



Nitrogen mineralization and nitrification following land conversion in montane Ecuador

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Abstract

The lower montane zone of northwestern Ecuador, like many parts of the tropics, is undergoing rapid conversion from native forest vegetation to crop and pastureland. The current landscape is a mosaic of agricultural land, forest fragments and second-growth vegetation in various stages of development. While there is abundant research documenting the effects of land-use change in the lowland tropics, such information is scarce for montane regions on young volcanic soils. We compared foxtail pasture (*Setaria sphacelata*, [(Schumach.) Stapf and C.E. Hubb.]) and traditional, mixed-species pasture with undisturbed old-growth forest, 15–20 y-old secondary forest and 5–10 y-old shrubby regrowth. At two replicates of each vegetation class, we measured soil nitrogen and carbon pools, *in situ* net nitrogen mineralization and nitrification, soil respiration and soil physical properties. *Setaria* pasture decreased soil NO_3^- -N pools and net mineralization and nitrification rates compared to mature forest, secondary vegetation, and mixed-species pasture. Soil NO_3^- -N in *Setaria* pastures, during wet and dry seasons, was 40 and 25% of amounts measured in other vegetation types. Net nitrification rates were also lower beneath *Setaria* during both seasons, the greatest difference occurring during the wet season. Net nitrification rates increased considerably (two-fold and greater) under wet season conditions beneath all vegetation types except *Setaria* pasture. Soils beneath both pasture types were wetter and had higher bulk density than mature and second-growth forests. Conversion to pasture produces widely varying effects on soil N dynamics depending on characteristics of the pasture species, such as *Setaria*'s extremely dense root system. Reduced soil N availability beneath *Setaria* pasture will affect both long-term pasture productivity and subsequent forest regeneration in abandoned pastures. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

The consequences of land conversion on soil nitrogen processes are poorly understood for tropical montane ecosystems. The major source of land-use change in Latin America is increasing pasture production (Houghton et al., 1991). In the Andes Mountains of Ecuador, the rate of pasture expansion has increased considerably during the last two decades as new roads improve access to previously isolated valleys and link them to major population centers.

In the lowland tropics, conversion from forest to

pasture reduces plant available soil N (Reiners et al., 1994; Neill et al., 1995; Johnson and Wedin, 1997), and alters soil physical properties (Spaans et al., 1989; Wielemaker and Lansu, 1991). Net N mineralization and nitrification rates in lowland tropical pastures of Central and South America were less than half that of adjacent intact forest (Reiners et al., 1994; Neill et al., 1995). For the tropical montane regions, comparable information quantifying the effects of pasture management compared to other land use options is lacking.

Young, tephra-derived soils, such as those found in the volcanically active Andes, are characterized by low soil N availability (Riley and Vitousek, 1995; Tanner et al., 1998). Productivity is constrained by the absence of mineral nitrogen in tephra or lava deposits and by slow release of plant available N forms from organic

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Table 1
Properties of volcanic ash derived soils in lower montane tropical forests of northwestern Ecuador

Depth (cm)	Total C Mg C ha ⁻¹	Bulk density (g cm ⁻³)	1.5 MPa gravimetric water content (%)	Soil pH	
				Water	1 M NaF 2:1
0–5	25.1	0.5	22.6	5.3	10.8
5–15	48.7	0.7	16.7	5.0	11.3
15–30	31.0	0.8	14.0	4.9	11.5
30–60	39.9	1.0	14.0	5.0	11.3
60–100	44.8	1.0	12.1	5.1	9.5

matter. The amorphous, allophane minerals found in volcanic soils form physically stable aggregates and chemically stable organic-aluminum complexes that inhibit soil N turnover (Shoji et al., 1993). Cool temperatures and frequently waterlogged montane soils further retard organic matter decomposition and nutrient release (Vitousek and Matson, 1988). In tropical mountain forests, soil N availability increases with pedogenic development (Riley and Vitousek, 1995; Tanner et al., 1998) and with decreased elevation (Vitousek and Sanford, 1986; Marrs et al., 1988).

Here, we compare soil N cycling in intact forest with the two dominant pasture types found in the lower montane region of northwestern Ecuador. We also examine soil N variables in second-growth forest and shrub vegetation regenerating after agricultural land use.

2. Materials and methods

2.1. Study sites

This research was carried out at the Maquipucuna Forest Reserve, located in the province of Pichincha on the western slope of the Ecuadorian Andes (0° 5' N; 78° 37' W). The study site is situated at 1400 m elevation in tropical lower montane forest (Grubb, 1977). Annual precipitation at a nearby meteorological

station (< 10 km) averaged 3198 mm (INHERI, 1987). On-site precipitation from 1994 to 1996, averaged 3630 mm y⁻¹. A dry period occurs during August and September, when monthly rainfall is less than 100 mm. Daily minimum and maximum air temperature average 17–26°C with little seasonal change.

