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Soil carbon dynamics in regrowing forest of eastern Amazonia

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Abstract

The future flora of Amazonia will include significant areas of secondary forest as degraded pastures are abandoned and secondary succession proceeds. The rate at which secondary forests regain carbon (C) stocks and re-establish biogeochemical cycles that resemble those of primary forests will influence the biogeochemistry of the region. Most studies have focused on the effects of deforestation on biogeochemical cycles. In this study, we present data on the recuperation of carbon stocks and carbon fluxes within a secondary forest of the eastern Amazon, and we compare these measurements to those for primary forest, degraded pasture, and productive pasture. Along a transect from a 23-y-old degraded pasture, through a 7-y-old secondary forest, through a 16-year-old secondary forest, and to a primary forest, the $\delta^{13}\text{C}$ values of soil organic matter (SOM) in the top 10 cm of soil were -21.0 , -26.5 , -27.4 , and -27.9% , respectively, indicating that the isotopic signature of SOM from C3 forest plants was rapidly re-established. The degraded pasture also had significant inputs of C from C3 plants. Radiocarbon data indicated that most of the C in the top 10 cm of soil had been fixed by plants during the last 30 years. Differences in soil C inventory among land use types were small compared to uncertainties in their measurement. Root inputs were nearly identical in primary and secondary forests, and litterfall in the secondary forest was 88% of the litterfall rate of the primary forest. In contrast, the secondary forest had only 17% of the above ground biomass. Because of rapid cycling rates of soil C and rapid recovery of C fluxes to and from the soil, the below ground C cycle in this secondary forest was nearly identical with those of the unaltered primary forest.

Keywords: Amazonia, carbon-13, carbon-14, forest, soil

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Introduction

Large areas of forest in Amazonia have been replaced by pasture in recent decades (Skole & Tucker 1993). Depending on the type of management, pasture may remain active or become degraded, with the growth of secondary forest, locally called 'capoeira' (Buschbacher *et al.* 1988; Uhl *et al.* 1988). Serrão & Toledo (1990) estimated that half of the area cultivated with pasture in the Amazon ($100\,000\text{ km}^2$ – $120\,000\text{ km}^2$) is degraded land, which has less carbon in above-ground biomass than the original forest vegetation, and in which recovery

to the original forest state may occur only with difficulty (Buschbacher *et al.* 1988). As the biomass associated with pastures and secondary growth forest is always smaller than the original forest, the tropical regions of the world are considered to be a net source of CO_2 to the atmosphere due to deforestation in the last two decades (Houghton 1990). If secondary forests are allowed to regrow, however, a significant C sink could develop.

The role of tropical soils in the carbon balance after land-use changes is poorly understood. In Amazonia, soil C stocks to 1 m depth have been estimated to be 47 Gt (Moraes *et al.* 1995). Consequently, small changes in this large carbon reservoir may be fundamental to the carbon dynamics of the region. The degree to which changes in soils will play a role in regional C dynamics depends on

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how much of the C stored in soils is in a form that will respond quickly to land-use change, and how much is stable carbon that does not change with land use. It has been suggested that soil fertility may depend on the faster cycling organic matter pools (Tiessen *et al.* 1994). It is therefore important to determine the dynamics of soil C in tropical ecosystems.

Several studies on the effects of land-use change on soil C dynamics have been conducted recently in tropical regions, mostly in Brazil (Choné *et al.* 1991; Martins *et al.* 1991; Fernandes 1993; Davidson *et al.* 1995; Trumbore *et al.* 1995; Moraes *et al.* 1996) and one in Costa Rica (Veldkamp 1994). Generally these studies considered only the initial forest and pastures with different ages, without considering the subsequent secondary forest regrowth. Although there is considerable variation in the results of these studies, in general, where pasture productivity was high in well-managed pastures, soil C stocks increased, and where pasture productivity declined in degraded pastures, soil C stocks declined.

The objective of this research was to determine the rate at which carbon fixed by the vegetation of a secondary forest in the eastern Amazon accumulates in the soil. We used carbon concentration and soil density in order to calculate soil C stocks under primary and secondary forests, and pastures. To aid in determining soil C dynamics, we separated soil organic matter by density into components with faster and slower turnover times. Carbon inputs to and losses from the soil were estimated from measures of litterfall, root turnover, and CO₂ emissions from the soil. In addition we used measures of stable and radioactive carbon isotopic composition in organic matter and soil CO₂ to address the origin of the soil organic matter (SOM) and its rate of cycling, respectively.

Site description

The study was conducted in 1992–93 at Victoria Ranch, which is a typical ranch located near the city of Paragominas (2°59' S; 47°31' W), in the south-east part of the Brazilian state of Pará, eastern Amazon. The mean annual precipitation is 1750 mm, which is less than the Amazon average of 2200 mm. There is a pronounced dry season from June to November, when less than 250 mm of rain falls, which is typical of the eastern half of the Amazon Basin. Soil in the area is classified as 'Latossolo Amarelo' in the Brazilian soil classification, equivalent to Haplustox in the USDA Soil Taxonomy. The undisturbed forest remains evergreen in spite of the severe dry season due to the existence of deep roots extracting water stored deep in the soil (Nepstad *et al.* 1994).

