Rapid accumulation and turnover of soil carbon in a re-establishing forest

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Present understanding of the global carbon cycle is limited by uncertainty over soil-carbon dynamics[1–6]. The clearing of the world's forests, mainly for agricultural uses, releases large amounts of carbon to the atmosphere (up to 2×10^{15} g yr^{-1}), much of which arises from the cultivation driving an accelerated decomposition of soil organic matter[1–4]. Although the effects of cultivation on soil carbon are well studied, studies of soil-carbon recovery after cultivation are limited[4–11]. Here we present a four-decade-long field study of carbon accumulation by pine ecosystems established on previously cultivated soils in South Carolina, USA[7]. Newly accumulated carbon is tracked by its distinctive ^{14}C signature, acquired around the onset of forest growth from thermonuclear bomb testing that nearly doubled atmospheric $^{14}CO_2$ in the 1960s. Field data combined with model simulations indicate that the young aggrading forest rapidly incorporated bomb radiocarbon into the forest floor and the upper 60 cm of underlying mineral soil. By the 1990s, however, carbon accumulated only in forest biomass, forest floor, and the upper 7.5 cm of the mineral soil. Although the forest was a strong carbon sink, trees accounted for about 80%, the forest floor 20%, and mineral soil <1%, of the carbon accretion. Despite high carbon inputs to the mineral soil, carbon sequestration was limited by rapid decomposition, facilitated by the coarse soil texture and low-activity clay mineralogy.

Our most precise understanding of how land use affects soil carbon comes from decades-long field experiments that directly estimate soil change under controlled land-management regimes[7–11]. Although long-term soil studies are highly valued[11–15], nearly all such studies examine agricultural ecosystems; remarkably few test soil changes associated with reforestation, reclamation or natural plant succession[7,16].

One exception is a four-decade-long experiment at the Calhoun Experimental Forest in South Carolina, USA, which has documented changes in soil chemistry during pine-forest development from 1957 to 1997[7,10,16–19]. Before 1957, the Calhoun soil was cultivated for cotton and other crops for more than a century, practices that depleted soil organic matter and enhanced nutrient availability from fertilization and liming. The upper 35-cm layer of mineral soils at the Calhoun forest is coarse textured (68% sand, 15% clay), which ensures macroporosity and a highly oxidized environment. Clay minerals that are present are low-activity kaolinite with little potential to physically protect organic carbon inputs from microbial attack. Similar soils are found over extensive areas of southeastern North America and the warm temperate zone and tropics[20,21].

Soil studies conducted near the Calhoun forest suggest that from the early 1800s to the middle of the twentieth century, agricultural use (primarily for cotton, corn, hay and pasture) reduced organic carbon in the upper 30 cm of the Calhoun mineral soil by about

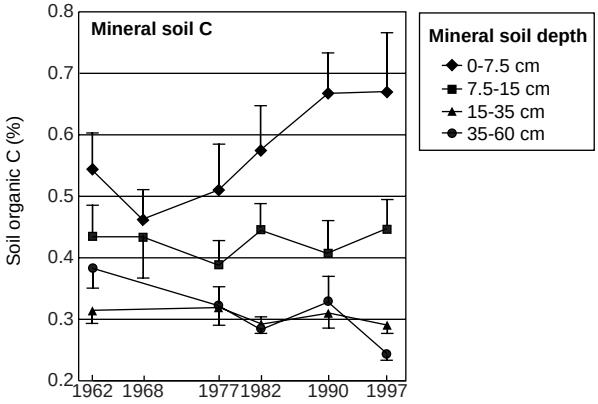

Figure 1 Mineral-soil carbon (1962–97) in eight permanent plots of the Calhoun Experimental Forest, South Carolina, USA. Plots were planted with loblolly pine seedlings in 1957 following long-term cultivation for cotton and other crops. Error bars depict the spatial variation (as standard errors) among the eight permanent plots. The randomized complete block analysis of variance indicated highly significant increases over the 40 years in soil carbon at 0–7.5 cm depth ($p < 0.001$), and decreases at 35–60 cm depth ($p < 0.05$).