Montane soils of northwestern Ecuador are formed on andesitic ash and pumice deposits (Clapperton, 1993). In the Maquipucuna forest reserve, the top 75–100 cm of soil formed from volcanic ash deposited 2500 y ago by the volcano, Pululagua (Papale and Rossi, 1993). Soil pH measured in 1 M NaF averages 10.9 in the top meter (Table 1), indicating the presence of allophane minerals (Fields and Perrott, 1966). Bulk density in mature forest averages 0.6 g cm⁻³ in field-moist soil sampled in the top 15 cm where gravimetric water content at 1.5 MPa is 19%. Soil texture estimated by the pipette method yields less than 10% clay. This contrasts with 22% clay estimated by hand and with 32% estimated from the relation (Soil Survey Staff, 1993)

$$2.5 \times (1.5 \text{ MPa moisture} - \text{Total soil carbon})$$

demonstrating the non-dispersive nature of the allophanic clay fraction. Surface soil reaction is strongly acid (Table 1). Labile soil phosphorus in the upper 15 cm average 8 and 15 µg P g⁻¹ for anion exchange resin and bicarbonate extractable forms, respectively.

Table 2
Forest structure and species diversity of trees of ≥5 cm diameter at breast height

Vegetation type	Replicate	Height (m)		Diameter (cm)		Basal area, (m ² ha ⁻¹)	Species per plot, (225 m ²)
		Max	Mean	Max	Mean		
Old-growth forest > 50 y	1	30	11	58.7	12.9	25.5	20
	2	22	9	23.8	10.2	10.2	15
Secondary forest 15–20 y	1	25	10	31.5	10.9	22.7	15
	2	28	14	29.5	12.8	18.0	8
Shrub regeneration 5–10 y	1	9	7	12.3	6.4	1.6	3
	2	2	4	17.7	7.2	6.8	3

The five vegetation types studied are dominant landscape features of the mid-elevation region of northwestern Ecuador. The vegetation types are interspersed across a 1 km² area of the Maquipucuna Reserve. We sampled two replicate patches of each vegetation type. Limited availability of undisturbed forest patches prevented further replication. Morphological and physical characteristics of the top 50 cm of soil indicate that all vegetation developed upon the same ash deposit (C. Rhoades, unpub. PhD thesis, University of Georgia, 1997). Replicated trials that monitor change following land conversion would require 5 to 10 y to provide conclusive results; in this study we take advantage of a series of existing land-use patches to gain an immediate estimate.

Old-growth forest replicates had been undisturbed for a minimum of 50 y, according to local residents (Table 2). Secondary forests were 15–20 y-old stands regenerating from abandoned cropland. Shrubby regrowth develops within 5 y of abandoning cropland or traditional pastures. The shrub communities are dense mixtures of remnants from previous production systems (*Musa paradisiaca* L., *Psidium guajava* L.) along with common successional shrubs (*Heliconia* spp., *Piper* spp., *Vernonia patens* H.B.K.). *Setaria sphacelata* pastures were hand-planted between 1980 and 1986, after clearing the forest and burning the brush. Traditional, mixed-species pastures (also established 1980 to 1986) contain both annual and perennial plants. Dominant grasses include *Digitaria sanguinalis* (L.) Scopoli, *Panicum polygonatum* Schrader and *Paspalum paniculatum* L.

2.2. Field and laboratory methodology

Net N mineralization and nitrification rates were measured using *in situ* incubations (Binkley and Hart, 1989). Seasonal comparisons of soil N availability were made under dry (September 1994) and wet (May 1995) season conditions. Soil incubation chambers consisted of 10 cm dia PVC tubes driven into the top 15 cm of mineral soil. Aboveground portions of vegetation were excluded from the chambers and plant roots were severed by core installation. Chambers were covered with loose fitting, aluminum foil-shielded caps that allowed gas movement, but prevented leaching. Within each tube, changes in inorganic-N content during the 14-d period represent net nitrogen mineralized from organic sources. Assuming no losses to leaching, plant uptake or gaseous N emissions, net mineralization and nitrification were calculated as follows (Hart et al., 1994):

$$\text{Net mineralization} = (\text{NH}_4^+ - \text{N} + \text{NO}_3^- - \text{N})_{t+1} \\ - (\text{NH}_4^+ - \text{N} + \text{NO}_3^- - \text{N})_t$$

$$\text{Net nitrification} = (\text{NO}_3^- - \text{N})_{t+1} - (\text{NO}_3^- - \text{N})_t$$

