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Substantial labile carbon stocks and microbial activity in deeply weathered soils below a tropical wet forest

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Abstract

Contrary to large areas in Amazonia of tropical moist forests with a pronounced dry season, tropical wet forests in Costa Rica do not depend on deep roots to maintain an evergreen forest canopy through the year. At our Costa Rican tropical wet forest sites, we found a large carbon stock in the subsoil of deeply weathered Oxisols, even though only 0.04–0.2% of the measured root biomass (>2 mm diameter) to 3 m depth was below 2 m. In addition, we demonstrate that 20% or more of this deep soil carbon (depending on soil type) can be mobilized after forest clearing for pasture establishment. Microbial activity between 0.3 and 3 m depth contributed about 50% to the microbial activity in these soils, confirming the importance of the subsoil in C cycling. Depending on soil type, forest clearing for pasture establishment led from no change to a slight addition of carbon in the topsoil (0–0.3 m depth). However, this effect was countered by a substantial loss of C stocks in the subsoil (1–3 m depth). Our results show that large stocks of relatively labile carbon are not limited to areas with a prolonged dry season, but can also be found in deeply weathered soils below tropical wet forests. Forest clearing in such areas may produce unexpectedly high C losses from the subsoil.

Keywords: Costa Rica, deforestation, land-use change, microbial activity, pasture, soil organic carbon, tropical rain forest

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Introduction

Recent estimates show that the amount of carbon stored in the top 3 m of soils below tropical evergreen forests (474 Gt C) is about one fifth of the global soil carbon stock (Jobbagy & Jackson, 2000). This amount is almost 80% of the total estimated amount of carbon stored in global terrestrial vegetation (~610 Gt C, Schimel, 1995). It also demonstrates the important role that soils below these forests could play in the global carbon cycle. However, the role of these soils now and in the future strongly depends on the lability of this soil carbon and its availability to the soil microbial biomass.

Most studies on the effects of land-use change on soil organic carbon (SOC) have been limited to the topsoil or at most the top meter of the soil. This is understandable, given that the strongest effects of land-use change, the highest carbon concentrations (e.g. Veldkamp, 1994) and the greatest microbial activity (e.g. Luizão *et al*., 1992) have been found in the topsoil. Furthermore, SOC in the subsoil is traditionally considered (e.g. Sombroek *et al*., 1993) to be stable, relatively inert humus that is not likely to be affected by a change in land use. Since the mid 1990's, however, there has been increased recognition that there can be large carbon stocks below the A-horizon, especially in some deeply weathered soils in the tropics. Although SOC concentrations are low in the subsoil of these soils, the volume of these deep soil horizons is very large. As a result, the total carbon stored below the first meter may actually be higher than the carbon stock in the top meter of the soil profile (Nepstad *et al*., 1994; Trumbore *et al*., 1995). An increasing awareness of the importance of deep soil carbon is reflected in the increasing global estimates of soil carbon stocks. In the 1980's, the total amount of carbon stored in the top meter of soils of the tropics was estimated at 316 Gt C (Post *et al*., 1982). A subsequent review of carbon stocks in the first 2 m resulted in an estimate of 616–640 Gt C for soils of the

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tropics (Batjes, 1999), and a more recent review estimated the carbon stock down to 3 m depth in soils of the tropics at 1037 Gt C (Jobbagy & Jackson, 2000). These authors also concluded that the biomes with the most SOC at 1–3 m depth were tropical evergreen forests and tropical grasslands/savannas.

In their study in Pará, Brazil, Nepstad *et al.* (1994) were the first to point out the importance of deep soil carbon in Amazonian forest soils. They demonstrated that the forest soil below 1 m depth at their study site contained more carbon than the aboveground biomass. Further, they showed that 15% of this subsoil carbon turns over on annual to decadal timescales. They explained the occurrence of the deep carbon by the presence of deep roots, which are needed by that evergreen forest to maintain a green canopy during dry periods that can last up to 5 months.

Our study was conducted in the old-growth forest and adjacent pastures of La Selva Biological Station in the Atlantic Zone of Costa Rica. In contrast to the forest in Pará, this tropical rain forest has a perudic moisture regime with a weak dry season and on average no month receiving less than 100 mm of rain (Sanford *et al.*, 1994). We address the following questions:

- How important is deep soil carbon in deeply weathered soils below a tropical forest with a perhumid climate?
- What is the effect of forest clearing for pasture on this deep soil carbon?
- Is there measurable microbial activity in the subsoil of these deeply weathered soils, and what is the relative importance of microbial activity in the subsoil compared to in the topsoil?

Because no long-term data as yet exist for assessing the effects of conversion of forest to pasture, we measured total soil carbon, ^{13}C carbon isotopes and indices of soil microbial activity in replicated old-growth forest sites and in adjacent pasture sites and we assumed that conditions before pasture establishment were equivalent between the paired sites.

Materials and methods

Site description

Our study was conducted in and around the La Selva Biological Station of the Organization for Tropical Studies (OTS), in NE Costa Rica. La Selva is located between the Atlantic coastal plain and the foothills of Costa Rica's Central Cordillera. The bulk of the La Selva reserve is old-growth forest that has been protected and used for ecological research since the 1960's. The unprotected areas adjacent to La Selva have been largely cleared for cattle pastures, a process that mainly took place in the 1970's (Butterfield, 1994). Thus, the effect of cattle pastures on soil characteristics and processes can be deduced from comparison of sites within and outside La Selva on equivalent soils.

The forest of La Selva is classified as a tropical wet forest in the Holdridge life zone system (Hartshorn & Hammel, 1994). The climate is classified as perudic: the average annual rainfall is 3962 mm with a slightly drier period from February to April; however, even during this period the average monthly rainfall exceeds 100 mm and precipitation is higher than evapotranspiration. The annual mean temperature averages 25.8 °C (Sanford *et al.*, 1994).

Soils

The landscape in and around La Selva is dominated by old lava flows and river terraces. La Selva is situated at the footslopes of the Barva volcano, the source of these basaltic lava flows. One of the three principal flows underlying La Selva has been aged at ca. 1.2 million years (Alvarado, 1990). Soils on these lava flows are deeply weathered, reddish-brown clays (augering showed that on stable geomorphological units, saprolite occurs at 5 to >6 m depth) with a low ECEC (9.5 $cmol_c\,kg^{-1}$ in the top 0.1 m, decreasing to 2.5 $cmol_c\,kg^{-1}$ at 1–2 m depth) and low base saturation (16% in the top 0.1 m, decreasing to 9% at 1–2 m depth). A recent soil mineralogical analysis showed that the clay minerals Kaolinite, Halloysite and Gibbsite dominate the entire soil profile; considerable amounts of Goethite, Hematite and Magnetite also occurred, but 2:1 phyllosilicates were not detected (Kleber *et al.*, in press). Prior to this analysis, these soils were classified as Ultisols (Sollins *et al.*, 1994); multiple characteristics, however, show that these are Oxisols (Typic Haploperox): a low silica: sesquioxide ratio; low base exchange capacity (<16 $cmol_c\,kg^{-1}$ clay), low activity of clays and low content of weatherable minerals (Kleber *et al.*, in press). By La Selva convention, these soils are termed 'Residual'. The two major rivers at the site (Rio Puerto Viejo, Rio Sarapiquí) have deposited a complex of river terraces. The terraces we studied have not been dated, but are regarded as Pleistocene (Sollins *et al.*, 1994). These soils are deeply weathered, yellowish-brown clay soils, typically with strongly weathered coarse material at 3 m depth, with low ECEC (7.7 $cmol_c\,kg^{-1}$ in the top 0.1 m, decreasing to 4.2 $cmol_c\,kg^{-1}$ at 1–2 m depth), and with low base saturation (17% in the top 0.1 m, decreasing to 8% at 1–2 m depth). Mineralogical analysis (Kleber *et al.*, in press) has shown that also in this soil type the dominant clay minerals are Kaolinite, Halloysite and Gibbsite throughout the soil profile;