The forest in our study area was cut and pasture established in 1969 with *Panicum maximum* and later with

Brachiaria humidicola. The subsequent fate of these pastures has varied. Some have remained active pasture with only periodic burning up to 1992–93, when we sampled. We refer to these as degraded pasture, since fertility is low and pasture grasses are mixed with regrowing trees and shrubs. Other pastures were maintained for a few years, then abandoned to secondary forest regrowth. Finally, some of the degraded pastures were disked, fertilized and replanted with *Brachiaria brizantha*, a highly productive grass, in 1987. This land-use type, which we refer to as managed pasture, has been suggested to sequester significant amounts of carbon due to increased root biomass (Fisher *et al.* 1994).

We report data from two kinds of sampling undertaken at Victoria Ranch. To study changes in total carbon stocks and fluxes among different land-use types, we sampled 2–3 soil pits to a depth of 8 m for each of four land uses: primary forest, degraded pasture, managed pasture and secondary forest (degraded pasture abandoned in 1976). Data collected at these sites include C inventory and isotopes in soil organic matter to 8 m depth, above- and below-ground biomass, root production (Nepstad *et al.* 1995), CO₂ emissions and CO₂ concentrations and isotopes measured in the soil atmosphere. Some of these data were reported previously in Trumbore *et al.* (1995) and Davidson & Trumbore (1995); we present them here for comparison with new data from secondary forests. Because of the large amount of variability in the 0–10 cm soil layer, we composited 8 cores collected around each pit. Samples from greater depths in the soil pits were collected after augering at least 1 m into the side of 3 forest, 3 closed canopy secondary forest, 2 managed pasture and 2 degraded pasture sites.

To study variability in C and C isotopes in the uppermost part of the soil, we collected soil cores (0–10 cm) along a 600-m transect reflecting the typical mosaic of vegetation formed in the eastern Amazon after forest clearing. The transect covers four land use types. A degraded pasture planted with *Panicum maximum* in 1969 dominated the first 75 m of the transect. This degraded pasture was burned four or five times and cattle were excluded from it in 1984. The next part of the transect had vegetation locally called 'capoeira aberta' (open secondary forest, consisting of a mixture of grass, woody shrubs, vines and treelets) extending between 75 m and 235 m. This area remained pasture from 1969 to 1985, after which a typical forest vegetation was allowed to regrow. An area that was abandoned slightly earlier, in ≈1976, extended from 235 m to 435 m. Here trees were thicker and bigger, the biomass of woody shrubs increased, and grasses were almost undetectable. This type of vegetation is locally called 'capoeira fechada' (closed secondary forest), and is in the same stand as the

soil pits for secondary forest. Finally, the original forest (undisturbed except for edge effects) comprised the 435 m to 600 m portion of the transect. Surface soil samples (0–10 cm depth after litter removal) were collected every 30 m along the transect. In total, we collected 3 samples from degraded pasture; 5 from open secondary forest; 7 from closed secondary forest and 6 from forest. The managed pasture land use type was not included in the transect.

Methods

Soil C inventory and C isotopes

Soil samples were sieved to <2 mm, and a portion ground for bulk soil analysis. The remaining <2 mm soil was separated by density into fractions <2 g cm⁻³ (low density fraction) and >2 g cm⁻³ (high-density fraction) using sodium polytungstate solution. The low-density fraction is composed mainly of relatively undecomposed vascular plant material and charcoal. The high-density fraction represents a mixture of labile and refractory material associated with the soil mineral phase. (For details of the analytical procedure see Trumbore 1993.)

Our experience has shown that the high-density fraction of C (>2 g cm⁻³) isolated from SOM is not homogeneous with respect to turnover, but instead is a mixture of more rapidly and more slowly cycling components. We applied an acid-base-acid hydrolysis procedure (0.5 N HCl–0.1 N NaOH/0.1 N Na-pyrophosphate–6 N HCl; see Trumbore & Zheng 1996, for procedural details) and measured C and ¹⁴C content in the unhydrolysed residue for forest soils to further isolate the refractory component of soil organic matter.

Soil organic carbon and nitrogen concentrations were determined in the bulk soil samples and in organic matter fractions by combustion of organic carbon to CO₂ and measurement in a Carmograph device, or using a Fisons NA1500 elemental analyser. No carbonate is present in these soils.

Sample preparation for stable isotope analysis was done through combustion with CuO in evacuated Pyrex tubes. Isotope measurements were performed with a Micromass 602 E mass spectrometer fitted with double inlet and double collector systems. Results are expressed in $\delta^{13}\text{C}$ relative to the PDB standard, defined as:

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}} - R_{\text{std}}}{R_{\text{std}}} \right) \times 1000, \quad (1)$$

where R is the ratio $^{13}\text{C}:^{12}\text{C}$

Samples were analysed at least in duplicate with a maximum difference of 0.3‰ between replicates.

