Biogeochemistry (2005) 72: 315–336
DOI 10.1007/s10533-004-0368-7

Regional variation in soil carbon and $\delta^{13}C$ in forests and pastures of northeastern Costa Rica

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Received 22 January 2004; accepted in revised form 13 April 2004

Key words: Costa Rica, Land-use change, Pasture, Soil carbon, Stable carbon isotopes

Abstract. Recent studies suggest that the direction and magnitude of changes in soil organic carbon (soil C) pools following forest-to-pasture conversion in the tropics are dependent upon initial soil conditions and local factors (e.g. pre-conversion soil C content, soil texture, vegetation productivity, and management practices). The goal of this study was to understand how landscape-scale variation in soil-forming factors influenced the response of soil C pools to forest clearing and pasture establishment in northeastern Costa Rica. We measured soil C and its stable isotopic composition in 24 paired pasture and reference forest sites distributed over large gradients of edaphic characteristics and slope throughout a 1400 km^2 region. We used the large difference in stable C isotopic signatures of C3 vegetation (rain forest) versus C4 vegetation (pasture grasses) as a tracer of soil C dynamics. Soil C pools to 30 cm depth ranged from 26% lower to 23% higher in pastures compared to paired forests. The presence of non-crystalline clays and percent slope explained between 27 and 37% of the variation in the direction and magnitude of the changes in soil C storage following pasture establishment. Stable carbon isotopes ($\delta^{13}C$) in the top soil (0–10 cm) showed a rapid incorporation of pasture-derived C following pasture establishment, but the vegetation in these pastures never became pure C4 communities. The amount of forest-derived soil C in pasture topsoils (0–10 cm) was negatively correlated to both pasture age and the concentrations of non-crystalline iron oxides. Together these results imply that site factors such as soil mineralogy are an important control over soil C storage and turnover in this region.

Introduction

Soils contain the largest terrestrial carbon pool and it has long been recognized that land management activities and land-use changes impact soil C storage (Greenland and Nye 1959; Jenkinson and Rayner 1977). Earlier global scale assessments of changes in soil C storage have concluded that deforestation (defined here as the conversion of forests to pastures) in the tropics contributes a significant flux of carbon dioxide to the atmosphere as soil C pools decrease following clearing (Detwiler 1986; Melillo et al. 1996). However, field-scale studies have shown both increases and decreases in soil C storage following conversion of tropical forests to pastures (Allen 1985; Brown and Lugo 1990; Fisher et al. 1994; Trumbore et al. 1995), and recent literature syntheses suggest soil C inventories, on average, increase slightly following pasture establishment in the tropics (Veldkamp in press; Guo and Gifford 2002; Murty et al. 2002). The variable response of the soil C pool to forest clearing and pasture establishment implies that a greater understanding of regional soil carbon dynamics is necessary to better constrain global C budgets.

A number of mechanisms may determine the direction and magnitude of changes in soil C storage following conversion of forest to pasture. In areas where less productive forested sites are replaced with deep-rooted pasture grasses, soil C inventory may increase following deforestation due to increases in detrital carbon inputs (Fisher et al. 1994; Feigl et al. 1995; de Moraes et al. 1996; Bernoux et al. 1998). In other sites, the soil C inventory may decline with conversion from forest to pasture or agriculture, presumably due to lower carbon inputs, increased soil C mineralization as microclimatic conditions are altered by deforestation, or erosion (Veldkamp 1994; Johnson and Wedin 1997; Saikh et al. 1998). Last, altered microbial community size, composition and dynamics may impact the biogeochemical cycles of C, phosphorus and other nutrients in the soil, resulting in increases or decreases in soil C storage (Cleveland et al. 2003). Together these studies suggest that both initial site conditions and management practices determine the fate of soil C pools following pasture establishment.

In this study we investigated regional variability in the response of soil C pools to forest clearing and pasture establishment in northeastern Costa Rica. During the past five decades this region has undergone rapid land-use change with the dominant transition being the conversion of forests to pastures (Read et al. 2000). The area has large geographic gradients in edaphic properties such as soil C content, topographic relief, soil texture, and clay mineralogy (Powers and Schlesinger 2002a), and thus provides an excellent setting to examine the effects of site factors on soil C storage. We measured soil C and its stable isotopic composition ($\delta^{13}C$) in 37 pastures and 24 forest sites distributed throughout a 1400 km^2 region to understand how variation in site factors across the landscape influenced the response of soil C pools to forest clearing. We also assessed the usefulness of stable C isotopes as a tracer of soil C dynamics, because pasture forage species in the tropics are typically C4 grasses and have very different isotopic signatures than the C3 forests they replace. This approach is similar to that taken by de Koning et al. (2003) to investigate regional variation in soil C pools following secondary forest regrowth in Ecuador.

In order to estimate the effects of the conversion of forest to pasture on soil C storage, we used a ‘space for time substitution’. This approach explicitly assumes that each pair of sites was in equilibrium prior to deforestation and that the paired forest sites represent pre-clearing soil C in the pasture sites. It is often impossible to verify these assumptions, but recent work has shown that a space for time substitution and a longitudinal study (i.e. archived and contemporary soil samples) yielded similar conclusions about the rate of recovery of soil properties following landslip erosion in New Zealand (Sparling et al. 2003). Although the pastures we studied vary in age, they do not form a chronosequence of sites because the pairs of sites were located across a regional gradient of soil forming factors. Thus, we use differences in soil C stocks between paired forest and pastures to examine the spatial variability across the landscape, and estimates of soil C turnover rates derived from stable isotope analyses to make inferences about the temporal dynamics of soil C and how these vary regionally.

We also measured leaf litter and fine root C stocks in both forests and pastures, as these may indicate changes in detrital C inputs to the soil. A widely regarded conceptual model developed for northern hardwood stands suggests that forest floor C decreases immediately following disturbance such as harvesting, and gradually accrues with time (Covington 1981). However, recent re-examination of this model concluded that the dynamics of both forest floor or leaf litter stocks and fine root biomass stocks following land-cover change are considerably more complex than previously recognized (Yanai et al. 2003).