Initial and final soil NO₃⁻-N and NH₄⁺-N content for each incubation period were extracted from fresh soil within 12 h of sampling using 2 M KCl (10 g moist soil in 50 mL of extractant). Soil was stored in plastic coolers prior to extraction. Filtered extracts were frozen until colorimetric analysis (Perstorp Inc., Wilsonville, Oregon). Subsamples of soil were dried for 24 h at 105°C to determine gravimetric moisture content; both the initial and final inorganic-N concentrations are expressed on a dry-weight basis. To verify the relationship between soil N indices and plant N uptake, we carried out a 60-d bioassay with grain sorghum (*Sorghum bicolor*) grown in soil from the various vegetation types (0–15 cm depth; secondary forest was not included). Oven-dried, ground soil and plant samples were analyzed for total N and C using a Carlo Erba model 1500 CN analyzer (Carlo Erba Instruments, Milano, Italy). Bulk density was measured on intact soil cores (0–15 cm; *n* = 10 per vegetation replicate). Soil pH was measured in a 2:1 deionized water to air-dried soil suspension after 30 min of agitation. Field-moist pH was analyzed on a subset of samples. Fine roots (≤ 2 mm) were hand-sorted from six 10 cm dia soil cores for the 0–15 cm depth per replicate. Water-filled pore space (WFPS), synonymous with relative saturation (Linn and Doran, 1984) was calculated as follows:

$$\% \text{ WFPS} = (\theta_v / \text{TP}) \times 100$$

where θ_v = volumetric water content, TP = total porosity = (1 – Bulk Density/2.65).

In situ soil respiration was analyzed using static chambers and 0.5 M NaOH base traps during the 1995 wet season. The static chamber method integrates respiration from plant roots and soil microorganisms (Coleman and Sasson, 1978). Base traps were titrated to a phenolphthalein endpoint within 8 h of terminating the 24-h respiration assay (Zibilske, 1994).

Within each replicate of the five vegetation types, three 5 × 15 m blocks were established perpendicular to the slope. Sample locations were randomly selected within each block. Effects of vegetation type, vegetation replicate, block and season were tested on extractable soil N and net N transformations with repeated-measures, nested analysis of variance (SPSS Inc., 1997). Season was the within-subject factor; replicates were nested within vegetation types and blocks were nested within replicates. For each replicate of the five vegetation types, six mineralization incubations

Table 3

Soil N pools, net N transformations and water-filled pore space (WFPS) for wet and dry seasons (means with standard error of the mean in parentheses, $n = 6$)

Vegetation type	Replicate	Extractable soil N pools (kg N ha ⁻¹)				Net N transformations (kg N ha ⁻¹ 14 d ⁻¹)				WFPS (%)	
		NH ₄ ⁺ -N		NO ₃ ⁻ -N		Mineralization		Nitrification		Wet	Dry
		Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Mature forest	1	4.88 (0.3)	1.07 (0.1)	1.85 (0.3)	2.65 (0.7)	6.01 (0.8)	3.18 (1.1)	7.43 (0.9)	2.98 (1.0)	56.32 (3.5)	20.80 (0.5)
	2	2.06 (0.2)	1.00 (0.1)	2.53 (0.3)	3.92 (0.4)	8.98 (1.9)	5.87 (0.9)	9.38 (1.8)	5.88 (0.8)	55.98 (2.6)	24.03 (2.3)
Secondary forest	1	4.23 (0.6)	1.74 (0.6)	2.64 (0.5)	4.58 (0.5)	4.95 (0.6)	2.32 (0.9)	6.13 (0.5)	2.63 (0.9)	52.07 (3.9)	25.20 (1.1)
	2	2.76 (0.4)	1.58 (0.2)	2.76 (0.5)	3.49 (0.9)	10.32 (0.7)	3.75 (1.0)	10.50 (0.7)	4.25 (0.9)	58.33 (3.1)	31.87 (0.5)
Shrub regeneration	1	4.03 (0.8)	1.82 (0.4)	2.25 (0.1)	3.31 (0.2)	12.07 (1.6)	1.60 (0.4)	13.24 (2.0)	1.46 (0.5)	102.87 (6.1)	41.35 (1.1)
	2	5.05 (0.7)	2.10 (0.4)	2.36 (0.4)	1.84 (0.3)	4.41 (1.1)	4.40 (0.8)	5.01 (1.3)	2.78 (0.6)	76.47 (8.2)	33.28 (2.7)
<i>Setaria</i> pasture	1	4.64 (1.4)	1.68 (0.3)	0.78 (0.1)	0.35 (0.1)	-2.28 (1.1)	1.36 (0.4)	-0.61 (0.2)	0.54 (0.2)	78.13 (6.3)	43.82 (2.8)
	2	5.02 (0.9)	1.44 (0.4)	1.20 (0.1)	1.06 (0.1)	0.03 (1.4)	4.10 (0.8)	1.73 (0.7)	1.12 (0.4)	101.90 (5.0)	58.47 (3.8)
Mixed pasture	1	4.60 (0.8)	0.55 (0.2)	3.00 (0.6)	1.77 (0.3)	10.04 (4.8)	4.11 (0.8)	9.90 (4.5)	2.62 (0.8)	100.00 (7.7)	36.42 (5.6)
	2	3.95 (0.4)	1.69 (0.5)	2.76 (0.2)	0.80 (0.2)	16.41 (1.6)	5.03 (1.8)	17.62 (1.8)	3.29 (1.5)	74.19 (3.3)	37.92 (4.2)

were deployed during wet and dry seasons. Soil respiration, total soil C and N pools, and fine root biomass were analyzed with a simple, nested analysis of variance. Relationships between N variables and other soil properties were compared using linear regression (SPSS Inc., 1997).