Radiocarbon ¹⁴C was measured in an accelerator mass spectrometer at the Lawrence Livermore Laboratory. graphite targets were prepared from soil samples according to standard methods (Vogel 1992). The ¹⁴C content is expressed as $\Delta^{14}\text{C}$ (where sample is corrected to $\delta^{13}\text{C} = -25\text{‰}$) and is estimated according to the following equation:

$$\Delta^{14}\text{C} = \left(\frac{A_{\text{sample}} - A_{\text{std}}}{A_{\text{std}}} \right) \times 1000. \quad (2)$$

Positive values of $\Delta^{14}\text{C}$ indicate the presence of ¹⁴C produced by atmospheric detonation of atomic bombs (bomb carbon) and negative values indicate that ¹⁴C had undergone significant radioactive decay (the half life of radiocarbon is 5730 years).

Carbon stocks were calculated by multiplying the respective carbon concentration times the soil bulk density and by interval depth. Bulk density was measured in the pit samples only; we assumed bulk density values for the 0–10 cm transect samples, equalled the average bulk density for the 0–10 cm depth interval in the pits representing the same land use. For surface samples there was a correction in the soil density due to the soil compaction in the pasture and secondary forest, for details see (Davidson & Ackerman 1993; Trumbore *et al.* 1995; and Veldkamp 1994). Bulk density in the 0–10 cm increased from $\approx 0.96 \text{ g cm}^{-3}$ in forest to 1.01 g cm^{-3} in 'capoeira' and to 1.12 g cm^{-3} in degraded and managed pastures, below this layer the value of bulk density is almost the same for all land cover soils and around 1.30 g cm^{-3} (Trumbore *et al.* 1995).

Plant C stocks and production

Above-ground biomass for the primary forest was measured by Nesptad (1989). We estimated the above ground biomass of the 16-y-old secondary forest (closed 'capoeira') by measuring the heights and diameters at breast heights (dbh) of all trees and lianas (5 cm dbh in ten 5 × 5 m plots, then calculating biomass using the allometric equations of Uhl *et al.* 1988). The biomass of the smaller trees and lianas was estimated from subplots. The degraded pasture estimate was made by harvesting, weighing in the field, and determining moisture content, of all of the above-ground biomass in five 5 × 5 m plots located within the areas of the degraded. The estimate of the managed pasture above ground biomass was made by harvesting, weighing and determining moisture content of all of the above-ground biomass in 30 1 × 0.5 m plots located along randomly placed transects.

Root production rates are based on assuming annual turnover of fine live roots (0–2 mm). Determination of root biomass was described in Nepstad *et al.* (1994) and is based on separation of roots from known volumes of soil during pit digging. Values used here are based on collections in both wet and dry seasons. Litterfall data are annual averages based on monthly collections in 0.5×0.5 m litterfall traps in primary and secondary forest ecosystems. Pasture data are based on clipping dead plant components.

Soil CO₂

Fluxes of CO₂ were measured using a dynamic chamber technique, with increasing CO₂ concentrations in the chamber headspace monitored by a LiCor infrared gas analyser. Concentrations of CO₂ in the soil atmosphere were measured using the LiCor analyser as described in Davidson & Trumbore (1995). We report annual CO₂ flux data that are averages of monthly measurements at 2–3 pits per land use type, with eight chambers measured at each pit. Soil gas CO₂ was measured less frequently, but showed little variation except in the surface meter.

Samples for carbon isotope measurements of soil CO₂ were collected from soil gas tubes inserted in the pit wall using pre-evacuated canisters (electropolished aluminium, 500 cm³). The CO₂ was purified from the air collected by concentrating it in the lab on molecular sieve (Bauer *et al.* 1992). Purified CO₂ was analysed directly on the mass spectrometer for ¹³C or reduced to graphite targets for accelerator mass spectrometer (AMS) analysis at Lawrence Livermore. No correction for N₂O has been made for the ¹³CO₂ measurements; N₂O mixing ratios may reach 1000 ppb in the soil atmosphere.

Partitioning soil carbon using ¹³C

The change of vegetation accompanying conversion of forests to pastures involves a shift in the ¹³C signature of organic matter inputs to the soil. Primary and secondary forest vegetation fix carbon through the predominantly C3 photosynthetic pathway, while tropical grasses used in pastures are C4 plants. A simple mass balance approach is widely used to determine what fraction of the soil carbon is stable (largely C3 carbon remaining in the soil after years to decades after conversion to pasture) or labile (derived from recent C4 plant inputs) (Vitorello *et al.* 1989; Cerri *et al.* 1991)

$$\%C3 * (\delta^{13}C3) + \%C4 * (\delta^{13}C4) = 100 * (\delta^{13}C_{\text{sample}}). \quad (3)$$

This approach assumes that the end member forest and pasture are pure C3 or C4 components.

Partitioning soil carbon using ¹⁴C

Radiocarbon data may also be used to determine C that is of recent origin from that which have been stabilized in soils over a long time period. Carbon originally fixed from the atmosphere over the past 30 years will reflect the influence of ¹⁴C produced by atmospheric weapons testing, and will have positive $\Delta^{14}C$ values. In contrast, stable carbon will not be influenced to a great degree by recent changes in atmospheric ¹⁴C, but will reflect the residence time of C in organic matter by the degree to which ¹⁴C has been depleted compared to pre1950 atmospheric levels (negative $\Delta^{14}C$ values).