The specific objectives of this study were to: (i) describe regional variation in soil and detrital C stocks under forest and pasture vegetation, and relate these patterns to topo–edaphic factors, (ii) determine the direction and magnitude of the differences in litter and soil C pools following deforestation in paired forest-to-pasture comparisons, (iii) determine if the differences in soil C inventories were related to initial site conditions including elevation, slope, soil particle-size distributions, and soil mineralogical composition, and (iv) relate indices of soil C turnover rates derived from $\delta^{13}C$ measurements to topographic and edaphic variables. This study complements previous work in the same region of northeastern Costa Rica that examined patterns of soil C storage under forest vegetation (Powers and Schlesinger 2002a), the effects of agricultural intensification and reforestation on soil C storage (Powers 2004), and temporal changes in regional soil C budgets (Powers et al. 2004).

Methods

Study area

Field sites were located in a 1400 km^2 study region in northeastern Costa Rica (the northwestern corner is 84°13′57″W longitude and 10°34′28″N latitude; southeastern corner is 83°52′12″W, 10°14′41″N). The study region comprises the northern flank of Volcáns Barva and Poás, and the range of elevation for the sampled sites ranged from 44 to 796 m above sea level. Mean annual temperature and soil chemical and physical properties vary along the elevation gradient, but mean annual precipitation is fairly similar throughout the region. Mean annual temperatures for the sampled sites ranges from 20.9 °C in the high-elevation sites to 25.3 °C in the low-elevation sites. Precipitation is high (mean annual precipitation is 4065 mm averaged over the study area, standard deviation is 415 mm) and only weakly seasonal (Powers and Schlesinger 2002a). All soil parent materials are volcanic, but there are important differences in the stage of weathering and geomorphic positions of soils throughout the landscape. Soils in the higher elevations are developed *in situ* from volcanic lava and mudflows, and have less clay, lower bulk densities, and allophanic clay mineralogy.

Low-elevation soils (<100 m.a.s.l.) are either residual (i.e. weathered in place from lava flows) or derived from Quaternary alluvial deposits. In general, the low-elevation soils are more weathered than the high-elevation soils: they have higher clay concentrations, lower sand concentrations, and little evidence of allophane or other non-crystalline clays that form early in the weathering sequence (Powers and Schlesinger 2002a). Thus, the elevation gradient likely represents a weathering gradient, as both soil age and temperature vary continuously over the gradient. Further data on soil C concentrations and isotopic values of the forest sites used in this paper are presented in Powers and Schlesinger 2002a, b.

Site selection, management, and land-cover history

Thirty-seven cattle pastures from 3 to 60 years old were sampled. Sites were chosen based upon consent of the owner and the availability of suitable reference forest sites on similar soil types and landforms. Most of the pastures were on small farms, only two farms exceeded 100 ha, and none were located on experimental farms. Farmers in this area employ similar management regimes; following clearing of the native forest by hand (i.e. heavy machinery is not typically used), some sites are burned (Reiners et al. 1994; Veldkamp 1994). *Ischaemum timorense* Kunth., an introduced, invasive, C4 African grass, is commonly planted or invades following clearing. The lack of a pronounced dry season prevents frequent burning of pastures. Very few land owners fertilize their pastures, but localized application of herbicides is common. Stocking densities are $\sim$2 animals ha^{-1}.

Each of the pastures was paired with a reference forest site located <10 km away with similar edaphic characteristics and topography. Several lines of evidence suggest the pastures were well matched with the forests: soil color did not vary between the pairs, the average difference in slope between forest and paired pastures was 6.3%, and there were no statistically significant differences in soil particle-size distributions between the pairs despite large regional gradients in soil texture (see below). The forest sites were ‘primary’ or selectively harvested, and are described in detail in Powers and Schlesinger, 2002a. The locations of all forest and pasture sites were mapped with a global positioning system (based on the approximate center of the sampled area) and the data compiled in a geographic information system (Arc/Info).

We used a combination geo-referenced land-cover maps and interviews to estimate pasture age. Digital land-cover maps derived from aerial photography and satellite remote sensing were available for the study area (1960, 1976, 1983, 1986, 1992, and 1996/1997), although not every study site was represented on each map (Read et al. 2000; Powers 2001). We overlaid the study site map onto all of the landcover maps to obtain initial estimates of pasture age. The date of forest clearing was calculated as the average year between two map dates where the land cover changed (i.e. a site that was in forest in 1986 and in pasture in 1996 was estimated to have been converted in 1991). All dates of pasture clearing provided by land owners or managers were corroborated by the digital land-cover record.

Field sampling

Within each patch of forest or pasture, we established a 0.5- to 1.0-ha plot. Ten sampling points distributed ~25 m apart were placed within each plot. We chose this sampling intensity and spatial arrangement based upon a previous study that showed no spatial autocorrelation of soil C beyond 25 m in three 1 ha plots (Powers unpublished data). Although it may be advantageous in some studies to sample by genetic horizons (Davidson and Ackerman 1993), it is easier to precisely and accurately estimate soil C contents by sampling soil layers at fixed depth intervals, especially in highly weathered soils where horizon boundaries are diffuse. Ten soil samples were collected from each site with an auger (~ 7 cm diameter) after removing the leaf litter. Within each site, the soil samples were composited in the field for the following fixed depth intervals: 0–10, 10–20, and 20–30 cm. The soil samples were air dried at ambient conditions, passed through a 2-mm sieve, and transported to Duke University or the University of Göttingen for analysis.

Prior to soil sampling, forest floor material (leaf litter excluding large twigs and seeds) was collected from ten 0.10-m^2 quadrats. In the pasture sites, all grasses were clipped to the soil surface and sorted into live and dead shoots. The dead shoots were retained as an estimate of leaf litter, while the live shoots were discarded. All leaf litter samples were oven-dried at ~65 °C for >48 h and then weighed. Subsamples of leaf litter were composited by site and finely ground prior to further analyses.

