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Effects of forest clearing and succession on the carbon and nitrogen content of soils in Puerto Rico and US Virgin Islands

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Abstract

Soil samples from mature and secondary forests and agricultural sites in three subtropical life zones of Puerto Rico and the US Virgin Islands were collected to determine the effects of forest conversion to agriculture and succession on soil organic carbon (C) and nitrogen (N) contents. Site characteristics that may affect soil C and N (slope, elevation, aspect, and texture) were as uniform as possible. Carbon contents (to 50 cm depth or bedrock) of cultivated sites, as a percent of corresponding mature forests, were lower in the wet (44%) and moist (31%) than in the dry (86%) life zones whereas N contents were relatively high regardless of life zone (60–130% of the mature forests). Conversion of forests to pasture resulted in less soil C and N loss than conversion to crops. The time for recovery of soil C and N during succession was approximately the same in all three life zones, about 40–50 yr for C about 15–20 yr for N. However, the rate of recovery of soil C was faster in the wet and moist life zone, whereas N appeared to recover faster in the dry life zone. Evidence for loss of soil C during cultivation and gain during succession to soil depths of 50–100 cm is presented.

Introduction

Conversion of tropical forest lands to agriculture affects the soil through its effect on soil organic matter and nutrients as well as on physical properties. Organic matter is an important component of soils because of its influence on cation exchange capacity, soil structure, soil-water balance, and a source of plant nutrients (Lal and Kang, 1982; Sanchez, 1976). Losses of organic matter may lead to soil degradation and low crop yields. These trends are reversed during forest succession or fallow when the organic matter and nutrient contents generally increase. Understanding the dynamics of soil organic matter and nutrients in tropical forest soils undergoing change (both deforestation and succession) and the factors influencing these dynamics is important for addressing such issues as the fragility of tropical soils, their sustainability for production, and global biogeochemical cycles.

Available studies on tropical soils suggest a rapid decline in organic matter and nitrogen due to continuous cultivation (*e.g.*, Allen, 1985; Aweto, 1981; Ayanaba *et al.*, 1976; Brams, 1971; Nye and Greenland, 1964) which may or may not recover fully during forest succession (Aweto, 1981; Raich, 1983; Werner, 1984). However, most of these studies are short term (<15 yr), restricted to shallow depths, cover few tropical climate types, and are concerned with only one phase of the destruction/reconstruction cycle.

This study was designed to deal with some of these deficiencies by determining the differences in soil carbon (C) and nitrogen (N) content resulting from changes in forest land-use in three contrasting tropical environments in Puerto Rico and US Virgin Islands. Our emphasis was on both short and long-term changes in soil C and N pools that occur when forest land is converted to permanent agriculture and when agricultural land is abandoned and revegetated by secondary forests. The ideal conditions for such a study would be to sample the same sites over several decades. Because such long term plots are generally lacking in the tropics, we determined the soil C and N contents of sites of different ages and land use, but of similar soil types, that represented time series of forest conversion to agriculture followed by abandonment and forest succession.

Methods

Description of study sites

Soil samples were collected from three subtropical life zones (*sensu* Holdridge, 1967; although named subtropical, the life zones are located in the tropical latitudes): wet and dry forest life zones in Puerto Rico, and a moist forest life zone in St. John, US Virgin Islands. In all life zones, samples were collected from mature or very late secondary forests that served as controls, secondary forests (including plantations), and various ages and types of agricultural sites (Table 1). However, it was not possible to locate the same number of sites for each land-use type and age in each life zone for many reasons, including: great heterogeneity of soil types in each life zone, differences in past and present land-use and agricultural economic policies in each life zone, and inability to satisfactorily document ages of secondary forests.

Specific sites were selected on the basis of their present land-use and history. Slope, aspect, soil type and texture, and elevation within a life zone were selected as uniformly as possible. Aerial photographs for different time periods (1936, 1951, 1964, 1977, from the Puerto Rican Department of Public Works) and soils maps were used to locate potential sites in Puerto Rico and to estimate the ages of the present land-use. The actual ages of the sites and their land-use histories were determined with the help of the land owners and other people familiar with the area. Sites in St. John were selected with the assistance of John Matuszak (Cooperative Extension Service, College of the Virgin Islands), an expert on the land-use there.

The wet forest life zone is represented by two areas in Puerto Rico: in and adjacent to the Luquillo Experimental Forest (L) (18°21′N 65°55′W) and in and adjacent to the Carite State Forest (C) (18°5′N 66°4′W). The climate of these two areas is characterized by high rainfall (2200 mm yr^{-1} [C] to 3400 mm yr^{-1} [L]) and a fairly constant temperature of 23°C (Brown *et al.*, 1983; Ewel and Whitmore, 1973). The sites in the Carite area are higher in elevation (600–650 m) and have steeper slopes (40–60°) than those in the Luquillo area (200–450 m elevation and 20–40° slope). Soils in the wet forest life zone are ultisols of basic volcanic origin (Beinroth, 1971). The soils of all the study sites in this life zone belong to the Humatas series, classified as clayey, kaolinitic, isohyperthermic typic tropohumult (U.S. Department of Agriculture Soil Conservation Service, 1972, 1977).