Goethite and Magnetite occurred in considerable amounts, but Hematite and 2:1 phyllosilicates were not detected. Previously classified as Inceptisols, these river terraces are now also classified as Typic Haploperox, but are considered to be considerably younger than the residual soils (Kleber *et al*., in press). By La Selva convention, these soils are termed 'Old alluvial soils'. Throughout this paper, we use the terms 'old alluvial soils' and 'residual soils' to follow the usage in prior studies (e.g. Clark & Clark, 2000); the new classification treats both as Oxisols, albeit of contrasting age.

In this study, we performed a space-for-time substitution. Critical assumptions of this approach are that conditions before forest clearing were the same and that changes measured are caused by land use (cf., Veldkamp, 1994). Because we have no samples from the pasture sites before conversion, we cannot prove these assumptions, but we dealt with this problem by carefully selecting the study sites. From the old river terraces, we selected all sites to have a uniform, flat topography (slope not steeper than 2%). From the residual soils, we selected sites to all be on the summit or near the shoulder of the heavily weathered and dissected lava flows (slope not steeper than 5%). We also field inspected soil samples to ensure that soil material was similar in texture and color among the replicate sites.

In the old-growth forest, we selected three sites on old alluvial soils and three on residual soils. In pastures adjacent to La Selva, which were established in the 1970s, we also selected three sites on old alluvial and three on residual soils. At the time of sampling, the pastures were about 25 years old. All pasture sites were dominated by *Ischaeum indicum*, a C_4 grass considered to have relatively low biomass production (Van Dam *et al*., 1997). All sites were at elevations of 40–100 m above the sea level.

Soil sampling and sample processing

In 1997, soil shafts of 3 m depth (old alluvial soils) and 4 m depth (residual soils) were established at the old-growth forest sites (three sites on each soil type, one shaft per site). In each shaft, undisturbed soil samples (300 cm^3) were taken for bulk density measurements at the following depths (m): 0.05, 0.20, 0.40, 0.75, 1.5, 2.5 and (on the residual soils) 3.5. For each soil sample for bulk density, we carefully inserted a metal canister into the undisturbed soil layer. We took three such samples per shaft per depth. On the pasture soils (three sites on each soil type, one shaft per site), three undisturbed samples per site were taken at each of three depths: 0.05, 0.20 and 0.40 m. Earlier work in pastures on comparable soils at a separate study site 20 km away, had shown that increases in bulk density due to compaction only occurred at 0–0.3 m depth (Veldkamp, 1994).

At all 12 sampling sites, soil samples for chemical and microbiological analyses were taken vertically by auger in August and September 1999 for the following depth intervals (m): 0.0–0.10, 0.10–0.30, 0.30–0.50, 0.50–1.0, 1.0–2.0, 2.0–3.0 (and at 3.0–4.0 m depth at the residual soil sites). Care was taken not to contaminate the sampled soil with soil material from overlying layers. The soil samples were handled and homogenized using latex gloves. For microbial measurements, within each shaft two composite soil samples were made of three subsamples taken at different points across each depth layer. The samples were passed through a 2 mm sieve and stored field-moist in polyethylene bags for up to 2 days at 4 °C before microbial measurements were carried out. For soil chemical measurements, subsamples of the two soil samples for the microbial measurements were mixed to create one final bulk sample per soil depth. This bulk sample was air-dried for C and ^{13}C analyses. Microbial measurements were carried out at maximum water capacity (Forster, 1995). These assays for microbial activity were based on a single sampling during the wetter season. We expect minimal seasonal changes, however, given the small within-year fluctuations in temperature (about 2.5 °C in the topsoil and less than 1 °C at 2.5 m depth). Temporal variation in microbial activity would most likely occur in response to temporary soil dry-down during low-rain periods that can occur during the drier season at La Selva.

Soil carbon and ^{13}C analysis

The air-dried soil samples were passed through a 2 mm sieve and ground to powder using a ball mill. We determined the total organic C using an automated C & N analyzer (Heraeus vario EL, Hanau, Germany). The ^{13}C values were measured with an elemental C & N analyzer (Fisons EA11081, Beverly, MA, USA) coupled with an isotope ratio mass spectrometer (Delta plus, Finnigan MAT, Bremen, Germany). Plant material was prepared and analyzed in the same way. The isotope ratios were expressed as $\delta^{13}C$ values: $\delta^{13}C(‰) = [(R_{sam}/R_{std}) - 1] \times 10^3$ where $R_{sam} = {}^{13}C/{}^{12}C$ ratio for the sample and $R_{std} = {}^{13}C/{}^{12}C$ ratio of the reference (PDB). The amounts of soil carbon derived from forest and pasture were calculated using a simple mixing equation (Balesdent & Mariotti, 1996): $F = (\delta^{13}C_p - \delta^{13}C_f)/(\delta^{13}C_{C4} - \delta^{13}C_{C3})$, where F is the the fraction of new carbon in the pasture sample; $\delta^{13}C_p = \delta^{13}C$ value of sample from pasture soil; $\delta^{13}C_f = \delta^{13}C$ value of sample from forest reference; $\delta^{13}C_{C4} = \delta^{13}C$ value of pasture

residues; $\delta^{13}C_{C3} = \delta^{13}C$ value of forest residues. The average $\delta^{13}C$ values measured for plant tissues ($N = 4$ per tissue type) were: pasture leaves: $-12.08‰$; pasture fine roots (<2 mm diameter): $-15.25‰$; forest leaf litter: $-30.00‰$ and forest fine roots (<2 mm diameter): $-28.84‰$. The difference between the $\delta^{13}C$ signal of pasture leaves and fine roots was relatively large, which may be an indication that some of the fine roots sampled in the pasture were from C_3 plants. In our calculations, we used the average of leaves and roots for forest C_3 ($-29.42‰$) and pasture C_4 ($-13.67‰$). The advantage of this mixing equation compared to others is that it can be applied even if the isotope enrichments during C decay are high (Balesdent & Mariotti, 1996).