Bulk density was measured in two locations per site for three depths (0–10, 10–20, and 20–30 cm) by inserting 300 cm^3 steel rings into the soil, and then excavating the ring with a small spade. The samples were oven-dried at 110 °C for 48 h prior to weighing. Very few of the samples had stones or particles >2 mm, thus, there was no attempt to correct for gravel content. Roots were recovered from these samples using a hydropneumatic root elutriator. No attempt was made to separate live from dead roots, as the samples had already been dried at high temperatures (110 °C). Dried roots were sorted by size class and weighed. Fine roots (<1 mm diameter) were composited from all 6 samples per site, homogenized, and subsamples were ground in a mortar and pestle for carbon analysis. Slope (%) was measured using a clinometer in two locations per site and is reported as the mean value.

Laboratory analyses

Carbon concentrations were measured on ground soil (for each sampling depth), leaf litter, and root samples using an automated CN analyzer. Leaf litter and fine root stocks are reported as Mg C ha^{-1}. All mineral soil samples were analyzed in duplicate in two independent labs, and mean, oven-dried weight values are reported. Forest soil carbon inventories (Mg C ha^{-1}) were calculated for each fixed sampling depth by multiplying soil C concentrations by bulk density, sampling depth, and a unit conversion factor. Bulk density typically increases following conversion to pasture, as soils are compacted due to trampling by cattle. Thus, many workers suggest comparing soil C inventories on a common mass basis rather than a common volume basis (Davidson and Ackerman 1993;Veldkamp 1994; Fearnside and Barbosa 1998). Essentially, this reduces the effective sampling depth in compacted pastures. Because pasture soil C concentrations were sampled and measured at the same fixed depth intervals as forest soils, pasture soil C concentrations were adjusted to the effective sampling depths based on the changes in bulk density prior to calculating the inventories following Veldkamp (1994). For instance, if the soil mass in the top 10 cm of a pasture was 30% heavier than the corresponding soil mass in the paired forest, the soil C inventory for pasture (0–10 cm) was calculated using the measured C concentration and an effective sampling depth of 7 cm. To calculate soil C inventory for the next corresponding fixed depth, we used a combination of the remaining soil mass × soil C concentration for 3 cm soil depth, plus the soil mass × C concentration for the next lower sampling depth, to equal the equivalent soil mass in the forest soil 10–20 cm depth interval. These bulk density-corrected soil C inventories were summed over the three sampling depths to estimate the cumulative soil C inventories from 0–30 cm.

The stable isotopic composition of soil, roots, and above-ground litter was measured on a Finnegan Light Isotope Ratio Mass Spectrometer and is reported in standard delta notation of parts per thousand (‰) relative to the Pee Dee Belemnite standard. Fifty two of the mineral soil samples (11%) were analyzed in duplicate for $\delta^{13}C$, and the average difference between duplicates was 0.34‰. Twenty-four samples of fine roots and forest floor were analyzed in duplicate for $\delta^{13}C$, and the average difference between duplicates was 0.73‰.

Particle-size distributions were measured on all forest soils and a subset of the pasture soils (0–10 cm depth interval) via the pipette method following pretreatment with hydrogen peroxide to remove organic matter. Linear regressions of the particle-size fractions from paired forest and pasture sites showed that the sites were well matched with respect to soil texture (e.g. for percentage clay the slope coefficient from a linear regression was 1.06, the intercept was not different from 0, $r^2 = 0.961$, $F_{1,8} = 197.3$, $p < 0.0001$).

Acid oxalate and sodium pyrophosphate extractions were used to quantify clay mineralogy for the 0–10 cm depth interval of all forest and pasture samples (Parfitt and Henmi 1982; Parfitt and Childs 1988). Aluminum, silica, and iron concentrations in the extracts were quantified with inductively coupled plasma emission spectrometry (ICP). The acid oxalate extraction liberates 'active' Fe and Al contained in poorly ordered, amorphous or non-crystalline minerals such as ferrihydrite ($\approx Fe_o$), allophane, and imogolite (Hartwig and Loeppert 1993). Sodium pyrophosphate extracts all organically bound Al and an indeterminate fraction of the organically bound Fe (Hartwig and Loeppert 1993; Parfitt and Childs 1988). Ratios of pyrophosphate-extractable Al (Al_P) to acid oxalate-extractable Al (Al_o) < 0.5 are indicative of allophanic soil mineralogy, while ratios > 0.5 indicate that the active Al is present in an exchangeable form or complexed with humic materials (Mizota and Reeuwijk 1989; Dahlgren et al. 1993).

Statistical analyses of carbon stocks

To describe the patterns in soil C under forest and pasture, and differences between land covers, we used: (i) univariate statistics to summarize carbon contained in soil, litter and root stocks under forest and pasture vegetation, (ii) paired *t*-tests to assess differences in C stocks for a smaller subset of the data that included single pastures paired with nearby forests ($N = 24$ pairs), expressing the differences in soil C stocks on both absolute (pasture–forest) and proportional bases [(pasture–forest)/forest]*100, (iii) stepwise multiple regression with backward and forward selection techniques to select the independent variables (pasture age, elevation, forest soil texture, forest clay mineralogy, and %slope) that best predicted soil C stocks under forest, pasture or the differences between paired land covers, and (iv) correlation analysis to summarize the relationships among environmental variables, soil C stocks in forests and pastures, the differences between stocks, and the amount of remaining forest-derived soil C in pastures. For estimating the differences between forest and pasture C stocks for cases where two or more pastures of different ages were located near one forest site, we compared the pasture that had the most similar percentage slope value to the forest site. This reduced the total number of paired comparisons to 24, and avoided the problem of non-independent pairs.

Because our data showed that pasture establishment influenced soil mineralogical composition (but not particle-size distribution) (Powers 2001), we used the forest values of mineralogical variables in the multiple regressions, assuming that these represent initial conditions at the time of pasture establishment.