All forested sites in the subtropical moist forest life zone were located within the boundaries of the Virgin Islands National Park, St. John (SJ) (18°22′N 64°46′W) and the agricultural site was located near the park boundary. Practically all of St. John has been under agriculture at one time and undisturbed upland forests do not exist. The oldest forest that we could identify there was about 100 yr-old, and this was used as the control site. The area receives about 1250–1300 mm yr^{-1} rainfall, seasonally distributed, and has an average daytime temperature of 27°C. The sites were at 185–275 m in elevation with slopes of 10–20°. Soils of the study sites belong to the Cramer-Isaac association classified as fine, mixed, isohyperthermic typic argiustolls (G. Acevedo, U.S. Department of Agriculture

Table 1. Description of study sites in subtropical wet, moist and dry life zones of Puerto Rico and St. John (U.S. Virgin Islands)

Site	Age of present vegetation (yr)	Present vegetation	Past vegetation
Subtropical wet life zone			
LF1	mature	Mature forest	–
LF2	19	Mahogany[a] plantation	Young secondary forest
LF3	20–25	Secondary forest	Crops
LF4	40	Secondary forest	Coffee
LF5	38–47	Secondary forest	Crops
LF6	51	Mahogany[a] plantation	Crops
LA1	>50	Pasture	Forest
CF1	mature	Mature forest	–
CF2	10	Pine[b] plantation	Crops
CA1	0.6	Crops	Secondary forest
CA2	10	Crops[c]	Late secondary forest
CA3	10	Pasture/Crops[d]	Late secondary forest
CA4	>50	Pasture	Forest
Subtropical moist life zone			
SJF1[e]	100	Late secondary forest	Agriculture
SJF2	26	Secondary forest	Crops
SJF3	30–50	Secondary forest	Pasture
SJF4	50–60	Secondary forest	Agriculture
SJA1	>100	Pasture/Crops[f]	Forest
Subtropical dry life zone			
GF1a	mature	Mature forest	–
GF1b	mature	Mature forest	–
GF2	11	Secondary forest	Secondary forest
GF3	35	Secondary forest	Crops
GF4	50	Mahogany[g] plantation	Crops
GA1	60	Pasture/Crops[h]	Forest
GA2	60	Crops	Forest
GA3	>60	Pasture	Forest

[a] *Swietenia macrophylla.*

[b] *Pinus caribaea.*

[c] Annual food crops (mainly corn) for last 4 yrs and tobacco for previous 6 yrs.

[d] Pasture for last 4 yrs and tobacco in previous 6 yrs.

[e] No undisturbed forests exist on St. John; this was the oldest forest we could identify.

[f] The precise history of this site is unknown except that it has been used for both row-crops and pasture; it has been in pasture for at least the last decade.

[g] *Swietenia mahogani.*

[h] Pasture for last 5 yrs only.

Soil Conservation Service, Puerto Rico, 1988, pers. comm.)

Sites in the subtropical dry forest life zone were located along the south-west coast of Puerto Rico, in and adjacent to the Guanica State Forest (G) (17°58′N 66°52′W). The area receives about 750 mm yr^{-1} of rainfall, seasonally distributed, and the mean annual temperature is about 26°C (U.S. Department of Commerce National Oceanic and Atmospheric Administration 1966–80). All sites were at an elevation of 75–175 m with slopes of <5°. Soils in the study sites of this life zone belong to the Jacana series, a clayey, mixed, isohyperthermic lithic ustorthent (U.S. Department of Agriculture Soil Conservation Service, 1972).

Field sampling

Samples for C and N analysis were collected using a standard soil probe (inside diameter of 1.9 cm) or from soil pits. Most soil samples from Puerto Rico were collected in June 1982. These samples were collected with a probe after the loose litter was carefully removed to expose the mineral soil and each sample was a composite of three cores. Soil samples were randomly collected from an area of approximately 0.25–0.5 ha at each site. At each site in the wet life zone, a total of ten composite samples were collected from depths of 0–25 cm and 25–50 cm. Because the soils were shallow in the dry forest sites it was possible to collect between 5–9 composite samples only in the 0.25 ha area and to depths of 25 cm (generally the complete profile).

An additional five samples of soil of known volume to the two sampling depths were collected from each site to determine soil bulk density. Samples of soil were also collected from about half of the sites for textural analysis to confirm their classification.

Samples from St. John were collected in October 1984 from one soil pit in each site (0.25–0.5 ha in area). The pit was 1 m^2 in area and 50 cm deep (to the bedrock). Samples were taken from the mid-point of 10 cm intervals using 5 cm diameter × 5 cm deep metal rings. Two samples (one for C and N analysis and one for bulk density and texture) at each interval were collected from three to five profiles of the pit walls, with each sample treated as a separate one.

In addition to the sampling routine described above, we had the opportunity to collect samples from soil pits (in December 1984), dug to 1 m depth, from other ongoing studies in some of the wet life zone sites. The same sampling procedure used for the pits in St. John were used in these pits, with the additional collection of samples from the mid-point of 50–75 cm and 75–100 cm depths and the bottom 5 cm. These samples were used for measuring C and bulk density of each interval.

All soil samples were placed in cotton sample bags and air-dried in the field. They were then transported to the University of Illinois for further analysis.

Laboratory analysis

Samples for bulk density were oven-dried to constant weight at 105°C and weighed. Soil texture was determined by the hydrometer method after sieving through a 2 mm mesh (Bouyocous, 1962). None of the soils contained gravel or stones.

