

Land use change and soil nutrient transformations in the Los Haitises region of the Dominican Republic

Pamela H. Templer^{a,b,*}, Peter M. Groffman^b, Alex S. Flecker^a, Alison G. Power^a

^a*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA*

^b*Institute of Ecosystem Studies, Route 44a, Millbrook, NY 12545, USA*

Received 16 April 2003; received in revised form 18 June 2004; accepted 15 July 2004

Abstract

We characterized soil cation, carbon (C) and nitrogen (N) transformations within a variety of land use types in the karst region of the northeastern Dominican Republic. We examined a range of soil pools and fluxes during the wet and dry seasons in undisturbed forest, regenerating forest and active agricultural sites within and directly adjacent to Los Haitises National Park. Soil moisture, soil organic matter (SOM), soil cations, leaf litter C and pH were significantly greater in regenerating forest sites than agricultural sites, while bulk density was greater in active agricultural sites. Potential denitrification, microbial biomass C and N, and microbial respiration g^{-1} dry soil were significantly greater in the regenerating forest sites than in the active agricultural sites. However, net mineralization, net nitrification, microbial biomass C, and microbial respiration were all significantly greater in the agricultural sites on g^{-1} SOM basis. These results suggest that land use is indirectly affecting microbial activity and C storage through its effect on SOM quality and quantity. While agriculture can significantly decrease soil fertility, it appears that the trend can begin to rapidly reverse with the abandonment of agriculture and the subsequent regeneration of forest. The regenerating forest soils were taken out of agricultural use only 5–7 years before our study and already have soil properties and processes similar to an undisturbed old forest site. Compared to undisturbed mogote forest sites, regenerating sites had smaller amounts of SOM and microbial biomass N, as well as lower rates of microbial respiration, mineralization and nitrification g^{-1} SOM. Initial recovery of soil pools and processes appeared to be rapid, but additional research must be done to address the long-term rate of recovery in these forest stands.

© 2004 Elsevier Ltd. All rights reserved.

Keywords: Land use; Forest regeneration; Nutrient transformations; Dominican Republic

1. Introduction

Tropical land use change has important implications for biogeochemical cycles both regionally and globally (Scholes and Van Breemen, 1997). Much work has focused on the effects of forest conversion to cropland or pasture on C storage (Fisher et al., 1994; Nepstad et al., 1994; Van Noordwijk et al., 1997) and soil nutrient availability (Ewel et al., 1991; Keller et al., 1993; Reiners et al., 1994; Fernandes and Sanford, 1995; Neill et al., 1995, 1997;

Henrot and Robertson, 1994; Groffman et al., 2001). Often, C storage and soil nutrient availability are greater in forested land than pastures that replace them. Forest conversion to pasture can decrease soil C storage as natural vegetation is cut and decomposes, burnt, or replaced by crops that support lower C contents in the soil or aboveground plant biomass (Houghton, 1990). However, in some cases land converted to pasture may have amounts of stored C that equal or exceed the forest that preceded it (Moraes et al., 1996). There is some evidence that the abandonment of agriculture and the subsequent regeneration of forest may return C storage to pre-agricultural amounts, although the rate of recovery depends on the time frame one considers and whether the previous land-use was cropland or pasture (Post and Kwon, 2000; Guo and Gifford, 2002). Despite the fact that some studies have addressed C dynamics following

* Corresponding author. Present address: Ecosystem Science Division, Department of Environmental Science, Policy and Management, University of California Berkeley, 151 Hilgard Hall, Berkeley, CA 94720-3110, USA. Tel.: +1-510-643-3963; fax: +1-510-643-5098.

E-mail address: ptempler@nature.berkeley.edu (P.H. Templer).

reforestation in the tropics, it is not easy to predict the effects of tropical land use change on soil C transformations.

In addition to effects on C transformations, land use can have profound implications for soil N cycling in tropical systems. There is a consistent finding that intact tropical forests have higher rates of N mineralization and nitrification than agricultural sites (Piccolo et al., 1994; Reiners et al., 1994; Neill et al., 1995, 1997), suggesting that N availability is greater (Nadelhoffer et al., 1983) where there is less human disturbance. However, soil stocks of inorganic N can be higher in agricultural sites than forest sites because of lower plant uptake (Neill et al., 1995). Moreover, converting forests to pastures can influence how much N₂O is emitted to the atmosphere through denitrification (Keller et al., 1993; Neill et al., 1997; Verchot et al., 1999). It is important to understand patterns of N₂O loss because it is both a greenhouse gas and a contributor to stratospheric ozone destruction. In tropical soils, N is often emitted to the atmosphere through denitrification rather than being taken up by plant biomass because N is often in high supply relative to other essential nutrients (Vitousek and Sanford, 1986; Vitousek and Matson, 1988; Vitousek and Farrington, 1997). Unlike net mineralization and nitrification rates, the pattern of N emissions with land use change is not well understood or reliably predicted (Erikson and Keller, 1997). Research suggests that there is sometimes a transient increase in N emissions from soils once forests are cut, but that over time older pastures can have lower N emissions than intact forests (Keller and Reiners, 1994; Verchot et al., 1999).

Compared to the study of effects on N and C cycling caused by forest conversion to pastures, few studies have focused on the conversion to other agricultural uses (e.g. Ewel et al., 1991; Fernandes and Sanford, 1995). However, understanding the effects of a wide variety of agricultural activities on forest regeneration processes is very important because a significant amount of forest land in the tropics is converted to agricultural use other than pasture. Thus, the major objective of our study was to compare soil N and C cycling in a series of sites that have experienced different land use legacies.

Like many other tropical countries where deforestation is occurring at high rates, the Dominican Republic has a very high rate of land conversion to agriculture. Between 1930 and 1980, 60% of its original forest was cut (Bolay, 1997). Much of this land has been converted to farmland, including pastures, oil palm plantations, sugar cane and cacao. In 1968, the government of the Dominican Republic legally protected 208 km² of forest land in the northeastern region of the country (Bolay, 1997). This area became Los Haitises National Park in 1976 and was enlarged to 1600 km² in 1993 by presidential decree. An extensive amount of land was taken out of agriculture with the park expansion.

The abandonment of agriculture in 1993 within the park presented an opportunity to evaluate the effects of land use change in the Los Haitises region of the Dominican Republic. The park has been shown to have an extensive

amount of floral (Rivera et al., 2000) and faunal diversity (Glor et al., 2001) that varies across the landscape with time since agricultural abandonment and topography (e.g. forests on hill tops of mogotes vs valley bottoms). To date, there have been few studies to examine how land use change affects soil nutrient and C transformations in Caribbean forest systems. We therefore sought to characterize a range of soil pools and fluxes during the wet and dry season across a variety of land use sites. Our objectives were (1) to compare patterns of C, N and cation availability and loss in a variety of active agriculture, regenerating and intact forest sites and (2) to explore the role of organic matter quality in influencing patterns of C and N storage and availability in this tropical landscape.

