Effects of Soil Texture on Belowground Carbon and Nutrient Storage in a Lowland Amazonian Forest Ecosystem

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ABSTRACT

Soil texture plays a key role in belowground C storage in forest ecosystems and strongly influences nutrient availability and retention, particularly in highly weathered soils. We used field data and the Century ecosystem model to explore the role of soil texture in belowground C storage, nutrient pool sizes, and N fluxes in highly weathered soils in an Amazonian forest ecosystem. Our field results showed that sandy soils stored approximately 113 Mg C ha^{-1} to a 1-m depth versus 101 Mg C ha^{-1} in clay soils. Coarse root C represented a large and significant ecosystem C pool, amounting to 62% and 48% of the surface soil C pool on sands and clays, respectively, and 34% and 22% of the soil C pool on sands and clays to 1-m depth. The quantity of labile soil P, the soil C:N ratio, and live and dead fine root biomass in the 0–10-cm soil depth decreased along a gradient from sands to clays, whereas the opposite trend was observed for total P, mineral N, potential N mineralization, and denitrification enzyme activity. The Century model was able to predict the observed trends in surface soil C and N in loams and sands but underestimated C and N pools in the sands by approximately 45%. The model predicted that total belowground C (0–20 cm depth) in sands would be approximately half that of the clays, in contrast to the 89% we measured. This discrepancy is likely to be due to an underestimation of the role of belowground C allocation with low litter quality in sands, as well as an overestimation of the role of physical C protection by clays in this ecosystem. Changes in P and water availability had little effect on model outputs, whereas adding N greatly increased soil organic matter pools and productivity, illustrating the need for further integration of model structure and tropical forest biogeochemical cycling.

Key words: roots; soil carbon; century model; soil texture; biogeochemistry; tropics.

INTRODUCTION

Soil texture exerts a strong influence on many hydrologic and biogeochemical processes in forest

ecosystems by affecting the ability of soils to retain C, water, and nutrient ions (Jenny 1980). For these reasons, soil texture is also a key parameter in models of terrestrial biogeochemistry, which generally show that soil organic matter (SOM) increases linearly with clay content at regional and global scales (Parton and others 1993; Schimel and others

1994). Despite the well-demonstrated importance of soil texture, many questions remain about the role of texture in belowground C allocation, soil C storage, ion exchange capacity, and ecosystem scale processes, such as primary productivity and decomposition. This is especially true for lowland tropical forests, which exhibit considerable spatial heterogeneity in soil texture at both local and regional scales (Cuevas and Medina 1986, 1988; Matson and Vitousek 1987; Moraes and others 1995).

The interactions of soil texture and biogeochemical cycling are complex. Clay soils can facilitate the formation of passive C pools with slow turnover times due to the physical protection of SOM by clay minerals (Christensen 1992). Clay soils also tend to have higher cation exchange capacity, net primary productivity (NPP), and litter decomposition rates in the tropics under natural conditions (Uehara 1995). Sandy soils are often associated with high fine root biomass in tropical forests due to greater C allocation to roots for nutrient and water capture (Klinge 1973b, 1975; Cuevas and Medina 1988). Sandy soils may also have slower litter turnover rates due to nutrient and water limitations on decomposition (Cuevas and Medina 1986).

Soil textural properties vary in response to weathering rates and the initial mineralogy of the parent material or the deposition of material from streams, runoff, and erosion. In general therefore, soil texture tends to change at local scales along topographic gradients and at landscape or regional scales associated with changes in parent material or weathering rates. The nature of soil-forming processes that lead to spatial heterogeneity in soil texture are also generally associated with differences in micro- and macroclimate, vegetation, and hydrologic inputs and exports making it difficult to control for texture while holding several other environmental variables constant.

In this study, we use both an empirical and a modeling approach to examine the relationship of soil texture to patterns in belowground C and nutrient pools and N transformation rates in a lowland Amazonian forest. The Amazon basin is a geologically old region that is diverse with regards to soil texture (Furch and Klinge 1978; Moraes and others 1995). Patterns in biogeochemical and ecological processes with soil texture have been described along topographic gradients in Amazonian forests (Cuevas and Medina 1986, 1988; Matson and Vitousek 1987; Livingston and others 1988; Vitousek and Matson 1988; Medina and Cuevas 1989), and larger, regional-scale gradients (McKane and others 1995; Moraes and others 1995). In this study, we were interested in how belowground

processes varied in relation to soil texture while holding landscape position, climate, and cover type relatively constant. Our site occurred at the contact between a relic depositional surface and an upland landscape, all of which is now upland, Tierra Firme forest with little or no topographic variation.

We were also interested in using a modeling approach to test our understanding of the processes contributing to patterns in belowground C and nutrient pools in tropical forests. Soil texture is often used as a primary parameter controlling SOM stabilization in biogeochemical models. To examine the role of texture in greater detail, and to test mechanisms by which texture influences the biogeochemistry of a moist lowland tropical forest, we used the Century biogeochemistry model (Parton and others 1987) to simulate the forest on the different soil textural classes at our site. The Century model originally was developed for use in temperate grasslands and agricultural systems but has since been extended and re-parameterized for use in temperate and tropical forests (Sanford and others 1991; Comins and McMurtrie 1993; Vitousek and others 1994, Raich and others 1997), as well as for analyses of global biogeochemical dynamics (Schimel and others 1997). Whereas the applicability of Century has been tested extensively for temperate ecosystems, less testing of the model has been done for tropical ecosystems (but see Vitousek and others 1994; Gijsman and others 1996; Raich and others 1997). Our motivation for using Century is twofold. First, we examine the ability of the model to capture the trends we observe along our soil texture gradient. This exercise is helpful both because it allows us to evaluate our understanding of textural controls on tropical forest biogeochemistry, and because it represents a validation test for a key parameter influencing the behavior of this model. Second, we examine the potential role of feedbacks among texture, nutrients, and water in the model by examining model sensitivity to changes in N, P, and water availability.

METHODS

Site Description

The study was conducted in the Tapajos National Forest (TNF) located 50 km south of Santarem, Para, Brazil. The region has a mean annual temperature of 25°C, and receives approximately 2000 mm of rain per year with a dry season lasting from May through October (Parrotta and others 1995). The 1000-ha study site was located on an old, nearly flat, erosional remnant plateau (planalto) with a very

limited drainage network formed on sediments of the Barreiras formation. The underlying bedrock geology consists of slanted beds of sedimentary rocks deposited as a fluvial-lacustrine sequence. The soil textural differences at this site most likely reflect the underlying sedimentary bedrock that consists of alternating sandy and clayey beds.

Soil textural classification of the larger study area was determined by field inspection of samples from 551 control points spaced at 50-m intervals in a regular pattern throughout the 1000-ha area (5 x 2 km). In total, transects covered approximately 28 km. A limited number of points was skipped because of the difficulty of access including a small area of poorly drained soil. Soils were divided into two categories: (a) those having clay and clay loam texture (found at 375 points); and (b) the remainder having coarser textures (mainly sand and sandy loam found at 176 points). Assuming the regular transect pattern is representative of the area, approximately 68% of the area surveyed is on clays or clay loams (ultisols and oxisols) and 32% on sands and sandy loams (ultisols).

Field Sampling

We sampled surface soils (0–10 cm depth), forest floor, and fine root biomass along six 10 x 60–m transects located perpendicularly to a 400-m gradient from sand to clay soils. Transects were located at 0 and 50 m (sands), 150 and 200 m (sandy loam to clay loam), and 350 and 400 m (clays) along the textural gradient (Figure 1). Additional samples of forest floor and fine root biomass were taken on sands and clays to facilitate comparison of these two textural extremes (see below). To estimate soil chemical and physical properties and root C, N, and P to 1 m depth, we took samples from five large 3 x 1 x 1–m quantitative soil pits randomly located at 0, 50, 200, 350, and 400 m along the texture gradient and 18 additional 1 x 1 x 1–m soil pits with nine each on sand and clay soils.