Soils for C and N analysis were ground to pass a 0.55 mm sieve and oven-dried to constant weight at 70°C. Organic C of samples collected in Puerto Rico in 1982 was determined by the Walkley–Black wet oxidation method (Allison 1965). The C concentration of the samples from St. John and the samples from pits in Puerto Rico was determined by a dry-oxidation method, using a Leco furnace, with the C as CO_2 determined gravimetrically. To determine if the two methods of measuring C concentration gave comparable results, 70 arbitrarily selected samples of the 1982 Puerto Rican soils (35 from each of the two depths) were reanalyzed for C using the dry-oxidation method. A paired t-test of these samples (dry *versus* wet-oxidation C concentration) exhibited no statistical significance ($p = 0.01$), thus results by both methods are reported and considered as giving equivalent results. Total N (to depths of 0–25 cm only) was determined by the aluminum block digestion (Gallaher *et al.*, 1976) and semimicro-Kjeldahl unit (Bremner, 1965).

Data analysis

Carbon and N concentrations were converted to total content to a given depth as the product of bulk density, concentration, and depth of sample, and expressed in units of kg m^{-2}.

Conversion of forest land to agriculture often results in increases in bulk density, thus sampling to a fixed depth can result in the collection of more soil per unit of depth. It has been recognized that in order to study changes in the chemical properties of soil over time, comparisons must be based on the same soil mass rather than the same depth (Ayanaba *et al.*, 1976; Nye and Greenland, 1964). To determine the implications of differences in bulk densities between control and disturbed sites, we recalculated their C content based on a mass of soil equal to that of the control sites using the methods given in Mann (1986).

Results

Soil texture

Results of the soil texture analysis for all three life zones confirmed their classification and demonstrated the general textural similarity among all sites within a life zone (Table 2). Within the dry and moist life zones, the soil texture of the sites sampled were equal to each other (with the exception of SJF1) and to the USDA analysis for that soil series. Site SJF1, the control forest site, had less clay and more sand than the other sites but it was still classified as a clay loam (Table 2). Significant differences in the texture of the wet life zone sites were exhibited particularly between sand. However, the range for clay and silt was generally similar to the USDA analysis for the Humatas series.

Bulk density

The conversion of forests to agriculture had no effect on soil bulk density in the wet life zone sites with the exception of CA1 (Fig. 1A and 1B). This exception, with a low bulk density, was the youngest agricultural site which had been tilled just prior to sampling. In the dry and moist life zones, the agricultural sites had significantly ($p = 0.05$) higher bulk densities than the control forests (Fig. 1C and 1D). Age of secondary forests did not appear to influence bulk density within a life zone because bulk densities of all forest sites were not significantly different from each other ($p = 0.05$, Fig. 1).

Table 2. Texture analysis of soils; no gravel occurred in any of the soils. Values followed by the same letter within a life zone group are not significantly different (Duncan's Multiple Range Test, $p = 0.05$)

Site	Clay %	Sand %	Silt %	Soil type
Subtropical wet life zone				
LF1	69.0^{a}	13.8^{ab}	17.2^{a}	clay
LF2	52.5^{b}	18.6^{ab}	28.9^{b}	clay
LF5	68.5^{a}	8.1^{b}	23.4^{b}	clay
LF6	53.7^{b}	21.0^{a}	25.3^{b}	clay
LA1	70.8^{a}	8.6^{b}	20.6^{a}	clay
Humatas series[a]	58.4	4.6	37.0	clay
	66.7	6.4	26.9	clay
Subtropical moist life zone				
SJF1	28.4^{b}	42.0^{a}	29.6^{ab}	clay loam
SJF2	32.8^{ab}	32.2^{ab}	35.0^{b}	clay loam
SJF3	43.6^{a}	33.5^{ab}	22.9^{a}	clay/clay loam
SJF4	39.6^{a}	28.0^{b}	32.4^{b}	clay/loam
SJA1	39.6^{a}	28.0^{b}	32.4^{b}	clay loam
Cramer series[a]	45.1	28.0	26.9	clay loam
	45.5	24.9	29.6	clay loam
Subtropical dry life zone				
GF1b	56.5^{a}	15.2^{a}	28.3^{a}	clay
GF2	53.1^{a}	15.1^{a}	31.8^{a}	clay
GA2	50.6^{a}	17.8^{a}	31.6^{a}	clay
GA3	52.8^{a}	26.4^{a}	20.8^{a}	clay
Jacana series[b]	52.3	17.1	30.6	clay
	57.4	15.0	27.6	clay

[a] From U.S. Department of Agriculture Soil Conservation Service (1967).

[b] From U.S. Department of Agriculture Soil Conservation Service (1965).