2. Materials and methods

2.1. Study area

This study took place in Los Haitises National Park (19°00'N, 69°40'E), located in the northeastern region of the Dominican Republic. We examined the effects of land use on soil N and C processes in the Trepada Alta region of the park and adjacent agricultural sites surrounding the park. The region is characterized by karst topography and mogotes, which are steep 'haystack hills' that are covered by distinct vegetation (Rivera et al., 2000) and rise approximately 50 m a.s.l. (Zanoni et al., 1990). Mogotes are composed of rocks that are Miocenic and Pleistocenic limestone and are characterized by relatively thin soils and shorter stature trees than the surrounding valleys (Zanoni et al., 1990). The soils of the valleys are red clays from the Los Haitises Association. We are not aware of publications that describe in greater detail the classification of soils within the park or the surrounding area. The area has an average annual temperature of 25.2 °C and receives approximately 2000 mm rain year⁻¹, mainly occurring from April to December (Bolay, 1997). Native vegetation is comprised of subtropical broadleaf forest (Zanoni et al., 1990).

Our experimental design compared four major land use classes: old forest, mogote forest, regenerating forest and active agriculture sites. Agricultural activities largely modified forests on the valley floor, but not on the hilltops within Los Haitises National Park. In general, the mogote tops of Los Haitises were disturbed less than the valley floors because of the very steep slopes leading up to them. However, fires or selective harvesting of trees have affected some mogote tops. Regenerating sites were either abandoned pasture or abandoned conuco mixed gardens containing species such as banana, coconut, beans, pineapple and citrus trees. Previous land uses were determined from oral histories communicated by park guards. The design was not completely balanced due to the uneven availability of habitat

types. Pastures ($n=3$) were abandoned approximately 5–7 years before the start of our study and at the time of our study was dominated by *Piper aduncum* L. and *Psidium guajava* L. (Rivera et al., 2000). Young mixed garden sites ($n=2$) were abandoned less than 5 years before the start of our study, whereas old mixed garden sites ($n=2$) were abandoned more than 5 years before our study. The younger mixed garden sites were dominated by *Piper aduncum* L. and *Triumfetta* spp, while older mixed garden sites were dominated by *Piper laeteviride* Ekman ex Trelease and *Inga vera* Willd (Rivera et al., 2000). Our old forest ($n=1$) and mogote forest ($n=3$) sites within Los Haitises had never been disturbed. The old forest site was dominated by *Guarea guidonia* (L.) Sleumer and *Piper laeteviride* (Rivera et al., 2000). We were unable to locate more than one old forest site and park personnel knew of no others in the Trepada Alta region of the park. The mogote forest sites were dominated by *Ocotea coriacea* (Sw.) Britton and *Bombacopsis emarginata* (A. Rich) A. Robyns (Rivera et al., 2000). Our mogote sites showed no evidence of recent human disturbance such as cutting or fires. While the mogote forest sites cannot be used as reference sites, we include them within our study because of the distinct composition and relatively high diversity of plants (Rivera et al., 2000) and fauna (Glor et al., 2001) found within them.

Outside of the park, where the land is currently disturbed by human activity, we sampled soils from three active pasture sites, three active African oil palm plantations, and three active cacao groves. Pasture sites had been used for cattle grazing for several decades. The oil palm plantations had trees regularly spaced in a grid approximately 6 m apart with the understory cleared for weed control. Our sites overlap with those where plants were sampled by Rivera et al. (2000) and lizards sampled by Glor et al. (2001) in Trepada Alta and the surrounding region of Los Haitises.

2.2. Soil sampling

Within the experimental design described above, we randomly sampled three soil cores (6 cm d; 10 cm depth) from each site during July 1997 (wet season) and five soil cores from each site during January 1998 (dry season). We augmented our sample size in 1998 to increase our statistical power. Samples were transported to the Institute of Ecosystem Studies in Millbrook, New York and refrigerated for approximately 4 days before analyses were carried out. We quantified soil moisture by drying soils in an oven at 105 °C to determine mass loss of water over 2 days. We determined soil organic matter content (SOM) by loss of dry mass on ignition at 450 °C for 4 h. Bulk density was determined by excavating three 10 cm × 10 cm × 10 cm soil pits per site in January 1998 and weighing the soil after oven drying at 105 °C. Within the mogote forest sites, we could not sample to a depth of 10 cm because of the presence of a very thin soil layer and the extremely rocky nature of these sites.

2.3. Determination of microbial biomass C and N

We used the chloroform fumigation incubation method (Jenkinson and Powlson, 1976) to determine microbial biomass C and N. A subsample of 20 g of fresh soil, from each of the 3 and 5 soil cores per site during the wet and dry seasons, respectively, was fumigated with chloroform for 24 h to lyse microbial cells. Following the fumigation, 0.2 g of fresh (non-fumigated) soil were added to the fumigated soil and placed into tightly sealed mason jars. Soils were incubated for 10 days at room temperature. Following the incubation of these soils, 9 ml of head space gas were taken from each jar to determine rates of microbial respiration. We measured CO₂ with a gas chromatograph (Tracor Model 540, ThermoFinnigan, Austin, TX) fitted with a thermal conductivity detector. At the end of the incubation, inorganic N was extracted by adding 80 ml of 2 M KCl to each jar and shaking them for 1 h on an orbital shaker at 125 rpm. The extraction solution was subsequently filtered through Whatman 42 filters. Ammonium and NO₃⁻ were quantified using an Alpkem auto-analyzer (O.I. Analytical, Wilsonville, OR) in the Institute of Ecosystem Studies (IES) Analytical Laboratory. Microbial biomass C was assumed to be proportional to the amount of CO₂ evolved at the end of the 10-day incubation (correction factor=0.41; Jenkinson and Powlson, 1976; Voroney and Paul, 1984), assuming that the extraction efficiency was 41% and not subtracting out the unfumigated control values. Microbial biomass N was determined from the amount of inorganic N extracted by the KCl at the end of the 10-day incubation (correction factor=0.54; Jenkinson and Powlson, 1976; Voroney and Paul, 1984).

2.4. Determination of N mineralization

We determined rates of net mineralization in incubated soils that were not fumigated by calculating the amount of NH₄⁺ and NO₃⁻ produced over 10 days. We determined rates of net nitrification by calculating the amount of NO₃⁻ produced in these incubations.

