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SOIL CARBON DIFFERENCES AMONG FOREST, AGRICULTURE, AND SECONDARY VEGETATION IN LOWER MONTANE ECUADOR

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Abstract. In the lower montane region of northwestern Ecuador, forest clearing for sugar cane and pasture production occurs simultaneously with recolonization of secondary forest vegetation on abandoned agricultural lands. We estimated the loss of forest-derived soil C (light in ^{13}C) and the accumulation of C from replicate sugar cane and pasture vegetation (heavy in ^{13}C) using a stable C isotope technique. We also measured differences in the proportion of soil C derived from C_3 and C_4 plants across a land-use progression from agricultural fields through successional communities and undisturbed forest. Total soil C was 23 Mg/ha lower in the upper 30 cm following 50 yr of sugar cane production (24% decrease) compared to old-growth forest. The net change (-0.4 Mg·ha^{-1}·yr^{-1}) in soil C consisted of 1.3 Mg/ha annual losses of original forest C and 0.9 Mg/ha annual gains of C from sugar cane. After 15 yr beneath pasture, soil C was 11 Mg/ha less in the upper 30 cm than beneath forest (12% decrease). During that period, 33% of the original forest C was lost, compared to 68% released during 50 yr of sugar cane cultivation. Rate of forest C loss, C_4-C accumulation, and net soil C change differed little between two distinct pasture types. *Setaria sphacelata* pasture and a traditional mixed-species pasture both contained more total soil C and added C_4-C more rapidly than sugar cane. Under second-growth forest, soil C increased by 1.9 Mg·ha^{-1}·yr^{-1}, the result of a 3 Mg/ha annual increase in C_3 carbon and a 1.1 Mg/ha annual loss of C_4 carbon. The total soil C pool returned to preclearing levels within 20 yr. While widespread reforestation may be thwarted by high demands for land in northwestern Ecuador, agricultural land-use options exist that can contribute to increased soil C stocks.

Key words: deforestation; Ecuador; pasture; secondary forest; Setaria sphacelata*; soil carbon sequestration; soil organic matter; stable carbon isotopes; sugar cane agriculture.*

Introduction

Soils contain 75% of the terrestrial C inventory (Houghton et al. 1985, Schlesinger 1986), and tropical soils contain 32% of the global soil carbon (Eswaran et al. 1993). It follows then that land-use change that influences soil C storage and release within the tropics can have large implications for global C cycling. Changes in soil C following tropical deforestation have become an international policy concern in terms of both sustained production at a local or regional scale (Tiessen et al. 1994) and the global consequences relating to increased emissions of CO_2 from terrestrial systems (Houghton 1991, IPPC 1994).

Conversion from native forest to agricultural land has varying influence on soil C inventories, depending on the type of forest ecosystem undergoing change and the postconversion land management. In tropical America, transition from forest to cropland typically reduces soil C by 20–50% (Detwiler 1986, Mann 1986, Eswaran et al. 1993). Formation of tropical pasture typically results in 18–20% reductions of soil C (Veldkamp 1994, Fearnside and Barbosa 1998). However, in some cases where pastures are managed under ideal conditions, soil C can increase 15–50% (Trumbore et al. 1995, Neill et al. 1996).

While agricultural conversion continues to threaten tropical forests, a large proportion of previously cleared land now abandoned from agriculture has been revegetated by secondary forest (Moran et al. 1994, Skole et al. 1994). Carbon sequestration within second-growth biomass and soils may partially offset C emissions associated with forest clearing and other land-use practices (Lugo and Brown 1992, Houghton et al. 1993). In their studies of Puerto Rican second-growth forest, Brown and Lugo (1990) estimated that soil C stocks increase 0.5–2.0 Mg·ha^{-1}·yr^{-1} and are restored to original forest levels within 40–50 yr. *Eucalyptus saligna* plantations growing on abandoned Hawaiian sugar cane fields returned soil C to within 12% of native forest levels after a decade (Bashkin and Binkley 1998).

Analysis of the isotopic composition of soil C has greatly improved our ability to investigate soil C dynamics (Balesdent et al. 1987, Vitorello et al. 1989, Cerri et al. 1991). Land-use changes that convert C_3 vegetation (i.e., forest) to C_4 crops or pasture alter the isotopic signature of the litter inputs, resulting in

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in situ labeling of soil organic matter (Balesdent et al. 1987). Comparison of C isotopes beneath original forest and land conversion sites allows simultaneous measurement of loss of original soil C and sequestration of C inputs. The converse is possible where C_3 vegetation replaces either natural (Martin et al. 1990, Trouve et al. 1994) or cultivated (Jastrow et al. 1996) C_4 communities.