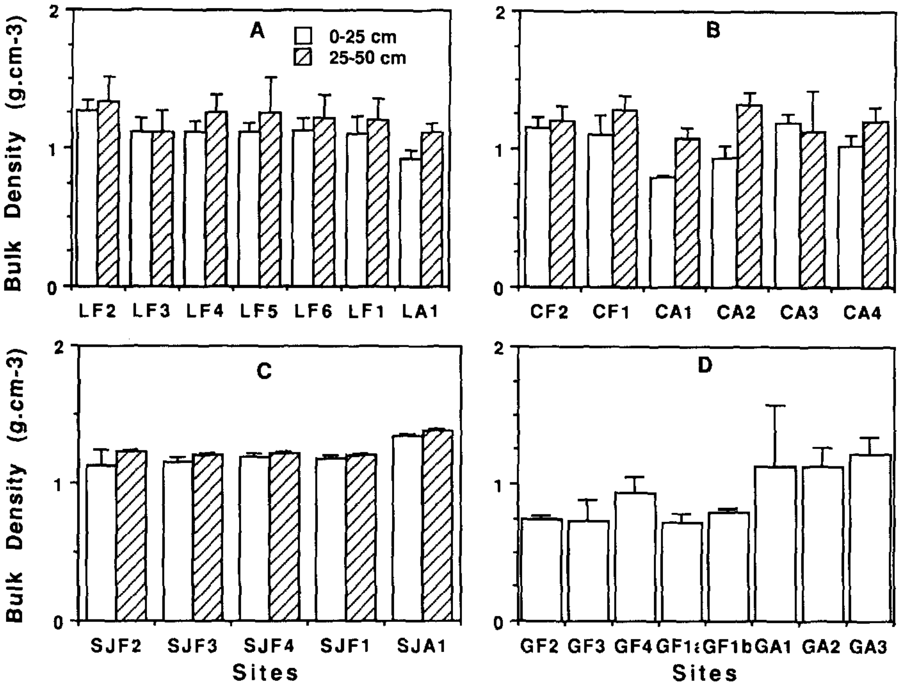

Fig. 1. Mean bulk density (+95% confidence interval) for soils in the study sites of the subtropical wet (**A** and **B**), moist (**C**), and dry (**D**) life zones. Forest (F) and agricultural (A) sites are arranged in order of increasing age (refer to Table 1 for description of sites).

Carbon and nitrogen concentrations and C/N ratios

The C concentrations in the top 25 cm of soil of the dry forest sites (2.3–4.3%) tended to be the highest, followed by the wet (1.8–3.9%) and moist (1.5–2.8%) forest sites. Not surprisingly, C concentrations decreased with increasing depth, although the relative decrease was less in the moist than in the wet sites. Furthermore, soil C concentrations tended to increase with increasing age of the secondary forest, but the differences were only significant ($p = 0.05$) between the youngest secondary and control forest in the wet and moist life zones. Carbon concentrations of soils under crops (cultivated >10 yr) were significantly lower ($p = 0.05$) than control forests in all life zones (1.4–1.5% in wet, 1.0% in moist, and 1.8% in dry) and lower than those under pastures (2.5–3.1% in wet and 2.5% in dry).

Concentrations of soil N (0–25 cm) ranged from 0.11–0.26% in all wet, 0.19–0.23% in all moist, and 0.17–0.40% in all dry life zone sites. The patterns of N concentrations among sites were similar to C within a life zone.

Carbon to nitrogen (C/N) ratios were low, ranging from about 6–22 for forest sites and about 4–19 for agricultural sites (Fig. 2). The C/N ratios tended to be highest in the wet forest sites and no obvious pattern with age was exhibited (Fig. 2A). For the moist and dry secondary forest sites, C/N ratios tended to increase with increasing age.

The C/N ratios for the agricultural sites were similar to those for the secondary forest sites in the corresponding life zone with the exception of site SJA1 in the moist life zone (Fig. 2B). This site had the lowest C/N ratio of all. The C/N ratios for all sites that we obtained are comparable to those found by others for tropical soils (*e.g.*, Ayanaba *et al.*, 1976; Aweto 1981; Nye and Greenland, 1964; Sanchez, 1973) and indicate that a large amount of N is potentially available in the soil (Sanchez, 1973).

Vertical distribution of carbon

The C content in soil under a mature wet forest (LF1) declined fairly rapidly with depth in the top 40 cm with little change beyond this depth

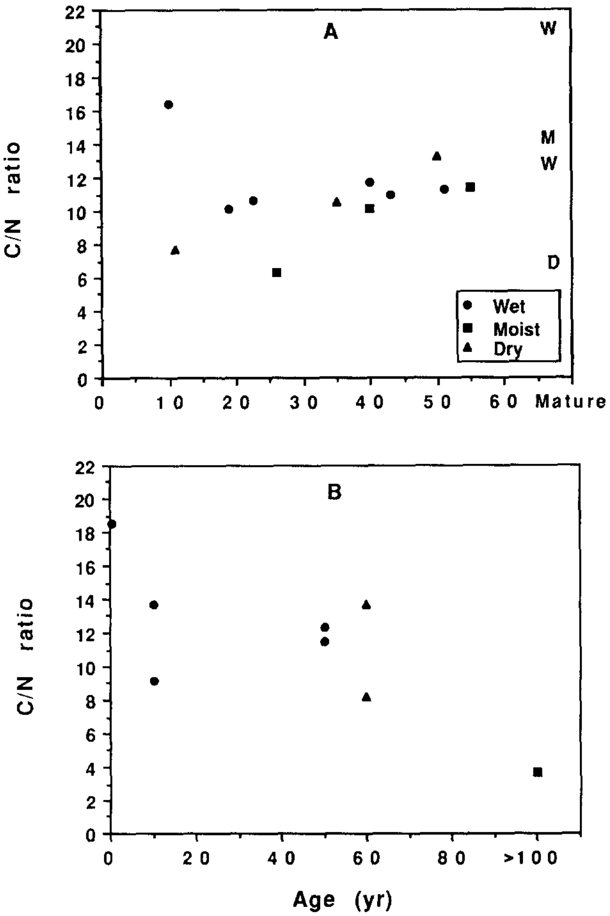

Fig. 2. Variation in C/N ratios with age of (**A**) forest sites and (**B**) agricultural sites. The C/N ratios for the mature forest sites are designated as W = wet, M = moist, and D = dry.

