

# Effect of Pasture Trees on Soil Nitrogen and Organic Matter: Implications for Tropical Montane Forest Restoration

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## Abstract

In lower-montane ecosystems of Ecuador, *Setaria sphacelata* (foxtail grass), the predominant introduced pasture species, forms a tussock grassland that reduces soil nitrogen and resists recolonization of forest vegetation. We compared the influence of individual trees or small clusters of nitrogen-fixing (*Inga* sp., Fabaceae) and non-nitrogen-fixing trees (*Psidium guajava* L., guava) on the soil and abiotic conditions that affect further regeneration of forest vegetation within pastures. Pasture trees ameliorated air temperature and light intensity to levels similar to those in adjacent intact forest. Beneath *Inga*, soil  $\text{NO}_3^-$ -N was four times higher than in open pasture. Nitrification was five times higher under *Inga* canopies than in open pastures for both field and laboratory incubations. This suggests that the increased soil N transformations under *Inga* are derived mainly from improved soil rather than microenvironmental conditions. *Psidium* canopies slightly increased field nitrification but had no effect under laboratory conditions. We also compared the natural abundance  $^{13}\text{C}$  signature and

the carbon and nitrogen content of subcanopy soil with adjacent open pasture soil. *Inga* increased the C and N content of the upper 5 cm of soil and increased by 7% the fraction of soil organic matter derived from  $\text{C}_3$  plants. The improved soil and abiotic conditions beneath the canopies of N-fixing pasture trees favor the establishment and growth of woody montane species, suggesting that these trees could be used to accelerate forest regeneration within abandoned pastures.

## Introduction

Conversion of forest into pasture is responsible for 75% of the tropical forest cleared annually (Uhl et al. 1988; Myers 1991). In the face of continuing deforestation, concern over managing tropical biodiversity and ecosystem function has shifted from strict forest protection toward restoration of cleared areas by expanding forest remnants. The majority of research on land degradation following deforestation and on the role of forest patches and fragments in forest restoration has been conducted in lowland tropics (Guevara et al. 1986; Uhl et al. 1988; Nepstad et al. 1990, 1996b). Neotropical montane ecosystems are similarly imperiled by anthropogenic disturbance (Kattan & Alvarez-López 1996), where planted pastures have become the predominant land-use type (Aide & Cavellier 1994). In this tropical ecoregion, little information exists about the influence of pasture conversion on ecosystem processes or on pathways of forest restoration.

Restoration of forest in areas converted to pasture is complicated by multiple factors (Nepstad et al. 1990, 1996a; Aide et al. 1995). In lowland tropics, pastures are established on large tracts of cleared forest, grazed until soil fertility is depleted, and then abandoned (Serrão & Toledo 1990). In the typically large lowland pastures (10–100 ha), low rates of seed dispersal into pastures, along with harsh abiotic conditions (intense light and water stress) and seed and seedling predation, limit recolonization rates of woody plants. Reduced soil fertility in pastures and competition with dominant herbaceous vegetation further reduces the potential for woody vegetation to recolonize pastures (Aide et al. 1995). In montane landscapes, where rugged topography limits the extent of pastures (<5 ha), seed dispersal into the interior of the pasture is less of a constraint to forest regeneration than are soil conditions and competition within the pasture. *Setaria sphacelata* ([Schumach.] Stapf & C. E. Hubb, foxtail grass), the dominant pasture grass in the montane region of northwestern Ecuador, reduces the availability of soil nitrogen to less than 20% of that found in intact montane forest (C. C. Rhoades, unpublished data). Unlike other pasture types where invasion by weeds may halt grazing after a short period of time (Serrão & Toledo 1990), *Setaria* pastures form a dense

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root mat that may deter establishment of other plant species.

In the Andes, incorporating scattered trees within pastures has been promoted as an agroforestry option to improve soil fertility and to provide shade for livestock and multiple products for rural households (Galloway 1986; Lojan-Idrobo 1992; Añazco-Romero 1996). From the standpoint of forest regeneration, trees dispersed within pastures provide improved microsites that may help forest seedlings overcome soil fertility and abiotic barriers to regeneration, as well as reduce competition from pasture grass. Shade beneath trees growing within tropical pastures has been shown to decrease grass growth by over 50% (Somarriba 1988). Attenuated light and lower heat load beneath tree canopies approximate microclimatic conditions of the forest interior that favor regeneration of forest species.