Although there have been numerous applications of stable isotope techniques to evaluate land-use change in the lowland tropics, the montane tropics and in particular the volcanic soils of these regions have not been studied. We examined total soil C and its isotopic composition in lower montane forest, in C_4 crop and pastures, and in secondary shrubland and forest in montane areas of northwestern Ecuador. While the general pattern of land use in this region is similar to that found throughout the tropics, the naturally high soil C content of these volcanic soils makes questions about the effects of changing land management on soil C stocks especially interesting. Trials that monitor change following land conversion require decades to provide conclusive results. On the other hand, studies that compare contemporary land-use types provide more timely results, but are subject to the risk of confounding natural spatial variation with differential effects of land conversions. In this study, we used the latter approach, comparing replicates of existing land-use patches; we minimized the risks through careful site selection.

METHODS

Study site

This research was carried out on the western slope of the Ecuadorian Andes (00°05′ N, 78°37′ W) at 1400 m elevation. The study site was located in tropical lower montane forest (Grubb 1977) within the Maquipucuna Forest Reserve. Average annual precipitation at a nearby ($<$10 km) meteorological station is 3200 mm (INHERI 1987). Average daily minimum and daily maximum air temperatures were 17° and 26°C, respectively.

Soils within the Maquipucuna reserve and surrounding areas developed from andesitic volcanic ash deposited 2500 years ago (Papale and Rossi 1993). Allophane mineralogy dominates the young ash-derived soils as indicated by high 1-mol/L NaF pH and oxalate-extractable Si (Rhoades 1997). The region is characterized by high and seasonally uniform soil moisture and temperature regimes (perudic and isohyperthermic, respectively). Nearby soils of similar age, origin, and morphologic characteristics have been classified as Andic humitropepts (Beinroth et al. 1985).

Land-use sequence

The six vegetation types studied (sugar cane, *Setaria sphacelata* pasture, mixed-species pasture, shrub fallow, second-, and old-growth forest) are dominant features of the mid-elevation region of northwestern Ecuador. During most of the 20th century, sugar cane production has dominated the agricultural economy of the mid-elevation region of northwestern Ecuador (Wunder 1996). In the past two decades, new roads have improved access to isolated mountain valleys and clearing for cattle pasture has become the leading source of land conversion (Southgate and Whitaker 1992, Wunder 1996). Currently, pasture and sugar cane cover approximately equal amounts of land within the lower portions of mid-elevation valleys. Old-growth forest fragments remain on steep slopes and the upper portions of the watersheds. Secondary shrub and forest vegetation is interspersed throughout the landscape.

We selected two replicate patches of each land-use type. We sampled side-slope positions with slopes ranging from 10 to 45%. Morphological and physical characteristics of the top 50 cm of soil indicate that soils at all 12 sites formed from the same ash deposit (Rhoades 1997). Forest, pasture, and secondary vegetation replicates do not form a spatially contiguous series of vegetation types, but are interspersed within a 1-km² area of the Maquipucuna reserve. Active sugar cane fields were sampled 5 km from the reserve at equal elevation.

We studied two distinct pasture types: pure *Setaria sphacelata* [(Schumach.) Stapf & C.E. Hubb.] and mixed-species pastures. All pasture sites were established between 1980 and 1986 after forest clearing and slash burning. Before 1970, portions of the pasture sites underwent 3–4 mo periods of maize (*Zea mays*) interspersed with 2–4 yr forest fallow. The sites were cropped $\leq$5% of the 50 yr prior to pasture conversion. *Setaria* is an introduced C_4 grass that forms tussock grasslands with a thick surface root mat. Planted *Setaria* pastures have become the dominant grazing system on mid-elevation slopelands of western Ecuador since their introduction ~1980. Traditional pastures in the lower montane region contain a mixture of C_4 grasses and invading C_3 forbs and shrubs. The dominant grasses include *Digitaria sanguinalis* (L.) Scopoli, *Panicum polygonatum* Schrader, and *Paspalum paniculatum* L. Traditional pasture grasses are rhizomatous, but unlike *Setaria*, do not form tussocks or a dense root layer. The sugar cane (*Saccharum* sp.) fields that we studied were hand-planted and hand-harvested and were not fertilized or burned. Sample cane plots have been under continual production for 50 yr. Prior to establishing sugar cane, the fields were either banana plantations or forest vegetation.

In the lower montane region, secondary vegetation re-establishes rapidly after abandonment of cropland or traditional pastures. Within 5 yr, fallow fields are occupied by shrubs (*Baccharis*, *Piper*, *Vernonia*). Closed-canopy forest dominated by *Nectandra acutifolia* [(K & P) Mez, Lauraceae] is formed within 10–15 yr. We sampled 5–10 yr old shrub vegetation and 15–20 yr old secondary forest plots that were abandoned from sugar cane production or traditional pasture. We were unable to determine the duration of agricultural activities prior to abandonment.

