca* Aiton	Yes	Yes
American hornbeam	*Carpinus caroliniana* Walter	Yes	Yes
black gum	*Nyssa sylvatica* Marsh.	Yes	Yes
Carolina laurelcherry	*Prunus caroliniana* Aiton	Yes	Yes
cedar elm	*Ulmus crassifolia* Nutt.	Yes	Yes
cherrybark oak	*Quercus pagoda* Raf.	Yes	Yes
Chinese tallow	*Triadica sebifera* (L.) Small	Yes	Yes
chinkapin oak	*Quercus muehlenbergii* Engelm.	No	Yes
Devil's walkingstick	*Aralia spinosa* L.	No	Yes
green ash	*Fraxinus pennsylvanica* Marsh.	Yes	Yes
hawthorn	*Crataegus* spp.	Yes	Yes
Loblolly pine	*Pinus taeda* L.	Yes	Yes
red maple	*Acer rubrum* L.	Yes	Yes
river birch	*Betula nigra*L.	No	Yes
sassafras	*Sassafrasa albidum* (Nutt.) Nees	Yes	Yes
shagbark hickory	*Carya ovate* (Mill.) K. Koch	Yes	Yes
Shumard oak	*Quercus shumardii* Buckley var. *shumardii*	Yes	Yes
Southern crabapple	*Malus angustifolia* (Aiton) Michx.	Yes	Yes
sugarberry	*Celtis laevigaeta* Willd.	No	Yes
Southern sugar maple	*Acer barbatum* Michx.	No	Yes
sweetbay	*Magnolia virginiana* L.	No	Yes
sweetgum	*Liquidambar styraciflua* L.	Yes	Yes
tuliptree	*Liriodendron tulipifera* L.	No	Yes
water oak	*Quercus nigra* L.	Yes	Yes
wax myrtle	*Morella ceriferum* (L.) Small	No	Yes
white oak	*Quercus alba* L.	No	Yes
willow oak	*Quercus phellos* L.	Yes	Yes
winged elm	*Ulmus alata* Michx.	No	Yes
yaupon	*Ilex vomitoria* Aiton	Yes	Yes