2.5. Determination of potential denitrification

We determined rates of potential denitrification for each soil sample ($n=3$ per site in the wet season and $n=5$ in the dry season) using a denitrification enzyme activity assay (Smith and Tiedje, 1979). We added 10 ml of media solution (1.44 g KNO₃ l⁻¹, 500 mg glucose l⁻¹ and 125 mg chloramphenicol l⁻¹) to 5 g fresh soil that were subsequently incubated under anaerobic conditions in the presence of C₂H₂ and shaken at 125 rpm for 90 min. We sampled the head-space for N₂O after 30 and 90 min of incubation. N₂O concentration was measured on a gas chromatograph (Tracor Model 540, ThermoFinnigan, Austin, TX) fitted with an Electron Capture Detector.

2.6. Determination of leaf litter C and N content

We determined the C and N contents of leaf litter collected from the soil surface during January, 1998 from three 10×10 cm quadrats within each site. Samples were dried at 60 °C for 2 days and ground (<0.4 mm). We analyzed C and N contents, using acetanilide as a reference standard, on a Carlo-Erba C-N Analyzer (Carlo Erba, Milan) in the IES Analytical Laboratory.

2.7. Determination of soil base cation concentration and pH

Three randomly selected soil samples (10 cm depth) collected from each site in January, 1998 were analyzed by the Cornell College of Agriculture and Life Sciences Analysis Laboratories for K, Ca, and Mg. These base cations were extracted with a ratio of 1:5 sample:Morgan's solution (a Na acetate/acetic acid solution, pH 4.8). The concentration of these elements was determined using an inductively coupled plasma emission spectrophotometer. Soil pH was determined by allowing one part water and one part soil to stand at room temperature for 1 h. The pH of this suspension was determined using a standard pH meter.

2.8. Statistical analysis

We conducted nested two-way analyses of variance (ANOVA) using SAS JMP software (Version 3.2.5, 1999) with land use class and season as the main effects. In our model, site was nested within land use class. When necessary, data were log-transformed prior to statistical analysis to meet the requirement of normal distribution of data. We conducted linear contrasts of the means comparing

active agriculture, regenerating forest, old forest and mogote forest sites to test the hypothesis that various land uses had different effects on soil fertility and C and N cycling. We also conducted linear contrasts of the means of old and young mixed gardens, as well as active and abandoned pasture to determine whether specific land uses had affected soil properties. Statistical significance was determined at a level $P < 0.05$, except if indicated. We calculated each soil characteristic as g^{-1} dry soil, g^{-1} SOM and cm^{-3} .

3. Results

3.1. Soil physical and chemical properties

There was significantly more soil moisture in the wet season (July 1997) than in the dry season (January 1998) and the amounts were greater in the regenerating and old forest sites compared to active agricultural sites (Table 1). We measured greater SOM (Table 1) in the regenerating and old forest sites compared to the active agricultural sites, and the greatest amount g^{-1} soil in mogote forests. Bulk density was significantly higher in the agricultural sites compared to regenerating and old forest sites (Table 1).

Amounts of soil base cations (Mg, Ca, K) were significantly greater in regenerating sites compared to agricultural sites (Table 1). Mogote forest soil contained the largest amount of base cations (Table 1). Abandoned pasture soils had approximately five times the amount of base cations as active pasture soils (Table 1). Soil pH was highest in mogote forests, followed by old forest, regenerating forest and active agriculture (Table 1).

Table 1
Soil (top 10 cm) properties with standard error across land uses

Land use	Dry season moisture (mg $\text{H}_2\text{O g}^{-1}$ soil)	Wet season moisture (mg $\text{H}_2\text{O g}^{-1}$ soil)	Organic matter (% dry wt)	Organic matter (mg cm^{-3})	Bulk density (mg cm^{-3})	pH	Base cations (g kg^{-1})
<i>Active agriculture</i>							
Oil palm	200.1 ± 13.9	199.5 ± 19.2	7.00 ± 0.64	60.0 ± 4.0	915.1 ± 57.4	5.56 ± 0.34	1.87 ± 1.02
Active pasture	297.9 ± 20.2	311.1 ± 30.6	13.01 ± 1.43	105.0 ± 13.0	779.3 ± 44.3	5.07 ± 0.10	0.94 ± 0.17
Cacao	320.4 ± 13.7	412.6 ± 29.0	12.79 ± 1.26	92.0 ± 11.0	774.1 ± 45.4	5.91 ± 0.18	2.40 ± 0.17
Mean	273 ^a ± 12.0	295 ^a ± 20	10.9 ^a ± 0.70	86 ^a ± 7.0	823 ^a ± 21	5.50 ^a ± 0.14	1.74 ^a ± 0.36
<i>Regenerating forest</i>							
Abandoned pasture	407.2 ± 10.8	424.2 ± 9.1	22.70 ± 1.72	94.0 ± 11.0	441.9 ± 26.6	5.62 ± 0.16	4.58 ± 0.58
Young mixed gardens	442.0 ± 18.3	415.9 ± 14.0	29.28 ± 5.82	173.0 ± 54.0	516.0 ± 14.0	6.02 ± 0.13	3.53 ± 0.43
Old mixed gardens	442.8 ± 25.1	424.2 ± 24.8	26.94 ± 1.08	144.0 ± 10.0	544.0 ± 44.0	6.23 ± 0.16	6.51 ± 1.17
Mean	427 ^b ± 9	422 ^b ± 9	25.7 ^b ± 1.8	131 ^b ± 17	492 ^b ± 16	5.91 ^b ± 0.10	4.83 ^b ± 0.48
Old forest	433 ^{b,c} ± 35	523 ^{b,c} ± 38	26.8 ^b ± 3.21	142 ^{a,b} ± 13	595 ^b ± 23	6.14 ^{a,b} ± 0.11	4.21 ^{a,b} ± 0.40
Mogote	522 ^c ± 20	563 ^c ± 25	62.08 ^c ± 3.53	ND	ND	6.90 ^c ± 0.28	20.86 ^c ± 2.76

Base cations include K, Mg and Ca. Different letters above means represent statistically significant differences at $P < 0.05$. ND indicates no data available.

3.2. Microbial biomass and activity among four major land use classes

Amounts of microbial biomass N and C g^{-1} varied significantly among land use classes and were approximately two-fold larger in regenerating sites than in active agricultural sites (Fig. 1). On g^{-1} SOM basis, microbial biomass C was greater in active agricultural sites than regenerating sites (Fig. 1). Per unit soil volume (cm^3), soil microbial biomass N was approximately 40% greater in the regenerating sites ($229.7 \pm 11.6 \mu g N cm^{-3}$) than the active agricultural sites ($164.2 \pm 16.8 \mu g N cm^{-3}$; $P < 0.01$). There was no difference in microbial biomass C cm^{-3} between active agricultural ($1415.3 \pm 187.4 \mu g C cm^{-3}$) and regenerating sites ($1512.7 \pm 134.5 \mu g C cm^{-3}$) sites ($P = 0.66$).