Sampling and analysis

At two replicate patches of the six vegetation types, soil was sampled at 0–5 and 5–15 cm depths in five randomly selected sampling points; deeper soil layers (15–30, 30–60, and 60–100 cm) were sampled at three of these points. Deeper samples were removed from the sides of 1 m deep soil pits, in order to reduce compaction and contamination among soil layers. Soil samples were mixed, air-dried and passed through a 2-mm sieve to remove coarse fragments and roots. Bulk density was measured on replicate field-moist cores (7.5 cm diameter) sampled from each depth ($n = 10$ for two upper layers; $n = 6$ for other layers). Soil pH was measured in suspensions with a 1:2 ratio of air-dried soil to water. Roots were sampled from two replicate cores (7.5 cm diameter) from each soil depth. Root samples were hand-sorted into fine (<1 mm) and coarse (1–3 mm) size classes. In situ soil respiration was analyzed during a 24-h incubation using 0.5 mol/L NaOH in static chambers (Zibilske 1994).

Soil, litter, and roots samples were oven-dried at 60°C and ground with a ball mill prior to analysis. Soil and tissue samples were combusted at 900°C in a sealed quartz tube with a CuO catalyst. The CO_2 released during combustion was purified and analyzed with a Finnigan MAT Delta-S mass spectrometer (Finnigan, Bremen, Germany). Carbon isotope results are expressed in $\delta^{13}C$ notation relative to the international Pee Dee Belemnite $CaCO_3$ standard (Boutton 1991). Standard deviation for repeated measurements of a homogenized standard sample was $\pm 0.2‰$ ($n = 25$). Total C content of soil and plant tissue was determined using a Carlo Erba model 1500 CN analyzer (Carlo Erba, Milan, Italy).

Calculations and statistical analyses

Soil C stocks were calculated for each soil layer from bulk density and C concentration data. Due to increased bulk density in surface layers of managed sites, pasture and cane C stocks were corrected for vertical compaction (Davidson and Ackerman 1993, Veldkamp 1994). For these sites, the sample depth used to calculate soil C stocks was reduced proportional to the increase in bulk density relative to original forest.

In pasture and cane sites, the proportion of residual forest C (CC_3) and of C originating from C_4 vegetation (CC_4) was calculated using the $\delta^{13}C$ of soil, aboveground litter and root inputs from the following mixing models (Balesdent et al. 1987, Vitorello et al. 1989):

$$CC_3 = (\delta^{13}C_s - \delta^{13}CC_4)/(\delta^{13}CC_3 - \delta^{13}CC_4)$$

$$CC_4 = (\delta^{13}C_s - \delta^{13}CC_3)/(\delta^{13}CC_4 - \delta^{13}CC_3)$$

where $\delta^{13}C_s$ is the δ value of soil sampled in pasture or cane, $\delta^{13}CC_4$ is the δ value of C_4 litter inputs, and $\delta^{13}CC_3$ is the δ value of C_3 forest soil.

To calculate the increment in C_3-derived soil C after abandoning agriculture, the δ value of soil and litter from successional vegetation was compared to the isotopic signature of sugar cane and traditional pasture soils.

The effect of land use on soil $\delta^{13}C$, total soil C stocks and C_3- and C_4-derived soil C was tested (six vegetation types with two sites per vegetation type) by analysis of variance design with replicates nested within land-use type (SPSS 1997). Orthogonal contrasts were used to compare old-growth forest with sugar cane and to compare successional vegetation with sugar cane. Tukey's means comparison test (critical value: 0.05) was used to separate land-use effects.

RESULTS

Native forest

In old-growth lower montane forest, soil pH averaged 5.0 in the top 100 cm (Table 1). Bulk density increased from an average of 0.67 Mg/m^3 in the upper 15 cm to 0.84 Mg/m^3 in the 15–30 cm layer. Soil C averaged 6.5% and 2.7% in the 0–15 and 15–30 cm depths, respectively. The total C content in these layers was 61.4 and 34.1 Mg/ha (Table 2). The 30–100 cm depth of old-growth replicate 2 had much higher clay (Rhoades 1997) and bulk density, and lower percentage C (Table 1) than any other replicate. This forest replicate was on a steeper slope, and abrupt change in soil conditions in the lower profile delineates a substrate not found in the upper meter of any other site. Thus, the 30–100 cm depth of old-growth replicate 2 was excluded from calculations of C stocks or turnover.

The $\delta^{13}C$ value of forest litter ranged from $-29.2‰$ to $-29.0‰$ ($n = 10$). Surface soil $\delta^{13}C$ was $-27.6‰$ beneath old-growth forest and increased to $-25.6‰$ in the 15–30 cm layer (Fig. 1). There was an additional 3‰ enrichment in the 30–100 cm layer. Typically, there is a 2‰–3‰ enrichment of soil $\delta^{13}C$ with soil depth (Nadelhoffer and Fry 1988). At our site, the cause of greater isotopic enrichment at depth is unknown, but may be associated with burial of organic matter or C_4 vegetation by volcanic tephra (Vitorello et al. 1989, Desjardins et al. 1994). Pottery shards found at lower depths of several sample pits indicate prior human occupancy of the site. Due to concerns about incongruities at the lower soil levels, statistical inferences are restricted to the upper 30 cm of the soil profile.

