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Legacies of agriculture and forest regrowth in the nitrogen of old-field soils

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Abstract

In the Carolina Piedmont of the USA, agricultural and forest management in the 19th and 20th centuries has greatly altered soil organic nitrogen (N). The objective of this study is to evaluate effects of two centuries of land use on N in upland Piedmont soils that are derived from the region's most common bedrock, granitic gneiss. Effects of agriculture on total soil N were examined by comparing soils cropped mainly for cotton since about 1800 with soils that remained under hardwood forest without cultivation or fertilization. Effects of forest regrowth on the N of old-field soils were examined in eight permanent plots resampled on seven occasions from 1962 to 1997 at the Calhoun Experimental Forest in South Carolina.

Together, the soil-comparative study and the four-decade field experiment illustrate how soil N in the southern Piedmont has been altered by agricultural management during the 19th and 20th centuries. Not only have agricultural harvests removed considerable N from Piedmont soils, but soil organic matter has been enriched in N by agricultural fertilization, a practice that has now contributed greatly to N cycles of many old-field forests in the region.

In old-field pine stands (*Pinus taeda*) at the Calhoun Experimental Forest, 40 years of forest growth accumulated 366 kg ha^{-1} of N (CV=9.3%) in tree biomass and 740 kg ha^{-1} (CV=9.7%) in forest floor between planting in 1957 and the last sampling in 1997. In the four decades, mineral-soil N was diminished by 823 kg ha^{-1} (CV=39.5%), a reduction in N accompanied by substantial decreases in mineralizable N as well. On the other hand, N accretion in the whole forest ecosystem averaged 5.9 kg ha^{-1} per year over this period (significant at a probability of <0.07), an accretion attributed mainly to atmospheric N deposition rather than N_2 fixation. Despite the N accretion and legacy of agricultural fertilization, the 40-year-old Calhoun forest has grown into a state of acute N deficiency. Future N research should include support for a network of long-term field studies which investigates N dynamics in forest floor and logging slash, and estimates N-use and N-retention efficiencies of fertilized pine-forest ecosystems.

Keywords: Nitrogen cycling; Biogeochemistry; Forest ecosystems; Agro-ecosystems; Long-term soil-ecosystem experiments

1. Introduction

Managing soil nitrogen (N) in the 35-million hectare pine and pine–hardwood forests of the southeastern USA is far from trivial in the 21st century. For example,

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- Acidic, advanced weathering-stage soils (Ultisols) dominate the region. Many of these soils are characterized by generally low native fertility.
- Most soils in the region are highly disturbed by 150–300 years of agriculture. A legacy of agriculture is prominent in southeastern soils as cultivation, accelerated erosion, fertilizer inputs, and crop harvests have greatly altered soil fertility.
- Southeastern forests have nearly doubled in standing wood volume between the 1950s and 1990s, as the regional agricultural landscape has changed to one that is largely forested with a mixed set of uses. The nutrient requirements of this rapidly growing forest have made large demands on soil fertility, as have the forest harvests that have accompanied forest regrowth across the region. More wood is currently harvested for industrial products from southeastern forests than from any other wood-producing region on earth, about 250 million m^3 per year (Powell et al., 1993; Jaakko Pöyry Group, 1994).
- The fraction of the southeastern forest that is most intensively managed for high fiber production relies fundamentally on management of soil fertility. A part of the new soil management includes forest N and P fertilization, a practice used in the 1990s on more than a half million hectares of high-productivity southeastern forest.

The forest N cycle, including inputs, returns, and losses, is relatively well quantified throughout the world in studies that span one to several annual cycles (Johnson and Lindberg, 1992). On the other hand, we have hardly any estimates of changes in the forest N cycle and in particular in soil N over time-scales of decades. Although computer simulations are important for understanding changes in N in ecosystems over these time-scales, they are no substitute for direct observations of soil and ecosystem change. Even small errors in annual estimates of N circulation carried over time-scales of decades magnify our uncertainties of whether soil N inputs are outpaced by removals and whether ecosystems are actually gaining or losing N. Ecosystem experiments which quantify soil change over decades of management are therefore invaluable to our perspectives of ecosystem sustainability (Jenkinson, 1991; Leigh and Johnston, 1994; Mitchell et al., 1996).

A simplified, generic N budget illustrates how managed southeastern pine forests may gain or lose N over time-scales of decades (Table 1). Nitrogen removals in timber harvest plus hydrologic leaching range from <120 to 400 kg ha^{-1} in pine forest stands harvested on a 25-year rotation (Table 1). Compensating these removals are inputs of N from atmospheric deposition plus N_2 fixation that range from 5 to 10 kg ha^{-1} per year (Binkley et al., 1989a; Johnson

Table 1
A simplified N budget for a southern-pine ecosystem managed on a 25-year harvest rotation without fertilization[a]

N flux	Low (kg ha^{-1})	High (rotation^{-1})	Comment
Inputs			
Atmospheric deposition	125	250	Estimated at 5–10 kg ha^{-1} per year (Johnson and Lindberg, 1992)
N_2 fixation	25	50	Estimated at 1–2 kg ha^{-1} per year by free-living fixers (Grant and Binkley, 1987)
Total inputs	150	300	
Removals			
Stem harvest	100	300	Wood and bark (Wells and Jorgensen, 1975; Binkley et al., 1989a; Johnson and Lindberg, 1992, this paper)
Leaching	<20	100	Estimated <0.2–1 mg l^{-1} in 40 cm per year of drainage (Wells and Jorgensen, 1975; Johnson and Lindberg, 1992; Markewitz et al., 1998)
Total removals	<120	400	
Surplus or deficit	−250	+>180	Estimated range from relatively low removals plus high inputs (surplus) to high removals plus low inputs (deficit)

[a] On individual sites, the main variations are attributed to relatively large measurement errors of inputs (that affect N inputs by both atmospheric deposition and fixation) and to the wide range of productivity in forest ecosystems (that affects stem harvest removals).

and Lindberg, 1992; Fox and Mikler, 1995; Richter and Markewitz, 1995), inputs that over a 25-year forest-rotation may amount to 150–300 kg ha^{-1}. The N balance hypothetically ranges from a surplus of 180 kg ha^{-1} to a deficit of 250 kg ha^{-1}, a range that depends substantially on ecosystem productivity, harvest utilization, and measurement errors. Table 1 helps to demonstrate why long-term soil–ecosystem experiments are important to quantifying ecosystem-N dynamics over time-scales of decades (Stone, 1975; Powers and Van Cleve, 1991; Richter and Markewitz, 2000).

In this paper, we estimate changes in soil N in a four-decade soil–ecosystem experiment (at the Calhoun Experimental Forest in South Carolina), and we place these relatively recent changes in soil N in the context of soil N as it was affected by more than a century of prior agricultural use (1800–1950).

1.1. Objectives

In the upland Piedmont of southeastern USA, changes in soil N are particularly interesting because three distinctly different ecosystems (Fig. 1) correspond to major changes in the regional N cycle over time-scales of millennia, centuries, and decades (Table 2):

- A primary forest ecosystem, mainly of oak and hickory species, that covered the upland Piedmont for thousands of years prior to 1700.
- An agro-ecosystem, that dominated the southern Piedmont region from about 1800 to the early 20th century, a system managed for cotton, tobacco, corn, wheat, and other agricultural products.
- A secondary, old-field forest ecosystem, that in the late 20th century grows on >35 million hectares, much of which was established in pine between 1920 and 1960.