Net mineralization and net nitrification g^{-1} soil were highest in mogote forest sites (Fig. 2). Rates of net mineralization and net nitrification g^{-1} SOM were significantly greater in agricultural sites than regenerating sites (Fig. 2) and were largest in mogote forests (Fig. 2). There was no difference in rates of net mineralization and nitrification cm^{-3} among land use types.

Microbial respiration g^{-1} soil was significantly greater in regenerating than in active agricultural sites and was highest in mogote forests (Fig. 2). Microbial respiration g^{-1} SOM was higher in the agricultural sites compared to all of the other sites (Fig. 2).

Potential denitrification g^{-1} soil was significantly greater in the regenerating sites compared to any other

land use type (Fig. 2). Potential denitrification SOM^{-1} was significantly higher in the regenerating and active agricultural sites than the mogote forest sites (Fig. 2).

While we found significant differences between agricultural and regenerating sites, we found few differences between the old forest and other sites we examined. There was no significant difference between regenerating and old forest sites in net mineralization, net nitrification, microbial respiration (Fig. 2), biomass C and N g^{-1} soil or g^{-1} SOM (Fig. 1). However, potential denitrification g^{-1} soil was significantly lower in old forest than regenerating sites (Fig. 2). The only significant differences between active agricultural sites and old forest was in microbial biomass N g^{-1} soil which was higher in old forest sites (Fig. 1) and microbial respiration g^{-1} SOM (Fig. 2), which was higher in active agricultural sites.

3.3. Variation of microbial biomass and activity within active agricultural sites

There was a significant amount of variation in soil and microbial properties among the agricultural sites. For example, oil palm soils had the lowest amounts of SOM, moisture, microbial respiration, microbial biomass C and N and potential denitrification (Tables 1, 2a, and 2b), while cacao sites had the highest moisture (Table 1), microbial biomass C (Tables 2a and 2b) and potential denitrification (Tables 2a and 2b; $P = 0.058$).

Abandoned pastures differed markedly in soil properties from active pastures. Compared to active pastures,

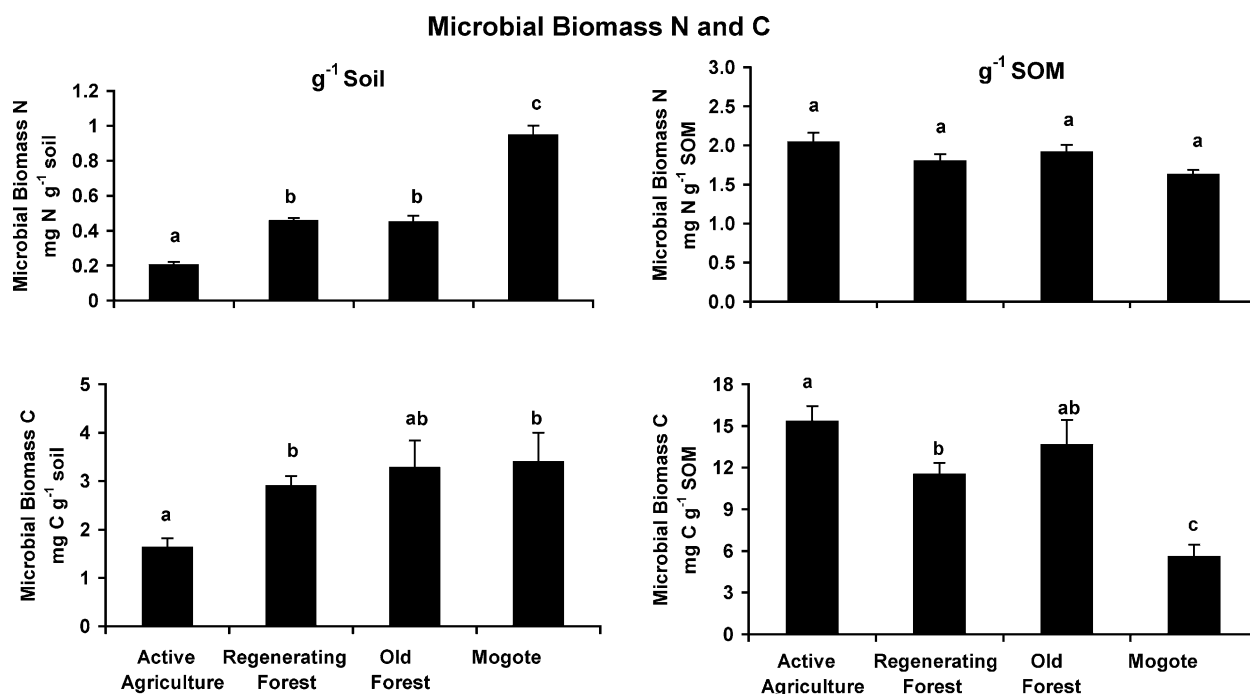


Fig. 1. Microbial biomass N and C g^{-1} soil and g^{-1} SOM (error bars represent standard error). Different letters above bars represent statistically significant differences at $P < 0.05$.