Microbial activity

Basal respiration (BR) was measured as one indicator of microbial activity using the 'syringe incubation method' (Heilmann & Beese, 1992). The CO_2 production of a soil sample is calculated by incubating the sample in a gas-tight glass syringe and measuring the CO_2 increase over a period of 20 h. Preliminary tests showed that in 24 hours, the syringes lost less than 1% of a CO_2 standard with a concentration of 4.93%. CO_2 was measured using a Shimadzu gas chromatograph with a TCD detector. For more details on the CO_2 analyses, see Schwendenmann *et al.* (2003).

A second indicator of relative microbial activity was estimated based on substrate-induced respiration (SIR) using the 'syringe incubation method' (Heilmann & Beese, 1992). SIR is measured by adding an easily decomposable substrate (glucose) to the soil sample to induce a maximum respiration rate; this maximum respiration rate has been shown to be correlated with the active glucose-responsive microbial biomass (Anderson & Domsch, 1978). To facilitate mixing of the soil sample with the glucose, the soil sample was mixed with a pulverized mixture of 50% quartz sand and 50% glucose. We carried out preliminary tests with glucose levels between 0.4% and 1.4% of the moist weight of the soil sample, to determine the amount of glucose needed to induce a maximum respiration rate; no increase in CO_2 production was measured above 1.0% glucose addition. We therefore used 1.0% glucose addition in the experiments. Normally, the CO_2 production rate is converted into microbial biomass using a conversion factor (Anderson & Domsch, 1978). However, published conversion factors have been developed for temperate topsoils and several authors have demonstrated that SIR should be calibrated for specific soil conditions. As we did not have the ability to calibrate the SIR values of our soils against a standard microbial biomass method, we use our numbers only to estimate differences in relative glucose-responsive microbial activity (GRMA), across our study sites and at different soil depths. Absolute comparison with other studies should only be made if the SIR method has been calibrated against a standard method for microbial biomass.

Root sampling

We quantified roots ≥2.0 mm in diameter in half of the soil column taken from each of the six shafts excavated in the old-growth forest sites when the six pits were excavated. The reason for the use of this sampling was to detect the maximum depth at which different root classes occur. We did not sample roots to make reliable stand-level estimates of coarse root biomass, and the data should not be used for this purpose. A square soil column 0.8 m on a side was excavated by depth layer: 0.0–0.1, 0.1–0.3, 0.3–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0 m and for the residual soil pits: 3.0–4.0 m. Using a 2 mm sieve, roots ≥2.0 mm in diameter were sieved from the soil from each depth, and returned to the laboratory. There, roots were washed and sorted into diameter classes (2–5, 5–10, 10–20 and >20 mm) and dried at 65 °C to stable mass (to 0.1 g on two consecutive weighings).

Soil water monitoring

We measured soil water content using frequency domain sensors (CS615, Campbell Scientific, Inc. Logan, UT, USA). We used a calibration function that we developed for each of our two soils (Veldkamp & O'Brien, 2000). Sensors were inserted horizontally into the shaft wall of all forest soil shafts, at the following depths (m): 0.05, 0.2, 0.4, 0.75, 1.5, 2.5, and for the residual soil shafts: 3.5. Sensors have been read bi-weekly since April 1998 using a portable reader (O'Brien & Oberbauer, 2001).

Calculations and statistical analyses

Carbon concentrations (kg C kg^{-1} soil) were converted into total organic carbon stocks (Mg C ha^{-1}) using measured bulk density values for each soil type and the volume of the sampled horizon. Because of the higher bulk density in the pasture topsoil, comparison of SOC was made on a mass (rather than volume) basis, to avoid artifacts from soil compaction (Veldkamp, 1994). Microbial activity and basal respiration are commonly expressed on a mass basis. We also calculated our results on a soil volume basis using bulk density and volume of the sampled soil horizon. We compared the two soil types using the data down to 3 m depth (the maximum depth of the old alluvial soil).

Normal distribution of the carbon data and the microbial parameters was demonstrated with a goodness-of-fit test using the Kolomogorov–Smirnov D statistic. We used analysis of variance to test for significant effects of land use and soil type, at each soil depth interval.

Results

Soil chemical and physical characteristics

In the forest soils, pH increased significantly with soil depth (r, soil depth and mean pH of three samples in each soil = 0.69 and 0.64 in residual and old alluvial soils, respectively; $P < 0.001$ in both cases); in the pasture soils, there was no clear relation between soil depth and pH (Table 1). Compared to the residual soil, the old alluvial soils had slightly higher pH values at 0.1–0.3, 0.5–1.0 and 1.0–2.0 m depth, but the strongest effect on pH was land use. The pH of the pasture soils was higher than forest soils at all depths, with the strongest effect in the topsoil. In all cases, the highest pH measured was <5.0, too low for carbonates to exist. The bulk density below forest was low in both soil types (Table 1); values increased with depth from 0.63–0.71 Mg m^{-3} to about 1.0 Mg m^{-3} at 2–4 m depth. The topsoil of the pastures (0–0.1 m depth) was compacted in comparison to the forest soils (t-test, $P < 0.001$). At 0.1–0.3 m depth, only the old alluvial soil showed a higher bulk density in the pasture (t-test, $P = 0.05$). The 0.3–0.5 m soil layer showed no difference between land-use types in bulk density, and we assumed no land-use-related differences in bulk density at greater depth. Both soils are clay soils (Table 2). In the residual soil, clay content was 68–79% in the top 2 m and decreased slightly at 2–4 m depth. In the old alluvial soils, clay content was 61–70% in the top 2 m and decreased between 2.0 and 3.0 m depth.

Soil organic carbon stocks and dynamics

The total organic carbon in the forest soils down to 3 m depth (Fig. 1) was higher for the residual soils (330 Mg C ha^{-1}) than for the old alluvial soils (214 Mg C ha^{-1}). Similarly, in the pasture sites there was greater SOC down to 3 m depth in the residual soil (300 Mg C ha^{-1}) than in the old alluvial soil (201 Mg C ha^{-1}). Analysis of variance ($N = 3$ sites in each soil type, in the pasture and forest) revealed that in the topsoil (0.0–0.3 m depth) there was a significant effect of soil type ($P = 0.001$), with more SOC in the residual soil, but there was no significant effect of land use ($P = 0.062$). In the subsoil (0.3–3.0 m depth) results were different; the pasture subsoil contained less SOC than the forest subsoil ($P = 0.014$), and the residual soils contained more SOC than the old alluvial soils ($P < 0.001$). At neither depth was there an interaction between land use and soil type.