3. Results

Soil NH₄⁺-N did not vary among vegetation classes, but declined nearly three-fold during the dry season (Tables 3 and 4). Extractable soil NO₃⁻-N was uniform across vegetation with the exception of *Setaria* pasture, where it decreased to 25–40% of the dry and wet season averages of the other vegetation types (Table 3). Soil NO₃⁻-N increased in the dry season beneath forest,

decreased under pasture and varied beneath shrub vegetation.

Vegetation and seasonal effects on net mineralization and nitrification rates agreed with patterns of soil NO₃⁻-N (Table 3). Net N transformations were substantially lower in *Setaria* pastures than in other land-use classes (Tables 3 and 4). Mineralization rates were -2–0 kg N ha⁻¹ during wet season incubations in *Setaria* soils, compared to an average of 9 kg N ha⁻¹ for the other vegetation types. Wet and dry season nitrification rates in *Setaria* pastures were 6 and 24%, respectively, of those measured under all other vegetation classes. In forest sites, nitrification rates doubled from 4 to 8 kg N ha⁻¹ 14 d⁻¹ during the dry and wet seasons, respectively. Nitrification increased nearly five-fold during the wet season beneath mixed-species pasture. There was no seasonal change in nitrification beneath *Setaria*. Similarity between mineraliz-

Table 4

F-ratios and significance levels for repeated measures; season was the within-subject factor; *, **, *** significant at the 0.05, 0.01, and 0.001 probability levels, respectively

Sources	Extractable N pools			Net N transformations		WFPS
	NH ₄ ⁺ -N	NO ₃ ⁻ -N	Sum	Mineralization	Nitrification	
Between subject						
Vegetation	1.99	23.87***	3.82**	15.92***	16.71***	52.30***
Replicate (Vegetation)	2.01	3.94**	0.82	3.14*	4.53**	14.28***
Block (Replicate)	0.92	5.60***	2.02	1.61	1.79	4.70**
Within subject						
Season	115.21***	0.81	50.58***	27.36***	73.60***	491.23***
Season × Vegetation	1.10	8.40***	4.71**	9.49***	8.73***	7.09***
Season × Replicate (Vegetation)	1.92	1.35	1.75	4.51**	5.03**	3.21*
Season × Block (Replicate)	0.81	1.10	1.23	2.82*	2.17	1.78

ation and nitrification rates indicates that N generated by mineralization is rapidly nitrified beneath forest and secondary vegetation. Negative wet-season net transformation rates below *Setaria* probably resulted from microbial immobilization of inorganic soil N.

Soil NO_3^- -N and net nitrification rates were well correlated to the tissue N content of bioassay-grown sorghum (Fig. 1). Leaf N concentration was 40% higher for sorghum grown in forest versus *Setaria* soil. Sorghum leaf N was similar for plants grown in mixed-species pasture and shrub soil.

Soil bulk density increased from 0.6 g cm^{-3} in mature and second-growth forest to $0.8\text{--}0.9 \text{ g cm}^{-3}$ under both pasture types and shrub regeneration (Table 5). Water-filled pore space (WFPS) ranged from 21% during the dry season to 100% during the wet season (Table 3). Both types of pasture had higher WFPS than forests during both seasons ($P < 0.05$); WFPS was 1.7 and 2.5 times greater in *Setaria* pasture than in mature forest during wet and dry seasons. Shrub regeneration had WFPS similar to the pastures. Soil pH in water ranged from 5.4 to 4.8 across vegetation classes (Table 5). There were larger differences in soil pH between replicates than between vegetation types (Table 5). Field-moist soils were consistently 0.5 pH units higher than air dry samples.

S. spachelata is a tussock-forming grass with a very dense root mat near the soil surface. Fine root biomass was three- and five-fold greater in *Setaria* pasture than in mature forest and mixed-species pasture (Table 5).

Wet season soil respiration increased nearly two-fold, from 14 to $26 \text{ kg C ha}^{-1} \text{ d}^{-1}$ between mature forest and *Setaria* pasture (Table 5). For the upper 15 cm depth, total soil C and N pools did not differ significantly between vegetation classes (Table 5).