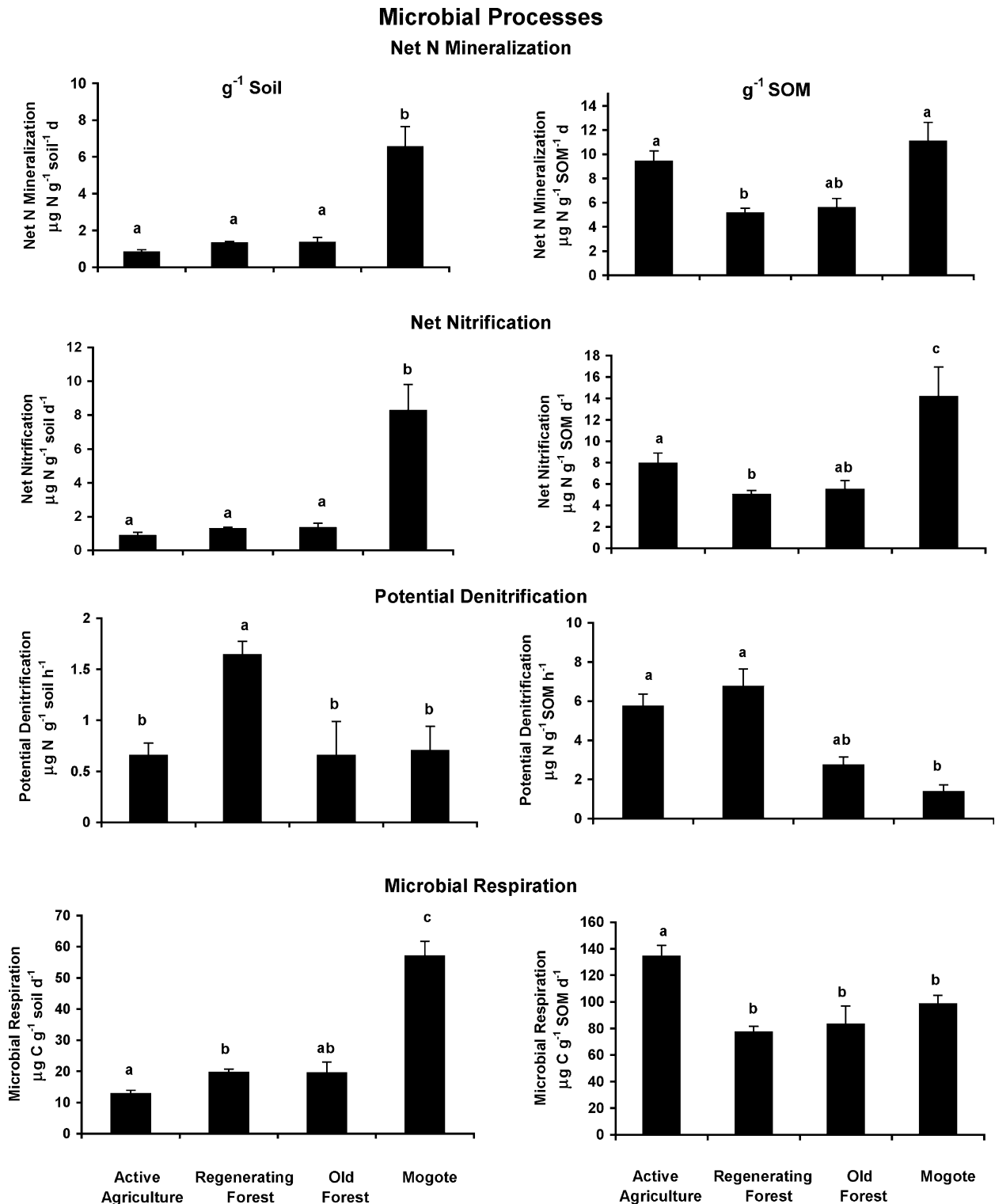


Fig. 2. Microbial processes including net mineralization, net nitrification, potential denitrification and respiration g^{-1} soil and g^{-1} SOM (error bars represent standard error). Different letters above bars represent statistically significant differences at $P < 0.05$.

abandoned pastures had greater soil moisture in the wet and dry seasons (Table 1) in addition to greater amounts of base cations (Table 1), microbial biomass N and C g^{-1} soil (Table 2a), and rates of potential denitrification g^{-1} soil

(Table 2a). In contrast, on g^{-1} SOM basis, active pastures had higher net mineralization (Table 2b), microbial biomass C (Table 2b) and microbial respiration (Table 2b) compared to abandoned pastures.

Table 2a
Microbial biomass and processes g^{-1} dry soil (top 10 cm) with standard error across land uses

Land use	Microbial biomass N (mg N g^{-1} soil)	Microbial biomass C (mg C g^{-1} soil)	Net mineralization ($\mu\text{gN g}^{-1}$ soil d^{-1})	Net nitrification ($\mu\text{gN g}^{-1}$ soil day^{-1})	Microbial respiration ($\mu\text{gC g}^{-1}$ soil day^{-1})	Potential denitrification (ngN g^{-1} soil h^{-1})
<i>Active agriculture</i>						
Oil palm	0.12 ± 0.01	0.78 ± 0.10	0.51 ± 0.06	0.98 ± 0.47	5.6 ± 0.6	225 ± 199
Active pasture	0.24 ± 0.02	1.90 ± 0.33	0.74 ± 0.28	0.41 ± 0.28	16.8 ± 2.0	806 ± 195
Cacao	0.25 ± 0.04	2.56 ± 0.46	1.31 ± 0.21	1.27 ± 0.22	16.5 ± 1.7	1074 ± 246
<i>Regenerating forest</i>						
Abandoned pasture	0.42 ± 0.03	2.79 ± 0.32	1.26 ± 0.16	1.24 ± 0.17	18.3 ± 1.6	1696 ± 199
Young mixed gardens	0.42 ± 0.03	2.56 ± 0.32	1.30 ± 0.14	1.23 ± 0.14	19.1 ± 1.3	1842 ± 239
Old mixed gardens	0.53 ± 0.04	3.42 ± 0.41	1.43 ± 0.17	1.43 ± 0.16	22.3 ± 2.3	1342 ± 246
Old forest	0.45 ± 0.04	3.27 ± 0.56	1.36 ± 0.26	1.34 ± 0.27	19.4 ± 3.6	652 ± 337
Mogote	0.95 ± 0.05	3.39 ± 0.61	6.55 ± 1.09	8.27 ± 1.54	57.1 ± 4.7	700 ± 239

Table 2b
Microbial biomass and processes g^{-1} SOM (top 10 cm) with standard error across land uses

Land use	Microbial biomass N (mg N g^{-1} SOM)	Microbial biomass C (mg C g^{-1} SOM)	Net mineralization ($\mu\text{gN g}^{-1}$ SOM day^{-1})	Net nitrification ($\mu\text{gN g}^{-1}$ SOM day^{-1})	Microbial respiration ($\mu\text{gC g}^{-1}$ SOM day^{-1})	Potential denitrification (ngN g^{-1} SOM h^{-1})
<i>Active agriculture</i>						
Oil palm	1.79 ± 0.13	12.10 ± 1.63	8.57 ± 1.31	8.24 ± 1.87	101.6 ± 13.5	3100 ± 4320
Active pasture	2.09 ± 0.14	15.40 ± 1.90	8.52 ± 1.76	5.40 ± 1.54	150.3 ± 16.0	5950 ± 3977
Cacao	2.24 ± 0.33	19.93 ± 1.78	11.31 ± 1.19	10.57 ± 1.14	149.7 ± 10.6	8123 ± 5957
<i>Regenerating forest</i>						
Abandoned pasture	1.71 ± 0.18	11.21 ± 1.58	5.14 ± 0.80	5.01 ± 0.84	74.8 ± 8.7	6823 ± 7840
Young mixed gardens	1.78 ± 0.14	10.92 ± 1.46	5.02 ± 0.47	4.74 ± 0.47	76.8 ± 5.6	8053 ± 1669
Old mixed gardens	1.96 ± 0.10	12.46 ± 1.17	5.24 ± 0.49	5.23 ± 0.44	81.3 ± 5.1	5364 ± 3917
Old forest	1.91 ± 0.10	13.64 ± 1.80	5.60 ± 0.76	5.51 ± 0.80	83.1 ± 13.8	2730 ± 1181
Mogote	1.62 ± 0.06	5.59 ± 0.87	11.08 ± 1.55	14.18 ± 2.76	98.3 ± 6.5	1380 ± 1400

3.4. Leaf litter

Leaf litter associated with regenerating and mogote forest sites had significantly higher %C than active agricultural sites (Table 3). There were no differences in leaf litter %N or the C-to-N ratio between regenerating, active agricultural sites, old forest and mogote forest sites (Table 3). However, leaf litter associated with cacao had the lowest C:N, while active pastures had the highest (Table 3).