Of the paper's five specific objectives, two evaluate changes in soil N associated with forest clearing and agricultural use of these soils for more than a century, two investigate changes in soil N in aggrading pine stands that grow on former agricultural fields abandoned since the 1950s, and one integrates these changes in soil N over time-scales of centuries and decades. Explicitly stated, the objectives are to estimate:

1. soil N under unfertilized and uncultivated deciduous hardwood forests, selected to represent

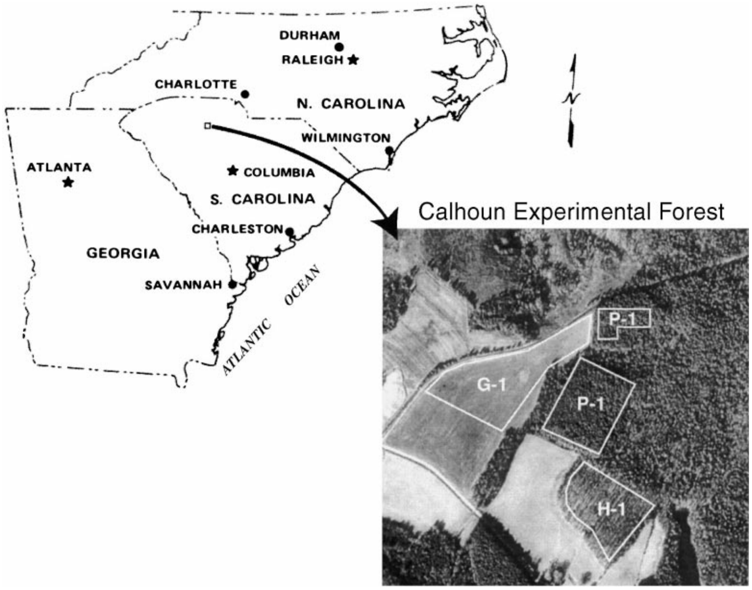

Fig. 1. Location of the Calhoun Experimental Forest in South Carolina, USA. Soil sampling plots illustrated for experimental loblolly pine, old hardwood, and hayfield (P-1, H-1, and G-1, respectively).

Table 2
Three time-scales of ecological processes that affect mineral-soil organic N in upland ecosystems of the Carolina Piedmont in the southeastern North America

Time-scale	Ecosystem	Dates	Processes controlling total N in mineral soil	
			Input	Output
Millennia	Primary forest	Pre-1700	Atmospheric N deposition, N_2 fixation, litter return, canopy leaching	Hydrologic leaching, nutrient accumulation in biomass and forest floor, fire, erosion, denitrification
Centuries	Agricultural[a]	1800 to mid-1900s	Atmospheric N deposition, N_2 fixation, diminished organic matter return, fertilizer amendments	Hydrologic leaching, fire, harvest removals, accelerated erosion, denitrification
Decades	Secondary pine forest	Mid-1900s to present	Increased atmospheric N deposition, N_2 fixation, litter return, canopy leaching	Hydrologic leaching, nutrient accumulation in biomass and forest floor, fire, harvest removals, erosion, denitrification

[a] In the early 1800s, a no-input, shifting field method of agriculture was common (Gray, 1933). After the Civil War, relatively low but increasing amounts of fertilizers were used, and more continuous field cultivation was common. By the early 20th century, fertilizers were commonly used throughout the region.

conditions close to those of the primary forest before 1700;

2. changes in soil N that are associated with long-term cotton and other agricultural uses from about 1800 to present;
3. changes in mineral-soil N in old-fields over four decades of pine-forest development;
4. N accretion in the four-decade-old pine ecosystem (biomass plus soil); and
5. a N budget of upland Piedmont soils that spans the period from pre-1800 to the present.

2. Methods

To accomplish the paper's objectives, we used a soil-comparative study and a long-term field experiment with all plots on or near the Calhoun Experimental Forest, SC, USA (Richter and Markewitz, 2000). The fifth objective combines data from both the comparative and experimental studies with information from the history of cotton cultivation in the Piedmont and across the southeastern USA (Vance, 1929; Gray, 1933; Sheridan, 1979; Mitchell et al., 1996).

2.1. The Calhoun ecosystem

The Calhoun Experimental Forest is located in southwestern Union County of upstate South Carolina (Fig. 1), at about 34.5°N, 82°W (Richter et al., 1994b). Elevation is about 300 m, and geologic material of all soils and ecosystems used in the study is part of Piedmont's most common bedrock, a partly metamorphosed granitic gneiss. Soils that have formed on broad interfluves of Piedmont's granite gneiss are typically Ultisols, one of the world's most common soil orders (Buol et al., 1989; Richter and Babbar, 1991). Surface horizons of these Ultisols derived from granitic gneiss are relatively coarse, i.e., sandy loams or loamy sands. Soil series sampled in this study include the Appling, Cecil, and Madison series, three soils that together cover about a third of the southern Piedmont from Maryland to Alabama.

The Calhoun ecosystem currently has a warm temperate, humid continental climate with long, hot summers and short, mild winters. Annual precipitation currently averages about 1250 mm (1973–1987, Whitmire, SC), annual evapotranspiration about 880 mm, and annual drainage about 370 mm (Gnau, 1992). Mean annual air and soil temperature is about 16°C. Soil temperature within the year ranges between 5 and 25°C at about 20 cm depth (D.D. Richter, unpublished data). Soil temperature and moisture regimes are thermic and udic, respectively (Buol et al., 1989; Soil Survey Staff, 1992).

On upland sites, vegetation prior to about 1800 was predominantly mixed deciduous forest. Common species of upland forests were white, black, and northern and southern red oak (*Quercus alba*, *Q. velutina*, *Q.*

rubra, and *Q. falcata*), shagbark, mockernut, and pignut hickories (*Carya ovata*, *C. tomentosa*, and *C. glabra*), and many other species. The Piedmont in the Carolinas was subdivided with royal and state grants in the mid- to late 18th century, and by the beginning of the 19th century, upland hardwood forests were being extensively cleared and converted to agricultural fields.

From about 1800 to the beginning of the US Civil War in 1861, agricultural fields in the Carolina Piedmont were managed for cotton (*Gossypium* spp.), corn (*Zea mays*), tobacco (*Nicotiniana tabacum*), wheat (*Triticum aestivum*), and other crops, almost always with a minimum of fertilization. After forests were cut and burned, large ash effects promoted a short-lived increase in nutrient bioavailability. Following several years of cropping, cotton and tobacco were often abandoned when fertilizer effects of ash diminished. Farmers typically switched to less demanding crops such as wheat before abandoning fields entirely, and moving on to "fresh soil" (Gray, 1933).