Surface Soil Physical and Chemical Properties along the Transects

Soils were sampled from the 0–10-cm depth by using a 2.5-cm diameter soil corer. We took multiple core samples at each of five randomly selected points along each transect yielding 30 aggregate soil samples. Samples were refrigerated immediately after collection and until analyses could be conducted (approximately 3–7 days). Roots and litter were manually removed from field moist samples, which then were passed through a 2-mm sieve. Soil texture was determined using a Bouyoucos hydrometer in a soil suspension of 50 g of soil in 1 L of H_2O (Gee and Bauder 1986). Samples were pretreated
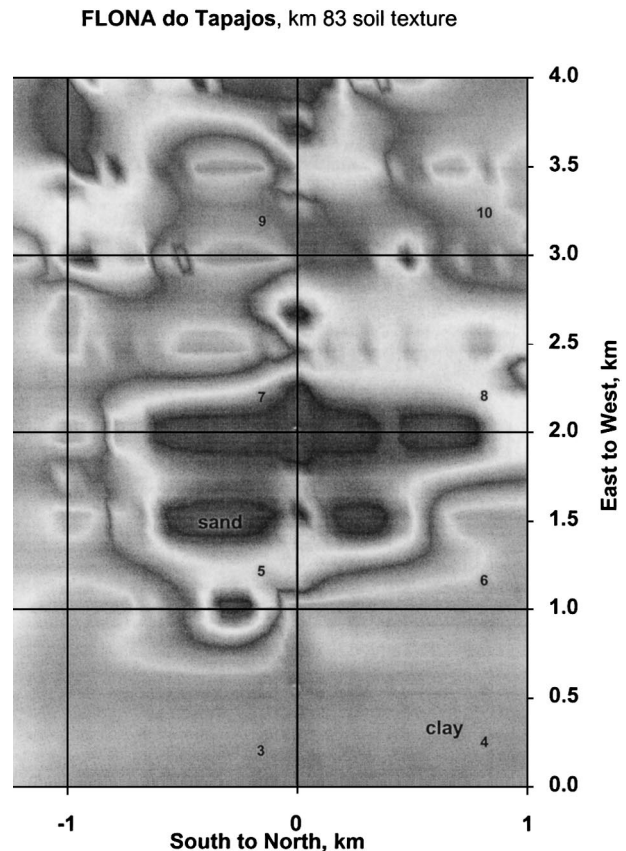

FLONA do Tapajos, km 83 soil texture

Figure 1. Soil texture map of the study site in the Tapajos National Forest, Para, Brazil. The map was generated from texture samples collected every 50 m along 0.5-km transects through the research area. The texture transect was located at the contact between sands and clays in block 6. Additional samples were collected in high clay and high sand soils.

with heat and H_2O_2 to remove organic matter and with NaHMP as a dispersal agent to minimize foaming. Soil pH was determined on fresh soils in a slurry of 4 g in 8 mL deionized H_2O.

We measured denitrification enzyme activity (DEA) according to Tiedje (1994) with some minor changes because of the high activity measured. A 10-g sample of field moist soil was placed in a 250-mL Erlenmeyer flask and 25 mL of a solution containing 1 mM glucose, 1 mM $NaNO_3$ and 1 g L-1 chloramphenicol was added. The flasks then were evacuated and flushed six times with He to produce an anaerobic environment. Acetylene (made from calcium carbide) was added to a final concentration of 10 kPa. The flasks were incubated during a 30-min anaerobic assay on a rotary shaker (100 rpm). Head space gas was sampled after 10, 20, 30, and 40 minutes and analyzed for N_2O on a gas chromatograph with electron capture detector (Keller and Reiners 1994). The DEA was calculated

from the linear increase in N_2O taking the dissolved N_2O into account by using the Bunsen relationship.

Potential net N mineralization and net nitrification were measured using aerobic laboratory incubations (Hart and others 1994). Two 15-g subsamples of field moist soils were weighed into plastic Nalgene bottles. One set of subsamples was immediately extracted with 100 mL of 2 M KCl; the other set was covered with perforated parafilm and incubated at ambient temperatures (approximately 25°C) for 7 days before extraction. Net nitrification and N mineralization were analyzed and calculated according to Hart and others (1994).

Samples for other chemical analyses were air-dried and ground to pass through a 2-mm sieve. Approximately 5-g samples were extracted separately with 55 mL 1 M NH_4Cl for exchangeable cation concentrations and with 50 mL of NH_4F for extractable P (Olsen and Sommers 1982) by using a vertical vacuum extractor (Johnson and others 1991). Samples were analyzed for exchangeable Ca, Mg, K, Al, Mn, Fe, and P on a Direct Current Plasma Spectraspan V spectrophotometer, Fullerton, CA USA at the International Institute of Tropical Forestry (IITF). For total C and N, samples were reground to a fine powder and analyzed upon combustion by using a Fisons CN analyzer, Suffolk, UK. Standard reference material, procedural blanks, and replicate samples were run for quality assessment at the rate of 1 per 10 samples. Subsamples of all soils were dried at 105°C to determine moisture content. All data reported here are on an oven dry soil basis. Bulk density of the 0–10-cm depth was determined at three random points on each of the six transects along the gradient ($n = 18$) by using a known volume bulk density corer. Samples were dried at 105°C to a constant weight and weighed for bulk density determinations.

Forest Floor Mass and Elemental Content

The forest floor was sampled at five random locations along each transect ($n = 30$), and at 10 additional random locations each on clay and sandy soils by using a 15 x 15–cm template (inside area). The forest floor contained recent litter and humified organic matter. Samples were dried at 65°C, weighed to determine mass, ground in a Wiley mill, and redried. Ground samples were predigested in H_2O_2 and then digested in concentrated HNO_3 by using a block digestor (Luh Huang and Schulte 1985) and analyzed at Boston University for Ca, Mg, K, Al, P, Fe, and Mn at IITF and for total C and N. Standard reference material (citrus and apple leaves), procedural blanks, and replicate samples were run for quality assessment at the rate of 1 per 10 samples.

Fine Root Biomass

Fine root standing stocks (0–10 cm depth) were sampled from five random locations along each transect ($n = 30$) by using a root corer of 4.1 cm inside diameter (Vogt and Perrson 1991; Silver and Vogt 1993). Cores were refrigerated until they were processed by sorting live and dead roots by size class (less than or equal to 2 mm diameter; greater than 2–5 mm diameter) from washed sieves. This technique yielded few samples in the greater than 2–5-mm size class, so these data are not reported here. Instead, we use data from the large quantitative pits described below to estimate the coarse root fraction. Root samples were dried at 65°C and weighed to determine mass. We took 10 additional randomly located samples for fine root standing stocks (less than or equal to 2 mm diameter) on both sand and clay soils ($n = 20$). To characterize patterns in fine root standing stocks by depth, we took three root cores from both the 20–30-cm and the 30–40-cm depths each on sand and clay soils ($n = 12$). All cores were processed as above. Root C and N were measured on a C.E. Instruments CN analyzer at U.C. Berkeley, and root P was measured at IITF after a H_2O_2-H_2SO_4 digest (Parkinson and Allen 1975).

Coarse Roots

A total of 23 large quantitative pits were excavated for coarse root biomass. We sampled the five pits located at 0, 50, 200, 350, and 400 m along the soil texture gradient, as well as 18 1 x 1 x 1–m pits with nine each on sand and clay soils. Each pit was sampled for root biomass at the 0–10-cm, 10–40-cm, and 40–100-cm depths. In the 0–10-cm depth, we separately weighed the mass of fine roots that could be easily separated from soil in the field. This technique undoubtedly excluded a proportion of the very fine (less than 1 mm) roots and root fragments, which are better sampled using the coring technique mentioned above. At the two deeper depths, fine root biomass was low, so we took samples of total root biomass combining all size classes together. Roots were cleaned of adhering soil and weighed in the field by using a spring balance (± 50 g), and subsampled for moisture determinations. Samples were dried at 65°C and weighed to determine mass, and to estimate a conversion factor from field wet weight to oven dry weight. Ground subsamples were predigested in H_2O_2 and digested in H_2SO_4 for total P and analyzed on a DCP at IITF (Parkinson and Allen 1975). Additional subsamples were analyzed for C and N on a CN analyzer at Stanford University.

Soil Chemical and Physical Properties to 1 m Depth

Soil textural properties, bulk density, soil $\delta^{15}N$, and soil cation, P, C, and N content were determined in 1-m deep quantitative soil pits located along the soil texture gradient and in additional pits located on sands and clays. An aggregate soil sample was collected at the 0–10-cm, 30–40-cm, and 90–100-cm depths from pits located at 0, 50, 200, 350, and 400 m along the gradient ($n = 15$) for textural properties, exchangeable cation concentrations, extractable and total P, and pH. Soil pH was determined in water as above, and in a slurry of 4 g of soil in 8 mL of 1 M KCl. Soil texture, exchangeable cations, and extractable P were measured as above. To estimate total P concentrations, we digested approximately 5 g of soil in H_2O_2 and concentrated H_2SO_4 by using a block digestor (Parkinson and Allen 1975). Solutions were analyzed at IITF. Standard reference soils, replicate samples, and blanks were used for quality control.