Using the difference in $\delta^{13}C$ isotope signature (Table 3) between C_3 trees (in forest) and C_4 grasses (dominant

Table 1 Soil pH and bulk density in residual and old alluvial soils (both Oxisols) below forest and pasture at La Selva, Costa Rica

	Residual soil				Old alluvial soil			
Depth (m)	Forest		Pasture		Forest		Pasture	
pH (H_2O)								
0.0–0.1	4.0	(0.2)	5.0	(0.5)	4.1	(0.0)	4.9	(0.4)
0.1–0.3	3.9	(0.2)	4.8	(0.4)	4.2	(0.1)	4.6	(0.1)
0.3–0.5	4.3	(0.1)	4.7	(0.2)	4.4	(0.1)	4.7	(0.1)
0.5–1.0	4.4	(0.1)	4.6	(0.1)	4.5	(0.1)	4.7	(0.0)
1.0–2.0	4.4	(0.1)	4.6	(0.1)	4.5	(0.1)	4.7	(0.0)
2.0–3.0	4.5	(0.1)	4.6	(0.2)	4.6	(0.0)	4.7	(0.1)
3.0–4.0	4.5	(0.1)	4.8	(0.1)				
Bulk density (Mg m^{-3})								
0.0–0.1	0.63	(0.05)	0.81	(0.04)	0.71	(0.02)	0.84	(0.07)
0.1–0.3	0.76	(0.07)	0.76	(0.08)	0.82	(0.01)	0.89	(0.02)
0.3–0.5	0.84	(0.05)	0.77	(0.04)	0.85	(0.03)	0.84	(0.02)
0.5–1.0	0.92	(0.03)	nm	nm	0.85	(0.03)	nm	nm
1.0–2.0	0.98	(0.03)	nm	nm	0.95	(0.03)	nm	nm
2.0–3.0	1.04	(0.12)	nm	nm	1.07	(0.06)	nm	nm
3.0–4.0	0.98	(0.16)	nm	nm				

$N = 3$ samples per soil type in each land-use type; SD in parentheses; nm = not measured.

Table 2 Soil texture in two soil types below forest and pasture

	Forest			Pasture		
Depth (m)	Clay (%)	Silt (%)	Sand (%)	Clay (%)	Silt (%)	Sand (%)
	Residual soil					
0.0–0.1	75.8 (5.1)	17.8 (3.7)	6.4 (2.4)	68.5 (2.0)	25.4 (2.3)	6.1 (2.3)
0.3–0.5	73.3 (1.9)	21.2 (2.8)	5.5 (1.2)	75.8 (1.1)	20.2 (0.7)	4.0 (1.0)
1.0–2.0	76.1 (5.7)	18.1 (2.1)	5.8 (3.6)	79.1 (1.2)	17.0 (1.0)	3.9 (0.5)
2.0–3.0	67.3 (11.3)	22.2 (8.1)	10.4 (7.6)	78.9 (6.7)	15.6 (3.7)	5.4 (3.1)
3.0–4.0	67.1 (10.9)	24.9 (9.3)	8.0 (8.6)	59.6 (9.4)	25.1 (8.8)	15.3 (8.5)
	Old alluvial soil					
0.0–0.1	68.4 (4.1)	22.3 (2.0)	9.4 (2.3)	61.1 (3.3)	28.3 (3.7)	10.6 (2.4)
0.3–0.5	70.1 (2.2)	22.7 (1.8)	7.2 (1.2)	62.9 (1.5)	29.9 (1.6)	7.2 (1.1)
1.0–2.0	67.5 (5.0)	24.2 (3.2)	8.3 (2.3)	42.0 (5.6)	41.1 (11.7)	16.9 (6.2)
2.0–3.0	37.5 (8.6)	43.0 (6.8)	19.5 (4.0)	26.8 (6.1)	62.3 (10.6)	10.8 (10.9)

$N = 3$; SD in parentheses.

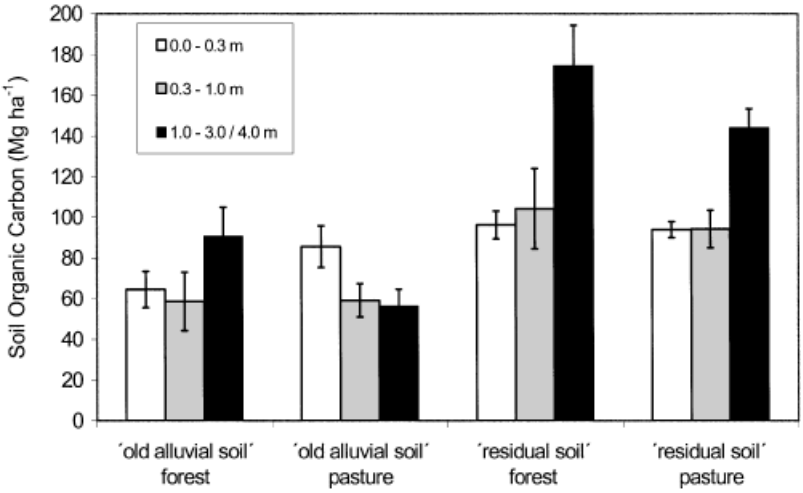

Fig. 1 Soil organic carbon stocks (mean and s.d.) at different depths for two soil types under old-growth tropical wet forest and pasture at La Selva, Costa Rica.

in the pastures), we distinguished forest-derived SOC from the grass-derived SOC (Fig. 2). In the pasture topsoil (0–0.3 m depth) on the old alluvial soils, SOC derived from C_3 (forest) vegetation had decreased from 64 Mg C ha^{-1} to 54 Mg C ha^{-1}, while 32 Mg C ha^{-1} had been added by the pasture grasses. This resulted in a net increase of 22 Mg C ha^{-1} in the topsoil of the old alluvial soil under pasture. For the topsoil of the residual soil, the decrease in forest C was from 96 Mg C ha^{-1} in the forest to 70 Mg C ha^{-1} in the pasture. This was accompanied by an increase in pasture (C_4-derived) C of 24 Mg C ha^{-1}. These changes together resulted in no net change in SOC in the topsoil. In the subsoil of both soil types, however, the forest-to-pasture transition was found to have decreased SOC. In the old alluvial soil pasture sites, SOC at 1.0–3.0 m depth that was derived from C_3 vegetation had decreased from 91 Mg C ha^{-1} to 53 Mg C ha^{-1}, while only 3 Mg C ha^{-1} SOC had been added by the C_4 vegetation; together these changes produced a net decrease of 35 Mg C ha^{-1}. In the residual soil pastures, the subsoil (1.0–4.0 m depth) similarly showed a net decrease of 30 Mg C ha^{-1} (a decrease from 174 to 140 Mg C ha^{-1} of forest-derived SOC, with 4 Mg C ha^{-1} added by the pasture C_4 vegetation).