After the Civil War, agricultural fields in the Carolina and Georgia Piedmont were more continuously cropped. As systems of sharecropping and tenant farming developed (Vance, 1929), fertilization and liming became more standard farm practices (Sheridan, 1979). Cotton production and area continued to increase in South Carolina and throughout the south until the 1920s when farms throughout the region began to be abandoned in large number. Cotton in the state of South Carolina declined from over a million hectares in 1920 to less than 40 000 ha in the mid-1980s. In response, naturally regenerating pine forests greatly expanded in area during the 20th century, becoming the dominant ecosystem of many old-fields. In the late 20th century, most old-fields in the Calhoun vicinity are pine or mixed pine-hardwood forests, hayfields, or pastures.

2.2. The Calhoun soil-comparative study

To evaluate the legacy of agricultural use on contemporary soils, a soil-comparative study was designed that included 15 plots at six different sites (Table 3), all within about 10 km of the Calhoun Experimental Forest. Four land-use histories are represented in the 15 plots, a history that is based on the status of the current ecosystem, whether hardwood

Table 3
Some details of the four ecosystems from which granitic gneiss-derived soils were sampled to investigate the effects of long-term agriculture on soil properties[a]

Ecosystem	Site code	Site name	Soil series	Approximate slope (%)	Bulk density (0–7.5 cm) (Mg m^{-3})
Oak–hickory	H-1	Calhoun	Appling	2	1.17
Oak–hickory	H-2	Murphy	Madison	10	0.93
Oak–hickory	H-4	Mt. Zion Church	Cecil	2	1.06
Oak–hickory	H-5	Rt. 196	Cecil	5	1.10
Loblolly pine[b]	P-1	Calhoun	Appling	3	1.30
Loblolly pine	P-2	Murphy	Madison	5	1.14
Loblolly pine	P-3	Padgett's Creek Church	Cecil	4	1.24
Loblolly pine	P-4	Mt. Zion Church	Cecil	2	1.14
Loblolly pine	P-5	Rt. 196	Cecil	5	1.19
Loblolly pine	P-6	Greer	Appling	3	1.28
Hay	G-1	Calhoun	Appling	2	1.32
Hay	G-2	Murphy	Cecil	5	1.29
Hay	G-3	Padgett's Creek Church	Cecil	5	1.06
Hay	G-4	Mt. Zion Church	Cecil	3	1.28
Hay	G-6	Greer	Appling	3	1.40
Rowcrop	C-1	Calhoun	Appling	2	1.26

[a] The soil-comparative study was analyzed with a randomized incomplete block design. Bulk density is the mean of five samples per site.

[b] Site P-1 is the Calhoun Forest Experiment. This site was not used in the soil-comparative study.

forest, old-field pine, hayfield, and rowcrop. All plots have soils derived from granitic gneiss, that are classified as Cecil, Appling, or Madison series. Plots were located on broad interfluves and have slopes <10%. At each of the 15 plots, a minimum of five 6-cm diameter undisturbed cores were taken within a 20×20 m area with cores subdivided into 0–7.5, 7.5–15, 15–30 cm depths. Bulk density and elemental concentrations and contents were estimated from these samples.

The four hardwood forests had no visible evidence of human-associated disturbance in the early 1990s. No evidence of cutting, burning, surface erosion, or overstory pine were observed in these stands, and we assume that they have never been completely cutover, cultivated, fertilized, or limed. On the other hand, these hardwood forests (Table 3) were no doubt used for free-range grazing, and have been harvested for fuelwood and timber in the distant past. Although hardwood forest soils have also received elevated N deposition in the 20th century (now at 5–10 kg ha^{-1} per year, Richter and Markewitz, 1995), hardwood forest soils are closest to those found on these sites prior to 1800, compared to most soils in the region that have been long used for agriculture.

The 11 other plots in the soil-comparative study have been cultivated for cotton, fertilized, and limed. Six of these plots are still under agricultural management: five plots that support hay fields and one that supports corn (Table 2). All of the latter receive periodic tractor traffic and amendments of lime and fertilizer, N, P, and K. Finally, there are five plots in old-field pine stands: old cotton fields that were abandoned between 40 and 50 years ago at which time they were planted with pine seedlings that have since grown into closed forest stands. These soils were almost certainly fertilized and limed when being cropped to cotton and other row crops, and have not received fertilizers when under pine. None of the pine forests have visual evidence of fire, cutting, severe erosion, or other disturbances other than former cultivation (furrows and occasional terraces).

2.3. The Calhoun forest experiment

To examine effects of four decades of forest development on N in old-field soils, we used the Calhoun forest experiment which includes permanent plots and soil archive (Richter et al., 1999). The experimental site is located on two adjacent cotton fields, in which 16 permanent plots were planted with pine seedlings in the winter of 1956–1957, eight plots of which are used for these studies of N. Tree height and diameter were measured on four occasions in the subsequent four decades (1972, 1978, 1982, 1990), forest floor sampled in 1997, and mineral soil sampled on seven occasions (1962, 1968, 1972, 1978, 1982, 1990, and 1997). Nearly all soil samples (1962–1997) are stored in an archive at Duke University.

All trees were measured for total height and diameter at 1.4 m height (DBH) in each of eight permanent plots ($n \leq 81$ trees per plot depending on tree mortality). Biomass was estimated by a combination of allometric equations depending on age and tree component (Nelson and Switzer, 1975; Pehl et al., 1984; Shelton et al., 1984; Van Lear et al., 1986; Baldwin, 1987; Kapeluck and Van Lear, 1995). At stand age 34 in 1991, site-specific equations were also estimated to predict aboveground biomass with the harvest and dimensional analysis of 10 trees (Urrego, 1993). Foliar biomass was estimated from monthly collections of litterfall (Urrego, 1993) for 2 years. Fine-root biomass (<2 mm diameter) was estimated with 6-cm diameter soil cores (O horizon plus 0–30 cm mineral-soil depth), which were taken every 3 weeks for 18 months. Nitrogen concentrations were estimated by on-site samplings of aboveground biomass made in 1991–1992. For N in root biomass, N concentrations were taken from Van Lear and Kapeluck (1995) and Shelton et al. (1984).

Forest floor was collected in 1997 with five 30-cm diameter samples in each of the eight plots. Samples were collected in three layers which approximated the Oi, Oe, and Oa layers of the organic layer.

Mineral soils were sampled in four depths (0–7.5, 7.5–15, 15–35, and 35–60 cm) by taking ≥ 20 2-cm diameter punch-tube cores and compositing samples by depth within each of the eight plots. Bulk density was sampled with a 6-cm diameter core in the early 1990s (Richter et al., 1994b).

To estimate whole-system accretion of N over four decades, N was estimated in the whole ecosystem in 1962 and in 1997, the 40th year of growth in the planted forest. In 1962 (the year of the first mineral-soil sampling, when the stand was 5 years in age), forest floor and tree biomass were not sampled. The N in these components in 1962 was estimated to total about 80 kg ha^{-1} from 5-year-old loblolly pine forests growing in old fields in Mississippi (Switzer and Nelson, 1972), and this lack of sampling was considered to present only minor problems in our estimate of ecosystem-N accretion.