4. Discussion

4.1. Tropical montane forest N transformations

Nitrogen cycling in Ecuadorian montane forest (1400 m) is consistent with other tropical sites at equal elevation on similar-age volcanic material. For our 2000 y-old tephra-derived soil, net mineralization in mature forests averaged 1.1 and $0.6 \mu\text{g N g}^{-1} \text{ d}^{-1}$ during the wet and dry seasons, respectively. In Hawaiian montane forest (1200–1300 m) along an volcanic ash age-sequence, Riley and Vitousek (1995) and Vitousek and Matson (1988) found that N transformations increased with substrate age. Daily net mineralization rates measured during 30-d incubations increased from $0.13 \mu\text{g N g}^{-1}$ on 1000 y-old tephra to $2.7 \mu\text{g N g}^{-1} \text{ d}^{-1}$ on 4000 y-old tephra (Vitousek et al., 1983). At 1500 m on volcanic soils in Costa Rica, Marrs et al. (1988) found net mineralization rates of $0.4 \mu\text{g N g}^{-1} \text{ d}^{-1}$.

Table 5

Soil pH_{water} , bulk density, fine root biomass, C and N stocks (0–15 cm) and soil respiration for forest, pasture and second-growth vegetation (mean and standard error of the mean); *, **, *** significant at the 0.05, 0.01, and 0.001 probability levels, respectively

Vegetation type	Replicate	$\text{pH}_{\text{w}}, 2:1$		Bulk density, (g cm^{-3})		Fine root biomass, (Mg ha^{-1})		Soil respiration, ($\text{kg CO}_2\text{-C ha}^{-1} \text{ d}^{-1}$)		C stock, (Mg ha^{-1})		N stock, (Mg ha^{-1})	
Mature forest	1	5.4	0.2	0.62	0.1	6.80	1.5	13.50	1.9	65.39	10.1	5.51	1.0
	2	4.9	0.2	0.60	0.0	3.79	0.7	15.64	1.9	56.21	4.9	4.98	0.4
Secondary forest	1	5.4	0.1	0.64	0.0	3.70	0.5	18.84	1.2	81.27	5.1	6.87	0.4
	2	4.8	0.1	0.74	0.0	6.02	0.4	21.16	1.6	58.03	2.3	5.28	0.1
Shrub regeneration	1	4.9	0.0	1.01	0.1	3.19	0.5	22.67	0.9	71.99	7.4	6.26	0.5
	2	5.3	0.1	0.82	0.0	3.58	1.2	20.84	1.3	73.99	10.3	6.40	0.9
<i>Setaria</i> pasture	1	5.1	0.1	0.71	0.0	14.46	4.8	29.05	2.0	61.09	4.0	5.39	0.3
	2	5.1	1.0	0.87	0.0	17.29	6.3	23.88	1.0	62.82	4.0	5.69	0.3
Mixed pasture	1	5.0	0.0	0.84	0.0	2.92	1.4	25.33	2.2	73.00	10.6	6.55	0.8
	2	4.9	0.1	0.86	0.0	3.71	1.6	23.84	2.2	64.45	4.8	5.64	0.4
ANOVA F-statistic													
Source													
Vegetation		0.67		17.45***		8.19***		14.73***		1.15		1.20	
Replicate (Vegetation)		7.18***		4.02**		0.65		1.47		1.42		1.08	

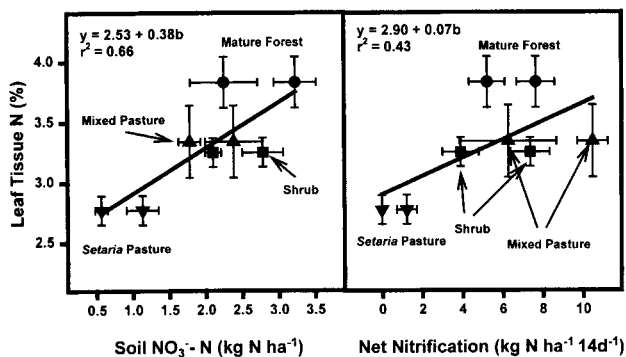


Fig. 1. Relationship between sorghum leaf N concentration and soil nitrate and net nitrification for combined wet and dry seasons. Sorghum was harvested after 60 d growing in *Setaria*, mixed-species pasture, shrub regeneration and mature forest soils (second-growth forest was not included). Points are means for each vegetation replicate; bars are 1 SE of the mean ($n = 5$ per replicate for bioassay data and $n = 12$ per replicate for soil N data).