(Fig. 3A). The profile of soil C in the mature moist forest (SJF1) exhibited a similar trend, but the pattern was compressed because of the shallower soils (Fig. 3D). However, sites that have been under agriculture for many decades exhibited lower soil C contents throughout the whole profile (Fig. 3B and 3E).

Carbon accumulated in all levels of the soil profile under secondary forests (Fig. 3C and 3F), although the pattern of accumulation appeared to be different between wet and moist forests. In the deep soils of the wet forests, C appeared to accumulate in the top 50 cm first, with only a slight change in the bottom 50 cm (Fig. 3C). In contrast, the vertical distribution of C in the moist secondary forest sites tended to parallel each other (Fig. 3D and 3F) suggesting that C accumulated at the same rate throughout the whole profile during succession.

Carbon and nitrogen content of soils

A test of the two methods of calculating C contents of agricultural soils to account for changes in bulk density (*i.e.*, equal depth *versus* equal mass; see methods) exhibited no significant differences between the two methods (t-test, $p = 0.05$). As both methods gave the same results, the C content to a fixed depth will be used in all subsequent discussions.

Total C contents to 25 cm and 50 cm for all sites are shown in Fig. 4, where the sites are arranged to represent a sequence of events in which mature forests are cleared for agriculture for various lengths of time followed by abandonment and forest succession. Conversion to crops resulted in a decline in soil C at all depths and in all life zones. Within 10 yr of continuous cultivation in the wet life zone, the soil contained about 44% of the C in the control forest site, or a change of about $0.8\,\mathrm{kg\,m^{-2}\,yr^{-1}}$ to 50 cm deep (Fig. 4A). In the moist life zone, the >100 yr-old agricultural site contained about 31% of the C of the control forest (Fig. 4B). Soils in the dry life zone experienced a smaller loss of C with cultivation than in the humid life zones. The sites cultivated for 60 yr or more contained about 86% of the control forests (Fig. 4C).

Soils under pasture contained more soil C than cultivated soils (Fig. 4). The two >50 yr-old pastures in the wet life zone had significantly more ($p = 0.05$) soil C at both depths than the 10 yr-old cultivated site, and about 70% of the C in the mature forests (Fig. 4A). In the dry life zone, the pasture contained 129% of the C in the mature forests, but in this case the difference between the pasture (GA3) and cultivated sites (GA1-GA2) was not significant ($p = 0.05$).

There was a general pattern of increasing soil C with increasing age of secondary forests (Fig. 4). The oldest secondary forest in all life zones (~50 yr-old) had approximately the same C content as the control forest. This suggests that it takes approximately the same length of time for soil C to recover in all life zones, *i.e.*, on the order of 50 yr. The two oldest secondary forests