2.4. Laboratory analysis

All samples were initially air dried. Organic matter was ground with a Wiley Mill and mineral soil crushed to pass a 2-mm screen. Mineral-soil samples have been archived throughout the study (1962–1997), and biomass and forest floor samples were archived starting in the 1990s. Subsamples were oven dried at 105°C for at least 24 h to provide an oven-dry basis to the data. Total C and N in pulverized subsamples were analyzed in 1997–1998 with a Perkin-Elmer dry-combustion instrument. These results were highly correlated with Kjeldahl-N determinations of mineral-soil samples made in 1979–1980 and with N determinations made with a Leco combustion instrument in 1987. Only the 1997–1998 analyses are used in this paper. Aerobic incubations of archived mineral-soil samples were conducted at 30°C for 30 days, at which time they were extracted with 2 M KCl and analyzed for NH_4 and NO_3 by conventional colorimetry.

3. Results and discussion

3.1. Legacies of primary forest and agricultural use in modern Calhoun soils

The hardwood forest soils (Table 3), which we assume have never been cultivated or fertilized, are our closest approximations to pre-agricultural soil conditions in these Piedmont ecosystems. Total N in the upper 30-cm soil of hardwood forests (Table 4) averaged 384 μg g^{-1} and 1551 kg ha^{-1} (CV=36.4%). Soils that support hayfields or row cropped corn have higher contents of soil N (Table 4), 2337 (CV=19.5%) and 1765 kg ha^{-1}, respectively, no doubt due to long-term N fertilization. Old-field pine soils, however, have relatively low concentrations and contents of soil N (Table 4), about 996 kg ha^{-1} (CV=27.7%). Old-field pine soils have not been fertilized since they came out of cultivation 40–50 years previously. As the pine forests have grown, they have transferred considerable N from the mineral soil to biomass and O horizons, apparently depleting mineral-soil N. Mineral-soil N in the old-field pine systems may also be low in comparison to currently fertilized systems, due to the generally lower rates of fertilization prior to 1950 compared with contemporary rates.

Table 4
Total soil N and bulk densities of 0–30 cm soil (collected 1992) from the four ecosystems near the Calhoun Experimental Forest, SC, USA[a]

Depth (cm)	Hardwood, n=4	Old-field pine, n=5	Hayfield, n=5	Rowcrop, n=1
Total N (μg g^{-1})				
0–7.5	853a (37.6)	375b (12.4)	1198a (23.6)	550
7.5–15	363ab (36.3)	195a (26.6)	414b (37.4)	500
15–30	218a (49.1)	192a (45.0)	304a (18.8)	280
0–30[b]	384 (36.4)	235 (23.8)	520 (19.5)	385
Total N (kg ha^{-1})				
0–7.5	701a (41.0)	340a (11.2)	1140b (25.8)	519
7.5–15	367ab (36.4)	213a (27.0)	477b (35.4)	569
15–30	483a (50.3)	442a (45.0)	720a (18.6)	677
0–30[b]	1551a (36.4)	996a (27.7)	2337b (19.5)	1765
Bulk density (g cm^{-3})				
0–7.5	1.08a (10.7)	1.21ab (5.0)	1.27b (10.0)	1.26
7.5–15	1.36a (6.7)	1.46ab (4.3)	1.56b (9.4)	1.52
15–30	1.48a (2.1)	1.53ab (2.2)	1.58b (4.8)	1.61
0–30	1.35a (3.6)	1.43ab (3.2)	1.55b (5.5)	1.53

[a] Coefficient of variation among the plots within each ecosystem is given in parentheses. Letters within a row indicate whether means are significantly different at $P<0.05$ (rowcrop was not included in the statistical analysis).

[b] Weighted by depth and bulk density.

Table 5
Total soil C and C/N ratios of 0–30 cm of soil (collected 1992) from the four ecosystems near the Calhoun Experimental Forest, USA[a]

Depth (cm)	Hardwood, $n=4$	Old-field pine, $n=5$	Hayfield, $n=5$	Rowcrop, $n=1$
Total C (%)				
0–7.5	1.927a (23.2)	0.747b (34.0)	1.475a (19.8)	0.814
7.5–15	0.808a (34.0)	0.446b (19.1)	0.577ab (29.4)	0.698
15–30	0.394a (7.2)	0.336a (24.4)	0.479a (44.1)	0.327
0–30[b]	0.805 (24.4)	0.449 (20.2)	0.712 (20.2)	0.529
Total C (Mg ha^{-1})				
0–7.5	15.73a (29.1)	6.67b (30.5)	14.01a (22.1)	7.69
7.5–15	8.08 (40.2)	4.86 (20.6)	6.67 (26.7)	7.96
15–30	8.70a (6.6)	7.54a (24.6)	11.31a (42.6)	7.90
0–30[b]	32.5a (24.4)	19.1b (12.5)	32.0a (20.2)	23.5
Ratio C/N				
0–7.5	22.6a (28.2)	21.5a (24.4)	12.3b (10.5)	14.8
7.5–15	22.3a (29.2)	22.7a (16.9)	14.0b (22.8)	14.0
15–30	18.1a (69.0)	17.3a (30.1)	15.8a (29.9)	11.7
0–30[b]	21.0a (37.2)	19.6ab (22.0)	13.7b (17.4)	13.4

[a] Coefficient of variation among the plots within each ecosystem is given in parentheses. Letters within a row indicate whether means are significantly different at $P<0.05$ (rowcrop was not included in the statistical analysis).

[b] Weighted by depth and bulk density.

Patterns of soil organic C and soil C/N ratio contrast with that of soil N. Uncultivated soils under hardwood forests not only have relatively high concentrations of organic C (0.81% in 0–30 cm soil), they have relatively large contents of organic C, 32.5 Mg ha^{-1} (CV=24.4%) despite relatively low bulk densities (Tables 4 and 5). There is relatively low organic C in the old-field pine soils and the soil currently under cultivation (18.8 Mg ha^{-1} for old-field pine (CV=14.2%) vs 32.5 Mg ha^{-1} under hardwood). On the other hand, soils that support hayfields have similar amounts of organic C in mineral soil as those under hardwood forests (Table 5). We hypothesize that yearly cultivation for crops such as cotton oxidizes soil C, decreasing C to about 0.5% in the upper 30 cm in these systems, but that grass hayfields are able to rapidly accumulate a relatively large amount of soil C, which we attribute to relatively high soil C inputs to mineral soils and perhaps reduced decomposition of C in the limed and fertilized grass ecosystems (Richter et al., 1994a; Richter and Markewitz, 1996, 2000).

The consequence of the differential effects of land use on soil N and C can also be expressed by the soil C/N ratio (Table 5). Uncultivated and unfertilized soils under hardwood forests have an average C/N ratio of 22.8 (CV=34.3%) in the surface 30 cm soil. Nitrogen-fertilized soils in hayfields or under corn have C/N ratios reduced to <14. Soils under old-field pines, that have not been fertilized or cultivated in 40–50 years, have a C/N ratio of 19.8 (CV=24.9%), mid-way between soils under hardwoods and those soils currently being fertilized.

3.2. Depletion of mineral-soil N during secondary forest development

One of the most striking patterns of soil change observed at the Calhoun Experimental Forest has been the four-decade depletion in N in the upper 0.6 m of mineral soil (Fig. 2, Table 6). This depletion closely parallels N accumulation in biomass (Fig. 3, Table 7) and forest floor (Table 7).