4. Discussion

4.1. Land use effects on soil nutrient transformations

Results from this work demonstrate that land use in the Los Haitises region of the Dominican Republic has had significant effects on N and C transformations within the top 10 cm of soil. Similar to Rivera et al. (2000) we do not use our four major land use classes as a chronosequence to make predictions about successional development of soils following abandonment of agriculture. This is because the sites undergoing modern cultivation are not fully representative of the abandoned land management practices.

For example, we analyzed soils taken from active oil palm plantations, but we do not have any samples taken from sites where this type of agricultural activity was abandoned. We use our experimental design to give us insight into soil

Table 3
Leaf litter %C and %N with standard error across land uses

Land use	Leaf litter		
	%N	%C	C-to-N ratio
<i>Active agriculture</i>			
Oil palm	1.90 ± 0.14	45.08 ± 0.96	24.77 ± 2.00
Active pasture	1.39 ± 0.09	39.48 ± 1.57	29.26 ± 2.16
Cacao	1.71 ± 0.08	33.79 ± 1.46	20.11 ± 1.25
Mean	$1.67^a \pm 0.07$	$39.45^a \pm 1.18$	$24.71^a \pm 1.26$
<i>Regenerating forest</i>			
Abandoned pasture	1.87 ± 0.10	45.00 ± 1.07	24.75 ± 1.76
Young mixed gardens	1.76 ± 0.16	43.16 ± 1.63	26.05 ± 3.34
Old mixed gardens	1.89 ± 0.19	44.39 ± 0.98	24.76 ± 2.50
Mean	$1.84^a \pm 0.08$	$44.30^b \pm 0.17$	$25.42^a \pm 0.81$
Old forest	$2.03^a \pm 0.05$	$44.86^{a,b} \pm 1.36$	$21.98^a \pm 0.40$
Mogote	$1.90^a \pm 0.06$	$48.01^b \pm 0.17$	$25.42^a \pm 0.81$

Different letters above means represent statistically significant differences between land use classes at $P < 0.05$.

properties, including nutrient availability and microbial biomass and activity, among a variety of land use types that occur at one or two points in time (e.g. mixed gardens that were abandoned less than 5 years ago vs those abandoned more than 5 years ago).

Our range of values for microbial biomass is similar to that found in other tropical sites (Groffman et al., 2001). Accumulation of soil nutrients and increased microbial activity in regenerating forest soils, compared to the active agricultural sites, suggests that they are more fertile. For example, soils from mixed gardens that had been abandoned for more than 5 years had larger microbial biomass N and C g^{-1} soil than those mixed gardens abandoned for less than 5 years, implying that the soil microbial community is beginning to rebound from intensive land use as the mixed gardens age and time since abandonment of agriculture increases. Also, the abandoned pastures had larger microbial biomass N g^{-1} soil than the active pastures. The regenerating forest soils were taken out of agricultural use only 5–7 years before the start of our study and already have similar soil properties and processes to the undisturbed old forest site. While agriculture can significantly decrease soil fertility and microbial processes, our data suggest that these effects can begin to change quickly with the abandonment of agriculture and the subsequent regeneration of forest.

4.2. Use of reference sites in estimating time of recovery

If we use the old forest site as a reference for the undisturbed forest condition in this region, we can estimate how long it will take for the regenerating sites to fully recover their SOM pools. The abandoned pasture sites were taken out of agriculture approximately 6 years before the start of this study and have approximately 66% of the amount of SOM per soil volume as the old forest reference site (Table 1). We calculated the minimum amount of time it would take the pasture sites to recover pre-disturbance amounts based on the assumption that SOM accumulation occurs linearly through time. Assuming linear accumulation in our sites, it would take the pasture sites approximately 9 years from the time of abandonment to recover their pre-disturbance SOM pools (6 years divided by 0.66). Recovery would likely be slower given that rates of recovery often decrease over time (Post and Kwon, 2000; Silver et al., 2000; Six et al., 2002). This may be why our prediction falls short of estimates produced by Rhoades et al. (2000) who found soil stocks of C to return to pre-agricultural amounts within 20 years in a tropical forest in Ecuador. Knops and Tilman (2000) predicted that it would take 180 and 230 years to reach 95% pre-agricultural amounts of soil N and C, respectively, in Minnesota. Recovery within a tropical ecosystem may be more rapid than in a temperate ecosystem due to higher turnover and storage of C (Brown and Lugo, 1982). However, it is important to note that our analysis does not include aboveground, root, or sub-surface (> 10 cm) accumulations of C. This may contribute to our estimates of relatively fast recovery rates compared to

predictions by Hughes et al. (1999) who found recovery to take 73 years in Veracruz, Mexico and Brown and Lugo (1990), who expected C recovery to take 40–50 years in tropical forests of Puerto Rico and the US Virgin Islands. Furthermore, we sampled from a fixed depth across all of our land use types, rather than by horizon. Davidson and Ackerman (1993) showed that this method could overestimate the amount of C stored in agricultural soils due to compaction caused by agricultural activity. Had we sampled by soil horizon, we may have found relatively smaller amounts of SOM in the abandoned pastures 6 years following abandonment, which could have contributed to a longer estimate of SOM recovery time for these soils.

It is important to consider that we were only able to find one old forest site within the region. However, this site more accurately represents the pre-agricultural state of the regenerating sites than the mogote forest reference sites (Rivera et al., 2000; Glor et al., 2001). We found no significant differences in soil base cations, microbial pools or processes between old forest and regenerating sites, with the exception of potential denitrification g^{-1} soil, which was lower in old forest. Either the regenerating sites are similar to old forest sites because they have recovered their pre-agricultural amounts of fertility, or we do not have adequate statistical power to detect differences between the reference and previously disturbed sites.

Although the mogote forest sites were undisturbed, we did not use them as a reference for the regenerating sites. The mogote forest sites were not used for agriculture before our study, yet they have very different characteristics from both the old forest site and the regenerating sites, which are likely partially due to inherent site differences and not land use change. The soils within mogote forest sites are atop hills that may not mirror the pre-disturbance fertility and C storage of the soils in the valleys below them because of differences in topography, water movement and soil erosion. The differences we found between the old forest and mogote forest sites underscore the importance of locating appropriate reference sites in land use change studies (Pickett and Parker, 1994; Aronson et al., 1995; Rheinhardt, 1996; White and Walker, 1997).

Our comparison between the regenerating and old forest sites suggests that initial regeneration of soil C and N pools and processes in this region is quite rapid. Further work needs to be done in Los Haitises National Park to address the long-term rate of recovery.