Total C and N were estimated from subsamples collected at 10-cm-depth increments (0–100 cm) from the pits at 0 m (sand), 200 m (loam), and 350 m (clay) along the texture gradient. We also took samples from six additional pits each on clay and sand soils at 7 cm, 40 cm, and 100 cm depth. We fit a logarithmic curve to these values and interpolated the soil C and N concentrations for the intermediate 10-cm-depth increments. The mean squared residuals for fitted C curves were 0.98 (± 0.01) for clays and 0.94 (± 0.03) for the sands, and for N they were 0.95 (± 0.02) for both sands and clays. All samples were analyzed on a CN analyzer at U.C. Berkeley and included replicate samples and reference soils. We interpolated total and extractable P concentrations by depth by using the values from the 0–10-cm, 30–40-cm, and 90–100-cm samples from pits along the texture gradient. Total P did not vary significantly with depth in the clays, so we used a mean value for all depths. Total P followed a decreasing pattern with depth in the sands ($r^2 = 0.84 \pm 0.01$). Total P data reported here represent a small sample size ($n = 4$) and thus should be viewed with caution.

Bulk density by depth was sampled on sands (50 m) and clays (350 m) at 10-cm-depth increments by using a know volume bulk density corer. Roots and rocks were removed, and the samples were dried at 105°C to a constant weight and weighed to determine mass. To estimate the mass of soil C, N, and P to a depth of 1 m, we multiplied the concentrations by depth with the bulk density estimations in sand and clay soils. Values were summed by depth to produce pool estimates for specific depth intervals. We had no bulk density estimates for subsurface loam soils, and so these soils were excluded from this analysis.

Soils were sampled for $\delta^{15}N$ from vertical profiles at 0 m (sand), 200 m (loam), and 350 m (clay) along the gradient. We took one sample from the surface to 2-cm, 2–5 cm, 5–10 cm depths and subsequent 10-cm-depth increments to 1 m in depth. Additional samples ($n = 4–6$) were taken from the surface and 90–100-cm depths in the sands (0 m) and clays (350 m). Soils were air-dried immediately after field sampling and again at 60°C to a constant weight. Soils then were ground to a powder and analyzed for $\delta^{15}N$ at the Natural Resource Ecology Lab at Colorado State University on a VG Isochrom Mass Spectrometer, Franklin, MA, USA with a dedicated Carlo Erba sample preparation system. The ^{15}N abundance is expressed in delta units relative to the $^{15}N/^{14}N$ ratio (R) of atmospheric N (^{15}N air/^{14}N air = 0.0036765). The $\delta^{15}N$ is calculated as $\delta^{15}N = [(R_{sample}/R_{standard})-1] \times 1000]$.

Model Application

We used the Century biogeochemistry model (Parton and others 1987) for our modeling exercise. Century has a three-compartment SOM model consisting of active, slow and passive pools of organic matter. Temperature, moisture, and nutrient constraints control the movement of C from plant pools to SOM pools, as well as between SOM pools. In addition, the movement of C from the slow to passive organic matter pools increases proportionally with clay content. We initialized Century by using parameters from tropical forest simulations done by Vitousek and others (1998) and Raich and others (1997) with rainfall and temperature data from the TNF. The tropical forest parameterizations differ from the original grassland and forest models in the stochiometry of C:N ratios and the relatively higher N inputs. One of the main biogeochemical differences between temperate system parameterizations and the TNF is the lack of parent material P in Brazil. For these runs, we initialized the model with no parent material P and high P sorption capacity to simulate the very low P conditions of this lowland tropical forest.

Our main objective was to evaluate the sensitivity of the Century model to soil texture and to compare the model simulated textural effects with pools of C and elements that we could measure at our site. To perform this sensitivity study, we "tuned" the model to achieve good correspondence between modeled and measured SOM carbon for our clay site. There are a number of ways to adjust Century, but one of

Table 1. Exchangeable Cations, Extractable P, Total C and N, and Soil Physical Properties[a] in the Tapajos National Forest, Para, Brazil

Soil Property	Meters along the Texture Gradient					
	0	50	150	200	350	400
Bulk density (g cm^{-3})	1.34 (0.05) ab	1.16 (0.11) abc	1.36 (0.04) a	1.14 (0.07) bc	1.23 (0.09) ac	1.02 (0.02) c
Sand (%)	80 (0.9) a	80 (0.7) a	52 (1.7) b	52 (0.6) b	37 (1.0) c	38 (1.1) c
Clay (%)	18 (0.4) a	18 (1.1) a	46 (1.7) b	45 (0.8) b	60 (1.1) c	60 (1.3) c
Silt (%)	2 (0.8)	3 (0.5)	2 (0.2)	3 (0.4)	3 (0.5)	2 (0.5)
pH (H$_2$O)	3.90 (0.03) ac	3.89 (0.08) ac	3.62 (0.14) a	3.79 (0.12) a	4.26 (0.18) bc	4.19 (0.13) c
Total C (%)	2.81 (0.54)	2.19 (0.43)	2.18 (0.08)	2.11 (0.13)	2.66 (0.11)	2.26 (0.06)
Total N (%)	0.15 (0.02)	0.13 (0.03)	0.15 (0.02)	0.15 (0.01)	0.18 (0.01)	0.17 (0.01)
Extractable P (µg g^{-1})	9.50 (1.44) a	6.50 (0.51) b	4.00 (0.49) c	4.28 (0.11) c	3.96 (0.25) c	3.01 (0.18) d
Ca (cmol$^+$ kg^{-1})	0.13 (0.04)	0.09 (0.02)	0.05 (0.01)	0.06 (0.02)	0.07 (0.01)	0.06 (0.01)
Mg (cmol$^+$ kg^{-1})	<	<	<	<	<	<
K (cmol$^+$ kg^{-1})	0.08 (0.01) a	0.06 (0.01) a	0.07 (0.01) a	0.06 (0.01) a	0.11 (0.01) b	0.08 (0.01) a
Mn (µg g^{-1})	8.06 (2.39) a	2.93 (0.74) b	2.13 (0.27) b	1.76 (0.36) b	1.72 (0.20) b	1.74 (0.29) b
Al (cmol$^+$ kg^{-1})	0.85 (0.14) a	0.58 (0.03) b	1.96 (0.06) c	1.74 (0.06) c	3.25 (0.13) d	2.56 (0.25) e

[a]0–10 cm depth.

Values are means ± 1 SE (in parentheses). Rows with different lowercase letters identify statistically significant differences among sites at the 95% level. Magnesium concentrations were below detection (<) by the analytical instrumentation (0.013 cmol$^+$ kg^{-1}).

the most sensitive aspects of the model is the strong potential N limitation to primary productivity (Vitousek and others 1998). By adjusting N inputs, we could alter the steady state content of SOM for the clay soil to achieve a good fit to our observed data. The equilibrium values of N additions required to obtain reasonable SOM C and N values for the clay site were additions of 2.2 kg N ha^{-1} y^{-1}. When the model inputs were set for the clay site, we altered only the bulk density and texture to reflect the conditions in the loam and sandy soils.

Once Century was parameterized for the clay site, we then compared the equilibrium soil and root C, N, and P contents from the model to measured values for sand and loam soils. To systematically explore the models simulated limitations to plant growth, and concurrently examine the sensitivity of Century to water and nutrient availability in the sands, we ran experiments where we doubled N inputs (from 2.2 to 4.4 kg ha^{-1} y^{-1}), P inputs (from 1.1 to 2.2 kg ha^{-1} y^{-1}), and rooting depth (60–120 cm depth). Because we could not adjust water use by vegetation in the model, we used rooting depth as a rough surrogate for water access and use, because rooting depth has been shown recently to correlate with ecosystem-level water use in seasonally dry tropical forests (Nepstad and others 1994).

The Century model output uses a fixed depth of 0–20 cm. To compare the Century model output with the field data, we used our measured bulk density, C and N values, and the measured and interpolated NH$_4$F-P and total soil P concentrations (see above). For the loam soil, we used the 0–10-cm bulk density measurement because there were no data for the deeper soil depths. Only clay and sandy soils were measured for root C, N, and P. Coarse root data were collected from the 0–10-cm, 10–40-cm, and 40–100-cm depths. We estimated the mass of coarse root C, N, and P for the 0–20-cm depth by adding one-third of the values for the 10–40-cm depth to the values for the 0–10-cm depth. Because root biomass tended to decrease with depth, this is likely to be a slight underestimation of the pool sizes of root C, N, and P.

Statistical Analyses

Statistical analyses were performed using Systat (Wilkinson 1990). Data were log transformed when necessary to meet the assumptions for analysis of variance (ANOVA). One-way and two-way ANOVAs were used to determine significant differences within variables along the gradient, and with texture and depth. Pairwise comparisons using the Least Significant Differences protocol were performed to determine where significant differences occurred. Pearson correlations were used to examine relationships among soil texture and soil and root properties. We also used simple and stepwise multiple linear regressions to identify trends with soil texture. We performed *t*-tests to examine differences in soil, root, and forest floor C, N, and P between sand and clay. Residuals from all analyses

were checked for normality and homogeneity of variances (Steel and Torrie 1980). We report significant differences at the 95% level unless otherwise noted. Values reported in the text are means followed by standard errors.