Agricultural sites

Soil pH did not differ between forest and agricultural sites (Table 1). Surface bulk density was 37%, 32%, and 26% higher beneath sugar cane, mixed-species, and *Setaria sphacelata* pastures, respectively, compared to native forest. Sugar cane and pasture soils had significantly higher bulk density in the upper 30 cm compared to old-growth forest ($P < 0.01$).

TABLE 1. Soil pH, bulk density, and soil carbon for the land-use type samples.

Vegetation type	Replicate	Depth (m)	pH (1:2 in water)	Bulk density (Mg/m^3)	Soil carbon (%)
Old-growth forest	1	0–15	4.8 (0.2)	0.63 (0.0)	6.17 (0.6)
		15–30	4.7 (0.3)	0.77 (0.0)	2.75 (0.6)
		30–100	5.3 (0.3)	0.99 (0.1)	1.97 (0.5)
	2	0–15	5.4 (0.3)	0.70 (0.0)	6.89 (0.7)
		15–30	5.1 (0.6)	0.91 (0.0)	2.67 (0.2)
		30–100	4.8 (0.3)	1.20 (0.1)	0.46 (0.2)
Second-growth forest	1	0–15	5.4 (0.2)	0.68 (0.0)	9.48 (0.7)
		15–30	5.2 (0.2)	0.94 (0.0)	2.30 (0.1)
		30–100	4.9 (0.1)	0.84 (0.1)	2.20 (0.1)
	2	0–15	4.7 (0.1)	0.78 (0.0)	5.50 (0.2)
		15–30	4.8 (0.1)	0.95 (0.0)	2.60 (0.2)
		30–100	5.3 (0.1)	1.06 (0.0)	1.10 (0.2)
Shrub regeneration	1	0–15	4.8 (0.0)	1.05 (0.1)	4.80 (0.6)
		15–30	4.9 (0.0)	0.98 (0.0)	2.31 (0.1)
		30–100	5.0 (0.0)	1.01 (0.0)	1.65 (0.3)
	2	0–15	5.2 (0.1)	0.85 (0.1)	5.84 (0.8)
		15–30	5.0 (0.1)	0.97 (0.0)	2.65 (0.2)
		30–100	5.3 (0.1)	1.03 (0.0)	1.47 (0.5)
Sugar cane	1	0–15	5.2 (0.1)	0.86 (0.0)	4.69 (0.2)
		15–30	5.3 (0.1)	1.06 (0.0)	2.31 (0.1)
		30–100	5.6 (0.1)	1.06 (0.0)	1.88 (0.4)
	2	0–15	5.5 (0.0)	0.96 (0.0)	4.41 (0.2)
		15–30	5.5 (0.1)	1.08 (0.0)	2.34 (0.3)
		30–100	5.7 (0.1)	1.15 (0.0)	1.33 (0.2)
Setaria pasture	1	0–15	5.1 (0.1)	0.76 (0.0)	6.12 (0.5)
		15–30	5.2 (0.1)	0.93 (0.0)	3.30 (0.3)
		30–100	5.5 (0.3)	1.02 (0.0)	1.73 (0.2)
	2	0–15	5.1 (0.1)	0.91 (0.0)	5.11 (0.3)
		15–30	5.2 (0.2)	1.06 (0.0)	2.26 (0.1)
		30–100	5.3 (0.1)	1.07 (0.0)	1.84 (0.3)
Mixed-species pasture	1	0–15	5.0 (0.0)	0.88 (0.0)	5.74 (0.9)
		15–30	4.8 (0.2)	1.00 (0.0)	2.37 (0.2)
		30–100	5.3 (0.1)	1.10 (0.0)	1.29 (0.4)
	2	0–15	4.9 (0.0)	0.87 (0.0)	4.99 (0.5)
		15–30	4.9 (0.0)	0.89 (0.1)	2.64 (0.2)
		30–100	5.5 (0.1)	1.07 (0.0)	1.48 (0.3)

Note: Values are mean (1 SE); $n = 5$ for 0–15 cm, and $n = 3$ for lower layers.

Setaria and sugar cane litter δ^{13}C values were −11.5‰ and −13.9‰, typical for C_4 plant tissue. Soil C in the top 5 cm of *Setaria* and mixed-species pastures was 5.5‰ and 3.5‰ more enriched in δ^{13}C than the forest soil (Fig. 1). In the upper 15 cm, both pasture types became rapidly depleted in ^{13}C. In the lower profile, the mixed-species pasture converged with the δ^{13}C of the forest soil, while *Setaria* soil was more enriched. The δ^{13}C of sugar cane soil averaged −23‰ to −22.5‰ in the top 30 cm, significantly enriched in δ^{13}C compared to forest vegetation throughout the sampled profile ($P < 0.001$). Old-growth forest soil had significantly lower δ^{13}C in the top 15 cm than the three agricultural land-use types ($P < 0.001$; Table 3).