Periodic tree measurements at the Calhoun indicate that N accumulation in biomass totaled 366 kg ha^{-1} (CV=9.3%) over the four decades (Fig. 3, Table 7). The rate of biomass accumulation of N averaged 17 kg ha^{-1} during the first 15 years, a substantial annual accumulation mainly due to the synthesis of the N-rich foliar canopy. Once the foliar canopy has grown fully, mainly stem wood and bark (with much lower N concentrations than foliage) continue to accumulate N. Between age 15 and 30, net accumula-

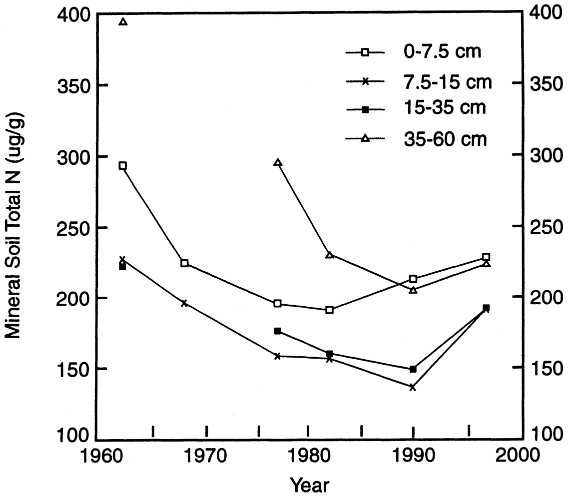

Fig. 2. Changes in total N concentrations in four layers of mineral soil at the Calhoun Forest Experiment, SC, USA (1962–1997). Means of eight permanent plots (site P-1). No samples were taken below 15 cm in 1968.

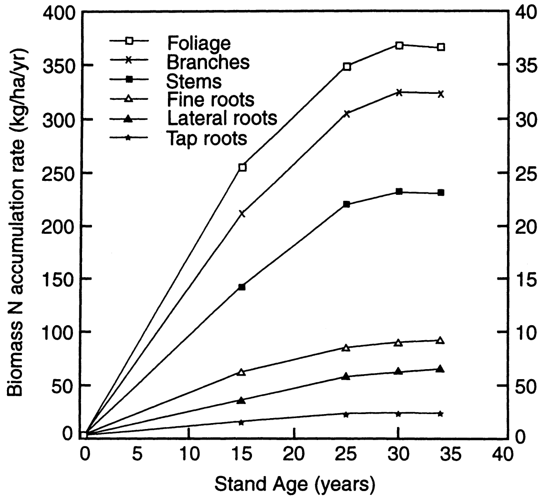

Fig. 3. Nitrogen accumulation in aggrading biomass over four decades at the Calhoun Forest Experiment, SC, USA. Estimates of mean N in biomass in eight permanent plots.

tion of N in biomass decreased to about 6 kg ha^{-1} per year, with N accumulating almost entirely in wood and bark of boles. After age 30, vegetation at Calhoun did not increase in biomass or N content (Fig. 3). Tree mortality at this period approximately compensated new biomass increment.

In addition to biomass N, forest floor heavily blankets the mineral soil at Calhoun and contains an enormous amount of N (Table 7). At age 40 (in 1997), the O horizon contained about 740 kg ha^{-1} of N (CV=9.7%). The nitrogen accumulated in biomass and forest floor thus totaled >1100 kg ha^{-1} by the mid-1990s (Table 7).

Mineral soil was the source for most of this N accumulated in biomass and forest floor, and over the four decades mineral-soil N decreased by 823 kg ha^{-1} with a CV=39.5% (Table 7). Total N in 0–0.6 m mineral soil amounted to 2687 kg ha^{-1} in 1962 (CV=15.0%) and 1863 kg ha^{-1} in 1997 (CV=16.3%). The reduction in mineral-soil N over this time was highly significant ($p<0.0001$), and was observed in all eight permanent plots (Table 6). Soil N was reduced to nearly 70% of its content in 1962.

The observed time series of mineral-soil N between 1962 and 1997 indicates that almost all of the draw down in mineral-soil N occurred during the first 25 years of forest growth (Fig. 2). The initial 25 years of most rapid transfer of N from mineral soil to biomass and forest floor have been followed by a relatively constant content of mineral-soil N from stand age 25–40 (1982–1997). Averaged throughout the upper 0.6 m of mineral soil, total N decreased from 301 μg g^{-1} (CV=15.0%) in 1962 to lows of 192, 178, and 209 μg g^{-1} in 1982, 1990, and 1997, respectively (Fig. 2).

Table 6
Depletion in total nitrogen of 0.6 m mineral soil of eight permanent plots at the Calhoun Forest Experiment, SC, USA (1962–1997)[a]

Plot	1962 (kg ha^{-1})	1997 (kg ha^{-1})	Change (kg ha^{-1})
1–8	1942.9	1357.1	−585.8
2–8	3099.0	1966.3	−1132.7
3–8	2338.9	1615.0	−723.9
4–8	2572.9	2202.9	−370.0
1–10	3013.9	1737.8	−1276.1
2–10	2933.7	2288.1	−645.6
3–10	2590.0	1902.1	−687.9
4–10	3001.5	1836.5	−1165.0
Mean	2686.6	1863.2	−823.4
Standard deviation	402.4	302.9	−325.0
CV (%)	15.0	16.3	−39.5

[a] The depletion of nitrogen was significant with a paired *t*-test at $p<0.0001$.

Table 7
Changes in total nitrogen in three ecosystem components (tree biomass, forest floor, and 0.6 m mineral soil) of eight permanent plots at the Calhoun Forest Experiment, SC, USA (1962–1997)[a]

Plot	1962 ecosystem[b] (kg ha^{-1})	1997			Ecosystem accretion[b] (kg ha^{-1})
		Biomass[c] (kg ha^{-1})	Forest floor (kg ha^{-1})	Ecosystem[b] (kg ha^{-1})	
1–8	2022.9	378.6	665.0	2400.7	377.8
2–8	3179.0	300.3	840.3	3106.9	−72.1
3–8	2418.9	359.3	711.1	2685.4	266.5
4–8	2652.9	408.6	687.7	3299.2	646.3
1–10	3093.9	343.3	673.3	2754.4	−339.6
2–10	3013.7	384.3	743.2	3415.6	401.9
3–10	2670.0	395.0	847.9	3145.1	475.1
4–10	3081.5	356.4	770.0	2962.9	−118.6
Mean	2766.6	365.7	742.3	2971.3	204.7
Standard deviation	402.4	34.04	71.9	339.73	341.9
CV (%)	14.5	9.3	9.7	11.4	167.0

[a] Ecosystem accumulation of N was significant at a $p<0.07$ by a paired t-test.

[b] Ecosystem represents the sum of nitrogen in vegetation, forest floor, and 60 cm mineral soil. In 1962, pine biomass and forest floor were estimated to contain 80 kg ha^{-1} in all plots (Switzer and Nelson, 1972).

[c] Estimated in 1991.