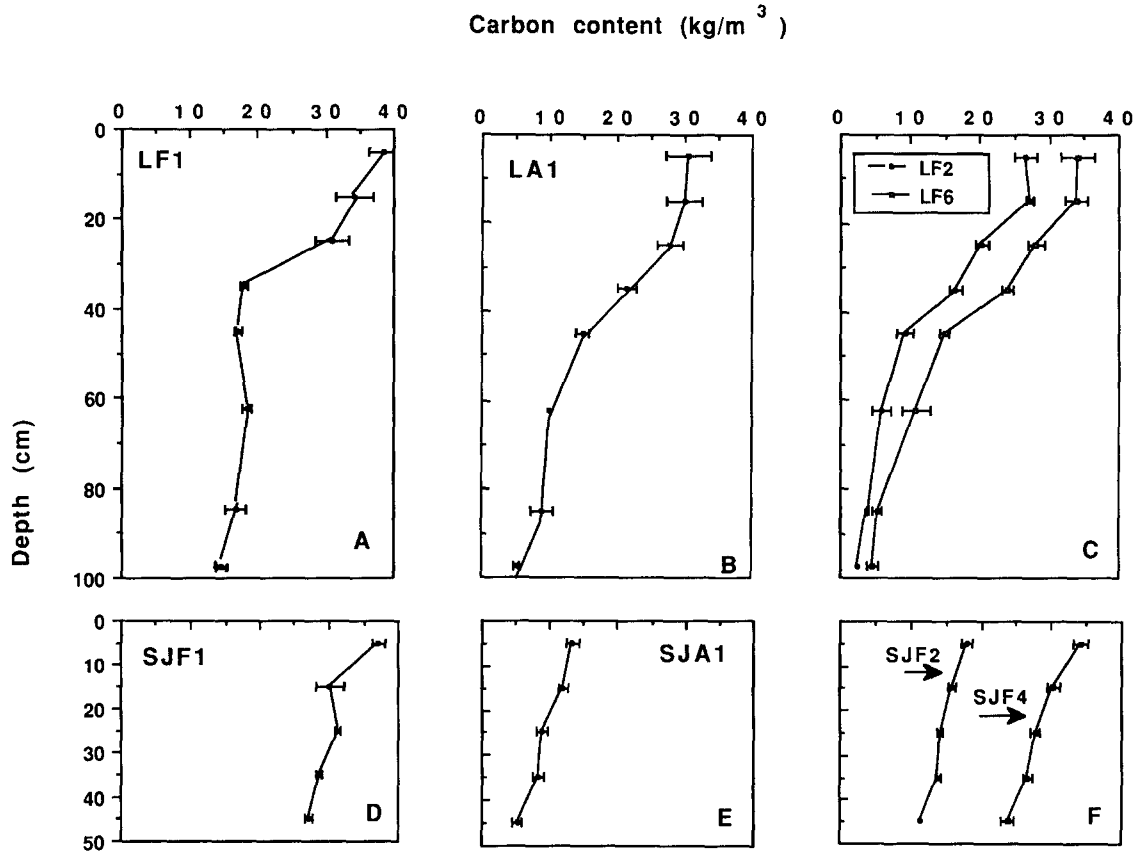

Fig. 3. Vertical distribution of organic carbon in forest and agricultural soils of subtropical wet (A–C Luquillo area of Puerto Rico) and moist (D–F; St. John) life zones. Each point is the mean ± one standard error (n = 3–5).

in the dry life zone had either the same or significantly ($p = 0.05$) higher C contents than the mature forest sites. The 50 yr-old site, a mahogany plantation, had high rates of litterfall and high litter standing stocks (Lugo *et al.*, 1978) which explains, in part, the high soil C. The litterfall rates in this plantation were some of the highest measured in this area (Lugo *et al.*, 1978), and suggests that in this case the use of a plantation to represent natural succession was not justified.

The pattern of N contents in the top 25 cm of soil by land-use of the sites varied by life zone (Fig. 5). The pattern in the wet life zone generally paralleled that for organic C (cf. Fig. 4A and 5A) as is demonstrated by the fairly constant C/N ratio for most sites (Fig. 2). In the moist life zone, soil N in all sites was as high or higher than in the control forest (Fig. 5B). The N content of the secondary forests in the dry life zone was higher than the control forests, and less than the control forest in the agricultural sites (Fig. 5C). The high N levels in the dry and moist secondary forests are partly due to the common occurrence of leguminous trees in these two life zones.

Discussion

Factors affecting loss of soil organic carbon and nitrogen

It has been suggested that soil texture, particularly the silt plus clay content, plays a role in determining the amount of organic matter in soil (Parton *et al.*, 1987; Sanchez, 1976). However, for our study areas, texture does not appear to explain the differences and similarities between the C contents. Sites in the dry and wet life