In *Setaria* pastures in the Ecuadorian Andes, seeds from trees with large, fleshy fruits are dispersed by livestock and become established. Our objective was to compare the impacts of nitrogen-fixing (*Inga* sp., Fabaceae) and non-nitrogen-fixing trees (*Psidium guajava*, guava) on available soil nitrogen and soil organic matter within monospecific *Setaria* pastures. The potential for improved soil and microenvironmental conditions beneath tree canopies has important implications for accelerating regeneration of montane forest.

## Methods

### Study Site

This research was carried out at the Maquipucuna Forest Reserve, located in the province of Pichincha on the west slope of the Ecuadorian Andes (0°5'N; 78°37'E). The study site is located in the ecotone between lower montane forest and cloud forest at an elevation of 1400 m. Long-term annual precipitation at a nearby meteorological station (<10 km from site) averaged 3198 mm (Instituto Ecuatoriano de Recursos Hidraulicos 1987). A dry period occurs during August and September, when rainfall is less than 100 mm per month. Daily minimum and maximum temperatures average 17° to 26°C, with little seasonal variation.

The soil is formed on a volcanic ash layer deposited 2500 years ago (Isaacson 1987; Papale & Rossi 1993). Soil reaction is strongly acid (pH in water = 5.3). Soil phosphorus averaged 8 and 15 µg P/g for anion exchange resin and bicarbonate extractable forms.

### Site Selection

We selected 10 *Inga* sp. and 5 *Psidium guajava* growing within a 3 ha *Setaria sphacelata* pasture (Table 1). The pasture was hand-planted in 1980 and had not been fer-

**Table 1.** Individual pasture and tree clump dimensions (mean and SE).\*

Tree Species	n	Canopy Height (m)	Main Bole Diameter (cm)	Stems Per Clump	Canopy Radius (m)	Canopy Area (m <sup>2</sup> )
<i>Inga</i>	10	6.54 (0.39)	11.24 (1.16)	2.64 (0.51)	3.36 (0.28)	36.82 (5.62)
<i>Psidium</i>	5	4.25 (0.32)	6.07 (.078)	9.80 (3.09)	2.99 (0.32)	29.31 (6.37)

\*Main bole diameter was measured 1.3 m above the ground. Stem count for stems over 2 cm in diameter.

tilized or weeded since that time. The density of scattered trees and groupings is approximately 30 trees/ha. *Inga* represented approximately 75% of pasture trees. All sample trees were located within a 2 ha pasture on similar soil and on a fairly uniform slope. Sample trees consisted of both solitary trees and multiple-stem clumps. Discrete, multiple-stem clumps were treated as single-canopy units. We measured the diameter of the largest stem of each tree and clump at 1.3 m. The radius of each canopy was averaged from four radial measurements.

### Field and Laboratory Methodology

Net nitrogen mineralization and nitrification were characterized with 14 day *in situ* incubations carried out in open pasture and beneath pasture tree canopies (Binkley & Hart 1989). Incubations were carried out in May 1995 under wet-season conditions. Soil incubation chambers consisted of PVC tubes 10 cm in diameter driven into the top 10 cm of mineral soil. Chambers were located randomly in open pasture, more than 10 m from the nearest tree canopy and were situated beneath pasture tree canopies, 1 m from the tree trunk. Chambers were covered with loose-fitting caps that allowed air circulation but prevented leaching losses. Caps were covered with aluminum foil to reduce heating within incubation chambers. Plant roots were severed when tubes were installed, so nitrogen loss to plant uptake is assumed to be negligible. Within each incubation tube, changes in inorganic N levels during the 14 day period represent net nitrogen mineralized from organic sources. Assuming no losses to leaching, plant uptake, or gaseous N losses, net mineralization and nitrification were calculated from the change in  $\text{NH}_4^+\text{-N}$  +  $\text{NO}_3^-\text{-N}$  and  $\text{NO}_3^-\text{-N}$ , during the incubation period, respectively (Hart et al. 1994).