The depletion of N from mineral soil greatly altered the quality of soil organic matter. The C/N ratio of mineral soil increased during the four-decade period from 18.8 in the upper 0.15 m of mineral soil to 30.6 in 1990. The C/N ratio had no doubt been reduced under cotton management (pre-1955) by N fertilization and C depletion by cultivation. During the growth of the Calhoun pine forest, the C/N ratio increased as N in mineral soil was transferred to tree biomass and forest floor and C was slowly accumulated (Richter et al., 1999).

3.3. *Forest floor as a governor of the N cycle*

Because forest floor was not sampled over the life of the experimental pine ecosystem, a computer simulation that predicted ^{14}C with apparent accuracy (Richter et al., 1999) was used with N release-coefficients of Jorgensen et al. (1980) to simulate the rate of N mineralization in forest floor through four decades (Fig. 4). The model suggests that a total of 1024 kg ha^{-1} of N has been deposited on the forest floor as litterfall and throughfall during a forest's 40-year lifetime. Net N mineralization is clearly low, and was simulated to amount to only 12.1 kg ha^{-1} per year by age 40 with the Jorgensen et al. (1980) model (Fig. 4). The effectiveness with which the pine forest floor has retained (formerly) bioavailable N, can be gauged by the fact that in 1997, 740 kg ha^{-1} of N (CV=9.7%) had accumulated in the forest floor (Table 7), about 72% of simulated 40-year N inputs.

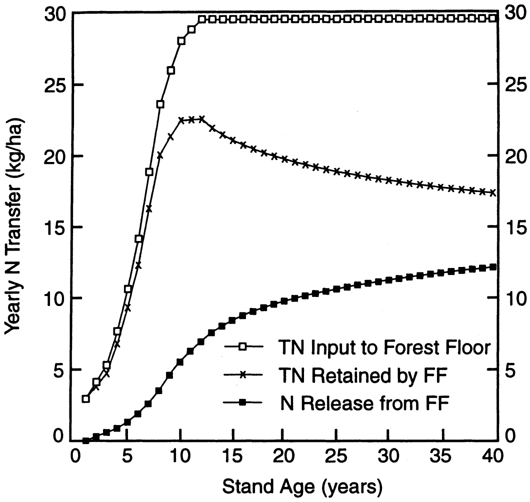

Fig. 4. Simulation of forest floor nitrogen dynamics based on mineralization coefficients of Jorgensen et al. (1980). The model simulated that 697 kg ha^{-1} of nitrogen accumulated in the Calhoun forest by 1997 compared with 740 kg ha^{-1} (CV=9.7%) that was measured. Nitrogen inputs to forest floor include litterfall plus throughfall.

The forest floor is a remarkably strong N sink and an effective governor of bioavailability of N and hypothetically the productivity of the was pine systems that was not fertilized.

3.4. Ecosystem N accretion during four decades of a re-establishing forest

Nitrogen accretion by ecosystems (soil plus vegetation) is highly significant to soil genesis, ecosystem development, and soil management, yet the rate that ecosystems gain N has high uncertainty and variability. The scientific literature is particularly intriguing on the topic (e.g., Stevenson, 1959; Jenkinson, 1971; Richards, 1973; Bormann et al., 1993). The rate that ecosystems gain N with and without N_2-fixing plants has been studied and debated for many years. *Pinus* species have figured prominently in this unsettled literature.

The Calhoun pine forest is an aggrading, N-deficient ecosystem with a tight N cycle, one that helps ensure that the ecosystem has been an effective N sink. Nitrogen inputs from atmospheric deposition and N_2-fixation are currently retained within the system, during this period in which biomass and forest floor accumulations have depleted mineral-soil N, and N leaching losses are remarkably low (Markewitz et al., 1998). This retention of inputs follows the "hypothesis" of Vitousek and Reiners (1975), that high biotic demand for N relative to supply ensures effective N retention by the ecosystem.

Based on a safe assumption that the Calhoun forest has retained most of its N inputs, the Calhoun experiment is well suited for making an estimate of N accretion and inputs from comparison of changes in total N in the 1962 and 1997 ecosystems (mineral soil, forest floor, plus vegetation) of the eight permanent plots (Table 7). In 1962, 5 years after pine trees were planted at the Calhoun forest, the ecosystem contained a total of about 2767 kg ha^{-1} of N (CV=14.5%). In 1997, the Calhoun ecosystem contained 2971 kg ha^{-1} of N (CV=11.4%) in the same eight plots. The 35-year accretion of ecosystem N totaled 204.7 kg ha^{-1}, which a paired *t*-test estimated to be significantly different from zero with a probability of <0.07. The mean annual N accretion was estimated to be 5.9 kg ha^{-1}, a modest N accretion, which we emphasize was not significantly different from 0 at $p<0.05$, although the p value is low at <0.07 (Table 7).

Despite the modest rate of N accretion, the estimated accretion is not likely to be underestimated, as the ecosystem has not lost much N during this period of reforestation. Nitrogen has not been lost by fire, as there has been no burning of the 40-year-old Calhoun forest. Moreover, for most of the life of the forest, denitrification and NO_3 leaching have likely been of minor significance to the N cycle of this unfertilized, N-deficient ecosystem.

Although some N may have been lost by leaching in the first few years after field abandonment, the pattern of soluble N concentrations in soil water in the 1990s illustrates how conservative the pine forest has been with respect to bioavailable N, and how little N has been lost to drainage water over the life of the forest. Between 1992 and 1994, concentrations of NH_4 and NO_3 averaged between 25 and 50 μmol l^{-1} in rainfall and throughfall, but once rainwater infiltrated into the soil, soluble NH_4 and NO_3 decreased to only 5–10% of concentrations found in water aboveground (Markewitz et al., 1998). Atmospheric N deposition may be up to 5–10 kg ha^{-1} per year, yet soil leaching through B and C horizons is <1 kg ha^{-1} per year. Even dissolved organic N (DON) is not apparently lost from the system in great amounts. Since leaching of DOC is <3 kg ha^{-1} per year (Richter and Markewitz, 1996), if a 10/1 C/N ratio is assumed for this DOC, leaching of DON would be <0.3 kg ha^{-1} per year.

In sum, inputs of N from atmospheric deposition, low N loss by leaching, and relatively modest rates of ecosystem-N accretion, all suggest that the 40-year pine forest has an N-accretion rate approximately equal to inputs from atmospheric deposition. Since nearly all N inputs have been retained by the pine ecosystem, N from associative N_2 fixers (Bormann et al., 1993) do not appear to contribute much N to the Calhoun pine ecosystem.