4.2. Influence of *Setaria* pasture on soil N transformations

Conversion to *Setaria* pasture considerably alters soil N transformations. Similar to conversion of lowland tropical forest to pasture, establishment of *Setaria* pasture reduces soil NO_3^- -N and decreases net nitrification and mineralization rates (Piccolo et al., 1994; Reiners et al., 1994; Neill et al., 1995; Johnson and Wedin, 1997). We measured 70 and 87% reductions in soil NO_3^- -N pools and net mineralization rates in *Setaria* pastures relative to undisturbed forest. Amazonian *Brachiaria brizantha* and *Panicum maximum* pastures reduced soil NO_3^- -N and net mineralization to the same degree (Neill et al., 1995). Reiners et al. (1994) measured 60 and 40% reductions in NO_3^- -N and net mineralization in Costa Rican, *Ischaemum indicum* pastures. Similar to our Ecuadorian site, the large drop in N availability and production of inorganic N after conversion to pasture occurred without change in total C and N pools (Buschbacher et al., 1988; Piccolo et al., 1994).

Lowland tropical forest-pasture comparisons have shown that in forest the majority of the inorganic soil N pool consists of NO_3^- -N, whereas pasture soils contain more NH_4^+ -N (Keller and Reiners, 1994; Piccolo et al., 1994; Neill et al., 1995). Soil NH_4^+ -N represented 66% in active pasture versus 23% in Costa Rican mature forest (Keller and Reiners, 1994). In Ecuadorian *Setaria* pastures, 77% of the total inorganic-N was NH_4^+ -N, compared to 42% in mature forest sites.

4.3. Sources of the *Setaria* pasture effect

The pattern of decreased N transformations after forest clearing and conversion to pasture is consistent

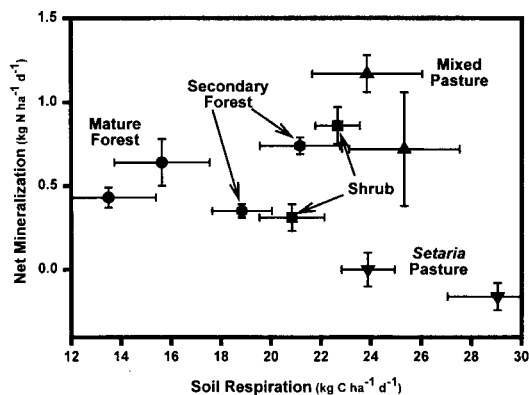


Fig. 2. Daily net mineralization and soil respiration during the 1995 wet season for two replicates of five vegetation types (mean \pm 1 SE).

with other tropical sites (Reiners et al., 1994; Neill et al., 1995) with notable exceptions (Montagnini and Buschbacher, 1989; Matson et al., 1990). Decreased soil N availability and N transformation rates have been attributed to chemical and physical conditions that restrict the activity of soil microbes that regulate soil organic matter turnover. In general, soil moisture, aeration, temperature, pH and NH_4^+ -N content (Paul and Clark, 1989) control nitrification. Soil pH, temperature and NH_4^+ -N did not vary significantly between the vegetation types we studied, so were not responsible for changes in nitrification. Lower net mineralization and nitrification rates may also result from high rates of microbial immobilization.

Soil compaction and waterlogged conditions following conversion to pasture produce conditions that may retard soil N transformations. Animal traffic in pastures increases bulk density and WFPS (Keller and Reiners, 1994) while reducing porosity (Spaans et al., 1989; Wielemaker and Lansu, 1991). For many non-volcanic soils, nitrification increases with soil moisture to a maximum at 60% WFPS (Linn and Doran, 1984). Beyond that point, anaerobic conditions slow nitrifiers and enhance denitrifier activity and nitrous oxide production. Because of their unique mineralogy and physical properties, volcanic soils continue to produce NO_3^- -N at WFPS above 80% (Doran et al., 1990). While bulk density and WFPS increased significantly under both *Setaria* and mixed-species pastures (Table 5), soil N characteristics differed considerably between the two pasture types. In spite of high wet season WFPS (87%), net mineralization and nitrification in the mixed-species pasture proceeded at a rate similar to mature forest. Soil N transformations in mixed-species pasture, forest and shrub sites all responded positively to increased soil moisture during the wet season. Conversely, seasonal change in WFPS had no effect on soil N transformations in *Setaria* pasture. While conversion to pasture increased soil com-

paction and moisture content, these changes favored rapid soil N transformations in one pasture type and had no effect in the other type.

Uptake of N by graminoids is much higher than by woody vegetation. For dense-rooted pastures, N uptake can exceed $500 \text{ kg N ha}^{-1} \text{ y}^{-1}$ (Whitehead, 1995). Annual net mineralization, estimated from wet (10 months) and dry (2 months) season averages, generates a maximum of $340 \text{ kg N ha}^{-1} \text{ y}^{-1}$ for any vegetation class in this study. Soil NO_3^- -N and net nitrification were inversely related to root biomass across our land-use types (Pearson $R = -0.87$; $P = 0.001$ and $R = -0.69$; $P = 0.026$). However, within our *in situ* incubation chambers, root N uptake is eliminated such that mineral N production is not influenced by N uptake in *Setaria* pasture soils. The sorghum bioassay verified that in sieved, root-free soil, plant available soil N was significantly lower in *Setaria* soils compared to mature forest (ANOVA $P < 0.03$; Fig. 1).