1,300 g m^{-2}, or by ~40% of the carbon present at 0–30-cm depth before cultivation[7]. Here we examine recovery of soil carbon during four decades of reforestation, by using eight permanent plots that were last harvested of cotton in 1955 and were planted in 1957 with seedlings of loblolly pine (*Pinus taeda* L.). On these permanent plots, soil samples have been collected on seven occasions between 1962 and 1997 using the same sampling procedures. Nearly all soil samples are archived and available for analysis.

Since 1957, the aggrading forest accumulated ~3,925 g m^{-2} of new carbon in the soil profile—that is, the forest floor (O horizon) plus mineral soil: this represents carbon accumulation of nearly 100 g m^{-2} yr^{-1} for 40 years (Table 1). Most of the new soil carbon, 3,780 ± 251 g m^{-2} (where ±251 indicates the standard error), is contained in the forest floor that now blankets the formerly cultivated mineral soil. Only 145 ± 26 g m^{-2} of carbon accumulated in the underlying mineral soil (Table 1), about 4% of the new soil carbon. Although carbon in 0–7.5-cm mineral soil increased significantly ($P < 0.001$) between 1962 and the 1990s, there were no significant increases in soil carbon deeper than 7.5 cm (Fig. 1). In fact, carbon in the lowermost soil layer sampled, at 35–60 cm depth, significantly decreased during the 40-year study, perhaps due to slow oxidation of organic-carbon input from crop roots during the period of farming.

Because the Calhoun forest was planted in 1957, new soil carbon derived from the forest has a distinctive isotopic composition because above-ground nuclear-bomb testing in the 1950s and 1960s greatly increased $^{14}CO_2$ in the atmosphere. The fate of new forest carbon can be examined in the ecosystem because the Calhoun forest has grown entirely within the period when the concentration of ^{14}C has been elevated in both the global atmosphere and in inputs of carbon to the reforested soil.

Changes in soil radiocarbon (^{14}C) during forest development show that soil carbon has been more dynamic than might be suggested by the gradual reaccumulation of total carbon alone. A decomposition model[22] indicates that by 1965, Δ^{14}C in the forest floor approached +700‰ only one year after the ^{14}C peak in the atmosphere (Fig. 2; Δ^{14}C is defined in Methods). By the 1990s, forest-floor Δ^{14}C declined to less than +300‰, lagging the decrease in atmospheric $^{14}CO_2$ owing to incorporation of ^{14}C into slow-to-decompose, humic compounds of the acidic pine forest floor (Fig. 2).

By the 1990s, bomb-produced ^{14}C was most concentrated in the basal layers of the forest floor and the 0–7.5-cm mineral soil (Fig. 2). In 1992, Oe and Oa horizons (the middle and the lowest layers

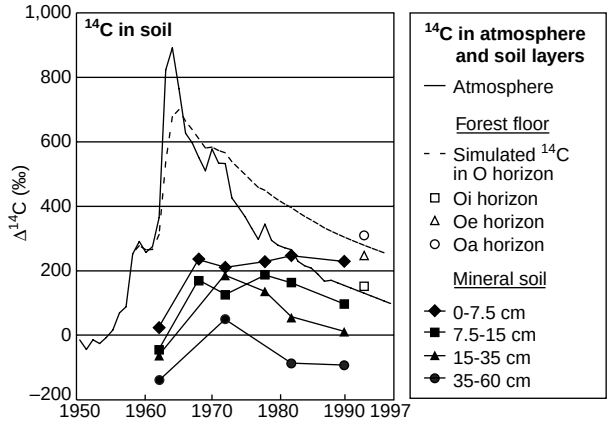

Figure 2 Time trends of ^{14}C in the Calhoun forest ecosystem. Shown are data for atmospheric CO_2 (1950–97); forest floor of Oi (L), Oe (F), and Oa (H) layers (in 1992); and mineral soil (in 1962, 1968, 1972, 1977, 1982 and 1990). Simulated changes in ^{14}C in forest floor (1957–96) are estimated from the decomposition model of Jorgensen and Wells[20] and estimates of annual litterfall input over the four decades. The Δ^{14}C for the 35–60-cm sample in 1962 was not measured, but was estimated conservatively by a soil-depth-based regression.