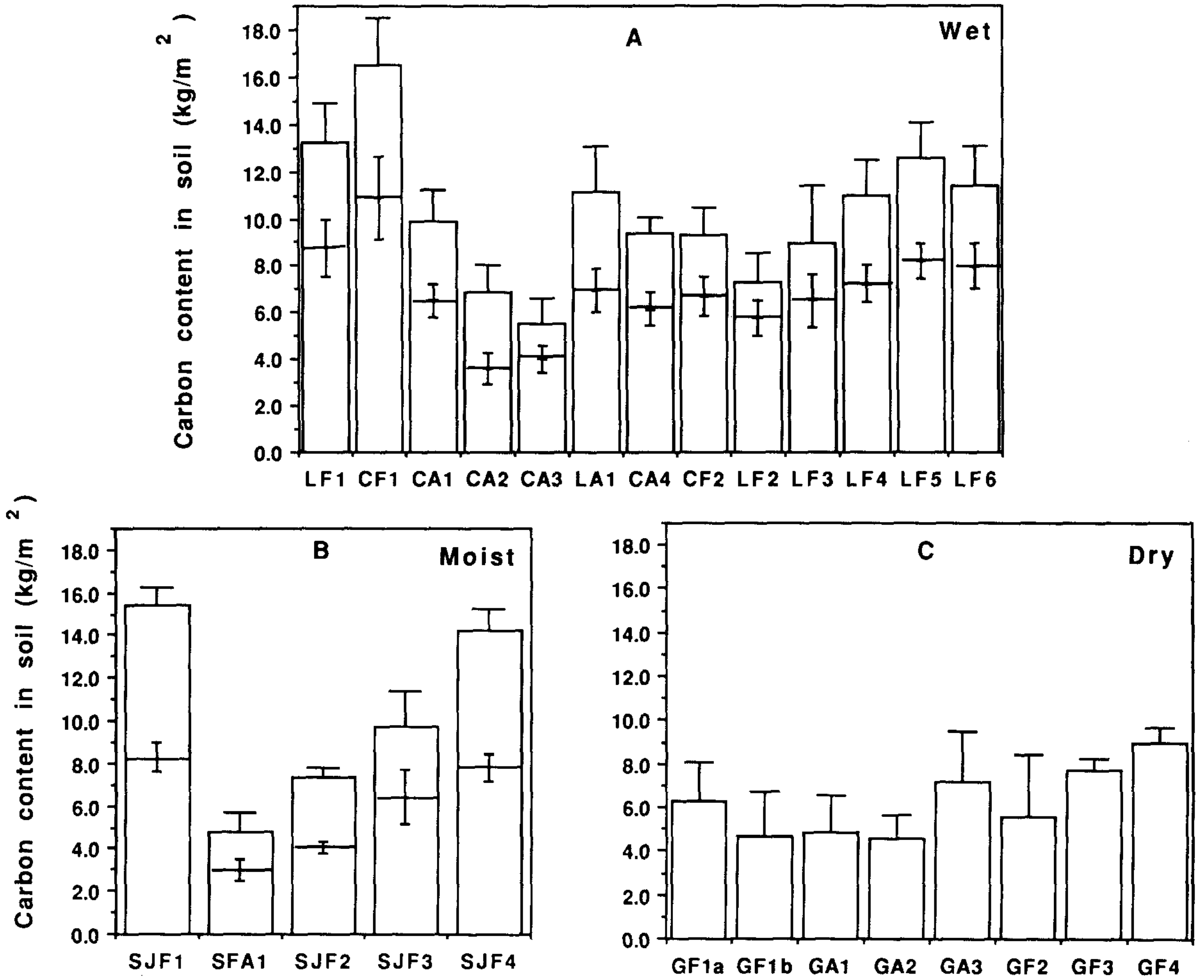

Fig. 4. Mean (±95% confidence interval) soil organic carbon content of sites arranged in a sequence from mature forests to conversion to agriculture, followed by abandonment and subsequent forest succession in subtropical (**A**) wet, (**B**) moist, and (**C**) dry life zones. The total height of the bar in (**A**) and (**B**) is to a sampling depth of 50 cm and the shorter bar is to 25 cm depth; the total height of the bar in (**C**) is to a sampling depth of 25 cm (refer to Table 1 for details of sites).

zones had soils that were texturally similar (Table 2), but their C contents to 25 cm depth were significantly different, whereas the wet and moist life zones had soils that are texturally different but were similar in C contents. Furthermore, any textural differences among our sites within a life zone are sufficiently small that we are confident that differences between C and N contents among sites are due to biotic factors rather than to inherent differences among the soils.

The loss of soil C upon conversion to agriculture has been shown to be proportional to the initial amount of C in the soil across a wide range of soil types, climates, and times since clearing (Allen, 1985; Mann, 1986; Weaver *et al.*, 1987). Results from our study confirm this trend. In the wet and moist life zones, the C content of the cultivated sites represented a loss of approximately 60–70% of the initial C based on the mature forest sites. In the dry life zone, where soil C content of the control forests was about 56–66% of the wet and moist life zone soils (comparing top 25 cm only), the C loss due to cultivation was only 14%. Although the age of the agricultural sites in these comparisons vary, Mann (1986) suggested that the greatest losses occur in the first one to two decades or so of cultivation when the soil C is approaching a new steady state level.