RESULTS

Physical and Chemical Properties of Surface Soils

The percent sand and clay varied significantly in the 0–10-cm depth along the texture gradient (Table 1 and Figure 2) ranging from 80% ($\pm$1) sand to 60% ($\pm$1) clay. Extractable soil P concentrations were significantly negatively correlated with clay content ($r^2 = 0.70$, $P < 0.01$; Table 2), and the combination of clay content and exchangeable K concentrations ($r^2 = 0.81$, $P < 0.01$). The correlation with K may be due to some K occlusion by the 1:1 clays, although K is likely to be sorbed less strongly than P (Graham and Fox 1971). A significant negative relationship also occurred with P and exchangeable Al concentrations ($r^2 = 0.57$, $P < 0.01$). Extractable soil P was
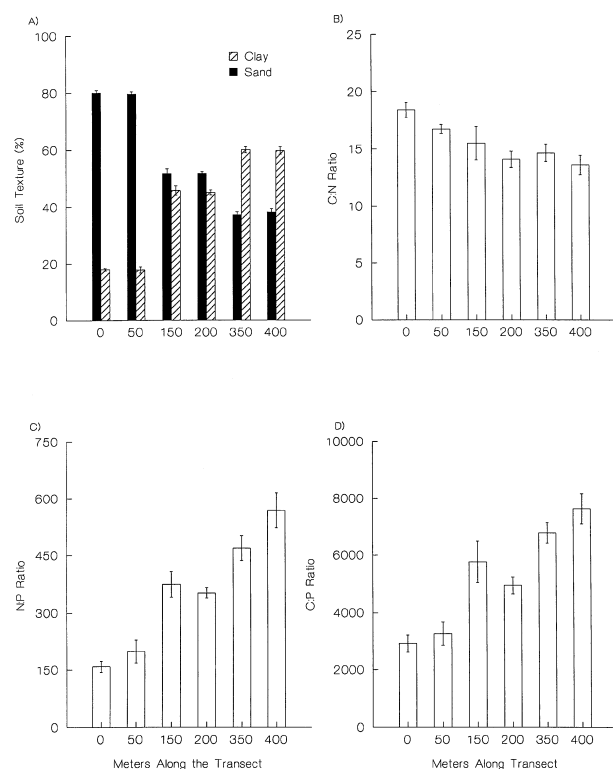
Table 2. Correlation Coefficients of the Relationship of Soil Chemical and Physical Properties, Fine Root Biomass, and Forest Floor Biomass to Clay Content in the Tapajos National Forest, Para, Brazil

Variable	Clay (%)
Ca cmol$^+$ kg^{-1}	-0.32
K cmol$^+$ kg^{-1}	0.47
Mn μg g^{-1}	-0.57
Al cmol$^+$ kg^{-1}	0.91*
P μg g^{-1}	-0.84*
C (%)	0.21
N (%)	0.49*
pH	0.35
Live roots (g m^{-2})	-0.47
Dead roots (g m^{-2})	-0.56*
Forest floor (kg ha^{-1})	-0.06
C:N	-0.73*
C:P	0.88*
N:P	0.93*
NH$_4$-N (μg g^{-1})	-0.26
NO$_3$-N (μg g^{-1})	0.60
Net nitrification (μg g^{-1} d^{-1})	0.70*
Net N mineralization (μg g^{-1} d^{-1})	0.56
DEA (ng g^{-1} h^{-1})	0.86*
Bulk density (g cm^{-3})	-0.24

$P < 0.01$.

Figure 2. Soil chemical and physical properties in the 0–10-cm depth along a soil texture gradient in the Tapajos National Forest, Brazil. (**A**) Texture; (**B**) C:N ratio; (**C**) N:P ratio; (**D**) C:P ratio. To calculate ratios, we used total C and N and extractable P.

very low in clays soils (3.0 μg g^{-1}), and increased by a factor of 3 in the sands (Table 1).

There were no significant trends in total C or N concentrations along the soil textural gradient in the 0–10-cm soil depth, but the C:N ratio decreased significantly from 18.4 in the sands to 13.6 in the clays (Figure 2). Total C and N in the soil were positively and significantly correlated along the gradient ($r^2 = 0.73$; $P < 0.01$). The soil C:P$_{extractable}$ and N:P$_{extractable}$ ratios both increased dramatically from sands to clay along the texture gradient (Figure 2), and were significantly positively correlated with clay content (Table 2). Total C pools in the surface soils ranged between 23 ($\pm$0.6) and 38 ($\pm$7.2) Mg C ha^{-1} and did not follow a significant trend with soil texture.

Nitrogen pools and fluxes varied significantly with soil texture. Ammonium-N concentrations were significantly lower in the loam soils than in the sands ($P = 0.05$), whereas NO$_3$-N was significantly higher in the loam soils than in the sands (Figure 3). Net nitrification rates increased significantly from 0.68–0.72 μg g^{-1} d^{-1} in the sands to 1.91–2.29 μg g^{-1}d^{-1} in the clays (Figure 3). Net nitrification rates
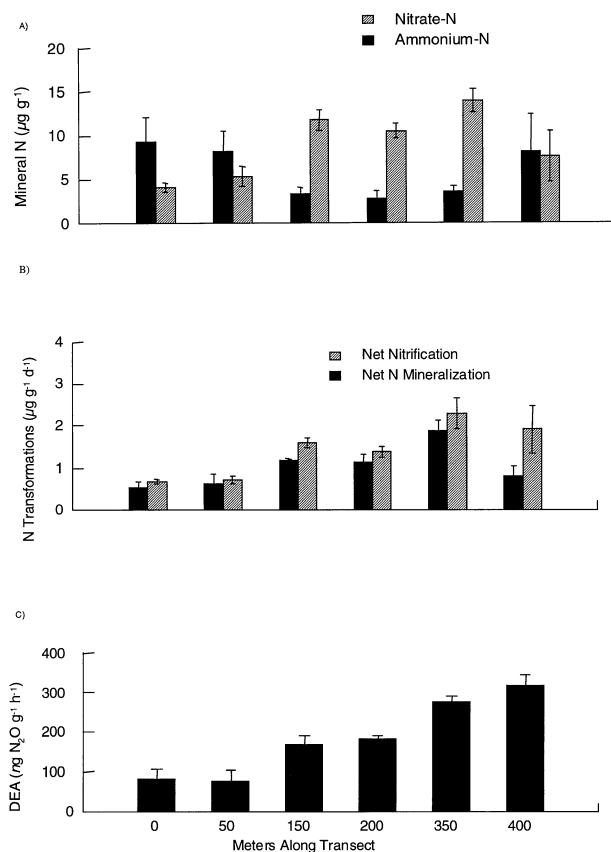
Figure 3. Initial mineral N concentrations **A**, potential net mineralization and nitrification **B**, and denitrification enzyme activity (DEA) **C** in the 0–10-cm soil depth along a soil texture gradient in the Tapajos National Forest, Brazil. Clay content increased along the gradient.

explained most of the trend in net N mineralization rates, which also generally increased significantly from sands to clays, with the exception of the last clay soil site along the gradient (Figure 3). Denitrification enzyme activity increased significantly from 77 ($\pm$23) ng g^{-1} h^{-1} in the sands to 317 ($\pm$24) ng g^{-1} h^{-1} in the clays and was significantly positively correlated with initial NH_4-N concentrations and clay content (Figure 3 and Table 2).

Concentrations of exchangeable Al increased significantly from sands to clays (Table 1), and clay content alone explained 84% of the variability in exchangeable Al (Table 2). Exchangeable nutrient cation concentrations were very low in the surface soils along the texture gradient (Table 1). Exchangeable Mg was below the detection limit of the analytical instrumentation (1.6 μg g^{-1} or 0.013 cmol$^+$ kg^{-1}). Pool sizes (kg ha^{-1}) of most elements followed similar trends as the elemental concentrations along the gradient. Soil pH was significantly lower in the loam soils than in the clays (Table 1).

Forest Floor and Root Biomass

Forest floor mass along the texture gradient averaged 6.9 ($\pm$0.7) Mg ha^{-1} (Table 3). Along the gradient, forest floor C concentrations were greater on the sands than on the other soil types, and forest floor N and P concentrations decreased slightly but significantly from sands to clays. When comparing just the two textural extremes ($n = 40$), forest floor C, N, and P content were significantly greater on sands than on clays (Table 4). Forest floor C:N and C:P ratios were very similar on sand and clays soils.