Soil C stable isotopes and dynamics

The bulk stable isotopic composition ($\delta^{13}C$) of C3 plants commonly ranges from -30 to $-28‰$, while that of C4 plants ranges from -11 to $-14‰$ (Balesdent and Mariotti 1996). $\delta^{13}C$ data in C3 to C4 vegetation conversions are commonly interpreted using simple, two end-member mixing models (Balesdent and Mariotti 1996). The fraction of C4-derived carbon or carbon derived from pasture grasses (F_p), is calculated as the ratio of the gradient in isotopic composition in soil C to that of detrital carbon sources to the soil as follows:

$$F_p = (\delta^{13}\text{C soil}_p - \delta^{13}\text{C soil}_f)/(\delta^{13}\text{C detritus}_p - \delta^{13}\text{C detritus}_f),$$

where δ^{13}C soil$_p$ is pasture soil, δ^{13}C soil$_f$ is forest soil, δ^{13}C detritus$_p$ is the input C signature from pasture grasses, and δ^{13}C detritus$_f$ is the input C signature from C3-forest vegetation.

These calculations are complicated by the fact that very few pastures are actually composed entirely of C4 grasses. Many tropical pastures have remnant trees, decaying slash and roots from forest vegetation, and C3 weeds (Camargo et al. 1999). Our approach to dealing with this limitation of interpreting δ^{13}C data was to calculate the fractional contribution of C4-derived C to the soil C pool (F_p) using two different assumptions about C4-end members. We then compared how our results depended upon the choice of end members. In all of the estimates, we used the measured isotopic composition of leaf litter plus fine roots (<1 mm diameter) at each site as the term for forest C input signatures, δ^{13}C detritus$_f$. Under Assumption 1, we assumed that all carbon inputs to pasture soils came from the dominant C4 grass, *Ischaemum timorense* Kunth., and we used the isotopic composition of foliage and fine roots (13.67‰) from this species as δ^{13}C detritus$_p$. However, if pasture vegetation contains a mixture of C4 and C3 plants, assuming a single C4 endpoint will underestimate the contribution of pasture vegetation to the soil C pool. Under Assumption 2, we used the average value of δ^{13}C for leaf litter plus fine roots that was measured in each pasture as the δ^{13}C detritus$_p$ term. Thus, the estimates of F_p under Assumption 1 are the lower boundaries for the fractional contribution of pasture vegetation to the soil C pool, and Assumption 2 provides the upper boundaries. All calculations were for the 0–10 cm soil depth interval.

To investigate how soil C dynamics varied regionally, we calculated the percentage of forest-derived carbon left in the pasture soil C pool (0–10 cm) as a measure of soil C turnover, i.e., $((C_f/C_i)*100)$. In this equation C_i = initial forest soil C stock and C_f is calculated from information on the fraction of pasture-derived soil C, F_p, and pasture soil C inventories, C_p, as follows: $C_f = (1\text{-}F_p)*C_p$. These values were estimated twice using both assumptions about pasture isotopic endpoints. We used this approach because it did not make assumptions about the partitioning of soil C into labile and refractory pools or estimate turnover times from single pool models, which did not fit our data (results not shown). Stepwise multiple regression with backward and forward selection techniques was used to investigate how the percent of forest-derived soil C remaining in pastures varied as a function of the following environmental variables: elevation, percent slope, Al_p/Al_o, Fe_o, %clay, %silt, %sand, and pasture age.

Results

Carbon stocks in forests and pastures

On average, soil C contents (to 30 cm depth) were similar for forests (80.5 Mg C ha^{-1}) and pastures (76.7 Mg C ha^{-1}, Table 1), but the range of values was large. Soil C under forest vegetation ranged from 51.4 to 138.6 Mg C ha^{-1}, and the range for pastures was similarly large, from 51.1 to 111.8 Mg C ha^{-1}. Forests had ~1 Mg C ha^{-1} in leaf litter, and pastures had roughly half of this value (Table 1). In contrast, pastures had slightly larger fine root C pools.

When analyzed as a group ($N = 24$), soil C stocks in forests increased with elevation and Al_p/Al_o (the index of non-crystalline clays), and these factors explained 40% of the observed variation (Table 2). Pasture soil C stocks ($N = 37$) also increased with elevation and with pasture age (Table 2, $r^2 = 0.59$). The positive relationship between pasture soil C stocks and age may be due to increases in soil C storage with time since clearing, or non-random patterns of deforestation with respect to initial forest soil C stocks (i.e. high C forest soils may have been converted before low soil C soils).

Differences between paired forests and pastures, and relationships to environmental factors

Because of the large spatial gradients in soil C stocks under forest vegetation, we calculated both the absolute and percent differences in C stocks between forest and pasture pairs (Table 3). On average, soil C stocks in pastures were 3.5 Mg C ha^{-1} lower than forests, a difference of less than 3% of initial forest soil C inventories (Table 3). Paired *t*-tests showed that there were no significant differences between forest and pasture soil C stocks (Table 3), although leaf litter stocks were significantly less in pastures compared to forests. For the paired forests and pastures, fine root pools were 60% higher in the pastures compared to forests ($p < 0.05$). The large average percent difference in root C

Table 1. Summary statistics for carbon pools (Mg C ha^{-1}) in soil (0–30 cm), leaf litter, and fine root biomass stocks (0–30 cm), in forests ($N = 24$) and pastures ($N = 37$)

Land cover	Mean	Minimum	Maximum	Standard deviation
Forest				
Soil C	80.54	51.14	138.60	16.88
Leaf litter	1.09	0.51	2.32	0.45
Fine roots	1.75	0.42	3.46	0.93
Pasture				
Soil C	76.66	51.13	111.82	13.41
Leaf litter	0.48	0.13	1.33	0.28
Fine roots	1.90	0.11	3.31	0.69

Table 2. Results from multiple regressions. Full models included the following explanatory variables : pasture age, elevation, Al_p/Al_o, Fe_o, %sand, %silt, %clay and %slope

	Intercept	Pasture Age	Elevation	Fe_o	Al_p/Al_o	%slope	%sand	d.f.	r^2	p
Carbon stocks (Mg C ha^{-1})										
Pasture	59.23	0.50	0.027	–	–	–	–	2,34	0.59	< 0.0001
Forest	54.30	NA	0.057	–	17.76	–	–	2,21	0.40	0.005
Differences in C stocks										
Absolute (Mg C ha^{-1})	–	–	–	–	–	−0.36	–	1,22	0.27	0.009
Percent	18.17	–	–	–	−16.30	−0.39	–	2,21	0.37	0.008
Percent forest-C Remaining (all data)										
Assumption 1	73.73	–	–	−37.03	–	–	0.86	2,21	0.38	0.007
Assumption 2	42.41	–	–	–	–	–	–	21	< 0.01	NA
Percent forest-C Remaining (sites < 50 years old)										
Assumption 1	101.70	−0.98	–	−31.38	–	–	–	2,19	0.49	0.002
Assumption 2	111.03	−1.61	0.07	−41.69	–	−0.85	–	4,15	0.71	< 0.001

All model terms significant at the $p = 0.10$ level.