3.5. Implications of rapid soil N depletion and low ecosystem N accretion

Low bioavailability of N in the Calhoun forest is expressed by the substantial decreases in mineral-soil total N, the gradually increasing mineral-soil C/N ratios, and the substantial accumulations of N in forest floor. Low bioavailable N is also expressed by low leaf

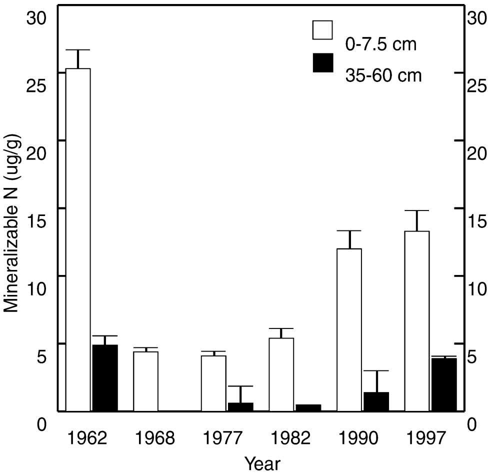

Fig. 5. Net mineralization of N in aerobic incubations (30°C) of mineral soil (0–7.5 and 35–60 cm layers) collected in permanent plots at the Calhoun Experimental Forest from 1962 to 1997.

area indices of the foliar canopies <2.5 $m^2\ m^{-2}$ when measured in the 1990s (H.L. Allen, unpublished data). Concentrations of total N in foliage of the upper crowns averaged only 1.06% N in the 1990s (Urrego, 1993), low for loblolly pine. Aerobic incubations of archived samples of Calhoun mineral soil indicate decreasing mineralizability of mineral-soil N (Fig. 5), especially during the early years of ecosystem development.

Taken together, results demonstrate not only that the ecosystem has sequestered relatively large amounts of (formerly) bioavailable N in biomass and forest floor (Table 7), but that the forest has grown into a state of acute N deficiency. Nitrogen in mineral soil is reduced to a low and generally constant content (Fig. 2), as mineralizable N in mineral soil was depleted by >800 kg ha^{-1}. Trees have increasingly met their N requirements for annual growth of foliage, wood, and bark, not so much from the continued net transfer from mineral-soil N, but from a relatively small pool of bioavailable N that includes: 24.0 kg ha^{-1}, from retranslocation of N within trees prior to leaffall (estimated from the difference between growing season foliage and litterfall); 12.0 kg ha^{-1}, from net N mineralization in the forest floor (simulated using a model derived from Jorgensen et al., 1980, Fig. 4), and 5–10 kg ha^{-1} per year, from N input in atmospheric deposition (Richter and Markewitz, 1995). We hypothesize that vegetation uses much of the N from these sources that total 41–46 kg ha^{-1} per year, but that net primary productivity (NPP) is limited by low bioavailability of N in the ecosystem.

The long-term N cycle at the Calhoun pine forest leads to three perspectives about sustaining N supply in soils that have previously been managed for agricultural crops, and that are now reforested with timber-producing trees.

From the perspective of agricultural crop harvests: From the perspective of agricultural crop harvests, the removal of N contained in cotton and corn harvests are relatively large. In the case of the Calhoun ecosystem, harvests of seed-cotton between 1935 and 1955 may have removed about 30 kg ha^{-1} of N per year (Mitchell et al., 1996). This relatively high rate of N drain was compensated by N fertilization, probably averaging 50–100 kg ha^{-1} per year during this period. Some of the N not taken up by harvested crops was accumulated in SOM and a fraction was lost as nitrate to groundwater.

From the perspective of wood harvests from the forest ecosystem: From the perspective of wood harvests from the forest ecosystem, conventional logging of the Calhoun pine forest would remove a total of about 140 kg ha^{-1} of N in stemwood plus bark at age 34 (Urrego, 1993). Expressed on an annual basis, this removal from the ecosystem is equivalent to about 4.1 kg ha^{-1} per year of N, or <15% of the annual removal rate in harvests of seed cotton. The removal rate of about 4.1 kg ha^{-1} is less than the atmospheric deposition input of about 5–10 kg ha^{-1} per year (Markewitz et al., 1998), so that even if logged, the Calhoun ecosystem may actually gain N. The greater drain of N from agricultural systems compared to forestry systems is commonly found in ecosystems throughout the world.

A caveat for modern forestry systems is that new systems of intensive management tend to increase nutrient drains compared with harvest regimes used in the past. A complete-tree harvest of aboveground biomass (foliage, branches, plus stem) might remove as much as 274 kg ha^{-1} of N from the Calhoun ecosystem (with 100% biomass utilization), equivalent to an annual N drain of 8.1 kg ha^{-1} per year. Although more intensive forest harvests of pine biomass may will increase nutrient removals, increased drain of N is likely to remain a small fraction of that with annual agricultural crops, if only because woody biomass has relatively low concentrations of N.

From the perspective of bioavailable N in forest soil: From the perspective of bioavailable N in forest soil, the relatively low rate of N drain from forest harvests does not mean that forest growth is not demanding on bioavailable N in soils. Quite the opposite is in fact the case. In the Calhoun forest, the relative balance of N supply vs demand is illustrated well by the rapid transfer of total N from mineral soil to biomass and forest floor. Although most of the N accumulated in biomass and forest floor is still within the ecosystem, such transfers of N without remineralization greatly diminish N bioavailability in the rooting zone (Fig. 5), and enhance N deficiencies that are commonly found in southern-pine ecosystems.

In the 40-year-old Calhoun forest, N that is accumulated in forest biomass and forest floor totaled 1108 kg ha^{-1}, equivalent to a mean annual accumulation rate of 27.7 kg ha^{-1} per year. This rate of accumulation is the same order of magnitude as N removal rates in seed-cotton harvests, 30 kg ha^{-1} per year (Mitchell et al., 1996). It is entirely understandable why an aggrading forest faces severe N deficiency when it has transferred >25 kg ha^{-1} per year of N from its mineral soil to biomass and forest floor over a period of 40 years.

The temporal dynamics of change are likely to be even more significant than is suggested by the mean annual rate of transfer over the four decades. Fig. 6 illustrates N accumulation in aggrading biomass based on repeated measurements and in forest floor based on computer simulations. The transfer of N from mineral soil to biomass plus forest floor peaks early in the life of the stand, but most especially for biomass. Considering that the net transfer of N from mineral soil to forest floor in Fig. 6 is modeled (Fig. 4) and not directly observed, N accumulation and mineralization in pine forest floor is a process of considerable importance to pine management. Hypothetically, massive transfers of N from mineral soil to forest floor (Figs. 4 and 6) can be manipulated by management and bioavailability of forest floor N enhanced to the benefit of productivity.

Although Calhoun forest's N demand outpaces its supply in mineral soil, it is significant that the depletion of mineral-soil N results from a transfer among ecosystem components, rather than a removal of N from the ecosystem. In contrast to agriculture, silviculture has the opportunity to manage the large pool of organic matter in forest floor and in logging slash and thereby regulate N mineralization, recirculation, and retention during forest development. An important challenge for intensive pine-forest management is to fertilize in such a way that decomposing forest floor and logging slash are transformed from strong N sink to well regulated source of N, all while minimizing N loss to drainage.

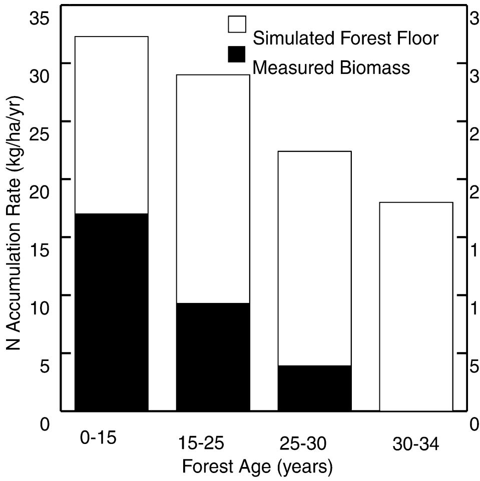

Fig. 6. Accumulation rates of N in biomass (measured) and forest floor simulated with model of Jorgensen et al. (1980) at Calhoun Experimental Forest.