Standing stocks of total fine root biomass (live plus dead) in the 0–10-cm depth decreased significantly from approximately 4.5 ($\pm$0.4) Mg ha^{-1} in the sandy soils to less than 1.9 ($\pm$0.4) Mg ha^{-1} in clays along the texture gradient (Figure 4). Both live and dead fine root biomass followed the same trend with soil texture; live fine root biomass was very low in all soil types (0.05–0.4 Mg ha^{-1}). Sandy soils had significantly greater live and dead fine root biomass to a depth of 40 cm than the clays (Figure 4). Total fine root biomass was significantly negatively correlated with N mineralization rates and positively correlated with extractable P pools ($r^2 = 0.48$; $P < 0.05$). Fine root C, N, and P content were significantly greater on sandy soils than on clays in the top 10 cm of soil (Table 4).

Total root biomass to a depth of 1 m ranged from 11 to 188 Mg ha^{-1} in the five pits along the texture gradient (Figure 4) and was greatest in the 0–10-cm depth at all sites. There was a general pattern of increasing total root biomass along the gradient from sands to clays. The exception was at meter 50 (sands) where we encountered an extremely heavy root (up to 15 kg m^{-2} wet weight) that penetrated from near the surface to 1 m in depth. Comparing all 22 pits on sand and clay soils (including the two clay and two sand pits along the texture gradient), there was significantly more coarse root C, N, or P in clays to a depth of 10 cm, and greater root P in 40–100-cm depth on clays. The ratios of root C:N and C:P were higher on the sands than on the clays for all soil depths (Table 4). The total root C pool to 1 m depth was approximately 26 $\pm$ 8 Mg ha^{-1} on sands and 17 $\pm$ 2 Mg ha^{-1} on clays.

Soil Properties to 1 m Depth

Total soil C pools to 1 m depth were very similar on clays (80 Mg C ha^{-1} $\pm$ 3) and sands (81 Mg C ha^{-1} $\pm$ 4; Table 4). There was significantly more C in the surface 20 cm of the clays but greater C in lower 50 cm in the sands ($P < 0.10$). Total N followed a

Table 3. Forest Floor Mass and Elemental Concentrations along a Texture Gradient in the Tapajos National Forest, Para, Brazil

Forest Floor Property	Meters along the Texture Gradient					
	0	50	150	200	350	400
Mass (g m^{-2})	839 (165)	840 (213)	652 (174)	564 (66)	538 (193)	720 (190)
C (%)	50 (0.5) a	51 (0.4) a	43 (2.6) b	46 (1.3) ab	42 (1.6) b	47 (1.6) ab
N (%)	1.89 (0.2) ac	2.69 (0.3) b	2.28 (0.2) ab	2.06 (0.1) abc	1.66 (0.1) c	1.77 (0.3) c
C:N	27 (2.5)	20 (1.8)	19 (1.7)	23 (1.7)	27 (2.1)	31 (8.0)
P (mg g^{-1})	0.49 (0.04) ab	0.67 (0.10) a	0.55 (0.06) a	0.53 (0.06) a	0.53 (0.03) a	0.37 (0.05) b
Ca (mg g^{-1})	3.97 (0.86)	5.78 (1.41)	6.02 (0.66)	7.88 (0.94)	5.45 (0.82)	4.49 (0.79)
Mg (mg g^{-1})	1.19 (0.11)	1.73 (0.37)	1.25 (0.10)	1.47 (0.14)	1.67 (0.18)	1.74 (0.45)
K (mg g^{-1})	1.50 (0.38)	1.81 (0.31)	1.63 (0.17)	2.53 (0.35)	1.62 (0.25)	1.16 (0.12)
Mn (mg g^{-1})	0.22 (0.05)	0.42 (0.10) b	0.51 (0.08)	0.24 (0.02)	0.25 (0.02)	0.33 (0.13)
Al (mg g^{-1})	0.46 (0.11) a	0.75 (0.33) ab	2.07 (0.45) c	1.87 (0.74) bc	6.31 (0.82) d	3.66 (0.66) cd

Values are means ± 1 SE (in parentheses). Rows with different lowercase letters identify statistically significant differences among sites at the 95% level; n = 30.

different pattern than C (Table 4). There was significantly more total soil N in clays to 1 m (8.5 Mg N ha^{-1} ± 0.4) than in the sands (6.6 Mg N ha^{-1} ± 0.4), due primarily to the significantly greater pools of N in the top 50 cm in the clays. Total C and N concentrations in the surface soils were lower when sampled from the large quantitative pits than from the core samples. It is unclear what caused these differences, but they could result from the smaller sample size and differences in the area sampled. We estimated a total belowground C pool (forest floor plus roots plus soil) of 113 Mg ha^{-1} C on the sands to 101 Mg ha^{-1} C on the clays (Table 4).

Total soil P concentrations and pools in the 0–10 cm depth followed the reverse trend of extractable P. Along the soil texture gradient, total soil P concentrations increased by a factor of 4 to 5 from sands to clays (Table 5). Total P concentrations tended to be greater at the deeper soil depths in the sands but followed no trend in the loam or clays soils (Table 5).

There were few trends in soil texture with depth along the textural gradient (Table 5). Sand content decreased slightly (-10%) with depth in the sand pits with a corresponding increase in clay content. Exchangeable nutrient cation and extractable P concentrations generally decreased with depth in the soil (Table 5).

Delta ^{15}N values ranged from 6.2 to 12.7. Sands had significantly lower δ^{15}N than clays in both the surface soils (Table 6). There were no statistically significant patterns in δ^{15}N between the surface and 1 m depth and no strong patterns with depth in the sand or loam soils. In the clays, the top 10 cm of mineral soil were slightly depleted in δ^{15}N relative to deeper soil depths (Table 6).

Model Results

The Century model simulation of the soil texture gradient predicted greater soil C, N, and P in clays than in loams or sands, respectively (Table 7). Century underestimated the soil C and N pools by 45% and 44%, respectively, on the sands, but captured the trends of lower C and N in the sands that we found with our samples from the large quantitative pits. Century has several P pools including mineral P, SOM P, secondary P, occluded P, and parent P. It is somewhat difficult to compare these model pools directly to data from P fractionation schemes (Gijsman and others 1996), and we lack the data for a comprehensive evaluation of the Century P model; however, there are several interesting patterns worth noting. We report the modeled SOM P fraction from Century in comparison to our NH$_4$F extractable P, forest floor P, and total P values. Interestingly, the vast majority of the P in the model simulations was located in the SOM P pool rather than in secondary or occluded P. Field measurements of NH$_4$F extractable P and forest floor P showed approximately three times more labile P in the sands than in the clays. In contrast, modeled P mineralization (an index of labile P) followed the opposite pattern and ranged from 0.15 g P m^2 y^{-1} in the sands to 0.2 g P m^2 y^{-1} in the clays. The model simulation predicted a threefold increase in SOM P from sands to clay, similar to the 2.7-fold increase we measured for total P in sands versus clays at this depth. The average pool size of total P measured on the clays (398 kg ha^{-1}) was considerably greater than the model SOM P output (129 kg ha^{-1}), and inclusion of parent, occluded, or secondary P pools in the model do not change this pattern.

Table 4. Forest Floor, Root, and Total Soil C, N, and P Pools by Depth in Sand and Clay Soils in the Tapajos National Forest, Para, Brazil

Depth	Sands	Clays	$P < 0.05$
Forest floor			
Litter C	4.39 (0.47)	3.10 (0.47)	*
Litter N	0.18 (0.02)	0.13 (0.02)	*
Litter P	4.44 (0.60)	3.13 (0.50)	*
Litter C:N	24.80 (2.03)	25.70 (2.65)	
Litter C:P	1030 (102)	1067 (92.8)	
0–10 cm			
Soil C	12.07 (0.68)	16.46 (1.25)	*
Soil N	0.89 (0.06)	1.48 (0.07)	*
Soil P	67.0 (5.00)	212.5 (19.5)	*
Soil C:N	13.03 (0.87)	9.95 (0.42)	*
Fine root C	1.48 (0.11)	1.06 (0.10)	*
Fine root N	0.05 (0.004)	0.03 (0.003)	*
Fine root P	1.59 (0.11)	0.80 (0.07)	*
Coarse root C[a]	6.00 (3.25)	6.77 (1.02)	*
Coarse root N	0.09 (0.05)	0.18 (0.03)	*
Coarse root P	2.99 (1.42)	4.49 (0.64)	*
Root C:N	72.37 (3.58)	38.72 (0.52)	*
Root C:P	1888 (116.3)	1515 (59.8)	*
10–40 cm			
Soil C	29.78 (1.84)	32.02 (1.69)	
Soil N	3.44 (0.21)	3.79 (0.27)	*
Soil P	277.5 (5.30)	569.0 (18.94)	*
Soil C:N	11.66 (1.04)	8.53 (0.55)	*
Total root C	13.88 (4.46)	6.35 (0.92)	
Total root N	0.20 (0.06)	0.17 (0.02)	
Total root P	5.18 (1.67)	5.22 (0.75)	
Root C:N	69.67 (0.07)	37.64 (0.09)	*
Root C:P	2682 (10.1)	1216 (0.10)	*
40–100 cm			
Soil C	39.28 (2.21)	31.68 (1.76)	*
Soil N	3.44 (0.21)	3.74 (0.26)	
Soil P	563.4 (0.51)	894.8 (5.46)	*
Soil C:N	11.56 (1.06)	8.55 (0.52)	*
Total root C	6.00 (2.44)	3.71 (1.13)	
Total root N	0.09 (0.04)	0.07 (0.02)	
Total root P	0.93 (0.38)	2.01 (0.61)	*
Root C:N	63.94 (0.04)	53.99 (0.04)	*
Root C:P	6523 (32.4)	1848 (1.40)	*
0–100 cm			
Total below-ground C	112.88 —	101.15 —	
Total below-ground N	8.38 —	9.59 —	
Total below-ground P	923.06 —	1691.90 —	