Table 3. Summary statistics for the absolute and proportional changes in carbon pools (Mg C ha^{-1}) in soil (0–30 cm), leaf litter, and fine root biomass stocks between paired forest and pasture plots ($N = 24$ pairs). Significant differences between forest and pasture pairs assessed with paired t-tests are indicated by asterisks

	Mean	Minimum	Maximum	Standard deviation
Absolute differences (Mg C ha^{-1})				
Soil C	−3.5	−26.8	20.2	12.8
Leaf litter	−0.64***	−1.92	−0.15	0.47
Fine roots	0.11	−2.90	2.41	1.31
Proportional differences (%)				
Soil C	−2.9	−25.6	23.0	15.1
Leaf litter	−55.58***	−93.59	−17.35	20.41
Fine roots	59.46*	−94.19	411.75	138.94

*p-value for paired t-test < 0.05.
***p-value < 0.001.

pools may be biased by particularly large values (i.e. root C pools in some pastures were four times greater than paired forests) (Tables 1 and 3).

Despite the small average differences between soil C stocks in forests and pastures across the landscape, the range of variability was large; soil C stock in

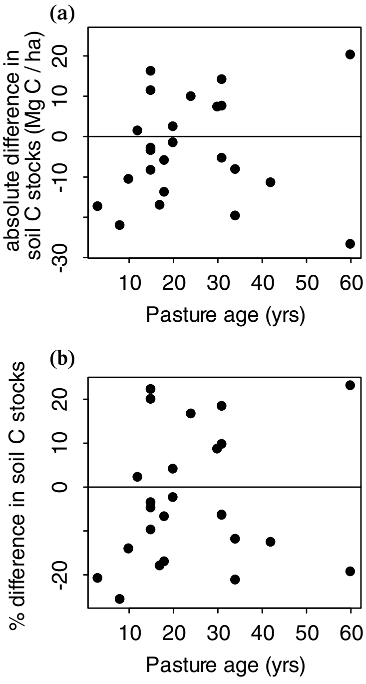

Figure 1. Differences in soil C stocks (0–30 cm depth) between paired pastures and forests as a function of pasture age (years), units are (a) absolute differences, Mg C ha^{-1}, and (b) differences expressed as a percent of forest soil C stocks.

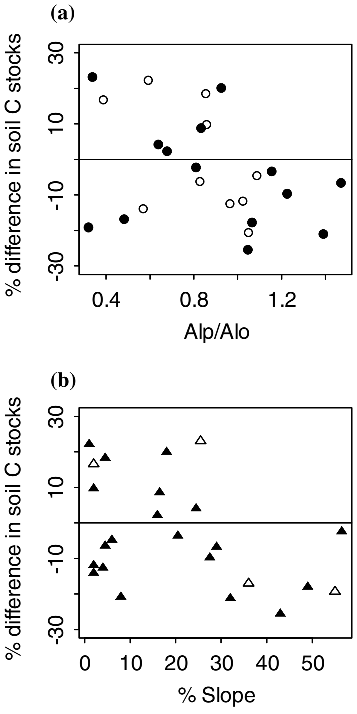

Figure 2. Percent difference in soil C stocks between paired pastures and forests as a function of topo-edaphic variables: (a) Al_p/Al_o, open circles are site with slope facets $< 10\%$ and filled circles are sites with $> 10\%$ slope, and (b) percent slope, open triangles soils with significant concentrations of non-crystalline clays ($< .5$), and filled triangles are sites with $Al_p/Al_o > 0.5$.

some pastures was 25.6% lower than paired forest sites and up to 23% greater than forest pairs at other sites (Table 3; Figure 1). In a multiple regression, percent slope explained 27% of the variation in the absolute differences between soil C stocks in pastures and forests, such that pairs with steeper slopes had larger differences in soil C stocks (Table 2). Together, percent slope and Al_p/Al_o explained 37% of the variation in percent difference between soil C stocks. Soil C stocks were lower in paired pasture sites located on more weathered soils, as indicated by higher values of Al_p/Al_o (Figure 2a). Pasture on soils with non-crystalline clays had higher soil C stocks than corresponding forests, unless these sites were located on steep soils, in which case they had lower soil C stocks than paired forests (Figure 2b).

Pasture age was not a significant predictor of the differences in soil C stocks between paired forests and pastures (Table 2), indicating that the temporal changes in C stocks do not confound inferences about the geographic factors that influence soil C changes. There were also no relationships between leaf litter and fine root C stocks in pastures as a function of pasture age (results not shown).

Table 4. Pasture characteristics and percent of forest-derived carbon remaining in pastures (0–10 cm depth)

Pasture site number	Pasture age (years)	Elevation (m.a.s.l)	Slope (%)	Sand (%)	Fe_o	Percent forest-derived soil C remaining in pasture, Assumption 1	Percent forest-derived soil C remaining in pasture, Assumption 2
1	31	103	0	11.5	0.65	60.6	38.6
2	18	93	25	15.6	0.80	67.9	–
3	8	94	34	10.1	0.62	63.3	60.3
4	15	87	1	11.5	0.83	71.6	59.5
5	42	49	0	9.4	0.84	26.7	22.8
6	30	519	14.5	10.7	1.29	47.2	46.7
7	20	395	56	34.0	1.07	50.3	13.8
8	34	80	32.5	10.1	0.46	44.9	21.9
9	34	61	1	9.4	0.60	31.5	13.8
10	20	273	17	8.6	0.78	47.8	42.4
11	12	60	10	20.1	0.51	95.7	94.4
12	15	69	0	20.1	0.70	100.2	84.8
13	10	51	0	42.7	1.21	53.7	39.7
14	15	48	1	3.6	1.37	36.0	23.9
15	15	99	40	9.2	0.55	60.5	0.8
16	3	70	21.5	11.1	0.43	72.0	57.7
17	18	106	48	8.7	0.70	53.0	12.4
18	17	301	46.5	20.7	0.63	48.3	45.3
19	31	75	1.5	11.5	1.03	45.4	23.1
20	15	380	20	20.3	0.65	67.2	63.2
21	31	185	3.5	5.6	0.44	73.9	41.2
22	24	44	1	5.6	1.27	22.6	21.9
23	60	796	42	48.7	1.54	51.7	42.8
24	60	579	21	56.6	1.43	81.5	62.5