4.3. Variation within specific land use classes

In addition to the broad differences found between agricultural and regenerating forest soils, there was considerable variation within each major land use type. For example, the oil palm sites were distinct from the other active agricultural sites, which may be due to the large amount of soil disturbance associated with understory clearing and movement of heavy agricultural equipment.

Lower amounts of SOM in agricultural sites in general have also been attributed to increased erosion and faster decomposition of residues as a result of increased exposure to sun and subsequently higher temperatures (Detwiler, 1986; Houghton et al., 1991).

Of all the active agricultural sites, the cacao agro-ecosystems most closely resembled forests in structure and vegetation density in that they had a thick understory, a large amount of leaf litter and a well-developed forest floor. The dense vegetative cover in cacao could have provided the organic substrate necessary for the relatively high soil fertility and microbial activity (Tables 1, 2a and 2b). Furthermore, the relatively low C-to-N ratio in leaf litter of the cacaos compared to other active agricultural sites may have contributed to a higher quality SOM source for the soil microbes (Taylor et al., 1989). For example, potential denitrification and microbial biomass C were higher in the cacaos than the other active agricultural sites. However, bulk density was still higher in cacaos compared to all regenerating sites, suggesting that current agricultural practices compact the soil. Cacao soils were intermediate in soil nutrient pools and microbial processes between the regenerating sites and other active agricultural sites. These results suggest that variation within agricultural practices can influence soil nutrient pools and microbial processes.

The old mixed garden sites differed from young mixed garden sites only in the amount of time since agriculture was abandoned. This provides us with a group of sites that had similar land use histories, but differed only in time since abandonment. Old mixed gardens had been out of production for more than 5 years, and young mixed gardens for less than 5 years, before our study began. Microbial biomass C and N, both significantly higher in old mixed gardens than young mixed gardens, were the only soil properties we found to be different between these land use classes. This suggests that microbial communities have begun to respond to the shift from agricultural use to regenerating forest. The similarity in all soil nutrient pools, as well as microbial processes, per unit SOM between old and young mixed gardens suggest that either time since abandonment does not affect the overall C quality of these soils, or that not enough time has elapsed since agricultural abandonment to observe a difference. This suggests that in some areas of Los Haitises Park, soil regeneration of nutrients and microbial processes lags behind the initial recovery of microbial communities and may not be detectable until at least 5 years after the cessation of agricultural practices. The variation in soil nutrient recovery across sites with different land use histories suggests that we need to focus on specific land use histories and that we cannot make broad generalizations about the effects of past agricultural practices.

4.4. Variation in soil organic matter quality

Our results suggest that the quality of SOM in agricultural plant residue plays an important role in the effects of land use changes on soil C and N transformations.

We observed larger amounts of microbial C (Fig. 1), as well as higher rates of net mineralization, net nitrification and microbial respiration g^{-1} SOM in agricultural sites compared to the regenerating sites (Fig. 2), implying that compared to regenerating sites the SOM within agricultural sites was more labile and more easily used by soil microbes. Additional evidence for this is that the active pasture soils had significantly higher rates of net mineralization and approximately 1.5 times higher amounts of microbial biomass C g^{-1} SOM than the abandoned pastures. However, the C-to-N ratio and N content of the leaf litter did not differ between regenerating and active agricultural sites, despite the fact that these factors often control decomposition (Taylor et al., 1989). A study examining the C and N content of other organic matter sources (e.g. plant roots or stems) needs to be done to better characterize the C and N inputs for these sites.

4.5. Soil physical and chemical properties

In addition to SOM, soil moisture and bulk density also had strong effects on soil microbial biomass and activity. Soil moisture was significantly lower within the active agricultural sites compared to the regenerating, old forest and mogote forest sites. This could have at least partially contributed to the smaller amount of microbial biomass N and C, denitrification and respiration g^{-1} soil in the agricultural sites compared to the regenerating sites (r^2 for relationships between soil moisture and each factor, respectively, equals 0.83, 0.57, 0.46, and 0.74; all $P < 0.05$). Bulk density also varied among land use types with greater values in the active agricultural than regenerating sites (Table 1), but the relationship to microbial activity such as microbial respiration was weaker than that of soil moisture ($r^2 = 0.59$; $P < 0.05$).

We found lower soil pH and soil base cations in the agricultural sites than the regenerating sites. There may have been significantly larger leaching losses of base cations in the agricultural sites, which may have resulted in higher soil acidity. We cannot attribute differences in soil pH to net mineralization or nitrification per soil volume because they were similar in both of these land use classes. Furthermore, we found lower rates of net mineralization and nitrification g^{-1} soil in the agricultural soils, which we would expect to cause a decrease in soil acidity (Brady and Weil, 1999).

4.6. Conclusions

Our results demonstrate that there is a significant amount of variation in soil nutrient transformations among intact forest, regenerating forest and active agricultural sites in and adjacent to Los Haitises National Park, Dominican Republic. Deforestation is common throughout the tropics and further changes in land use may have consequences for soil nutrient transformations. This study

suggests that in those areas in Los Haitises where agriculture is being abandoned and forest is regenerating, initial regeneration of soil C and N pools is quite rapid, but further work needs to address the long-term rate of recovery in this region.

Acknowledgements

The Global Environment Facility, Cornell Agroforestry Working Group, Cornell International Institute for Food, Agriculture and Development, and the Cornell Graduate School provided funding for this project. A National Science Foundation Research Training Grant supported P. Templer during the writing of this paper. We thank the Direccion de Parques Nacionales de La Republica Dominicana and Jose Ottenwalder of the Natural Resources Department of the Universidad Nacional Pedro Henriquez Urena (UNPHU) for logistical support in the Dominican Republic. We appreciate the laboratory assistance provided by Alan Loreface and Denise Schmidt at the Institute of Ecosystem Studies. We also thank Lou Verchot and Whendee Silver for very helpful comments on earlier drafts of this manuscript.