Perhaps the most remarkable outcome of N dynamics in the Calhoun study is not that the pine ecosystem gained only modest amounts of new N (at 5.9 kg ha^{-1} per year) or that the pine forest floor retains so much N (749 kg ha^{-1} in 40 years), but rather that the pine forest was able to take up such a large fraction of its mineral-soil N. About 30% of the total N in mineral soils in 1962 (or 823 of 2687 kg ha^{-1}) was transferred from mineral soil and mainly accumulated in biomass and forest floor during the four decades of forest development. Since losses of N from the ecosystem were inconsequential over this period, the N-retention efficiency of the unfertilized Calhoun pine forest has approached 100% (N accumulation relative to bioavailability). An open question for forestry research is how high a N-retention efficiency can be achieved for fertilized southern pine systems.

3.6. Soil N budgets over time-scales of centuries

Hypothetical changes in total soil N from 1800 to the present are contained in Table 8. The data in the table are derived from results of the comparative-soil study of land use effects on soils (Tables 4 and 5), the Calhoun Forest Experiment (Tables 6 and 7), from related Piedmont studies (McCracken et al., 1989; Van Lear et al., 1995), and from the agricultural history of the Carolina Piedmont (Vance, 1929; Gray, 1933; Sheridan, 1979; Mitchell et al., 1996).

Table 8 emphasizes the substantial changes that have transformed soil conditions in the Piedmont over the last two centuries. We conceive of this transformation of the upland Piedmont to have proceeded through five ecosystems.

Prior to being converted to agriculture, upland Piedmont mineral soils derived from granitic gneiss probably contained about 1500 kg ha^{-1} of N in their upper 30 cm (Tables 4 and 8). Primary forests were occasionally burned by Native Americans and by lightening, transferring small amounts of N to the atmosphere due to oxidation. These losses of N were compensated by relatively low inputs from N_2 fixation and atmospheric N deposition. Hydrologic and gaseous losses were similarly low as well.

In the first half of the 19th century, the primary forest in the Carolina Piedmont was extensively cleared and burned and N demand of new crops of cotton, corn, tobacco, and wheat were met almost entirely by N mineralization of native soil organic matter and from accelerated N mineralization from inputs of forest biomass and ash. In shifting field systems of agriculture that were typical of farms in the upland Piedmont at the time (Gray, 1933), soil N was affected relatively modestly compared with the systems of agriculture that were to follow the Civil War (Table 8). Fertilizers were rarely used in the Piedmont before the Civil War (Sheridan, 1979).

In the late 19th century, continuous cultivation for cotton on upland soils became increasingly prevalent, as share croppers and tenant farmers came to cultivate large areas of the region. Nitrogen losses in erosion and via crop harvest increased greatly, and fertilizer N became a part of standard farming practices. Fertilizer

Table 8
Hypothetical N fluxes in mineral soils of five Calhoun ecosystems[a]

Flux or property	Pre-1800 deciduous hardwood forest	1800–1860 no-input cotton, field rotation	1880–1930 low-input continuous cotton/corn	1930–1955 high-input continuous cotton/corn	1955–1990 no-input, old-field planted pine
N input[b] (kg ha^{-1} per year)	1–2	1–2	25	80	5–10
N removed in harvest[c] (kg ha^{-1} per year)	0	−2 to −4	−15	−25	−4
N sequestered in biomass, forest floor (kg ha^{-1} per year)	–	+5	–	–	−20
Hydrologic loss of N[d] (kg ha^{-1} per year)	0 to −2	−2 to −4	−15	−35	<−1
Annual mineral-soil N change (kg ha^{-1} per year)	0	+1.5	−5	+20	−18
Total soil N (kg ha^{-1})	1500	1590	1340	2090	1460
Soil C/N (unitless)	22	25	18	11	18

[a] Forests were cleared in 1800, converted to cotton with shifting field cultivation without fertilizer before 1860. In the latter 19th century, fields had continuous cotton with relatively low rates of fertilizer N. From 1930 to 1955, cotton was managed with higher N inputs. In the 1950s, the field was planted in pine seedlings that have grown for four decades.

[b] Atmospheric deposition taken as 1–2 kg ha^{-1} per year prior to 1950 and 5–10 kg ha^{-1} per year thereafter. Fertilizer accounts for inputs above these rates of atmospheric deposition. N_2 fixation in all systems is taken to be minimal.

[c] Assumes minimal harvest removal of N pre-1800. Antebellum rowcropping is taken to be shifting field cultivation, one fifth the time under cotton. Cotton harvest removals of N approximate those documented in Mitchell et al. (1996). Nitrogen sequestered (or released) from aggrading (or degrading) biomass plus forest floor.

[d] Assumes leaching drainage under forest or agricultural cover of 30 or 50 cm of water, respectively, and NO_3–N concentrations of <1, <1, 2, 5, and <1 mg l^{-1}, in the five ecosystems. Fluvial erosion is taken to be minimal under forest cover. Under cultivation, accelerated erosion is taken to be about 20 Mg ha^{-1} per year, with eroded soil having total N concentrations of 500 μg g^{-1}.

inputs remained modest, however, due to marginal economics of many farms, and because fertilizer N came mainly from organic sources and from extraction of N from coal. The continuous cultivation with limited N inputs reduced mineral-soil N (Table 8).

By the mid-20th century, crop yields were enhanced by a variety of agronomic practices, not the least of which was N fertilization, strongly promoted by agronomists and extension agents throughout the region. Accompanying these increases in inputs were increased N removals in harvests plus losses of N in leaching and erosion. Despite increased throughput of N in 20th century agro-ecosystems, mineral-soil organic matter was enriched with considerable N and C/N ratios declined (Tables 4 and 8).

After abandonment of rowcrops such as cotton and the planting of pine seedlings, soil organic matter, that had been enriched in N due to agricultural fertilization, was the chief source of N for pine-forest growth. Soil organic N was mineralized and redistributed to trees and forest floors over several decades of reforestation. An important fraction of N that is cycling in old-field pine forests is derived from fertilizer applied by nearly forgotten farmers many years in the past. The pine system appears to have remarkably high N demand and capability to retain bioavailable N.

3.7. Future of N research in the southern forest

Modern pine-forest management should aim to more broadly stimulate tree growth and benefit long-term rates of N mineralization from organic matter in forest floor, mineral soil, and logging slash. Three areas for N research include:

1. to institute an efficiently run set of soil–ecosystem studies that over several decades can quantify key processes of N circulation and the sustainability of managed southern-forest ecosystems;
2. to evaluate how the strong N sink in pine forest floor, mineral-soil organic matter, and logging slash, can be transformed to well regulated N source; and
3. to estimate fertilizer-use and fertilizer-retention efficiencies, which in rapidly growing pine forests may be relatively high compared with other intensively managed ecosystems.

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