The fraction of pasture-derived soil C was calculated using two-end member mixing models, assuming different end members for the C4-inputs to the soil from pasture vegetation (see Methods for a complete description of the Assumptions).

δ^{13}C and Soil C Dynamics

The stable C isotopic composition of soil in the forests was typical of C3 vegetation and ranged from −28.4 to −26.7‰ (0–10 cm depth), −27.7 to −26.0‰ (10–20 cm depth), and −27.3 to −25.3‰ (20–30 cm depth) (Powers and Schlesinger 2002b). In the pastures, the average δ^{13}C of litter and fine roots varied with pasture age, suggesting gradual replacement of C3 with C4 vegetation (Figure 3a). Scatter plots of δ^{13}C in the mineral soil versus pasture age reveal rapid incorporation of C4-derived carbon into pasture soil C pools, which decreases with depth in the profile (Figure 3b, c, d).

From 23 to 100% of the initial forest soil C inventory remained in the pastures (0–10 cm) under the assumption of a pure C4-isotope signature of pasture vegetation (Assumption 1), and 14–94% of forest-derived soil C was

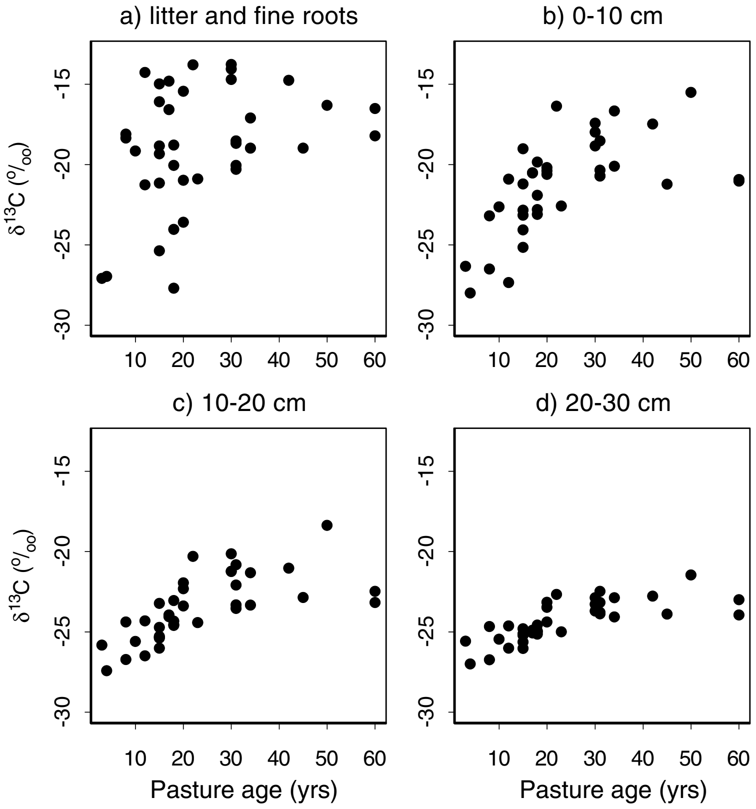

Figure 3. The isotopic composition (δ^{13}C ‰) in pastures of: (a) Leaf litter and fine roots, (b) mineral soil (0–10 cm), (c) mineral soil (10–20 cm), and (d) mineral soil (20–30 cm).

estimated to remain in pastures when calculated using the measured values of the isotopic composition of pasture vegetation (Assumption 2) (Table 4). In several pastures (2 and 15), the difference in isotopic composition between pasture and forest soils was greater than the difference between detrital signatures, resulting in $F_p > 1$, precluding the calculation of the percentages of forest-derived soil C Assumption 2. Excluding these sites from the Assumption 2 average, the average percent of forest-derived C remaining in pasture surface soils (0–10 cm) was 57% (A1) or 42% (A2). Despite the obvious incorporation of C4-derived C into soil C pools as pastures aged (Figure 3), there was considerably more variation in the decline in forest-derived soil C with pasture age under both assumed pasture endpoints (Figure 4).

Both soil mineralogy (Fe_o) and sand concentrations explained a significant part of the variation in remaining forest-derived soil C in this sample of pastures (Table 2), under the constant C4 endpoint assumption (Assumption 1). In contrast, when the measured isotopic values for pasture vegetation

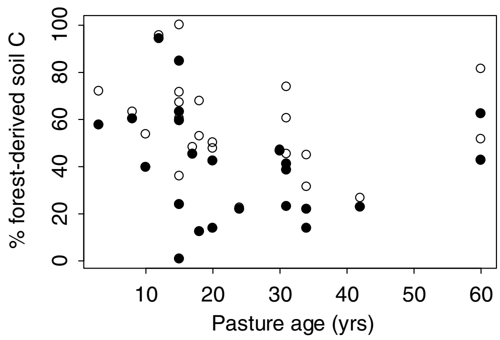

Figure 4. Estimated percent of forest-derived soil C remaining in pastures as a function of pasture age calculated under two assumed C4 endpoints (open circles were calculated under Assumption 1, filled circles are Assumption 2).

(Assumption 2) were used to calculate percent forest-derived soil C, none of the measured topographic or edaphic factors explained a significant portion of the variation in remaining forest soil C in pastures (Table 2). Pasture age did not appear as a significant variable in either multiple regression analysis.