Soil microbe mediated N and C mineralization are typically positively correlated (Franzuebbers et al., 1996). We found no such pattern across vegetation types. Regarding mature forest and *Setaria* pasture, increased respiration corresponded with decreased net N mineralization (Fig. 2). Low net N mineralization, coupled with high C efflux in the *Setaria* pastures suggests that the soil microbial community is actively immobilizing inorganic N into microbial biomass. Negative mineralization and nitrification rates in the *Setaria* pasture during the wet season (Table 3) also support this conclusion. The high root biomass in the *Setaria* pastures probably produces sufficient labile C, through root exudates and turnover to support an aggressive immobilizer community. Microbial biomass C contained in root-free soil (substrate induced respiration method; West and Sparling, 1986) was 2.6 times higher for *Setaria* than mature forest and was highly correlated with static chamber C efflux ($r^2 = 0.74$; C. Ettema, unpublished data). Comparing grasslands and forest, Sparling et al. (1994) found that microbial biomass C and N were 1.3 and 2.0 times higher in New Zealand pastures. Hart et al. (1993) also measured higher rates of N immobilization in California grassland relative to forest. Across a series of tropical forest soils, Vitousek and Matson (1988) found the highest rates of N immobilization and amounts of microbial biomass N in volcanically-derived montane forest soils.

4.4. Land conversion and soil N cycling in Northwestern Ecuador

Setaria pasture was the only land-use type that deviated significantly and consistently from undisturbed lower montane forest. In second-growth forest and shrub regeneration, variability between vegetation

replicates was high, yet N transformations were generally close to that of native forest and often higher. These similarities in soil N processes occurred in spite of large differences in stand structure and species diversity (Table 2). The increased bulk density that occurred during agricultural land use recovers more gradually, but returns to original amounts after two decades beneath second-growth vegetation.

Large differences between mixed-species and *Setaria* pastures demonstrate species-specific controls on soil nutrient and plant community dynamics. *Setaria*'s extremely dense root system not only alters soil N processes, but it also inhibits pasture colonization by woody vegetation. *Setaria* roots form both a physical barrier against seed establishment within pastures and also a competitive obstacle that limits soil resource availability to other plants. Conversely, mixed-species pasture has fewer roots and higher soil N availability and is more prone to woody plant invasion. The current advance of pasture production in mid-elevation areas of northwestern Ecuador is extending the range of *S. sphacelata*. While traditional pasture has little effect on soil N transformations and the effects of other agricultural practices diminish rapidly beneath second-growth vegetation, continued *Setaria* expansion will affect long-term pasture productivity and subsequent forest regeneration in abandoned pasture.

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References

- Binkley, D., Hart, S.C., 1989. The components of nitrogen availability assessments in forest soils. *Advances in Soil Sciences* 10, 57–112.
- Buschbacher, R., Uhl, C., Serrao, E.A.S., 1988. Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. *Journal of Ecology* 76, 682–699.
- Clapperton, C., 1993. *Quaternary Geology and Geomorphology of South America*. Elsevier, Amsterdam.
- Coleman, D.C., Sasson, A., 1978. Decomposer subsystem. In: Breyer, A.J., Van Dyne, G.M. (Eds.), *Grasslands, Systems*