Microbial activity

GRMA could be detected throughout all soil profiles, independent of land-use or soil type. As expected,

Table 3 Concentrations (%) and $\delta^{13}C$ (‰) of soil organic carbon below forest and pasture at La Selva, Costa Rica

	Residual soil				Old alluvial soil			
Depth (m)	Forest		Pasture		Forest		Pasture	
Soil organic carbon (%)								
0.0–0.1	5.59	(0.23)	5.89	(0.49)	4.02	(0.63)	5.32	(0.60)
0.1–0.3	4.02	(0.46)	3.05	(0.17)	2.19	(0.36)	2.30	(0.29)
0.3–0.5	2.43	(0.65)	2.01	(0.09)	1.48	(0.21)	1.41	(0.15)
0.5–1.0	1.38	(0.21)	1.38	(0.07)	0.78	(0.04)	0.84	(0.06)
1.0–2.0	0.79	(0.14)	0.69	(0.04)	0.68	(0.03)	0.45	(0.07)
2.0–3.0	0.50	(0.09)	0.43	(0.03)	0.24	(0.03)	0.13	(0.03)
3.0–4.0	0.44	(0.13)	0.32	(0.05)				
$\delta^{13}C$ (‰)								
0.0–0.1	−27.62	(0.26)	−21.99	(2.63)	−27.07	(0.32)	−18.54	(0.31)
0.1–0.3	−26.92	(0.35)	−24.67	(0.76)	−26.40	(0.37)	−23.48	(0.62)
0.3–0.5	−25.94	(0.38)	−24.46	(0.82)	−25.63	(0.32)	−23.96	(0.39)
0.5–1.0	−25.46	(0.38)	−24.01	(1.29)	−24.89	(0.44)	−24.29	(0.53)
1.0–2.0	−25.21	(0.38)	−24.90	(0.10)	−24.91	(0.26)	−23.89	(0.47)
2.0–3.0	−25.58	(0.56)	−25.14	(0.24)	−25.28	(1.04)	−24.99	(0.47)
3.0–4.0	−25.19	(0.14)	−24.51	(0.76)				

Data are means (SD in parentheses) from three sites in each land-use type, in both residual and old alluvial soils.

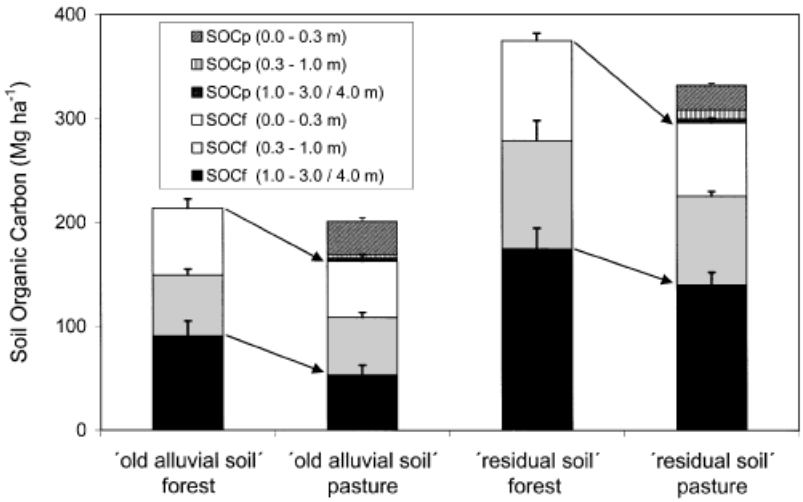

Fig. 2 Changes in stocks of forest- (SOCf) and pasture-derived (SOCp) carbon at different depths for two soil types following forest clearing and pasture establishment. Arrows indicate the inferred decreases in forest-derived SOC above and below 1 m depth.

GRMA calculated on a mass basis was highest in the topsoil and rapidly decreased with depth in both soil types and both land-use types (Table 4). Analysis of variance revealed that GRMA was higher in the pasture soil than in the forest soil at depths of 0.0–0.1 m ($P = 0.000$), 0.5–1.0 m ($P = 0.001$) and 1.0–2.0 m ($P = 0.014$). At other depths we detected no land-use effect. At no soil depth did we find a significant effect of soil type or an interaction between soil type and land use. We used our bulk density data (Table 1) to convert GRMA into an area basis; on this basis, in all soil and land-use combinations, the soil from 0.3 to 3 m depth contained GRMA levels comparable to those of the top 0.1 m, the soil that is normally sampled in studies of microbial biomass.

Basal respiration

We also detected basal respiration (BR) throughout all investigated soil profiles. As with GRMA, basal

Table 4 Basal respiration and glucose-responsive microbial activity (GRMA) in two soil types under forest and pasture at La Selva, Costa Rica

	Residual soil				Old alluvial soil			
Depth (m)	Forest		Pasture		Forest		Pasture	
Basal respiration ($\mu g\, CO_2$–$C\, g^{-1}\, dw\, h^{-1}$)								
0.0–0.1	1.58	(0.35)	1.49	(0.31)	1.25	(0.46)	1.13	(0.13)
0.1–0.3	0.50	(0.27)	0.29	(0.07)	0.28	(0.13)	0.17	(0.03)
0.3–0.5	0.16	(0.09)	0.11	(0.04)	0.14	(0.05)	0.08	(0.05)
0.5–1.0	0.07	(0.03)	0.06	(0.04)	0.06	(0.05)	0.05	(0.03)
1.0–2.0	0.06	(0.04)	0.04	(0.04)	0.06	(0.03)	0.06	(0.04)
2.0–3.0	0.09	(0.05)	0.04	(0.05)	0.05	(0.02)	0.04	(0.03)
3.0–4.0	0.11	(0.06)	0.07	(0.06)				
GRMA ($\mu g\, C\, g^{-1}\, dw$)								
0.0–0.1	999	(404)	1483	(295)	812	(289)	1550	(419)
0.1–0.3	346	(282)	389	(129)	253	(110)	276	(116)
0.3–0.5	205	(174)	177	(62)	111	(55)	173	(37)
0.5–1.0	52	(23)	108	(43)	56	(26)	91	(20)
1.0–2.0	40	(21)	62	(19)	32	(16)	48	(13)
2.0–3.0	37	(16)	39	(21)	28	(12)	38	(14)
3.0–4.0	47	(25)	45	(21)				

Data are means (SD in parentheses) from six sites in each land-use type, in both residual and old alluvial soils.

respiration was highest in the topsoil and rapidly decreased with soil depth (Table 4). Analysis of variance showed that BR in the top 0.0–0.1 m layer was higher in the residual than in the old alluvial soil ($P = 0.011$). In the 0.1–0.3 m layer this was also the case ($P = 0.018$); in addition, the forest had a higher BR than pasture ($P = 0.024$). In the 0.3–0.5 m layer, there was no difference in BR between soil types, but BR was higher in the forest than in pasture ($P = 0.049$). In the lower part of the profile, we detected no effect of either soil type or land-use. Basal respiration expressed on mass basis does not take into account the large soil volume that these soils have in the subsoil. For this reason, we also expressed the BR on an area basis using the bulk density data. While our laboratory data on BR cannot be assumed to parallel respiration levels in the field closely, the area-based values are heuristically useful in demonstrating that a relatively low basal respiration multiplied over a large volume of soil can result in large values of total respiration. For all soil and land-use combinations, such area-based values for BR (Fig. 3) were higher in the soil layers below 0.3 m than in the top 0.3 m. The area-based BR was not affected by land use.

Root biomass

The biomass of roots ≥ 2 mm in diameter was measured in the forest sites to detect the depth to which the larger root diameter classes occur. Variation in root biomass density was large and replication in each soil type was low ($N = 3$), and we found no significant differences with depth for the biomass of the four root diameter classes (Table 5). Only the total root biomass from 0–3 m depth in the diameter class $5 \leq 10$ mm was significantly higher for the residual soils.