Sugar cane soils contained 18 Mg/ha less soil C in the upper 15 cm than native forest (Table 2; $P = 0.00$). In the 15–30 cm depth, sugar cane soils contained 5 Mg/ha less soil C. The net decrease in soil C in the top 15 cm resulted from a 26 Mg/ha addition of C_4-C from sugar cane and a 43 Mg/ha loss of forest-derived C_3-C. Assuming 50 yr since conversion, the net annual loss was 0.35 Mg C/ha in the 0–15 cm layer; 0.5 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of added sugar cane C and 0.85 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of lost forest C. For the entire upper meter, sugar cane added 2.5 $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, and 3.2 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ of native C was lost.

Setaria and mixed-species pastures also accumulated C_4-C, while releasing native C. During the 15 yr since conversion from forest, *Setaria* added an average of 12 Mg/ha of C_4-C, while 22 Mg/ha of forest C was lost. This represents a 15% decrease in total soil C in the upper 15 cm, an annual loss of 0.6 Mg/ha. Mixed-species pasture contained 10 Mg C/ha or 17% less soil C than forest in the top 15 cm. Accumulation of C_4-C in the upper meter averaged 4.3 and 3.0 $\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ beneath *Setaria* and mixed pasture. The pasture and sugar cane sites contained significantly more C_4-C ($P < 0.001$), less C_3-C ($P < 0.001$), and less total C ($P < 0.01$) than old-growth forest (Table 3).

The C content of *Setaria* fine roots was 7.5 Mg/ha in the top meter of soil (Table 4). This was 5–7× more C than found in root systems of other land-use types ($P < 0.05$). In the lower 70 cm of the profile, sugar cane and *Setaria* both contained 2–4× more root C

TABLE 2. Contribution of C_3- and C_4-derived C to SOM pools beneath forest, sugar cane, and pasture.

			Soil C derived from:			Annual increment			
Vegetation type/age	Replicate	Depth (cm)	C_3 ($Mg \cdot ha^{-1} \cdot depth^{-1}$)	C_4 ($Mg \cdot ha^{-1} \cdot depth^{-1}$)	Total ($Mg \cdot ha^{-1} \cdot depth^{-1}$)	C_3 SOM ($Mg \cdot ha^{-1} \cdot yr^{-1}$)	C_4 SOM ($Mg \cdot ha^{-1} \cdot yr^{-1}$)	Net C ($Mg \cdot ha^{-1} \cdot yr^{-1}$)	Total C change (Mg/ha)
Old-growth forest (>50 yr)	1	0–15	56.3	0.0	56.3	0.0	0.0	0.0	0.0
		15–30	32.1	0.0	32.1	0.0	0.0	0.0	0.0
		30–100	131.6	0.0	131.6	0.0	0.0	0.0	0.0
		0–100	220.0	0.0	220.0	0.0	0.0	0.0	0.0
	2	0–15	66.6	0.0	66.6	0.0	0.0	0.0	0.0
		15–30	36.1	0.0	36.1	0.0	0.0	0.0	0.0
		30–100	34.1	0.0	34.1	0.0	0.0	0.0	0.0
		0–100	136.9	0.0	136.9	0.0	0.0	0.0	0.0
Sugar cane (50 yr)	1	0–15	19.6	24.6	44.2	−0.8	0.5	−0.3	−17.2
		15–30	14.9	13.6	28.5	−0.4	0.3	−0.1	−5.7
		30–100	50.9	86.6	137.5	−1.6	1.7	0.1	5.9
		0–100	85.4	124.8	210.2	−2.8	2.5	−0.3	−17.0
	2	0–15	16.8	26.6	43.4	−0.9	0.5	−0.4	−18.0
		15–30	10.5	19.1	29.7	−0.5	0.4	−0.1	−4.5
		30–100	27.9	77.9	105.8	−2.1	1.6	−0.5	−25.8
		0–100	55.2	123.7	178.9	−3.5	2.6	−1.0	−48.3
Setaria pasture (15 yr)	1	0–15	42.9	13.9	56.8	−1.2	0.9	−0.3	−4.6
		15–30	36.0	5.0	41.0	0.1	0.3	0.5	6.9
		30–100	82.8	37.7	120.5	−3.3	2.5	−0.7	−11.1
		0–100	161.8	56.6	218.4	−4.4	3.8	−0.6	−8.8
	2	0–15	36.3	11.2	47.5	−1.7	0.7	−0.9	−13.9
		15–30	22.4	6.3	28.8	−0.8	0.4	−0.4	−5.3
		30–100	82.0	53.7	135.7	−3.3	3.6	0.3	4.0
		0–100	140.7	71.2	212.0	−5.8	4.7	−1.0	−15.2
Mixed-species pasture (15 yr)	1	0–15	33.7	19.8	53.5	−1.8	1.3	−0.5	−7.9
		15–30	20.2	8.8	29.0	−0.9	0.6	−0.3	−5.1
		30–100	82.5	11.9	94.3	−3.3	0.8	−2.5	−37.3
		0–100	136.4	40.5	176.9	−6.0	2.7	−3.4	−50.3
	2	0–15	29.1	19.2	48.3	−2.2	1.3	−0.9	−13.1
		15–30	36.9	−4.4	32.5	0.2	−0.3	−0.1	−1.6
		30–100	73.8	34.7	108.5	−3.9	2.3	−1.5	−23.1
		0–100	139.8	49.5	189.4	−5.9	3.3	−2.5	−37.8