- Analysis and Man, International Biological Programme 19. Cambridge University Press, pp. 609–655.
- Doran, J.W., Mielke, L.N., Power, J.F., 1990. Microbial activity as regulated by soil water-filled pore space. In: Transactions 14th International, Congress of Soil Science, Kyoto, Japan, pp. 94–99.
- Fields, M., Perrott, K.W., 1966. The nature of allophane in soils. Part 3. Rapid field and laboratory test for allophane. *New Zealand Journal of Soil Science* 9, 623–629.
- Franzuebbers, A.J., Haney, R.L., Hons, F.M., Zuberer, D.A., 1996. Determination of microbial biomass and nitrogen mineralization following rewetting of dried soil. *Soil Science Society of America Journal* 60, 1133–1139.
- Grubb, P.J., 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Review of Ecology and Systematics* 8, 83–107.
- Hart, S.C., Firestone, M.K., Paul, E.A., Smith, J.L., 1993. Flow and rate of soil nitrogen in an annual grassland and a young mixed-conifer forest. *Soil Biology & Biochemistry* 25, 431–442.
- Hart, S.C., Stark, J.M., Davidson, E.A., Firestone, M.K., 1994. Nitrogen mineralization, immobilization, and nitrification. In: Weaver, R.W., Angle, J.S., Bottomley, P.S. (Eds.), *Methods of Soil Analysis, Part 2. Microbial and Biochemical Properties*. Soil Science Society of America, Madison, pp. 985–1018.
- Houghton, R., Lefkowitz, D., Skole, D., 1991. Changes in the landscape of Latin America between 1850 and 1985. I. Progressive loss of forests. *Forest Ecology and Management* 38, 143–172.
- INHERI 1987 Reporte hidrológico. Instituto Ecuatoriano de Recursos Hidráulicos, Quito, Ecuador.
- Johnson, N.C., Wedin, D.A., 1997. Soil carbon, nutrients, and mycorrhizae during conversion of dry tropical forest to grassland. *Ecological Applications* 7, 171–182.
- Keller, M., Reiners, W.A., 1994. Soil-atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica. *Global Biogeochemical Cycles* 8, 399–409.
- Linn, D.M., Doran, J.W., 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soils. *Soil Science Society of America Journal* 48, 1267–1272.
- Marrs, R.H., Proctor, J., Heaney, A., Mountford, M.D., 1988. Changes in soil nitrogen-mineralization and nitrification along an altitudinal transect in tropical rain forest in Costa Rica. *Journal of Ecology* 76, 466–482.
- Matson, P.A., Vitousek, P.M., Livingston, G.F., Swamberg, N.A., 1990. Sources of variation in nitrous oxide flux from Amazonian ecosystems. *Journal of Geophysical Research* 95, 16,789–16,798.
- Montagnini, F., Buschbacher, R., 1989. Nitrification rates in two undisturbed tropical rain forests and three slash-and-burn sites of the Venezuelan Amazon. *Biotropica* 21, 9–14.
- Neill, C., Piccolo, M.A., Steudler, P.A., Melillo, J.M., Feigl, B.J., Cerri, C.C., 1995. Nitrogen dynamics in soils of forests and active pastures in the western Brazilian Amazon Basin. *Soil Biology & Biochemistry* 27, 1167–1175.
- Papale, P., Rossi, M., 1993. A case of no-wind plinian fallout at Pululagua caldera (Ecuador): implications for models of clast dispersal. *Bulletin of Volcanology* 55, 523–535.
- Paul, E.A., Clark, F.E., 1989. *Soil Microbiology and Biochemistry*. Academic Press, San Diego.
- Piccolo, M.A., 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.
- Reiners, W.A., Bouwman, A.F., Parsons, W.F.J., Keller, M., 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. *Ecological Applications* 4, 363–377.
- Riley, R.H., Vitousek, P.M., 1995. Nutrient dynamics and nitrogen trace gas flux during ecosystem development in montane rain forest. *Ecology* 76, 292–304.
- Shoji, S., Nanzyo, M., Dahlgren, R., 1993. *Volcanic Ash Soils*. Elsevier, Amsterdam.
- Soil Survey Staff 1993 Keys to soil taxonomy. 5th ed. Soil Management Support Serv. Tech. Monogr. no. 19. Pochahontas Press, Blacksburg, VA.
- Spaans, E.J.A., Baltissen, G.A.M., Bouma, J., Miedema, R., Lansu, A.L.E., Schoonerbeek, D., Weilemaker, W.G., 1989. Changes in physical properties of young and old volcanic surface soils in Costa Rica after clearing of tropical rain forest. *Hydrological Processes* 3, 383–392.
- Sparling, G.P., Hart, P.B.S., August, J.A., Leslie, D.M., 1994. A comparison of soil and microbial carbon, nitrogen, and phosphorus contents, and macro-aggregate stability of a soil under native forest and after clearance for pastures and plantation forest. *Biology and Fertility of Soils* 17, 91–100.
- SPSS Inc 1997 SPSS for Windows, Version 8.0, Chicago, IL.
- Tanner, E.V.J., Vitousek, P.M., Cuevas, E., 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79, 10–22.
- Vitousek, P.M., Van Cleve, K., Balakrishnan, N., Mueller-Dombois, D., 1983. Soil development and nitrogen turnover in montane rainforest soils in Hawai'i. *Biotropica* 15, 268–274.
- Vitousek, P.M., Matson, P.A., 1988. Nitrogen transformations in a range of tropical forest soils. *Soil Biology & 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.
- West, A.W., Sparling, G.P., 1986. Modifications to the substrate-induced respiration method to permit measurement of microbial biomass in soils of differing water contents. *Journal of Microbiological Methods* 5, 177–189.
- Whitehead, D.C., 1995. *Grassland Nitrogen*. CAB International, Wallingford, UK.
- Wielemaker, W.G., Lansu, A.L.E., 1991. Land-use changes affecting classification of a Costa Rican soil. *Soil Science Society of America Journal* 55, 1621–1624.
- Zibilske, L.M., 1994. Carbon mineralization. In: Weaver, R.W., Angle, J.S., Bottomley, P.S. (Eds.), *Methods of Soil Analysis, Part 2. Microbial and Biochemical Properties*. Soil Science Society of America, Madison, WI, pp. 835–863.