Table 1 Soil carbon inputs and 40-yr accretions

	Forest floor	0–15 cm	15–60 cm
Annual soil carbon input* (g m^{-2} yr^{-1})			
Annual canopy litterfall‡	245 (11.9)	0	0
Annual DOC input‡	8 (13.1)	32 (28.1)	19 (34.5)
Annual rhizo-deposition‡	37 (23.0)	63 (14.1)	26 (26.5)
Annual carbon input	290	95	45
Total soil carbon accretion*† (g m^{-2})	3,780 (18.8)	145 (50.5)	0

* Annual soil carbon inputs (in the 1990s) and four-decade soil carbon accretion in eight permanent plots of the Calhoun Experimental Forest, South Carolina, USA. Reported are means and (in parentheses) coefficients of variation in % among the eight permanent plots.
† Soil carbon accretion is estimated for forest floor over 1957–97, and for 0–60-cm mineral soil over 1962–97. Carbon accretions were statistically significant in 0–7.5-cm mineral soils, but not in 7.5–60-cm layers. Bulk densities for mineral soils are 1.52 Mg m^{-3} in 0–35-cm layers of mineral soil and 1.44 Mg m^{-3} at 35–60 cm (ref. 18).
‡ Inputs of canopy litterfall to forest floor were estimated in 1991–92. Inputs of dissolved organic carbon (DOC) were estimated in bi- or tri-weekly collections over two years (1992–94): into forest floor from DOC in canopy throughfall; into 0–15-cm mineral soil from DOC in water infiltrating from the forest floor; and into 15–60-cm soil from DOC in water draining into soil at 15-cm depth. Inputs of carbon from rhizo-deposition were estimated in 1994–95 from 50% of the live fine-root (<2-mm) biomass in forest floor, or mineral soil at 0–15 and 15–30 cm depth. Fine roots were sampled in 1994–95, every three weeks over 18 months. The 50% factor is used as a conservative estimate of carbon inputs from rhizo-deposition.

of forest floor) had Δ^{14}C values of +247.3‰ and +309.8‰, respectively. These older forest litter materials are enriched in ^{14}C derived from plant biomass synthesized during the era of elevated $^{14}CO_2$ (Fig. 2). The surficial Oi horizon (litterfall deposited within the past three to four years) had Δ^{14}C of +152.2‰ in 1992, closely comparable to that of atmospheric CO_2 during the late 1980s and early 1990s (Fig. 2).

Despite the relatively modest 40-year changes in mineral-soil carbon (Table 1), organic matter had incorporated ^{14}C throughout the entire 0–60-cm layer of mineral soil within 8 years after the atmosphere peaked in $^{14}CO_2$ (Fig. 2). By 1968, Δ^{14}C of mineral soil at 0–15-cm depth had increased to +200‰, up from −10.4‰ in 1962. By 1972, Δ^{14}C of the entire 0–60-cm mineral soil averaged +125‰, compared to less than −100‰ in 1962.

Since the 1960s, however, only mineral soil at 0–7.5-cm depth has maintained its elevated ^{14}C (Fig. 2). This surficial layer of mineral soil is accumulating carbon in an incipient A horizon that is slowly reforming under the forest following long-term cultivation (Fig. 1). But below 7.5-cm depth, decreases in ^{14}C generally parallel atmospheric decreases in ^{14}C, a pattern that indicates that forest inputs of carbon are being rapidly decomposed (Fig. 2). We suggest that the 0–7.5-cm mineral soil continues to receive ^{14}C from relatively recalcitrant and enriched ^{14}C compounds that mainly reside in the lowest layers of the forest floor (Fig. 2).

To understand better these dynamics, we estimated carbon inputs to soils in the 1990s from three main processes: canopy litterfall, rhizo-deposition (fine-root sloughing and turnover), and hydrological leaching of dissolved organic carbon (DOC) from several sources.

Inputs of carbon to the forest floor in the mid-1990s totalled ~290 g m^{-2} yr^{-1} (Table 1), most of which was from canopy litterfall, although smaller amounts were derived from turnover of fine roots[23] and the DOC in canopy throughfall. The forest's 40-year accretion of forest-floor carbon, 3,780 g m^{-2}, is about 13 times greater than current annual input (Table 1). Accumulation of forest-floor carbon is attributed mainly to complex, acidic, and recalcitrant compounds derived from the coniferous leaf litter. The forest floor is classified as an acidic mor, perched atop the mineral soil, with relatively minimal mixing by soil animals of solid organic material with mineral soil below[7].