Notes: Values are means of $n = 5$ for 0–15 cm and $n = 3$ for other layers. C turnover is based on comparisons to the average of the two old-growth replicates for the top two depths and old-growth replicate 1 for the 30–100 cm depth.

than other vegetation types. Coarse roots (1–3 mm) represented <0.1% of total root biomass in *Setaria* pastures, but >50% of forest root systems.

Soil C efflux was 1.8× higher from *Setaria* and mixed pastures compared to old-growth forest (Table 4; $P = 0.00$). From sugar cane, respiration released 23% more C than the native forest ($P < 0.06$). Soil temperature was significantly higher in the agricultural sites and the shrub vegetation than beneath either forest type ($P < 0.05$).

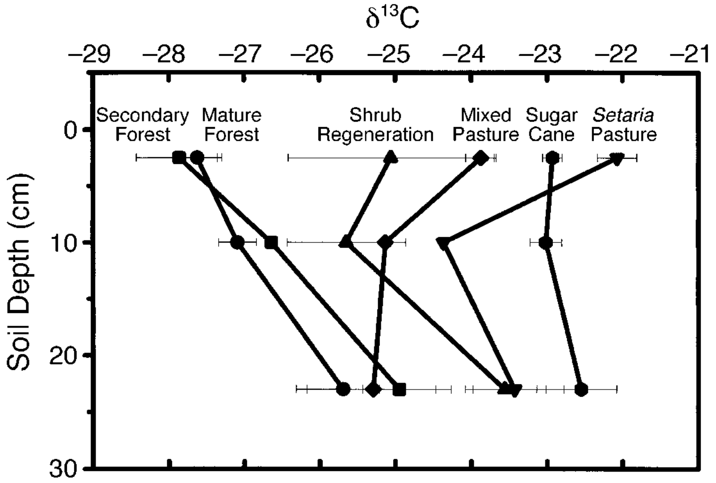

FIG. 1. Comparison of $\delta^{13}C$ profiles for six land-use types common to the lower montane region of northwestern Ecuador (0–30 cm depth). Data are means ±1 SE of two replicates per land-use type plotted at the midpoint of each sample layer.

TABLE 3. *F* ratios and significance for nested analysis of variance and orthogonal contrasts (0–15 cm depth).

Source of Variation	df	$\delta^{13}C$	Soil C Total	Soil C C_4-derived	Soil C C_3-derived
Nested ANOVA					
Vegetation	5	38.78***	10.90***	39.77***	35.83***
Replicate (vegetation)	6	2.28	3.81**	0.48	4.82**
Error	46				
Orthogonal contrasts					
Old-growth forest vs. cane and pasture sites	1	107.92***	11.25**	142.08***	86.41***
Sugar cane vs. shrub and forest sites	1	126.99***	22.78***	138.68***	115.32***

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Second-growth vegetation

In the second-growth vegetation plots, soil properties converged with those of the original forest. After 5–10 yr under shrub vegetation, the $\delta^{13}C$ value in the top 15 cm was within 2‰ of old-growth forest (Fig.1). Second-growth and old-growth forest sites had similar $\delta^{13}C$ values throughout the top 30 cm of the soil profile. Below 30 cm, soil of secondary vegetation plots was ^{13}C enriched, indicating sequestration of C_4-derived C.

As woody perennials recolonized abandoned agricultural land, new C_3-derived soil C apparently accumulated while the C_4-C sequestered during cropping was lost. Based on the assumption that sites originated from sugar cane or traditional pasture similar to those examined in this study, the top 15 cm of second-growth shrub and forest soils contained about one-third the C_4-C of sugar cane soil and about half the C_4-C of traditional pasture, respectively (Fig. 2). The proportion of soil C derived from C_4 inputs decreased from ~60% under sugar cane production to 20% and 15% beneath shrub and second-growth forest, respectively. Secondary forest contained 74 Mg C /ha in the upper 15 cm, 1.7 and 1.5× more than sugar cane and traditional pasture soil ($P < 0.05$). Shrub regeneration contained slightly more total C than sugar cane but did not differ from mixed pasture. Fine root C and soil respiration and temperature were intermediate between the old-growth forest and sugar cane or pasture (Table 4). Litter C inputs in shrub fallow and second-growth forest averaged 3.3 and 5.2 $Mg \cdot ha^{-1} \cdot yr^{-1}$ compared to 5.1 $Mg \cdot ha^{-1} \cdot yr^{-1}$ in old-growth forest (Rhoades 1997).