[a]P = 0.05. C and N values are in Mg ha^{-1}; values for P are in kg ha^{-1}. Fine roots are ≤2 mm diameter; coarse roots are >2 mm diameter. Asterisks signify statistically significant differences between soil texture types by using a 2 sample t-test. Standard errors are in parentheses.
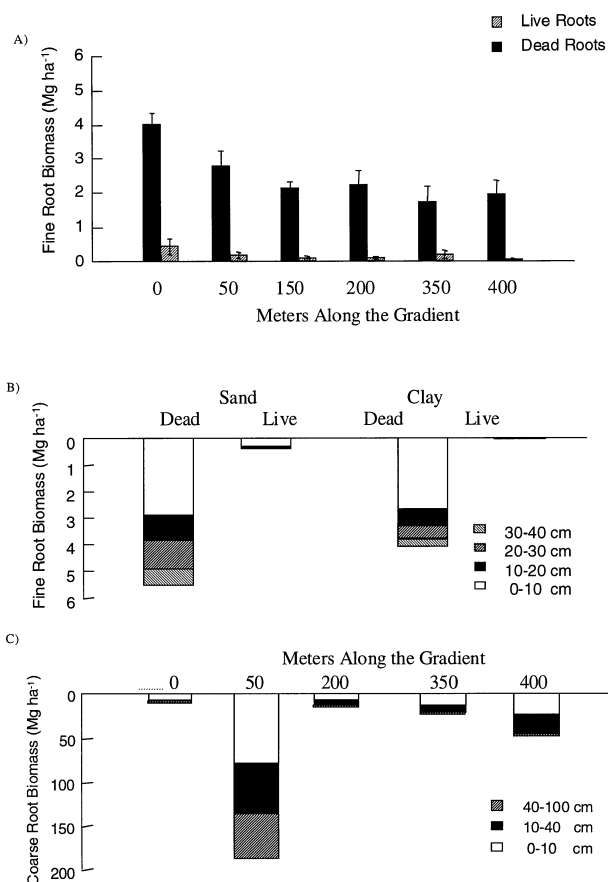

Figure 4. The distribution of fine and coarse root biomass in the Tapajos National Forest, Brazil. **A** The proportion of live and dead fine roots in the surface soils along the soil texture gradient. Error bars represent ±1 SE. **B** The distribution of live and dead fine root biomass by depth to 40 cm in sand and clay soil types. **C** Total root biomass by depth in five 3 x 1 x 1–m quantitative soil pits along the soil texture gradient. The high apparent biomass at meter 50 was heavily weighted by a single large and heavy root than passed through all three depths.

The model generally estimated fine and coarse root C content within 20% of the measured values, except for overestimating fine root C in the clays by 67%. The model closely predicted fine root N and P content in clays, but underestimated these in the sands. We measured greater coarse root N and P in both clay and sandy soils than Century predicted, but Century accurately captured the trends of greater coarse root N and P in clays than in sands (Table 7). Century underestimated the total belowground C (root plus soil) in the sands by 53%. Aboveground biomass C on sands was predicted to be 20% lower than on clays, whereas the total forest C pool was 30% lower on sands than on clays. Century predicted that total forest C would increase from sands to loams to clays (Table 7).

Table 5. Soil pH, Texture, Exchangeable Cations, Extractable (P_{ex}) and Total P by Depth in Five Large Quantitative Soils Pits[a]

Soil Property	0	50	200	300	350
0–10 cm depth					
pH (KCl)	3.59	3.70	3.47	3.73	3.72
pH (H_2O)	3.86	4.04	3.54	3.82	3.72
Sand (%)	86.25	84.34	58.81	50.56	37.70
Clay (%)	13.75	15.18	36.87	47.04	60.36
Silt (%)	0.00	0.48	4.32	2.40	1.93
Total P ($\mu g\,g^{-1}$)	58.17	41.80	121.93	201.87	189.28
Pex ($\mu g\,g^{-1}$)	2.48	1.89	6.22	3.45	3.31
Ca ($cmol^+\,kg^{-1}$)	0.02	0.02	0.05	0.04	0.03
Mg ($cmol^+\,kg^{-1}$)	<	<	<	<	<
K ($cmol^+\,kg^{-1}$)	0.03	0.02	0.05	0.05	0.07
Mn ($\mu g\,g^{-1}$)	0.58	<	0.81	2.18	1.75
Al ($cmol^+\,kg^{-1}$)	0.99	1.10	2.57	2.20	3.28
10–40 cm depth					
pH (KCl)	4.07	4.16	3.93	3.96	3.93
pH (H_2O)	4.28	4.18	4.91	4.25	3.91
Sand (%)	75.22	80.48	51.52	44.79	37.12
Clay (%)	22.39	19.52	48.48	54.25	60.00
Silt (%)	2.39	0.00	0.00	0.96	2.88
Total P ($\mu g\,g^{-1}$)	74.67	86.21	117.51	191.63	141.72
Pex ($\mu g\,g^{-1}$)	<	1.23	<	<	<
Ca ($cmol^+\,kg^{-1}$)	0.01	0.01	0.08	0.00	0.01
Mg ($cmol^+\,kg^{-1}$)	<	<	<	<	<
K ($cmol^+\,kg^{-1}$)	0.01	0.02	0.05	0.01	0.03
Mn ($\mu g\,g^{-1}$)	<	0.39	0.19	<	<
Al ($cmol^+\,kg^{-1}$)	1.53	1.27	1.87	2.40	2.31
40–100 cm depth					
pH (KCl)	4.23	4.18	3.96	3.88	3.93
pH (H_2O)	4.21	4.35	4.28	4.50	4.21
Sand (%)	75.27	73.32	50.14	44.91	39.31
Clay (%)	23.77	22.38	49.86	52.69	61.69
Silt (%)	0.95	4.30	0.00	2.40	0.00
Total P ($\mu g\,g^{-1}$)	79.42	78.25	128.36	na	219.51
Pex ($\mu g\,g^{-1}$)	<	<	<	<	<
Ca ($cmol^+\,kg^{-1}$)	0.01	0.01	0.01	0.01	0.01
Mg ($cmol^+\,kg^{-1}$)	<	<	<	<	<
K ($cmol^+\,kg^{-1}$)	0.01	0.01	0.01	0.01	0.01
Mn ($\mu g\,g^{-1}$)	<	<	<	<	<
Al ($cmol^+\,kg^{-1}$)	1.07	1.40	1.50	1.77	2.54

(Header: **Meters along the Texture Gradient**)

[a] $3 \times 1 \times 1$ m.
Values represent one pooled sampled per depth. Samples differ from those in Table 1. < signifies below detection of the analytical instruments. na = not available.

Table 6. Mean Delta ^{15}N by Depth in Three Soil Pits[a] along a Soil Texture Gradient in the Tapajos National Forest, Para, Brazil

Depth	Sands Meter 0	Loams Meter 200	Clays Meter 350
0–2	7.04 (0.40) a	nd	8.59 (0.49) b
2–5	9.08	10.02	8.38
5–10	9.55	10.11	9.18
10–20	8.99	8.82	9.52
20–30	9.99	10.03	9.73
30–40	10.20	7.06	10.34
40–50	9.57	12.49	12.64
50–60	7.05	6.59	9.22
60–70	6.20	12.28	9.53
70–80	6.58	9.54	9.62
80–90	6.62	6.72	12.74
90–100	7.31 (0.51) a	nd	9.45 (0.20) a

[a] $3 \times 1 \times 1$ m.
Replicate samples were taken from the 0–2-cm and 90–100-cm depths. For these depths, standard errors are in parentheses. Different lowercase letters indicate statistically significant differences between sand and clay by using replicate samples within depths. There were no statistically significant patterns with depth within sites (P < 0.05). nd, no data.

on the clays than on the other two soil types (Table 7). These model results agree with our experimental data that show higher DEA, mineralization, and more enriched $\delta^{15}N$ with depth on the clays than on the sands.