Turnover times for organic matter fractions may be estimated using a time-dependent model, assuming the pool of organic C under consideration is homogeneous and at steady state. The $\Delta^{14}C$ of C in year t is:

$$R^{14}C(t) = kR^{14}C_{\text{atm}}(t) + R^{14}C(t-1)(1-k-\lambda_{14}C), \quad (4)$$

where R is the fraction modern of ¹⁴C ($\Delta^{14}C/1000 + 1$), k is the rate constant for decomposition and $\lambda_{14}C$ is the decay constant for radioactive decay of ¹⁴C, and $R^{14}C_{\text{atm}}(t)$ is the radiocarbon activity of C inputs to the soil in year t (presumed here to equal that of the atmospheric $\Delta^{14}C$). In some cases, two different k -values will give the same $\Delta^{14}C$ in organic matter in 1992. In such cases, knowledge of the C fluxes into and out of the soil will constrain the k -value (Trumbore *et al.* 1995; Townsend *et al.* 1995).

Results and discussion

Ecosystem C stocks and fluxes

Carbon stocks, fluxes and isotope data derived from measurements at soil pits are compared for primary forest, secondary forest – ‘closed capoeira’, managed and degraded pasture in Table 1. The C inventory in above-ground biomass is greatest in the forest, which stores ≈ 30 times more C than degraded pasture. Managed pasture has slightly less above-ground biomass than degraded pasture, and secondary growth forest (regrowing at this site since 1976) is roughly 17% of the original forest value. The value for biomass in Table 1 is in accord with that of a 10-y-old secondary forest located in the same region (Guimarães 1993).

Litterfall and CO₂ efflux follow the same trends but with smaller difference between forest and closed capoeira compared with degraded and managed pastures (Table 1). Above-ground litterfall in the degraded pasture is only 31% of the rate observed in primary forest. Litterfall in secondary forest has recovered to slightly more than 84% of forest values (Table 1). Root inputs vary with soil depth, with 80–95% of inputs in the upper metre of soil. Highest inputs are found in managed pasture, and lowest values in degraded

Table 1 Values of selected parameters for soils under different land-covers

	Degraded pasture	Managed pasture	Closed Capoeira	Forest
Above-ground biomass (MgC ha ⁻¹)	4	3	22	132
Litterfall (MgC ha ⁻¹ y ⁻¹)	1.4	3.3	3.8	4.5
CO ₂ -flux (MgC ha ⁻¹ y ⁻¹) ^a	12.7	17.6	18.3	21.0
Roots inputs (MgC ha ⁻¹ y ⁻¹)				
0–10 cm	0.33	1.21	0.66	0.67
10–100 cm	1.21	2.26	1.29	1.36
100–300 cm	0.17	0.17	0.24	0.24
300–500 cm	0.10	0.03	0.18	0.27
Total	1.81	3.67	2.37	2.54
C-soil inventory (MgC ha ⁻¹) ^b				
0–10 cm	22	23	25	26
10–100 cm	78	84	78	76
100–300 cm	73	70	73	66
300–500 cm	51	45	51	38
500–800 cm	76	61	64	51
Total	300	283	291	257
δ ¹³ C-SOM/δ ¹³ C-CO ₂ (‰) ^c				
0–10 cm	-24.8/-18.3	-24.0/-13.0	-26.7/-25.0	-27.3/-25.3
100 cm	-25.4/-19.9	-25.4/-12.4	-25.6/-25.6	-25.7/-24.6
300 cm	-24.3/-19.8	-24.7/-13.6	-24.5/-24.4	-24.5/-24.1
500 cm	-23.7/-20.1	-24.5/-16.6	-23.9/-24.1	-23.9/-23.5
800 cm	-22.9/-20.6	-23.8/—	-23.8/-24.0	-23.4/-23.1
¹⁴ C-SOM/Δ ¹⁴ C-CO ₂ (‰) ^d				
0–10 cm	+106/+129	+117/+138	+126/+129	+138/+153
100 cm	-655/+156	-597/+120	-428/+132	-686/+155
300 cm	-778/+169	-738/+139	-696/+150	-798/+157
500 cm	-812/+161	-736/+155	-699/+147	-891/+169
800 cm	-796/+164	—	-788/+157	-865/+166

^a CO₂ flux, described by Trumbore *et al.* (1995) and unpublished data by Davidson and Verchot;

^b Soil C inventory, average values for 3 forest sites, 2 for degraded pasture, for 2 managed pastures and 3 'capoeiras'. Calculated using linear interpolation between discrete depths for which %C and carbon isotopes were measured. The minimum detectable difference (MDD), calculated by combining uncertainties in bulk density and C concentration analyses, was of 3, 8, 16, 11 and 17 MgC ha⁻¹ for the layers 0–10 cm, 10–100 cm, 100–300 cm, 300–500 cm and 500–800 cm. For more details see Trumbore *et al.* 1995.