DISCUSSION

Land management and soil C

Conversion from forest to crop or pasture typically leads to soil C loss, though data vary widely. At this mid-elevation region of Ecuador, soil C was 24%, 14%, and 9% lower in sugar cane, mixed-species and *Setaria* pasture sites, respectively, than in old-growth forest (Table 3). Typically, crop production results in larger reductions in soil C than pasture (Detwiler 1986) due to increased soil disturbance and erosion losses. In this region, however, differences in carbon pools are not significantly different between pasture and sugar cane ($P > 0.05$), despite differences in time since conversion. Because of different management practices, the higher apparent rate of net annual C loss following conversion to pasture is difficult to compare directly to the 50-yr-old sugar cane sites. However, soil C pools typically change most rapidly soon after conversion (Chone et al. 1991, Veldkamp 1994, Trumbore et al. 1995) and pasture loss rates are likely to slow with time.

Carbon isotope analysis showed that soil C turnover rates were more dramatic than net soil C changes. *Setaria* and mixed pasture soils lost 36% and 49% of the original forest C soil from the top 15 cm. In sugar cane sites, 70% of the original forest soil C was lost over 50 yr. The soil C turnover rates in this Ecuadorian montane site agree with results from other tropical studies, especially those also on high soil C volcanic soils. At 1700 m on Hawaiian volcanic tephra, Townsend and co-workers (1995) observed a 48% loss of forest-derived C in the top 20 cm of a 40–50 yr old pasture. Veldkamp (1994) observed comparable soil C losses in Costa Rican pastures on Andisols. Brazilian Ultisols with naturally low soil C content lost 8–35% of their original forest C in 20 yr (Neill et al. 1997). Brazilian Oxisols lost 40% of the original forest C following 50 yr of cropping with sugar cane (Vitorello et al. 1989).

Despite much higher fine root biomass in *Setaria* pastures, soil C inventories and turnover rates differed little from mixed-species pastures. The 7× higher *Setaria* root C content and equal respiration rates and soil temperature (Table 4) suggest that more C is available to be sequestered into soil C. Accumulation of C_4-C was slightly higher in the upper 30 cm of mixed pasture, but was twice as high at 30–100 cm in *Setaria* pastures (Table 2). At the lower depth, *Setaria* and sugar cane contain 3 and 8% less total soil C than native forest, compared to 23% less in mixed-species pasture. Further research is needed to understand how pasture grasses with different above- and belowground biomass influence soil C inventories.

TABLE 4. Fine (<1 mm) and coarse (1–3 mm) root carbon, soil respiration, and temperature (0–5 cm depth).

Vegetation type	Depth	Root C Fine (Mg/ha)	Root C Coarse (Mg/ha)	Soil respiration ($kg\ C \cdot ha^{-1} \cdot d^{-1}$)	Soil temperature (°C)
Old-growth forest	0–15	1.34 (0.2)	1.09 (0.3)	14.57 (1.3)	18.05 (0.2)
	15–30	0.28 (0.1)	0.51 (0.3)		
	30–100	0.30 (0.1)	1.03 (0.5)		
	0–100	1.91 (0.3)	2.63 (0.7)		
Second-growth forest	0–15	1.07 (0.1)	1.16 (0.3)	20.00 (1.0)	18.15 (0.2)
	15–30	0.15 (0.1)	0.22 (0.1)		
	30–100	0.12 (0.0)	0.17 (0.1)		
	0–100	1.34 (0.2)	1.54 (0.3)		
Shrub regeneration	0–15	0.99 (0.1)	0.56 (0.2)	21.75 (0.8)	19.50 (0.3)
	15–30	0.17 (0.0)	0.05 (0.0)		
	30–100	0.24 (0.0)	0.24 (0.1)		
	0–100	1.38 (0.1)	0.81 (0.2)		
Sugar cane	0–15	0.84 (0.1)	0.34 (0.1)	17.91 (1.2)	21.65 (0.6)
	15–30	0.20 (0.0)	0.13 (0.0)		
	30–100	0.64 (0.2)	0.23 (0.1)		
	0–100	1.67 (0.2)	0.71 (0.2)		
Setaria Pasture	0–15	6.19 (1.4)	0.01 (0.0)	26.46 (1.2)	19.45 (0.6)
	15–30	0.68 (0.2)	0.00 (0.0)		
	30–100	0.66 (0.1)	0.00 (0.0)		
	0–100	7.53 (1.4)	0.01 (0.0)		
Mixed-species pasture	0–15	1.17 (0.4)	0.33 (0.1)	24.59 (1.5)	20.55 (0.5)
	15–30	0.24 (0.0)	0.03 (0.0)		
	30–100	0.22 (0.1)	0.02 (0.0)		
	0–100	1.63 (0.4)	0.37 (0.1)		

Notes: Values are means (1 SE). Data from replicate sites were pooled within each land use type.