Doubling the rate of N inputs in the sands increased the model soil C content from 12.7 to 26.3 Mg ha^{-1}, whereas doubling the P inputs increased the soil C by only 0.4 Mg ha^{-1} (Table 7). Doubling the functional rooting depth from 60 to 120 cm depth also had only a minimal impact on soil C pools in sands with an increase of only 0.5 Mg ha^{-1} (Table 7).

DISCUSSION

The Effects of Soil Texture on Soil Nutrient Pools

The pool sizes and distribution of soil P and N varied significantly along the 400-m soil texture gradient in this forest. Sandy soils had more extractable P than the loam and clay-rich soils. In well-aerated soils such as these, P is easily complexed with exchangeable Al and Fe in the mineral soil, shown by the significant negative correlation of exchangeable Al and P along the gradient as clay content increased. There was significantly greater total P with increasing clay content along the gradient, probably due to the formation of Fe and Al phosphates and organically bound P, neither of which

The Century model also includes parameterizations of losses due to leaching and volatilization. Nitrogen losses generally followed the same trends as for total SOM N pools with higher rates of N leaching on the clays than on the loams or sands (data not shown), and higher rates of trace gas loss

Table 7. Century Model Simulation and Measured Values of the Belowground C, N, and P Pools and N Trace Gas Flux in the Tapajos National Forest, Brazil

Pools or Fluxes		Sands		Sandy Loams		Clays	
		CENTURY	Measured	CENTURY	Measured	CENTURY	Measured
Soil organic matter C	Mg ha^{-1}	12.7	22.9	24.0	31.4	31.2	29.8
Soil C 2 × N	Mg ha^{-1}	26.3	na	na	na	na	na
Soil C 2 × P	Mg ha^{-1}	13.1	na	na	na	na	na
Soil C 2 × water	Mg ha^{-1}	13.1	na	na	na	na	na
Soil organic matter N	Mg ha^{-1}	0.96	1.70	2.12	2.44	2.90	2.79
Soil organic matter P	kg ha^{-1}	44.1	5; 148	94.6	8; 305	129.1	5; 398
Fine root C	Mg ha^{-1}	1.78	1.94	2.11	na	2.24	1.34
Fine root N	Mg ha^{-1}	0.02	0.08	0.03	na	0.03	0.03
Fine root P	kg ha^{-1}	0.84	2.07	0.99	na	1.06	1.01
Coarse root C	Mg ha^{-1}	8.63	10.63	10.2	na	10.9	8.89
Coarse root N	Mg ha^{-1}	0.06	0.16	0.07	na	0.07	0.24
Coarse root P	kg ha^{-1}	1.25	4.72	1.48	na	1.58	6.23
Belowground C	Mg ha^{-1}	23.1	35.5	36.3	na	44.3	40.0
Aboveground C	Mg ha^{-1}	69.8	na	83.0	na	88.6	na
Total forest C	Mg ha^{-1}	92.9	na	119.3	na	132.9	na
Trace gas loss	kg N ha^{-1} y^{-1}	1.07	na	1.31	na	1.42	na

Model runs were parameterized as in Raich and others (1997) and Vitousek and others (1998) by using soil texture, bulk density, temperature, and precipitation from the TNF. The model was run for 10,000 y to quasiequilibrium by using fixed N and P inputs and no parent material P. We then doubled the model N inputs, P inputs, and rooting depth (from 60 to 120 cm) as a surrogate for water availability on the sands (see text). Model outputs are for the 0–20 cm depth. We used the 0–10-cm-depth bulk density value for modeled and measured estimates on sandy loams. Measured fine root values >10 cm depth were not available for the sandy loams so are not included here. Measured soil P is expressed as both extractable (first value) and total (second value). See text for details on measured and estimated values. na, not available or applicable.

are likely to be extracted with NH$_4$F. Phosphorus is cited frequently as a limiting element in lowland tropical forests and has been significantly correlated with rates of fine root growth, decomposition, and nutrient use efficiency by vegetation (Cuevas and Medina 1986, 1988; Medina and Cuevas 1989; Silver 1994). Tiessen and others (1994) did a detailed analysis of different P fractions along a topographic gradient in the Venezuelan Amazon and found that resin extractable P (their index of the plant available fraction) increased from ridges to valleys, corresponding to a gradient from more finely textured soils (17% clay) to more coarsely textured soils (2% clay). They also found more total and strong acid-extractable P in the finer textured soils on ridges than in sandier soils.

Contrary to the generalized patterns for P, N supply generally is considered adequate for plant growth in the lowland tropics (Vitousek and Sanford 1986; Vitousek and Matson 1988). Notable exceptions to this include quartz sands (psamments) in Brazil (Livingston and others 1988) and Venezuela (Cuevas and Medina 1986, 1988). Along the texture gradient, clays exhibited higher initial concentrations of NO$_3$-N and lower NH$_4$-N than sands and greater rates of potential net NO$_3$ production. Rates of potential net N mineralization and nitrification were strikingly similar to those re-

ported by Livingston and others (1988) and Vitousek and Matson (1988) for Amazonian soils along a topographic and soil texture gradient near Manaus, Brazil. They found that sandy soils of the lower topographic positions exhibited low potential net NO$_3$ production and relatively low levels of recovery of added ^{15}NO$_3$ compared with ridge and slope soils (Vitousek and Matson 1988). In this study, higher potential nitrification rates in clay soils were coupled with greater DEA and δ^{15}N indicating that N losses via denitrification and/or leaching also may be affecting N pools in the clays. Although denitrification is spatially and temporally dynamic, DEA generally is thought to be an integrative index of longer-term (annual) denitrification rates because enzymes can persist in the soil longer than actual denitrifier activity (Groffman and Tiedje 1989). Nitrous oxide fluxes and denitrification rates have been shown to decrease significantly with increasing sand content in temperate and tropical forests (Matson and Vitousek 1987; Livingston and others 1988; Groffman and Tiedje 1989), presumably in part because sandy soils often have better drainage and lower water holding capacity leading to better aeration. In this study, as in the study near Manaus, sandy soils also had lower net nitrification rates and NO$_3$ concentrations, which also are likely

to reduce denitrifier activity (Livingston and others 1988).

The $\delta^{15}N$ signature of soils provides additional information about the ecosystem N cycle. During decomposition, SOM tends to become enriched in $\delta^{15}N$ relative to plant litter due to fractionating losses of ^{14}N during mineralization (nitrification) and during trace gas and leaching losses (Blackmer and Bremner 1977; Mariotti and others 1982; Heaton 1986; Nadelhoffer and Fry 1988). Delta ^{15}N values often increase with depth as increasingly decomposed material moves down through the soil profile in leachate and as isotopically light N is lost to trace gases or leachate. The $\delta^{15}N$ values reported here are similar to those reported for other Amazonian forest soils, but depth profiles, and particularly the sand and loam profiles, showed less enrichment than other measurements in the Amazon basin (Piccolo and others 1994). The reason for the lack of enrichment with depth in the sand and loam soils is not clear, but it could be the result of faster downward movement of organic matter through the sands versus the clays. The higher $\delta^{15}N$ in the clays relative to sands is likely to result from greater rates of fractionating N losses via denitrification and N leaching, which is consistent with the higher DEA and nitrification rates we observed. Both denitrification and NO_3 leaching occur preferentially for ^{14}N rather than ^{15}N and leave the residual SOM enriched in ^{15}N (Karamanos and Rennie 1980; Kim and Craig 1993).

Unlike the patterns for N and P, pools of exchangeable Ca and Mg did not vary significantly along the texture gradient and were very low in the surface soils. Low exchangeable cation content is common in Amazonian soils (Stark 1971; Klinge 1977; Furch and Klinge 1978; Uhl and Jordan 1984) and may be partially moderated by high litter inputs and turnover and rapid and efficient cycling of nutrients from the forest floor (Stark and Spratt 1977; Stark and Jordan 1978; Cuevas and Medina 1986, 1988). In this study, forest floor Ca and Mg contents were greater than the exchangeable Ca and Mg content (in kg ha^{-1}) in the top 10 cm of mineral soil and are likely to be important sources of nutrients to plant roots. The lack of pattern along the gradient suggests that other factors, besides soil texture, may exert a strong influence on soil properties.