^c δ¹³C-SOM/δ¹³C-CO₂ and ^d Δ¹⁴C-SOM/Δ¹⁴C-CO₂, average values for 3 forest sites, 2 for degraded pasture, for 2 managed pastures and 3 'capoeiras'. 0–10 cm values are averages of 8 composited cores taken for each site.

pasture. Root inputs exceed surface litter inputs in pastures, but not in forests.

The efflux of CO₂ from the soil surface was highest in the forest and lowest in the degraded pasture. Secondary forest and managed pasture had intermediate CO₂ efflux rates (Table 1). The CO₂ fluxes for all ecosystems are 2.4–4.0 times the combined litterfall plus root inputs given in Table 1, indicating a large contribution of CO₂ production by root respiration.

The amount of C stored in this soil to 8 m depth (250–300 MgC ha⁻¹) is greater than that in above-ground biomass. Differences in soil C stocks among land cover types were not significant, however, given the large variability and uncertainties in percentage C analyses at

low concentrations deep in the soil. The minimum detectable differences among land-use types, based on uncertainties in the analyses of bulk density and carbon content, are 3 MgC ha⁻¹ for the 0–10 cm interval, and 8–17 MgC ha⁻¹ for the remaining depth intervals (Trumbore *et al.* 1995) (Table 1).

C isotopes in soil profiles

The δ¹³C and Δ¹⁴C of soil organic matter did not differ significantly among land-use types below the upper meter of soil (Table 1). A clear isotopic signature of C4 plants is observed in the upper 10 cm of soil in the degraded and managed pastures. Surface values of δ¹³C

for secondary forest were closer to C3 values. The $\delta^{13}\text{C}$ values for bulk organic matter increased by about 3‰ with depth for primary and secondary forest soils, from about -27‰ in the 0–10 cm layer to about -24‰ below 100 cm.

The isotopic composition of soil CO_2 reflects both the isotopic signature of root respiration and that of decomposing C in organic matter pools with fast turnover times. Large differences are seen between bulk organic matter and $^{13}\text{CO}_2$ in pasture soils, particularly in the managed pasture, which has $^{13}\text{CO}_2$ close to values expected for C4 vegetation. The degraded pasture, which has C3 shrubs growing in addition to C4 grasses, shows a mixture of C3 and C4 inputs to CO_2 production. For both of these soils, the ^{13}C content of CO_2 becomes lighter with depth, most likely because of increased inputs of C3-derived CO_2 at depth, either through decomposition of old C3 roots in managed pasture, or increased importance of C3 roots at depth in degraded pasture. Secondary forest $^{13}\text{CO}_2$ values were similar to those of the primary forest, indicating that mainly organic matter of C3 origin is being decomposed. In C3-dominated soils there was an increase in ^{13}C of CO_2 with depth in the soil.

The contrast in the $\Delta^{14}\text{C}$ values of organic matter and soil CO_2 are striking at depth, indicating that the bulk organic matter at depth, which is highly depleted in ^{14}C , is not contributing to organic matter decomposition. The $\Delta^{14}\text{C}$ values at depth are higher than the 1992 atmospheric values. Root respiration should have $\Delta^{14}\text{C}$ values close to plant tissues fixed in 1992 ($+142 \pm 5\%$). Hence, higher $\Delta^{14}\text{C}$ values in the soil atmosphere indicate that decomposition of organic matter, which was fixed by plants several years to decades ago when atmospheric $\Delta^{14}\text{CO}_2$ was higher, contributes significantly to CO_2 fluxes (Trumbore *et al.* 1995). The same pattern of increasing $^{14}\text{CO}_2$ with depth was observed for all four land use types. Thus, although the origin of the organic matter being decomposed may differ to some extent between C3 and C4 ecosystems, the turnover times of the material being decomposed are similar.

Fractionation of carbon – transect samples

Data for C storage in the upper 10 cm of soil based on the transect samples are given in Table 2. These data include results for samples separated into low-density ($<2 \text{ g cm}^{-3}$) and high-density ($>2 \text{ g cm}^{-3}$) fractions. About 91% of the soil mass of the upper 10 cm was present in the high-density fraction ($>2.0 \text{ g cm}^{-3}$), but the mean C concentration of the high-density fraction was only $2.81 \pm 0.30\%$ (Table 2). The C concentration in the low-density fraction was $22.8 \pm 3.4\%$. Combining soil mass and C concentration, about 56% of the carbon mass was in the mineral fraction and the

remaining 44% in the low density fraction for all ecosystems.

Bulk carbon content for the 0–10 cm samples from the transect are significantly higher (4.4–4.7% C) than those for the composited cores taken near soil pits (Table 1; 2.2–2.8% C). We attribute this difference to sampling biases introduced by differences in the removal of surface litter before sampling the mineral soil. Samples taken for soil pits typically had only 16–34% of the total C present as low density material (Trumbore *et al.* 1995), while transect samples had a higher proportion ($\approx 40\%$) of low density material with high percentage C. A second reason for systematic differences between the two data sets may be seasonal changes in the amount of low density material in the 0–10 cm layer. In either case, the variability of the transect data, together with the large differences possible in the same depth interval sampled by different people, underscores the uncertainty in using C inventory data alone to monitor soil C dynamics following land-use change.