In both soils, the maximum depth to which a given root class was found was inversely correlated with root diameter (Table 5). Only roots in the smallest root class ($2 \leq 5$ mm diameter) were sampled at depths of 2–3 m on both soils. In the residual soil, no roots in the sampled classes were found at 3–4 m depth. We did not sample roots finer than 2 mm diameter, but we did not observe fine roots below 2.5 m depth when the soil pits were excavated, nor did we observe them during augering for the soil samples used for the microbial activity.

Soil water content

Seasonal variation in soil water content was only detected down to 0.75 m depth (Fig. 4). Furthermore, the lowest volumetric soil water content detected over a period of 4 years at a depth of 0.4 m was 0.457 on the old alluvial soil and 0.386 on the residual soil. These values correspond with a tension of -60 kPa (pF = 2.8) for the old alluvial and -40 kPa (pF = 2.6) for the residual soil. Both values are only slightly drier than field capacity. At 1.5 m depth, we could not detect seasonality in the soil water content, and the lowest

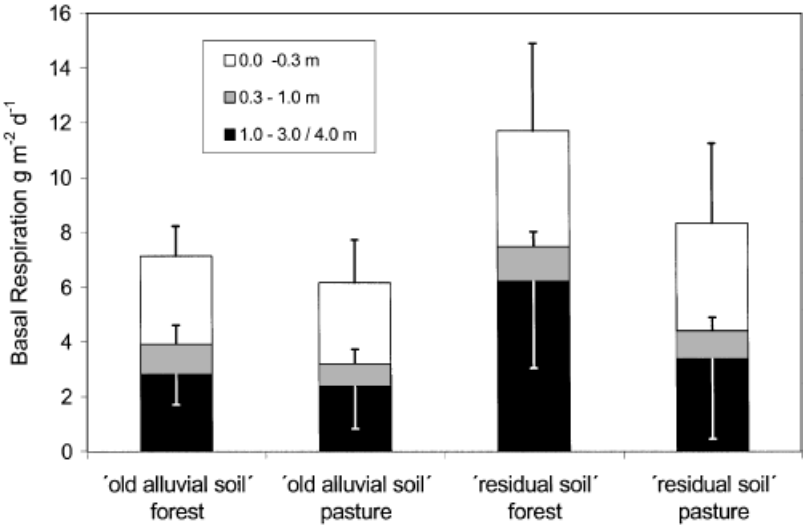

Fig. 3 Soil-volume-based basal respiration (mean + SD, $N = 6$ sites per condition) at different depths for two soil types under old-growth tropical wet forest and pasture at La Selva, Costa Rica.

Table 5 Dry root biomass density ($g\,m^{-3}$) in sites on the two principal soil types under old-growth forest at La Selva, Costa Rica

	Residual soil				Old alluvial soil			
Root diameter: Depth (m)	2≤5	5≤10	10≤20	>20	2≤5	5≤10	10≤20	>20
0.0–0.1	849 (353)	1504 (235)	1355 (216)	927 (809)	543 (170)	811 (515)	1041 (1417)	996 (1051)
0.1–0.3	421 (235)	931 (671)	851 (381)	686 (664)	188 (60)	191 (210)	241 (83)	1008 (881)
0.3–0.5	93 (53)	272 (154)	198 (197)	169 (293)	57 (22)	36 (14)	10 (17)	162 (220)
0.5–1.0	37 (20)	57 (49)	20 (35)	0	45 (10)	9 (13)	41 (71)	25 (43)
1.0–2.0	7 (2)	14 (13)	0	0	14 (6)	2 (3)	0	0
2.0–3.0	3 (6)	0	0	0	8 (7)	3 (5)	0	0
3.0–4.0	0	0	0	0				

Values are means (SD in parentheses) from three sites in each soil type.

volumetric water content measured at this depth over a 4-year period was 0.559 on the old alluvial and 0.567 on the residual soil. Tensions corresponding with these soil water contents are –1.6 kPa (pF = 1.2) for the old alluvial and only –0.25 kPa (pF = 0.4) for the residual soil. This means that at 1.5 m depth and lower, the soil water content is always wetter than field capacity, which means that there is never a considerable soil water uptake from 1.5 m depth or lower.

Discussion

Soil carbon stocks in forest soils and long-term C sequestration

The soil carbon stocks that we measured below this tropical wet forest are very high, especially when compared to carbon stocks in the aboveground vegetation. The estimated live aboveground biomass in old-growth forest at La Selva is 74.5 Mg C ha^{-1} for the residual soils and 83.5 Mg C ha^{-1} for the old alluvial terraces (Clark & Clark, 2000), and total standing and fallen coarse woody debris averages 25.4 Mg C ha^{-1} (Clark *et al.*, 2002). This means that on the old alluvial soil, 66% and on the residual soil 77% of the ecosystem carbon is stored in the soil organic matter. This proportion of belowground carbon stocks is substantially higher than numbers previously published for tropical forests. There are two reasons for this. First, the measured carbon stocks of this tropical wet forest are low compared to numbers for tropical moist forests published for the Amazon basin; this is mainly a result of the different allometric biomass equations between tropical wet and moist forests (Clark & Clark, 2000).

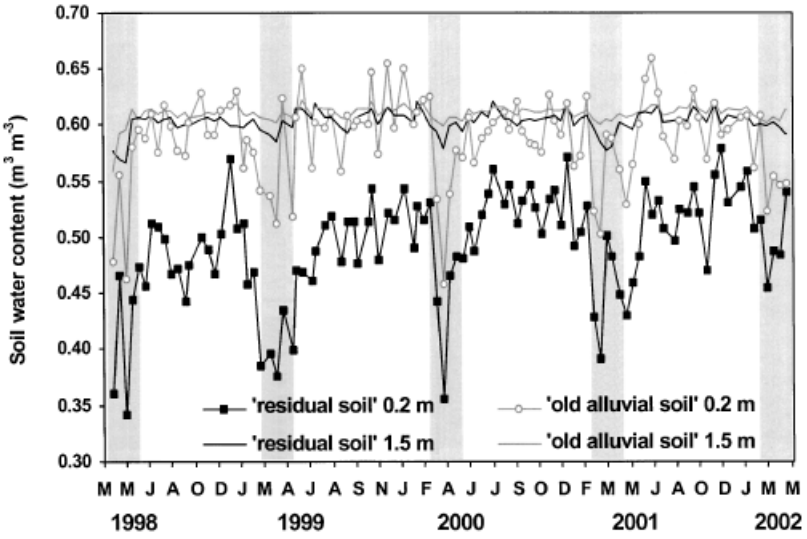

Fig. 4 Volumetric soil water content over a 4-year period at depths of 0.2 and 1.5 m, in old alluvial and residual soils under old-growth tropical wet forest at La Selva, Costa Rica.