Land management options

Our study suggests that on young volcanic soils in western Ecuador, two distinct land-use options may increase soil C pools. One option, conversion from sugar cane to pasture, maintains land in agriculture; the other returns agriculture land to forest.

Setaria pastures have surpassed traditional, mixed-species pastures in popularity due to ease of establishment, rapid growth, and resistance to weed invasion. Our results suggest that conversion from sugar cane to *Setaria* pasture may also increase soil C storage. Relative to the biomass C lost following forest clearing, the soil C difference between land-use options is small. In a region predominated by cleared lands, however, *Setaria* may provide a favorable agricultural option with regard to increasing soil C inventory.

Comparative studies have shown that well-managed pastures in Brazil (Trumbore et al. 1995) and high-yielding pastures in Colombia (Fisher et al. 1994) contain more soil C than associated degraded pastures or native savanna grasses may increase regional soil C. Likewise, Fisher et al. (1994) reported dramatic increases in soil C in sites converted from native savanna species to deep-rooted pasture grasses (26–70 Mg/ha after 3–9 yr). In eastern Amazonia, pastures receiving phosphorus fertilizer increase soil C inventories relative to unmanaged pastures (Trumbore et al. 1995), with the increase attributed to greater root production

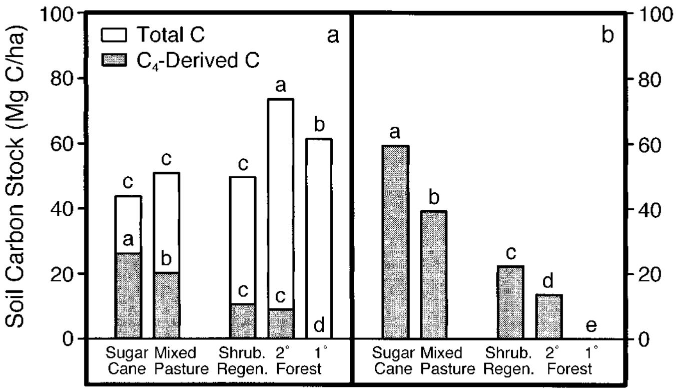

FIG. 2. (a) Total soil C and C_4-derived C stocks and (b) proportion of C_4-C beneath sugar cane, traditional pasture, successional vegetation, second-growth forest, and old-growth forest (0–15 cm soil depth). The C_4-derived soil C stocks of secondary vegetation were based on sugar cane values and were equal to values based on traditional pasture values. Data from two replicate sites are combined within each land-use type. The same letter above bars indicates that total soil C and C_4-C stocks and the proportion of C_4-C do not differ using Tukey's means comparison test (0.05 critical value).

in the managed pastures. Given that in Ecuador as in Brazil (Trumbore et al. 1995, Fearnside and Barbosa 1998), the vast majority of pastures are currently managed without fertilizer, increases in soil C storage may be possible through management.

Encouraging regrowth of secondary forest or establishing forest plantations is a second option for increasing soil C. Coupled with C sequestration within forest biomass, this option far exceeds the C storage potential of transforming cane to pasture. Our data demonstrate that second-growth forest soil C stocks are similar to levels found in native forest within two decades of abandoning sugar cane production or traditional pasture. Carbon in Ecuadorian second-growth forest soil exceeded that in sugar cane fields by 36 Mg/ha in the upper 30 cm, an estimated increase of 1.8 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$. There is similar evidence of soil C restoration under tropical forest plantations. Zou and Bashkin (1997) measured a 2.8 $\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$ increase in the upper 25 cm of Hawaiian *Eucalyptus* plantations growing on abandoned sugar cane land during the first decade after conversion. Cuevas and co-workers (1991) found that soil C content and vertical distribution was similar for Puerto Rican plantation and second-growth forests.

Land management objectives aimed at increasing C sequestration in tropical ecosystems favor increased reforestation (Montagnini and Porras 1998). In western Ecuador, concern for protection of faunal and floral biodiversity also advocates reforestation (Myers 1988, Dodson and Gentry 1991). Currently, however, $<10\%$ of the area cleared annually in the tropics is replanted (Bruenig 1996), and reforestation in Ecuador is rare. Our data suggest that even under socioeconomic conditions that preclude widespread reforestation, agricultural land-use options exist that can contribute to increased soil C stocks.

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