Inputs of carbon to the 0–15-cm layer of mineral soil totalled ~95 g m^{-2} yr^{-1}, much of which was from rhizo-deposition, although a substantial fraction was derived from DOC in leachates from the forest floor (Table 1). Even with carbon input estimated conservatively (Table 1), long-term soil carbon accumulation (145 g m^{-2}) is only 1.5 times that of estimated annual input in the 1990s. The short residence time for carbon input to mineral soils is notable[24]. Carbon inputs to surficial mineral soil in fine-root biomass and DOC (Table 1) are readily decomposed, as they have little protection from adsorption to organophilic clays in these surface soils with sandy loam textures[25,26].

From an ecosystem perspective, this aggrading forest is a strong carbon sink. Accumulation of carbon is especially pronounced in tree biomass and the forest floor relative to that in mineral soil. During the growth of this forest, trees accumulated 14,060 g m^{-2} of carbon (between 1957 and 1990), compared with 3,780 g m^{-2} in the forest floor (1957–97) and 145 g m^{-2} in surficial mineral soil (1962–97). Annual carbon accretions thus averaged about 426, 94 and 4 g m^{-2} in the three ecosystem components, respectively.

The overall pattern of carbon sequestration suggests a low carbon-storage potential for mineral soils compared to that in biomass and forest floor; a similar conclusion has been reached from a review of soil-carbon gains under primary vegetative successions[6]. Yet in comparison to other forested soils recovering from previous cultivation, the mineral soil at the Calhoun forest seems to be relatively slow to recover organic carbon. Previous estimates of mineral-soil carbon gains under forests[4,11] range from 21 to 55 g m^{-2} yr^{-1}, while soils at the Calhoun forest gained carbon at 4.1 g m^{-2} yr^{-1} (Table 1).

Although changes in soil carbon are not easy to estimate, the Calhoun experiment provides an approach for making these estimates: especially useful are its well replicated permanent plots, extensive within-plot composite sampling, and soil archive. The main factors driving relatively low carbon accumulations in Calhoun mineral soils are coarse soil texture, low soil surface area, low-activity clay mineralogy[26], and warm and humid climate. A network of long-term soil-ecosystem experiments similar to that at the Calhoun, at sites that encompass a range of controlling variables of soil and ecosystem carbon, would greatly facilitate future modelling and management of the carbon cycle[11,16]. □

Methods

Research area and field experiment. The Calhoun Experimental Forest is one of the world's longest running experiments in which forest-soil properties are measured periodically in replicated permanent plots with all soil samples archived.

The research area is located at 34.5° N, 82° W. Annual precipitation averages 1,170 mm (1950–87) and temperature 16 °C. In the early 1800s, primary deciduous forests at the site were cleared, mainly to grow cotton, and the site was managed for row crops, hay and pasture until the mid-twentieth century[7,16]. Soils are acidic Ultisols, classified as the Appling series (fine, kaolinitic, thermic Typic Kanhapludults). The Appling soil is a common soil of southeastern North America, and is formed from granitic gneiss, the bedrock from which about half the soils in the southern Piedmont region are derived.

In 1957, 16 permanent plots were installed on two cotton fields at the Calhoun Experimental Forest, eight of which are used in these carbon analyses. The mineral soils of these eight plots were sampled in 1962, 1968, 1972, 1978, 1982, 1990 and 1997. At each collection, each plot was sampled at least 20 times with a 2-cm-diameter punch tube in a systematic random fashion at four soil depths: 0–7.5, 7.5–15, 15–35 and 35–60 cm. Within each plot, the ⩾20 samples per soil depth were composited, that is, in one sample per depth.