However, the two oldest pastures in the sample are located at the highest elevations and have large concentrations of non-crystalline clays, which is likely why these two sites have from 43 to 82% of forest-derived soil C remaining after ~60 years in pasture (Table 4). We re-ran the regressions omitting these two sites and found considerably better fits to the models. Under the assumption of a constant C4 input to pastures, the percent of forest-derived soil C decreased with pasture age and Fe_o (Table 2). As expected, the intercept of this model was 102, i.e. approximately 100% of all soil C is derived from forest vegetation if the pasture age is 0. The regression model for forest-derived soil C remaining in pastures under Assumption 2 had a larger y-intercept (111) and was more complicated, including the variables pasture age, elevation, slope and Fe_o ($r^2 = 0.72$).

Correlations among variables

To facilitate the interpretations of environmental variables, soil C stocks, the differences between forests and pastures, and the remaining forest-derived soil C (C_f), we calculated the pairwise correlations among these variables (Table 5). These analyses were restricted to the paired sites ($N = 24$) and used estimates of C_f from Assumption 1. Importantly, pasture age was positively correlated with elevation, suggesting non-random patterns of deforestation. The changes in soil C stocks (absolute and proportional) were negatively correlated with forest soil C, but this is likely an artifact due to the fact that the changes in soil C are defined as a function of forest C stocks. Pastures with high soil C stocks also had large quantities of remaining forest-derived soil C (Figure 5a). The

Table 5. Pearson's product moment correlations between elevation, pasture age, forest and pasture soil C stocks (Mg C ha^{-1}), differences (Δ) between forest and pasture, the absolute and percent of forest-derived soil C (C_f) remaining in pastures (under Assumption 1), *p*-values in parentheses

	Pasture age	Forest soil C	Pasture soil C	Absolute Δ soil C	Percent Δ soil C	C_f, Mg Cha^{-1}	C_f as % total C_p
Elevation	0.60 (0.002)	0.55 (0.005)	0.64 (0.0008)	−0.01 (0.95)	0.06 (0.78)	0.19 (0.37)	0.05 (0.80)
Pasture age		0.52 (0.009)	0.69 (0.0002)	0.10 (0.65)	0.17 (0.44)	−0.04 (0.84)	−22 (0.30)
Forest soil C			0.67 (0.0003)	−0.56 (0.005)	−0.48 (0.02)	0.38 (0.07)	0.07 (0.76)
Pasture soil C				0.23 (0.27)	0.30 (0.16)	0.53 (0.007)	0.30 (0.15)
Absolute Δ soil C					0.98 (< 0.0001)	0.10 (0.64)	0.25 (0.24)
Percent Δ soil C						0.08 (0.72)	0.19 (0.36)
C_f, Mg Cha^{-1}							0.92 (< 0.0001)

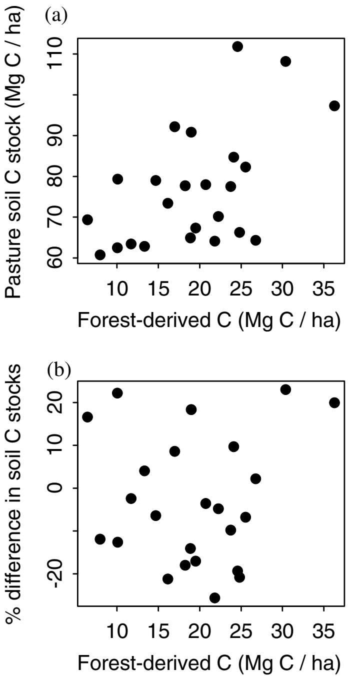

Figure 5. Relationship between forest-derived soil C remaining in pastures (estimated using a constant C4-endmember assumption) and (a) pasture soil C stocks, and (b) the percent difference in soil C stocks between paired pasture and forest.

differences in soil C between paired forests and pastures were not correlated with remaining forest-derived soil C (Table 5, Figure 5b).

Discussion

In our sample of 24 paired forests and pastures, the average change in soil C stocks across the landscape following the conversion of forests to pastures was not significantly different from 0. However, there was considerable variation in both the direction and the magnitude of the differences in soil C stocks. Site factors including topographic relief and soil mineralogy explained some of the variation in soil C stocks in both forests and pastures, and changes in soil C stocks following pasture establishment in this volcanic region of northeastern Costa Rica. Our results are consistent with many other studies that have found variable responses of soil C pools to pasture establishment following clearing of tropical forests (Fearnside and Barbosa 1998; Veldkamp (in press)). Together these studies suggest that this pattern is general, but the specific mechanisms may vary regionally.

We estimated the effects of converting forests to pastures on soil C stocks by sampling both forests and pastures of varying ages across a large regional gradient in soil texture and clay mineralogical composition. Interpretations of these data hinge on the ability separate site factors (geographic or spatial effects) from temporal effects (i.e. pasture age or time since clearing). In the larger sample of 37 pastures, soil C stock was positively correlated with pasture age (Table 4). There are two possible explanations for this pattern: (i) soil C storage may increase with time since clearing, or (ii) the initial clearing of forests for pastures may have occurred preferentially on forest soils with high initial C stocks, as other studies in the nearby region of Guapiles, Costa Rica have shown that fertile soils are deforested before infertile soils (Veldkamp et al. 1992). Several lines of evidence suggest the latter effect in this region as well as Guapiles. Both plots of the changes in soil C stocks following clearing (Figure 1) and the regression results (Table 2) indicate no consistent relationship between pasture age and the differences in soil C stocks between paired forests and pastures, although none of the youngest pastures ($<$ 10 years old) had higher soil C stocks than paired forests. Moreover, forest C stocks were positively correlated with pasture age (Table 5). This suggests the dominant influence of site factors in controlling both soil C storage under native forest vegetation and the fate of the soil C pool following land-cover change.