The C/N ratios of organic matter in bulk samples increased significantly from a mean of 13 in forest to 17 in degraded pasture. This increase reflects changes in both the low-density (C/N = 17 in forest to 20 in degraded pasture) and high-density (9 in forest to 15 in degraded pasture) fractions of organic matter. High-density fraction organic matter had lower C/N ratios than the light fraction in all ecosystems.

Differences in stable carbon isotopes among land cover types on the transect in the 0–10 cm soil samples are due to the differences in photosynthetic pathway for forest vegetation (all C3) and grasses planted for pasture (C4). The average value of $\delta^{13}\text{C}$ was heavier in the degraded pasture soil in relation to other land cover types for both organic matter fractions. This difference was especially pronounced for the low density fraction (Table 2), although the average value of -20.8‰ is lighter than would be expected for relatively undecomposed C4 plant material (-12 to -15‰), indicating the presence of organic matter derived from C3 plants. The $\delta^{13}\text{C}$ values in the low density fraction of primary and secondary forest surface soils averaged 0.6–1.7‰ lighter than mineral associated organic carbon. The $\delta^{13}\text{C}$ values in low density fractions of the 0–10 cm layer in soils were heavier than surface plant litter. In general, the standard deviations of the $\delta^{13}\text{C}$ values declined from the degraded pasture to open and closed capoeira, as the homogeneity of C3 plant inputs increases with secondary succession (Table 2). The primary forest had the lowest variability in the $\delta^{13}\text{C}$ values.

Whereas the $\delta^{13}\text{C}$ data indicate the source of C inputs (C3 vs. C4 plants) and the degree of decomposition (differences in $\delta^{13}\text{C}$ of forest density fractions) $\Delta^{14}\text{C}$ data reveal the fraction of soil organic matter derived from

Table 2 Carbon content (%), C/N, $\delta^{13}\text{C}$ (‰), $\Delta^{14}\text{C}$ (‰) and % soil mass [(%) s.m.], for the bulk, high-density ($>2\text{ g cm}^{-3}$) and low-density ($<2\text{ g cm}^{-3}$) fractions of soil

	$d > 2\text{ g cm}^{-3}$					$d < 2\text{ g cm}^{-3}$					Bulk				
	C	C/N	$\delta^{13}\text{C}$	$\Delta^{14}\text{C}$	(%) s.m.	C	C/N	$\delta^{13}\text{C}$	$\Delta^{14}\text{C}$	(%) s.m.	C	C/N	$\delta^{13}\text{C}$	$\Delta^{14}\text{C}$	
Degraded pasture	2.86 ± 0.12	15 ± 1.2	-22.9 ± 1.8	+109 ± 5	91.1 ± 3.8	22.8 ± 4.4	20 ± 0.8	-20.8 ± 2.9	+132 ± 11	8.9 ± 3.8	4.65 ± 0.77	17 ± 1.5	-21.0 ± 2.8	+112 ± 5	
Open capoeira	2.72 ± 0.33	11 ± 0.9	-25.0 ± 2.1	+124 ± 11	91.3 ± 2.9	22.7 ± 3.2	18 ± 0.2	-26.7 ± 1.8	+148 ± 4	8.7 ± 2.9	4.50 ± 1.01	14 ± 1.0	-26.5 ± 1.8	+150 ± 3	
closed capoeira	2.77 ± 0.30	13 ± 1.1	-26.9 ± 1.0	+134 ± 21	91.7 ± 4.3	23.0 ± 3.5	17 ± 2.0	-27.5 ± 1.1	+162 ± 18	8.3 ± 4.3	4.36 ± 0.82	15 ± 1.9	-27.4 ± 1.1	+151 ± 18	
primary forest	2.87 ± 0.45	9 ± 1.2	-27.2 ± 0.4	+125 ± 17	91.0 ± 17	22.6 ± 2.4	17 ± 2.0	-28.0 ± 0.6	+141 ± 25	9.0 ± 4.4	4.53 ± 1.16	13 ± 1.8	-27.9 ± 0.5	+138 ± 23	
total mean	2.81 ± 0.30				91.3 ± 3.8	22.8 ± 3.4				8.7 ± 3.8	4.51 ± 0.94				

The data are average values and standard deviation of 3 data of degraded pasture, 5 data of open capoeira, 7 data of closed capoeira and 6 data of forest.

bomb-carbon (i.e. C fixed since ≈ 1960). The $\Delta^{14}\text{C}$ values in Table 2 for bulk soil from the transect are all positive, indicating that most of the C in the 0–10 cm layer of these soils was fixed since atmospheric weapons testing ended in 1964. Radiocarbon contents in the high density fraction are consistently less than in low density carbon, although values still indicate the predominance of bomb-produced ^{14}C . The $\Delta^{14}\text{C}$ of low-density carbon are quite variable, and differences among land use types are not significant (Table 2). Again variability in C and C isotopes can arise from inconsistency in the sampling technique. Gradients of C and ^{14}C in particular are quite large within the uppermost 10 cm of soil (see Table 2 of Trumbore *et al.* 1995). Therefore, relatively small differences in sampling depth may affect the overall result. An additional cause of variability is the large degree of heterogeneity present in Amazonian soils. Downward mixing by animals, including insects, may dilute C and ^{14}C by varying degrees, especially in the upper 10 cm.