Soil archive, radiation and total carbon. The Duke Soil Archive stores air-dried soil samples at room temperature in sealed glass containers. Total soil carbon was analysed in powdered samples with a Perkin-Elmer CHN combustion instrument. Radiocarbon was measured by accelerator mass spectrometry (AMS) on graphite targets prepared from soil organic matter and is reported as $\Delta^{14}C$, the per mil deviation of $^{14}C/^{12}C$ compared with a decay-corrected oxalic acid standard[27]. Positive values of $\Delta^{14}C$ indicate presence of bomb-produced ^{14}C, and negative values indicate predominance of old soil organic matter with ^{14}C that has experienced significant radioactive decay (half-life is 5,730 yr). Radiocarbon was estimated using AMS of composite samples made from soil from the eight plots at each depth. Analysis of variance and means separation tests were used to test effects of time on soil carbon accumulation.

Soil carbon inputs. To estimate carbon inputs to soils, carbon in litterfall, fine roots, and soil water were estimated. Litterfall was sampled in each of the eight permanent plots with five collectors (each 0.72 m^2 in area) per plot. Canopy litterfall was collected monthly during 1991–92[28].

Fine roots were sampled volumetrically using a 6-cm-diameter corer that collected undisturbed cores of O horizon and mineral soil from 0–15 and 15–30 cm depths. Soil cores were taken every three weeks for 18 months in 1994–95. Samples were returned to the laboratory where fine roots (<2-mm) were separated from soil by wet-sieving and hand picking. Live roots were separated from dead, and the former were ashed to estimate carbon contents (taken as half the loss on ignition). Only the live fraction of the fine roots is reported here, and carbon inputs from fine-root turnover were simply estimated as 50% of live fine-root carbon in forest floor, or mineral soil at 0–15 and 15–30 cm depth. This factor (50%) is taken to be a conservative estimate of carbon inputs from rhizo-deposition.

DOC was determined in atmospheric precipitation (wet deposition), canopy throughfall, and solutions draining forest floor and several depths of mineral soils to 60 cm (ref. 19). Wet-only precipitation was collected by an Aerochem Metric sampler. Throughfall was collected in three bulk precipitation collectors in each of 8 plots using 16-cm-diameter funnels that were continuously open. Gravitational lysimeters were used to collect water from below O horizons and at 15-cm depth. Tension lysimeters of porous Teflon-quartz design collected solutions at 60-cm depths. Solutions were collected every two or three weeks over two years, 1992–94, and solutions were estimated for DOC concentration by combustion and infrared analysis, after purging solutions of CO_2 and H_2CO_3 by acidification and sparging with N_2 gas.

Received 8 January; accepted 4 May 1999.

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Acknowledgements. We thank P. Heine, N. Bethala, S. Buol, R. Christman, M. Hofmockel, V. Jin, J. Raikes, B. Megonigal, K. O'Neill, W. H. Schlesinger, J. Swanson and S. Zheng for contributions to this work. The Calhoun Experimental Forest was supported by the USDA Forest Service, Duke University, the Ecosystems Program of the NSF, and the National Research Initiative Ecosystems and Soils Programs of the USDA.

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Cretaceous age for the feathered dinosaurs of Liaoning, China

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The ancient lake beds of the lower part of the Yixian Formation, Liaoning Province, northeastern China, have yielded a wide range of well-preserved fossils: the 'feathered' dinosaurs *Sinosauropteryx*[1], *Protarchaeopteryx* and *Caudipteryx*[2], the primitive birds *Confuciusornis*[3] and *Liaoningornis*[4], the mammal *Zhangheotherium*[5] and the reportedly oldest flowering plant, *Archaefructus*[6]. Equally well preserved in the lake beds are a wide range of fossil plants, insects, bivalves, conchostracans, ostracods, gastropods, fish, salamanders, turtles, lizards, the frog *Callobatrachus*[7] and the pterosaur *Eosipterus*[1,8]. This uniquely preserved assemblage of fossils is providing new insight into long-lived controversies over bird–dinosaur relationships[1,2], the early diversification of birds[3,9,10] and the origin and evolution of flowering plants[6]. Despite the importance of this fossil assemblage, estimates of its geological age have varied widely from the Late Jurassic to the Early Cretaceous. Here we present the first $^{40}Ar/^{39}Ar$ dates unambiguously associated with the main fossil horizons of the lower part of the Yixian Formation, and thus, for the first time, provide accurate age calibration of this