In the volcanic soils of this study region, 40% of the variability in soil C pools under forests was accounted for by soil mineralogy and topographic relief. As previously documented, soil C stocks under forest vegetation increase with elevation (Powers and Schlesinger 2002a). Soil particle-size distributions and clay mineralogical composition co-vary along this elevation gradient, and represent a weathering or soil age gradient. At high elevations, the large soil C stock under forests is stabilized by non-crystalline clays, and thus indirectly related to elevation, and at lower sites in the landscape, soil C is stabilized in Al-humus linkages, as witnessed by positive relationship to Al_p/Al_o (Table 2) (Powers and Schlesinger 2002a). Non-crystalline clays have also been implicated in soil C stabilization in volcanic soils on Hawaii (Torn et al. 1997).

Both the absolute and proportional differences between paired forest and pasture soil C stocks were negatively related to %slope, suggesting that slope processes are an important mechanism accounting for C losses on steep slopes. However, non-crystalline clays, as indexed by Al_p/Al_o, also explained some of the variation in the proportional differences in soil C stocks between paired pastures and forests (Table 2). On flatter slopes with non-crystalline clays, pastures had higher soil C stocks than corresponding forests, and on steeper slopes, they had lower soil C stocks (Figure 2). Thus, both topography and soil mineralogy influence the response of the soil C pool to land-cover change. In addition, there was a considerable amount of variation in the response of soil C pools that was not accounted for by the variables we measured. Moreover, this study only examined changes to a depth of 30 cm, although there may be larger changes in C stocks below 30 cm (Trumbore et al. 1995) and translocation of forest-derived C to depths >30 cm in pastures (Osher et al. 2003).

In contrast to our results, in other studies changes in vegetation productivity, rooting patterns, and management have been invoked to explain the varying response of the soil C pool to pasture establishment (Fisher et al. 1994; Trumbore et al. 1995; Fearnside and Barbosa 1998). Several studies have shown that soil C pools increase in fertilized, well-managed pastures in Amazonia following clearing, and decrease in pastures under typical management practices (Trumbore et al. 1995). Similarly, the variation in soil C storage following pasture establishment in sites distributed across Rondônia, Brazil may be more related to site history and management practices than edaphic characteristics (Neill et al. 1997). Precipitation may also play a role in determining the direction and magnitude of the changes in soil C pools following landcover change. In the Southern United States, dry native grasslands (200 mm MAP) that were invaded by woody vegetation gained soil C, while wetter grasslands (1100 mm MAP) lost soil C (Jackson et al. 2002).

Because our forest-to-pasture comparisons cover a wide range of topo-edaphic conditions and represent common management practices on farms in this region, they can be used to assess the extent to which stable C isotopes are a useful tracer of soil C dynamics at the landscape scale. Although our single sampling period of root and litter isotopic composition may not reflect seasonal or short-term variability of inputs, we found strong suggestions that the isotopic composition of carbon inputs to the soil in pastures changed gradually with pasture age (Figure 3a), but never attained a pure C4-plant community. All of our methods for indexing soil C turnover times are sensitive to the assumption of pure C4 inputs, which clearly was not met in this sample of pastures. The violation of this assumption limits our ability to make inferences about soil C cycling rates using these data. However, using the two assumed endpoints for the isotopic composition of pasture vegetation allowed us to bracket the highest and lowest potential contributions of pasture vegetation to the soil C pool and to assess how sensitive our results were to violations of these assumptions. The average percent of forest-derived C remaining in pasture surface soils (0–10 cm) was 59% under Assumption 1 (pure C4 vegetation) or 45% under Assumption 2 (measured isotopic input composition), suggesting that the choice of end members influenced estimated soil C dynamics by an average of 14% in our dataset. The smallest difference between pairs of estimates was 0.43% and the largest difference was 40.5%, indicating the potential for large discrepancies between estimates of soil C dynamics.

Are gains in pasture-derived soil C or losses of forest-derived soil C responsible for the differences in soil C stocks between pastures and forests? Even though the remaining quantity of forest-derived soil C was correlated with soil C stocks in pastures (Figure 5a), there was no significant relationship between this pool of remaining C and the differences between forest and pastures (Figure 5b), suggesting that both new inputs from pasture vegetation and the decomposition of forest-derived C jointly control total soil C storage in pastures. As expected, the percent of forest-derived soil C in pastures decreased with increasing pasture age, but the rate of loss was modified by Fe_o, which is an index of the iron-bearing, non-crystalline clay ferrihydrite. The decoupling of the loss of forest-derived soil C with the differences between forest and pasture C stocks is consistent with work in *Eucalyptus* plantations established on former sugar cane fields in Hawaii. In these soils rapid decreases in cane-derived soil C were compensated for by rapid increases in *Eucalyptus*-derived C, leading to no net changes in soil C stocks (Binkley and Resh 1999).

Conclusions

This study has shown that the response of the soil C pool to forest clearing and pasture establishment can vary dramatically, even within a fairly small region (1400 km^2). In this volcanic landscape, the direction and magnitude of changes in soil C storage were correlated with soil mineralogy and topographic relief. Although explanations for the varying response of the soil C pool may differ in other regions, these results suggest that geographic variability in the changes in soil C pools following land-use change is the norm and not the exception. To better constrain regional, continental, and global C budgets, future studies should be stratified by the major gradients of soil forming factors in different regions. In our study landscape, the natural variability in plant community dynamics in unmanaged pastures limited the application of the ^{13}C natural abundance technique as a precise tracer of soil C dynamics, and was only useful in bracketing the contributions of C3-versus C4-derived vegetation to the soil C pool.

Acknowledgements

We would like to thank Peter Tiffin, Bill Schlesinger, Dan Richter, Elissa Levine, and three anonymous reviewers for helpful comments on earlier versions of this manuscript. We thank Jim Clark for statistical advice and help with the bootstrap analyses. Lars Szwec operated the mass spectrometer. This study was made possible through funding from the following sources to J.S.P.: a NASA Graduate Student Researcher Program Fellowship, an NSF Dissertation Improvement Grant (No. 9972569), an Andrew W. Mellon Foundation Fellowship for Ecosystem Studies awarded through the Organization for Tropical Studies, a National Security Education Program Fellowship, a Center for International Studies Travel Grant from Duke University, and a Tinker Field Research Grant from the Duke University Latin American Studies Program.

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