Patterns in Live and Dead Fine Root Biomass

Plants often respond to changes in nutrient and water availability by altering the allocation of C to root biomass (Cuevas and Medina 1988; Jackson and others 1990). High fine root biomass in surface soils facilitates ecosystem nutrient conservation through rapid and efficient nutrient capture and immobilization in tissues (Went and Stark 1968; Stark and Spratt 1977; Cuevas and Medina 1988; Silver and Vogt 1993). Fine root standing stocks along the texture gradient were similar to or greater than values reported for other tropical forests (Klinge 1973a, 1975; Gower and Vitousek 1989; Sanford 1989; Cuevas and others 1991; Silver and Vogt 1993) and decreased significantly from sands to clays in surface soils and to 40 cm depth. We found that fine root standing stocks were negatively correlated with N mineralization rates and positively correlated with extractable soil P concentrations. Although fine root standing stocks cannot be meaningfully extrapolated to productivity, other studies in the Amazon basin have shown that root growth responded to N additions on sandy soils and to P additions on clays (Cuevas and Medina 1986, 1988). Additionally, periodic water stress caused by rapid drainage and low water holding capacity in sands may lead to greater fine root biomass throughout the soil profile (Nepstad and others 1994).

The Distribution of Belowground C, N, and P

Recent studies have pointed to the importance of estimates of total (fine and coarse) root biomass for understanding the ecosystem C cycle and the relative importance of deeper roots (greater than 10 cm depth) in tropical forests (Nepstad and others 1994; Trumbore and others 1995; Jackson and others 1996; Cairns and others 1997). In this study, total root biomass C in the 0–10-cm soil depth amounted to up to 62% of the surface soil C pool (Table 6). Down to 1 m depth, root C amounted to 22% of the soil C pool on clays and 34% on sands. Few studies have measured coarse root biomass in tropical forests, and even fewer have attempted to consider the spatial heterogeneity of coarse roots by taking multiple samples. The data from the five large quantitative pits along the texture gradient were strongly influenced by one particularly heavy root found in the sands. Even with 11 large quantitative pits, there was still considerable spatial variability in coarse root biomass in sands. Our data illustrate the potentially large contribution of coarse roots to soil organic C and N and the spatial heterogeneity inherent in this ecosystem compartment.

The C:nutrient ratios of soils and plant tissues can be used to estimate the potential controls on elemental cycling across trophic levels within forest ecosystems and the regulation of exchanges of materials across ecosystem boundaries (Vitousek and others 1988). In the TNF, the C:N and C:P ratios of roots were much higher in the sands than in the clays (Table 4). The root C:P data suggest that root tissue

on clays may be able to access P not normally thought of as biologically available or that plants on clay soils have higher P-use efficiency than plants on sandy soils. Interestingly, the forest floor C:N and C:P ratios were similar on sands and clays suggesting that the big differences in soils may be a result of internal soil processes, or inputs from root tissues rather than a direct result of the chemical composition of the standing litter crop.

Modeling the Effects of Soil Texture on Belowground C and Nutrient Pools

Soil texture adds an extra layer of complexity to the ecosystem from both an empirical and modeling perspective. The Century model captures trends and pool sizes in soil C for temperate and tropical grasslands on a variety of soil textural classes (Parton and others 1993). Our comparison of the Century model output and the field collected data from the TNF demonstrates that the Century model is relatively successful at capturing the general trends in C and N as well as the distribution of C and N between SOM and belowground plant pools. However, the model appears to be overly sensitive to the effect of texture on SOM stabilization in the TNF.

Century represents the role of texture in SOM stabilization in two ways. First, the flow of carbon from slow turnover SOM to passive SOM is inversely scaled to sand content. In sites with high clay content, more passive SOM is formed reflecting the role of increasing soil surface area on C protection. Second, the efficiency of C transfers is affected by texture with more CO_2 lost during transformations between pools in highly sandy soils. Both of these mechanisms lead to increased C content in clays and scale linearly with clay content.

We measured substantially more C in the sands than Century predicted for the site based on our sensitivity analysis. The reasons for this may be simple and direct in that Century may overstate the influence of texture on passive SOM formation and efficiencies of C transformations. Alternatively, the parameters that govern these relationships in Century may simply fail to take into account nonmineral preservation of organic matter (Hedges and Oades 1997). The differences also could be influenced by complex interactions and feedbacks between texture, nutrient, and water availability and forest ecophysiology. Plant-soil feedbacks, such as increased belowground C allocation together with decreased root litter quality, could act to maintain higher belowground C pools and C retention time in sandy soils at the TNF. These patterns need to be interpreted with some caution because this is not a detailed study of SOM stabilization in tropical soils.

In our model analysis, we tuned the model to clays and then adjusted it to represent sands. Had we chosen the opposite approach of tuning first to sands and then predicting clay elemental content, our results would show an overestimation of element storage in the clay soils. Regardless of whether the model is underrepresenting C storage in sands or overestimating storage in clays, it is clear that the overall sensitivity of C storage to texture is significantly different in these tropical soils relative to the standard model representation.

We tested the sensitivity of the model to several mechanisms that may be important in determining the relationship of ecosystem C and nutrient cycling to soil texture. First, forests growing on sands may have different stand-level water-use efficiencies. If water availability constrains growth and/or decomposition during the dry season, then water-use characteristics may be important in determining SOC dynamics. As a preliminary assessment of the model sensitivity to changes in water availability, we increased the depth to which plants can access water in the model (for example, functional rooting depth). Doubling the functional rooting depth from 60 cm to 120 cm resulted in a small increase in equilibrium SOM content, but the change is not large and does not account for the differences in measured and modeled SOM for the sands (Table 7). There is good evidence that seasonally dry Amazon forest may have roots that extend several meters in depth (Nepstad and others 1994). Deep roots may be quite important for water uptake and might act to maintain higher levels of productivity (and therefore SOM content) than might be expected for forests with only shallow roots. Current versions of Century and most other ecosystem models do not have options for simulating deep rooting and as a result may not incorporate an important mechanism by which tropical productivity is maintained through the dry seasons and during drought years.

Our second exercise was to evaluate the role of nutrients in our modeled forests by doubling the input of N and P to the site (Table 7). In both sands and clays greater N inputs raised productivity and SOM content substantially, suggesting that in the "modeled" Tapajos forest the role of texture in forest dynamics acts primarily through availability of N. Because less SOM is stabilized on sands than on clays, less N is available for mineralization. With less N cycling through the system at equilibrium, productivity equilibrates at a lower value. In contrast, added P had very little effect in our model simulations. In Century, the N and P models appear to interact such that P limitation only can function as a transient phenomenon associated with the relative

demand for N and P. Whereas this approach may work in N-limited temperate systems, it causes potential problems in P-limited tropical soils. The interactions of P with texture, SOM, and productivity in Century are relatively complicated. Century includes modeled linkages between P mineralization and N/P availability, and when plant or microbial P availability in the model is low, P is mineralized. Once P enters the Century organic pools, it can be (and is) lost as dissolved organic P or sorbed into secondary forms in a manner independent of biotic demand for P (see Vitousek and others 1998 for a discussion of these losses). In our modeled systems, The combination of high rates of P mineralization, fertility independent P losses, and no parent P causes the system to crash without substantial atmospheric inputs of P. We found that we could maintain reasonable rates of productivity as long as P inputs (from the atmosphere) exceeded P losses through dissolved organic P and PO_4 sorption, but that below this threshold value, productivity would approach zero. These results highlight the discrepancies between the treatment of tropical biogeochemistry in simulation models and current conceptual models of the factors that should regulate tropical productivity.

The data and model simulations from the Tapajos textural gradient highlight several issues that will be important for evaluating the role of soil texture in tropical forest biogeochemistry. Clearly, more information is needed on the relative importance of both chemical and physical stabilization of SOM to refine our understanding of the relationship of soil texture to biogeochemical cycling. This may be critically important in tropical ecosystems where much of the soil nutrient capital is in organic matter rather than parent material (Sanchez 1976; Tiessen and others 1994). For P, this distinction may be especially important because of current difficulties in determining ecologically meaningful indices of labile and organic P (Gijsman and others 1996). The modeling exercises emphasized the relationships among nutrient availability and SOM content. Although, this particular model was most sensitive to N, the role of SOM in cycling of P and other nutrients also are likely to be important because SOM may be the dominant reservoir for N, P, and base cations in highly weathered tropical soils. Our results also highlight the important contribution of C allocation to roots in estimates of belowground C pools. Coarse roots frequently are ignored in estimations of ecosystem C cycling, but they clearly constitute a significant belowground C pool.

Models of biogeochemical cycling will need to be further evaluated if they are to be used successfully in tropical environments, and our results clearly demonstrate the need to better link conceptual and simulation models of tropical element cycling. Virtually all the major biogeochemical models have their origins in temperate systems and have been most extensively tested in these environments. Greater attention needs to be paid to variation in basic biogeochemical and physical factors, such as texture, P cycling, water use, and the role of base cations, for these models to be accurate in tropical environments.

ACKNOWLEDGEMENTS

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