High-density carbon, representing roughly 60% of the total C in the 0–10 cm layer, has $\Delta^{14}\text{C}$ values less than those of the 1992 atmosphere, but still $>100\%$. Further fractionation showed that acid and base hydrolysis solubilized much of the more labile carbon. The $\Delta^{14}\text{C}$ values for the nonhydrolysable residue in primary forest, closed capoeira and degraded pasture were +15, +75 and +17‰, respectively, representing 32, 37, and 32% of the total high density fraction carbon (19–22% of the total C in the 0–10 cm layer).

Rates of C turnover derived from isotopic data

The C isotopic data indicate that C turnover rates are rapid in the upper 10 cm of soil. Decreases in $\delta^{13}\text{C}$ and C/N ratio from pasture to secondary growth and primary forest along the transect indicate relatively rapid changes in soil carbon as a result of varying inputs from C3 (primary forest) to C4 (active pasture) and back to C3 (degraded pasture and secondary forest) during the last 20 years. Increases in $\delta^{13}\text{C}$ in pasture soils were observed in both density fractions, although the largest increase was in the low-density material. Hence, the high-density fraction of organic matter contains some fast cycling component that reflects C4 plant inputs.

Using the mass balance approach (eqn 3) to estimate the percentage of C derived from C4 plants incorporated in each soil, and assuming soil carbon in primary forest has $\delta^{13}\text{C}$ of -28% , and a C4 endmember soil has a $\delta^{13}\text{C}$ of -12% , we found that the highest percentage of C4 incorporated in surface soil organic matter was in degraded pasture (28–45%), mainly in the low-density fraction, followed by a sharp decrease in the open capoeira (8–15%), with less than 5% remaining in the

closed capoeira (Fig. 1). Given that the degraded pasture was about 23-y-old, the $\delta^{13}\text{C}$ data indicate that at least 30% of soil C in the 0–10 cm depth increment has turnover times less than 23 years. This estimate of decadal cycling C is a lower limit, because it is based on the assumption that there were no C3 inputs in the degraded pasture, which was not true at the time of sampling. If we instead assume the $\delta^{13}\text{C}$ of respired CO_2 measured in the degraded pasture (-19‰) is indicative of the $\delta^{13}\text{C}$ content of C inputs to the soil surface, we would calculate that 57% of the carbon in the 0–10 cm may be of recent origin. Rapid loss of the C4 signal in secondary forests is in accord with rapid turnover rates (<20 years) for the fast cycling organic matter.

Radiocarbon data show that the majority of soil C in the 0–10 cm interval contains bomb ^{14}C , and thus has been derived from C fixed from the atmosphere within the last 30 years. Profiles of ^{14}C show that soil organic matter below 10 cm depth is dominated by very old C and that it is difficult to detect changes in deep soil C following land use change.

We used a time-dependent model (eqn 4) to determine the turnover time ($1/k$) required for organic matter to reproduce observed values of $\Delta^{14}\text{C}$ in organic matter. For the low-density fraction in the 0–10 cm depth of primary and secondary forest soil, the $\Delta^{14}\text{C}$ values were equal to or greater than the values ($+143 \pm 5\text{‰}$) measured for plant material fixed in 1992 (the year of soil collection). These values are consistent with a range of turnover time for low density C of 1–3 years. Due to the shape of the atmospheric ^{14}C curve with time, and the fact that we are sampling ≈ 30 years after ^{14}C in the atmosphere peaked, $\Delta^{14}\text{C}$ values of $+140$ to $+165\text{‰}$ are also in accord with turnover times of 45–60 years (Fig. 2). We assume the shorter turnover times are correct, given the constraints of

Fig. 1 Proportions of C4 organic matter incorporated in SOM fractions under different land covers. Filled bar represent SOM fraction with density higher than 2 g cm^{-3} and open bars represent SOM fraction with density smaller than 2 g cm^{-3} .

C inputs to litter and 0–10 cm soil layers, and observations that surface layer litter has turnover times of less than 1 year (Trumbore *et al.* 1995). $\Delta^{14}\text{C}$ values for low-density carbon in the degraded pasture are lower than the present atmosphere, most likely due to the influence of charcoal derived from old forest wood.