The second reason is that the total amount of carbon in the soil of this tropical wet forest is about twice as high as the carbon stocks typically reported from the tropical moist forests in the Amazon basin. To illustrate this, Trumbore *et al.* (1995) measured 168 Mg C ha^{-1} down to 3 m depth and Sommer *et al.* (2000) reported 143 Mg C ha^{-1} down to 3 m, in both cases for Oxisols below forest in the state of Pará, Brazil. This is 46–71 Mg C ha^{-1} less than in La Selva's old alluvial soils and less than 50% of the C stock in our residual soil sites. The reason for the higher C stocks in our Costa Rican sites may lie in the life zone differences between sites (tropical moist forest in eastern Amazonia, tropical wet forest at La Selva). In his review, Post *et al.* (1982) found that the mean soil carbon density down to 1 m depth in tropical wet forest was almost double that found in tropical moist forest. This corroborates well with the difference between our residual soil C stocks down to 3 m depth and the C stocks reported by Trumbore *et al.* (1995) and Sommer *et al.* (2000).

In our data, soil type explained 68% of the variance of the carbon stocks. The parent materials of both the old alluvial and residual soils at La Selva have a very similar mineralogy; their main difference is caused by the difference in age (Sollins *et al.*, 1994; Kleber *et al.*, in press). If we consider the old alluvial and residual soils as being part of the same weathering chronosequence, then a comparison of C-stocks at different depths may reveal the long-term potential for C-sequestration in these soils below old-growth forest (Schlesinger, 1990; Fig. 1). This comparison indicates that the largest potential for C-sequestration is found in the subsoil, although the residual soil also has greater C stocks in the top meter. On a yearly basis, such C sequestration would be likely to be quite low. If we assume an age difference between the two soil types of about 10^6 years, and steady C accumulation in the soil over time, the long-term C sequestration potential would be only in the order of magnitude of about 160 g C ha^{-1} yr^{-1} (= 0.00016 Mg C ha^{-1} yr^{-1}). This rate is several orders of magnitude lower than the net C-sequestration rates (NEE) that have been attributed to some Amazonian forests based on eddy flux studies (Grace *et al.*, 1995; Mahli *et al.*, 1998).

Our results show that at La Selva, substantial soil carbon stocks exist below 1 m depth. Nepstad *et al.* (1994) reported similar results for their study site in the eastern Brazilian Amazon. They found that the forest soil below 1 m contained more carbon than the top meter, and they attributed these large subsoil carbon stocks to the deep root systems that characterize the tropical moist forests in large areas of the Amazon Basin; deep roots play an important role in these areas in maintaining dry season canopy greenness and evapotranspiration. In contrast, our tropical wet forest study site does not suffer from seasonal drought (Fig. 4), and we have found low total root biomass below 2 m depth (Table 5). Deep roots are therefore not a likely cause of the large C stock that we measured below 1 m depth in our soils. An important difference between our site and large parts of the Amazonian Basin is that, at La Selva, the average annual rainfall is about twice the average annual evapotranspiration (Sanford *et al.*, 1994). This means that about 2000 mm of rain drains through the soil profile each year, whereas in large parts of the Amazon basin such drainage through the soil is

much lower. This results at our sites in a net DOC transport of about 0.05 Mg C ha^{-1} yr^{-1} through the soil below 1.0 m depth (Schwendenmann, 2002). At the same time, DOC sorption isotherms showed a high affinity for DOC: between 1.0 and 3.0 m depth, the partition coefficients of the DOC sorption isotherms (that is the slope of the sorption isotherm and a measure of the affinity of the soil for DOC adsorption) were between 0.8 and 0.9 (Schwendenmann, 2002). These partition coefficients are higher than any of the partition coefficients published by Moore *et al.* (1992) who measured DOC sorption isotherms for 48 soil samples of a wide variety of soils. With DOC leaching rates of 0.05 Mg C ha^{-1} yr^{-1}, and a long-term C sequestration of 0.00016 Mg C ha^{-1} yr^{-1} (over a period of 10^6 years, see above), the net adsorption has to be only 0.32% of leached DOC to result in the high SOC stocks measured at our sites. We hypothesize that this process has contributed to the large carbon stocks below 1 m depth at La Selva.

Effects of land-use change on C stocks

Our data indicate that pasture establishment led to contrasting changes in carbon stock between soil types and between top- and subsoil. The increase in soil C-stocks in the topsoil (0–0.3 m depth) of the pastures on the old alluvial soil contrasts with the lack of change in soil C-stocks in the topsoil of the residual soil pastures. This difference may be mainly attributed to the expected differences in productivity of the pastures established on these soils, given their differences in soil fertility. In a period of about 25 years, considerably more pasture-derived carbon was added to the old alluvial sites (32 Mg C ha^{-1}) than to the residual sites (24 Mg C ha^{-1}). At La Selva, we found no changes in total carbon stocks for the soil horizons between 0.3 and 1.0 m depth. Surprisingly, we did find changes in soil C stocks below 1 m depth in both soil types: in both, total C-stocks below 1 m were substantially lower in the pastures compared to the forest sites (Fig. 2). This shows that a considerable part of the subsoil carbon can be mobilized within 25 years after forest conversion for pasture. For the residual soil, this labile carbon was about 20% of the total subsoil C stock of the old-growth forest. For the old alluvial soil, the net loss of C_3-derived carbon was even higher. In their study, Trumbore *et al.* (1995) used a simulation model to calculate the proportions of 'active', 'slow' and 'passive' carbon in the forest soil. Their best-fit simulation indicated that only 1% of the SOC at 1–3 m should be considered 'active', and that 14–19% should be considered 'slow' carbon (leaving 80–85% of total SOC in the 'passive' or recalcitrant class). In both soils, we found only quite small amounts of C_4-derived carbon below 1 m depth (4 Mg C ha^{-1} at 1–4 m in the residual soil and 3 Mg C ha^{-1} at 1–3 m in the old alluvial soil). This may be explained by the limited depth to which roots of these unproductive grasses can grow.

Care should be taken when using the change in ^{13}C to estimate the net changes in forest- (C_3) and pasture-derived (C_4) carbon, because pastures can also contain abundant C_3 herbs and bushes (Trumbore *et al.*, 1995). Although C_4 grasses currently dominate the vegetation at our sites, this is no guarantee that this has always been the case since forest clearing. The addition of recent C_3 carbon would mean that our calculated losses of forest-derived carbon and the calculated addition of pasture-derived carbon are both lower limits. This would mean that the size of the active and slow carbon pools could be even higher than we have estimated here.