References

- Aronson, J., Dhillon, S., Le Floch, E., 1995. On the need to select an ecosystem of reference, however imperfect: a reply to Pickett and Parker. *Restoration Ecology* 3, 1–3.
- Bolay, E., 1997. The Dominican Republic. A Country Between Rain Forest and Desert. Contributions to the Ecology of a Caribbean Island. Margraf, Germany.
- Brady, N.C., Weil, R.R., 1999. *The Nature and Property of Soils*. Prentice Hall, Upper Saddle River.
- Brown, S., Lugo, A.E., 1982. Storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14, 161–187.
- Brown, S., Lugo, A.E., 1990. Effects of forest clearing and succession on the carbon and nitrogen content of soils in Puerto Rico and US Virgin Islands. *Plant and Soil* 124, 53–64.
- Davidson, E.A., Ackerman, I.L., 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry* 20, 161–193.
- Detwiler, R., 1986. Land use change and the global carbon cycle: the role of tropical soils. *Biogeochemistry* 2, 67–93.
- Erikson, E., Keller, M., 1997. Tropical land use change and soil emissions of nitrogen oxides. *Soil Use and Management* 13, 278–287.
- Ewel, J.J., Mazzarino, M.J., Berish, C.W., 1991. Tropical soil fertility changes under monocultures and successional communities of different structure. *Ecological Applications* 1, 289–302.
- Fernandes, D., Sanford Jr., R., 1995. Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. *Conservation Biology* 9, 915–922.
- Fisher, M.J., Rao, I.M., Ayarza, M.A., Lascano, C.E., Sanz, J.I., Thomas, R.J., Vera, R.R., 1994. Carbon storage by introduced deep-rooted grasses in the South American savannas. *Nature* 371, 236–238.
- Glor, R.E., Flecker, A.S., Benard, M.F., Power, A.G., 2001. Lizard diversity and agricultural disturbance in a Caribbean forest landscape. *Biodiversity and Conservation* 10, 711–723.
- Groffman, P.M., McDowell, W.H., Myers, J.C., Merriam, J.L., 2001. Soil microbial biomass and activity in tropical riparian forests. *Soil Biology and Biochemistry* 33, 1339–1348.
- Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. *Global Change Biology* 8, 345–360.
- Henrot, J., Robertson, G., 1994. Vegetation removal in two soils of the humid tropics: effect on microbial biomass. *Soil Biology and Biochemistry* 1, 111–116.
- Houghton, R., 1990. The global effects of tropical deforestation. *Environmental Science and Technology* 24, 414–422.
- Houghton, R., Skole, D., Lefkowitz, D., 1991. Changes in the landscape of Latin America between 1850–1985. II. Net release of carbon dioxide to the atmosphere. *Forest Ecology and Management* 38, 173–200.
- Hughes, R.F., Boone Kauffman, J., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* 80, 1892–1907.
- Jenkinson, D.S., Powlson, D.S., 1976. The effects of biocidal treatments on metabolism in soil. A method for measuring soil biomass. *Soil Biology and Biochemistry* 8, 209–213.
- Keller, M., Reiners, W., 1994. Soil-atmosphere exchange of nitrous oxide, nitric oxide and methane under succession of pasture to forest in the Atlantic lowlands of Costa Rica. *Global Biogeochemical Cycles* 8, 399–409.
- Keller, M., Veldkamp, E., Weitz, A., Reiners, W., 1993. Effect of pasture age on soil trace-gas emissions from a deforested area of Costa Rica. *Nature* 364, 244–246.
- Knops, J.M.H., Tilman, D., 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* 81, 88–98.
- de Moraes, J.F.L., Volkoff, B., Cerri, C.C., Bernoux, M., 1996. Soil properties under Amazon forest and changes due to pasture installation in Rondonia, Brazil. *Geoderma* 70, 63–81.
- Nadelhoffer, K.J., Aber, J.D., Melillo, J.M., 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in southern Wisconsin (USA). *Canadian Journal of Forest Research* 13, 12–21.
- Neill, C., Piccolo, M., Steudler, P., Melillo, J., Feigl, B., Cerri, C., 1995. Nitrogen dynamics in soils of forests and active pastures in the western Brazilian Amazon Basin. *Soil Biology and Biochemistry* 27, 1167–1175.
- Neill, C., Piccolo, M., Cerri, C., Steudler, P., Melillo, J., Brito, M., 1997. Net nitrogen mineralization and net nitrification rates in soils following deforestation for pasture across the southwestern Brazilian Amazon Basin landscape. *Oecologia* 110, 243–252.
- Nepstad, D.C., De Carvalho, C., Davidson, E., Jipp, P., Lefebvre, P., Negreiros, G., Da Silva, E., Stone, T., Trumbore, S., Vieira, S., 1994. The role of deep roots in the hydrological and carbon cycles of amazonian forests and pastures. *Nature* 372, 666–669.
- Piccolo, M.C., Neill, C., Cerri, C.C., 1994. Net nitrogen mineralization and net nitrification along a tropical forest-to-pasture chronosequence. *Plant and Soil* 162, 61–70.
- Pickett, S.T.A., Parker, V.T., 1994. Avoiding old pitfalls: opportunities in a new discipline. *Restoration Ecology* 2, 75–79.
- Post, W.M., Kwon, K.C., 2000. Soil carbon sequestration and land-use change: processes and potential. *Global Change Biology* 6, 317–327.
- Reiners, W.A., Bowman, A.F., Parsons, W., Keller, M., 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. *Ecological Applications* 4, 363–377.
- Rheinhardt, R., 1996. The role of reference wetlands in functional assessment and mitigation. *Ecological Applications* 6, 69–76.
- Rhoades, C.C., Eckert, G.E., Coleman, D.C., 2000. Soil carbon differences among forest, agriculture, and secondary vegetation in lower montane Ecuador. *Ecological Applications* 10, 497–505.

- Rivera, L.W., Zimmerman, J.K., Aide, T.M., 2000. Forest recovery in abandoned agricultural lands in a karst region of the Dominican Republic. *Plant Ecology* 148, 115–125.
- Scholes, R.J., Van Breemen, N., 1997. The effects of global change on tropical ecosystems. *Geoderma* 79, 9–24.
- Silver, W.L., Ostertag, R., Lugo, A.E., 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restoration Ecology* 8, 394–407.
- Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. *Plant and Soil* 241, 155–176.
- Smith, M.S., Tiedje, J.M., 1979. Phases of denitrification following oxygen depletion in soil. *Soil Biology and Biochemistry* 11, 262–267.
- Taylor, B.R., Parkinson, D., Parsons, W.F.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70, 97–104.
- Van Noordwijk, M., Cerri, C., Woomer, P., Nugroho, K., Bernoux, M., 1997. Soil carbon dynamics in the humid tropical forest zone. *Geoderma* 79, 187–225.
- Verchot, L., Davidson, E., Henrique Cattanio, J., Ackerman, I., Erickson, H., Keller, M., 1999. Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia. *Global Geochemical Cycles* 13, 31–46.
- Vitousek, P., Farrington, H., 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry* 37, 63–75.
- Vitousek, P., Matson, P., 1988. Nitrogen transformations in tropical forest soils. *Soil Biology and Biochemistry* 20, 361–367.
- Vitousek, P.M., Sanford Jr., R.L., 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17, 137–167.
- Voroney, R.P., Paul, E.A., 1984. Determination of K_c and K_n in situ for calibration of the chloroform fumigation incubation method. *Soil Biology and Biochemistry* 16, 9–14.
- White, P.S., Walker, J.L., 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. *Restoration Ecology* 5, 338–349.
- Zanoni, T.A., Mejia, M.M., Pimentel, J.D., Garcia, R.G., 1990. La flora y la vegetacion de Los Haitises, Republica Dominicana. *Moscoso* 6, 46–98.