Fractionation of high-density carbon showed that it contained both a hydrolysable component, with more bomb ^{14}C , and a nonhydrolysable component, with ^{14}C values ranging from $+15$ to $+75\text{‰}$. For a steady-state C reservoir, which does not change in abundance or isotopic content over the past several decades, these ^{14}C values indicate an average turnover time for nonhydrolysable material of ≈ 50 –100 years. Assuming soils across the transect had on average 34% nonhydrolysable carbon with $\Delta^{14}\text{C}$ of $+35\text{‰}$ (≈ 75 years turnover time), we calculate that the 66% of the high-density fraction C hydrolysed had $\Delta^{14}\text{C}$ of $+147\text{‰}$ (degraded pasture), $+185\text{‰}$ (capoeira) and $+171\text{‰}$ (primary forest). Turnover times deduced from these ^{14}C values are 2–4 years or 21–51 years. On decadal timescales, only the primary forest satisfies the assumption of steady state required to determine turnover times from $\Delta^{14}\text{C}$ of hydrolysable C; the turnover time derived from $+171\text{‰}$ is either 4 or 41 years. Given the small changes in $\delta^{13}\text{C}$ observed for the high density fraction of pasture organic matter, the 41 years turnover time is more likely for the hydrolysable organic carbon. This is a longer turnover time than the 10–30 years estimated by Trumbore *et al.* (1995), who assumed a 'passive' $\Delta^{14}\text{C}$ of -250‰ , but did not directly measure it for the 0–10 cm interval.

Fig. 2 Temporal variability of $\Delta^{14}\text{C}$ values from 1950 to 1995 for atmospheric CO_2 (dashed fine line), for soil organic matter assuming a turnover time of 3 years (solid thick line) and for soil organic matter assuming a turnover time of 50 years (solid fine line). The arrow indicate the crossing point ($t = 1992$ and $\Delta^{14}\text{C} = +160\text{‰}$) between the 3 years and 50 years turnover times. For details see Trumbore (1993).

In summary, turnover times derived from interpretation of $\Delta^{14}\text{C}$ data were 1–3 years for low-density C ($\approx 40\%$

Fig. 3 Changes in (a) $\Delta^{14}\text{C}$ (b) carbon inventory and (c) $\delta^{13}\text{C}$ of bulk SOM in the upper 20 cm of soil predicted by the model for forest (thick dashed line), pasture (thick solid line), open capoeira (fine dashed line), and closed capoeira (fine solid line). Data from forest (closed circle – pit (●), open circle – transect (○)); pasture (filled square – pit (■), open square – transect (□)); open capoeira (open diamond – transect (◇)); closed capoeira (filled triangle – pit (▲), open triangle – transect (△)).

of total C), ≈ 40 years for hydrolysable, high-density C ($\approx 36\%$ of total C) and ≈ 100 years for nonhydrolysable, high-density C ($\approx 24\%$ of total C).

Figure 3 shows the predicted changes in C stocks and ^{14}C accompanying land use for conversion of forest to pasture, with either continued pasture, increased management of the pasture, or abandonment and regrowth of secondary forest. These predictions are based on assuming the partitioning of C into low-density, hydrolysable and nonhydrolysable pools with turnover times as derived from ^{14}C isotope data. We assume turnover times of C are unchanged with land use for the different fractions, and that C inputs to each organic matter pool are changed in proportion to the total above-ground and below-ground litter inputs for each land-use type. Degraded pasture soils are predicted to lose C, due to lower litter and root inputs, and secondary forest soils are predicted to start regaining this lost soil C. While this approach apparently overestimates C losses in the upper meter of soil in pastures, the differences between data and models are not significant because of the large uncertainty in soil C data. The predicted changes in $\delta^{13}\text{C}$ also exceed the observed values for pastures. The most likely explanation for this discrepancy is that the degraded pasture soils have significant C3 carbon inputs from herbaceous weeds, shrubs, and saplings. The $\delta^{13}\text{C}$ of soil CO_2 in degraded pastures (Table 2) demonstrates that C3 plants contribute significantly to soil respiration, thus indicating that root turnover and leaf litter inputs may also be important there.

The main conclusion resulting from this analysis is that soil C turnover rates are sufficiently high that the secondary forest has already regained the isotopic signatures characteristic of the primary forest. Most of the changes in C stocks take place in low-density pools, though these changes are small compared to measurement errors in this system. Hence, isotopic measurements provide a more sensitive indication of disturbance and recovery of soil carbon cycling processes than do measure of soil C stocks.

The rates of C inputs (litter and roots) and C outputs (CO_2 efflux) are not fully recovered in the secondary forest, but are significantly higher than in degraded pastures it is replacing. The secondary forest has also regained its function in the hydrologic cycle, with evapotranspiration rates nearly as large as the primary forest (Nepstad *et al.* 1995; Jipp *et al.* 1998). Above-ground biomass, in contrast, is still small relative to the C storage of the primary forest.

Because we have studied only one secondary forest with its particular land-use history, it would be premature to conclude that all abandoned pastures in the Amazon have the capacity to recover the C cycle of the primary forest as this one has. Degraded pasture is

estimated to cover an area of $\approx 50\,000\text{ km}^2$ in the Amazon (Serrão & Toledo 1990), but this large class includes pastures of widely varying intensity of use. Overgrazing and frequent use of fire can impoverish the pasture soil and impede regrowth of secondary forests (Buschbacher *et al.* 1988; Uhl *et al.* 1988). This study demonstrates, however, that relatively rapid recuperation of the C cycle, particularly below ground, is possible under conditions of moderate intensity of pasture use and subsequent regrowth of secondary forests following pasture abandonment.

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