Microbial activity in forest soils

With the SIR method, we infer the relative activity levels of active glucose-responsive microbes rather than the respective microbial biomass, because we as yet lack independent data from our site for a SIR/biomass calibration. Although traditionally it is assumed that the microbial activity is absent or insignificant below the topsoil, Richter & Markewitz (1995) reported considerable amounts of bacteria and fungi in a deeply weathered temperate-zone Ultisol. Our results provide clear evidence that this can also be the case for soils in tropical lowlands. Although we consistently measured the highest GMRA in the topsoil, we were able to detect microbial activity with the SIR method throughout all soil profiles in our study. Although the mass-based GMRA values from the subsoil were 20–30 times lower than those from the topsoil, the importance of GMRA at depth becomes apparent when this index is assessed on an area basis (Fig. 3). The amount of GMRA in the topsoil (0–0.3 m depth) of the forest old alluvial soil at La Selva was only about 50% of the total amount of glucose-responsive microbial activity detected over the whole soil profile. For the residual soil, this number was even lower (about 40%). The significant levels of microbial activity in the subsoil indicated by the SIR data are consistent with the CO_2 concentration profiles that we have independently measured in the forest soils. During a 2-year period of monitoring of CO_2 concentrations down the soil profiles at the old-growth forest sites, the highest CO_2 concentrations that we measured were consistently at the lowest sampling depth, 3.5 m in the residual soils and 2.5 m in the old alluvial soils (Schwendenmann *et al.*, 2003). That the highest CO_2 concentrations in the soil air space are

always sampled at the lowest depth can only be explained if there is a CO_2 source at or below the lowest sampling depth. The depleted stable isotope signature of this subsoil CO_2 points to a biological CO_2 source (E. Veldkamp, unpublished data), and microbial activity is therefore the most likely source of this deep CO_2.

Effects of land-use change on microbial activity

Microbial biomass, as part of the 'active' soil organic matter, reacts more rapidly to changes in land use and management than does the total soil C stock, and thus it has been considered to be a sensitive indicator for changes in soil organic matter (Powlson *et al*., 1987). In our study, the pasture sites had 30% (old alluvial soil) to 50% (residual soil) greater microbial activity than that of the forest sites. This difference was exclusively caused by different activity levels in the topsoil. The increased glucose-responsive microbial activity in the pasture topsoil may be related to a change in microbial community composition with the transition from forest to pasture. In a study in tropical Hawaii, Nusslein & Tiedje (1999) found a significant shift in the soil bacterial community associated with the forest-to-pasture transition. The higher pH in the pasture soils at La Selva (Table 1) may have provoked a shift from a fungal-dominated microbial community in the forest to a more bacterial-dominated community in the pasture sites, and such a shift could have produced the increased microbial activity.

Implications for the role of soils of tropical wet forests in the global carbon cycle

When Nepstad *et al.* (1994) reported that soil carbon stocks in deeply weathered soils in Eastern Amazonia are large and may be affected by changes in land use, they limited their conclusions to tropical evergreen forests that need deep soil water during the dry season. The input mechanism that they proposed for soil carbon below 1 m depth was the activity of deep roots that extract water during the dry season. Our results show that large stocks of soil carbon can also occur in deeply weathered soils below tropical wet forests that lack a clear dry season (at the 'wet' side of the rainfall spectrum for tropical forests). However, at our study site, the high water content throughout 4 years of measurements (Fig. 4) demonstrated that this forest does not depend in the dry season on deep roots to stay evergreen. While the contribution of root biomass below 1 m depth is less than 1% of the total root biomass, soil carbon stocks below 1 m depth contribute between 42% (old alluvial soil) and 46% (residual soil) of the total soil carbon. Although we cannot exclude deep roots as a source of this deep carbon, they are a less likely explanation at La Selva than at the study site of Nepstad *et al.* (1994). We propose that in the tropical wet forest at La Selva, where precipitation exceeds evapotranspiration, vertical transport of DOC followed by adsorption deep in the profile is the main mechanism of C input to the subsoil. Our results show that a substantial part of this deep carbon can be mobilized in about 25 years if this forest is cleared for pasture. A possible mechanism for this mobilization may be a diminished DOM adsorption capacity at higher pH (Kalbitz *et al*., 2000). In our study, this C loss from the subsoil affected the overall soil C balance in such a way that any increase in topsoil C stocks below pasture was more than offset by the C loss in the subsoil after forest clearing. How large a region in the tropics might be affected by similar processes? In Central and South America, the area where deeply weathered soils (Oxisols and Ultisols) occur and where precipitation exceeds 2500 mm is about 1.9 million km^2 (Fig. 5). Currently, the majority of this area is still below the tropical wet forest. Forest clearing in this area may be producing unexpectedly high C losses from the subsoil similar to those documented in this study.

From our results at La Selva, we cannot determine whether the subsoil of the studied soil types presently acts as a carbon source or sink. It is clear that on both soil types in our study sites, net losses of total organic carbon have followed forest clearing; however, the presence of C_4-derived carbon below 1 m depth in both soil types also indicates that new soil carbon has been sequestered since pasture formation. At this point, we cannot say whether this C sequestration has now reached the maximal levels possible for these soils or whether it is continuing. To address these critical questions, there is a clear need to carry out long-term process-level studies of the effects of land-use change on carbon storage in representative tropical systems.

Our results and earlier findings by Nepstad *et al.* (1994) demonstrate that we have to rethink sampling strategies when studying soil processes and the effects of land-use changes in deeply weathered soils. This is not only true for areas with a pronounced dry season, but also for areas below the tropical wet forest. When studies of the effects of land-use change on the global C cycle are limited to the topsoil, we could draw incorrect conclusions. Processes in the subsoil may contrast strongly with those in the surficial layer. Our findings also show that more than 50% of soil microbial activity may be found in the subsoil, indicating that a study of the topsoil gives an incomplete picture at best. We conclude that the results of global change models should be questioned as long as carbon cycling in the

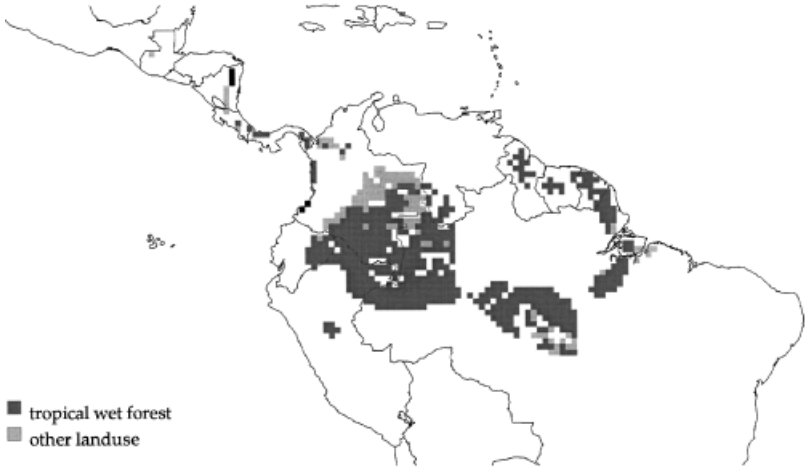

Fig. 5 Areas in Central and South America where deeply weathered soils (Oxisols and Ultisols) occur (FAO, 1996) and where annual precipitation exceeds 2500 mm (Leemans & Cramer, 1991). Black: areas currently still under tropical wet forest; gray: areas where forest has been cleared (World Conservation Monitoring Centre, 1997).

subsoil of deeply weathered soils in the tropics is not explicitly taken into account.

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