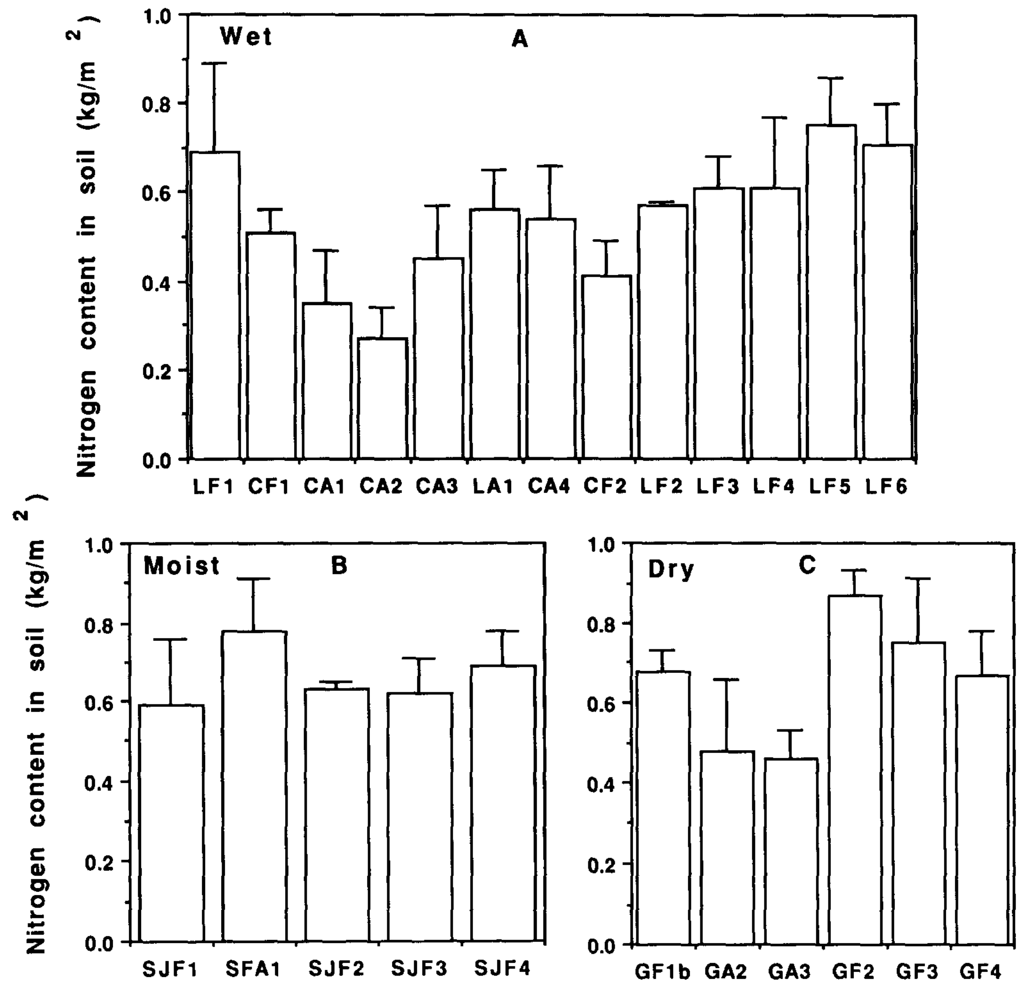

Fig. 5. Mean (+95% confidence interval) soil organic nitrogen content in the top 25 cm of soil of sites arranged in sequences of mature forest to conversion to agriculture, followed by abandonment and subsequent forest succession in subtropical (A) wet, (B) moist, and (C) dry life zones (refer to Table 1 for details of sites).

The loss of soil N due to forest conversion to crops has also been related to the initial N content (Allen, 1985). This appears to hold for our sites in the wet and dry life zones because the control forests have similar N contents and a similar decline (about 30–40% of the initial N with cultivation). In the moist life zone, however, the agricultural site contained more N than the forest most likely due to past cultivation practices (*e.g.*, fertilizer application).

The C and N content of tropical soils has been related to life zone or climate (Brown and Lugo, 1982; Post *et al.*, 1982; 1985) with high contents in very wet life zones and decreasing content towards drier life zones. Life zone also appears to be a factor that explains the pattern of C and, to some degree, N loss on conversion of forest soils to crops on more or less zonal soils. Upon conversion to crops, the high organic inputs typical of humid forests (Brown and Lugo, 1982) decrease markedly, but the warm humid climate favors continued decay of mineralizeable soil C and N and high rates of leaching. In contrast, organic matter production and decomposition in dry life zones are lower than in humid ones, and upon conversion to crops a slower rate of soil C and N loss occurs because organic inputs are only slightly reduced and microbial activity and leaching rates are low.

Conversion of forests to pastures exhibited less C and N loss. Unlike annual crops, pasture grasses maintain a constant cover of vegetation on the soil, reduce soil temperatures and rate of biological activity, and sometimes have high productivity and turnover rates that add organic matter, particularly from belowground, to the soil. Conversion of crop lands to pastures in Puerto Rico was shown to reverse the pattern of loss of soil C to one of accumulation (Lugo *et al.*, 1986).

Factors affecting the gain of soil carbon and nitrogen

The climatic factors that favor fast rates of C and N loss from the soil after forest clearing are also those that lead to fast rates of organic matter production and accumulation of soil C and N. The time for recovery of soil C and N suggested by this study was approximately the same in the three life zones (Figs. 4 and 5), with N recovering faster (about 15–20 yr) than C (about 40–50 yr). However, the absolute rate of recovery in the wet and moist life zones (about 0.1–0.2 $\mathrm{kg\,m^{-2}\,yr^{-1}}$) was faster than in the dry (about 0.05 $\mathrm{kg\,m^{-2}\,yr^{-1}}$) because of the different starting and ending points.

Climate is an important factor controlling the rate of recovery of soil C and N through its effect on the rate of reestablishment of vegetation during succession. During the first 20 yr or so of humid forest succession, roots develop rapidly (Ewel, 1971), and more of the organic matter production is recycled through litterfall and decomposition than is allocated to longer term storages in the vegetation (Brown and Lugo, 1990). These high inputs of organic matter to the forest floor lead to an accumulation of soil C at a relatively fast rate (Fig. 4). In drier climates, the input and turnover of organic matter during succession is slower, but because its depletion due to cultivation was less, soil C recovers in a similar amount of time.

Because the turnover rate of organic matter in young secondary forests is relatively high, the rate of increase in soil N is potentially most rapid during this time (Fig. 5). In younger secondary forests, N is used less efficiently by the vegetation and more is recycled via litterfall with accumulation in the soil. This fast rate of accumulation of soil N reinforces the suggestion that N is not a limiting factor for forest production and succession in the tropics (Vitousek, 1984).

Changes in soil carbon with depth

Many studies on the dynamics of soil C resulting from forest clearing have looked at the changes occurring in only the shallow soil horizons, top 30–40 cm or less. Sampling to these shallow depths is based on the assumptions that changes are expected to occur in the rooting zone or plough layer only and that the organic matter to this depth plays a significant role in plant nutrition.

In those sites where we sampled to greater depths we found that changes in C occurred throughout the profile. Others have also measured C changes to depths of 90 cm in tropical soils (Sanchez, 1976). The decline at greater depths upon conversion to agriculture is due to a reduction of organic inputs and a continuation of microbial activity and/or C leaching.

In the deeper soils of the wet life zone, C content of the forest and pasture sites to 30 cm represents only 40–52% of the total to 1 m depth. In the shallower soils of the moist life zone, C content to 30 cm represents 64% of the total to 50 cm deep. Clearly, sampling to 30 cm or so fails to include a large proportion of the total C to 1 m depth and fails to consider changes that may be occurring at these greater depths. This failure to include a large part of the soil C pool may not be so important in agricultural productivity studies but in studies of global biogeochemical cycles failure to include the C changes in the greater depths may be significant.

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