Initial and final soil  $\text{NO}_3^-\text{-N}$  and  $\text{NH}_4^+\text{-N}$  content for each incubation period was extracted from fresh soil within 12 hours of sampling by means of 2 M KCl (10 g moist soil in 50 mL of extractant). Filtered extracts were frozen and stored until transport and colorimetric analysis at the University of Georgia on an Alpkem RFA-300 autoanalyzer. Subsamples of soil were dried at 105°C to

determine gravimetric moisture content; all results are expressed on a dry-weight basis. Both initial and final inorganic N concentrations were corrected for soil moisture content at the time of sampling.

To differentiate changes in soil N transformations resulting from modified soil conditions below tree canopies (e.g., effects on the content or quality of soil organic matter) from those relating to the ameliorated microenvironment (e.g., differences in moisture and temperature), we compared soil N transformations during *in situ* incubations, with results measured under controlled conditions in laboratory incubations. Field incubations integrate both substrate and tree effects on microenvironment, while laboratory incubations eliminate microenvironmental differences (Binkley & Hart 1989). Laboratory incubation was carried out at 21°C for 14 days. Soil moisture was initially adjusted to near field capacity and maintained by periodic watering throughout the incubation period.

A 60 day bioassay using *Sorghum bicolor* (grain sorghum) grown in sieved (2 cm mesh), field-moist soil sampled from open pasture and tree canopy sites was performed to verify that soil N indices correlate to plant N uptake. *Setaria* leaf samples from open pasture and the subcanopy zone of five *Inga* and *Psidium* were analyzed for tissue N concentration.

Bulk density was measured by calculating the oven-dry mass of intact soil cores (0–5 and 5–15 cm depths;  $n = 10$ ). Soil pH in water and 0.01 M CaCl<sub>2</sub> were measured in a 1:2 ratio of air-dried soil to water suspension after shaking for 30 minutes.

Tree canopy influence on soil CO<sub>2</sub> evolution was analyzed during the 1995 wet season with static chambers and 0.5 M NaOH base traps (Coleman & Sasson 1978; Zibilske 1994). The static chamber method integrates respiration from plants roots and soil microorganisms. Prior to their installation, all vegetation was clipped from the area encompassed by the chamber. Each PVC chamber (15 cm diameter) was covered with aluminum foil and inserted 2 cm into the soil to prevent gas leaks. Chambers were installed beneath each sample *Inga* ( $n = 10$ ) and *Psidium* ( $n = 5$ ) and in randomly selected open-pasture sites, more than 10 m from the nearest tree.

Litterfall was collected monthly from 0.25 m<sup>2</sup> traps placed below three *Inga* and three *Psidium* canopies (May to December 1996). Leaf litter was sorted from other fine litter (twigs, bark, seed pods) and dried for 48 hours at 55°C to determine monthly litter inputs. Samples of *Inga* and *Psidium* leaf litter were composited from the litter traps for further analysis. Senesced *Setaria* litter was composited from open pasture areas more than 10 m from the nearest tree. Prior to analysis, soil and litter and bioassay samples were oven-dried at 60°C and ground with a ball mill.

Total soil and plant tissue C and N content and natural abundance <sup>13</sup>C for the 0–5 and 5–15 cm soil depths

were determined by means of a Carlo Erba model 1500 CN analyzer interfaced with a Finnigan MAT Delta-S mass spectrometer. Carbon isotope results are expressed in  $\delta^{13}\text{C}$  notation relative to the international Pee Dee Belemnite CaCO<sub>3</sub> standard (Boutton 1991). The relative proportion of soil C originating from C<sub>3</sub> plants was calculated using the  $\delta^{13}\text{C}$  of the soil in open-pasture and tree-canopy sites, along with tree and pasture litter samples (Martin et al. 1990; Wolf et al. 1994). The proportion of soil carbon derived from the pasture trees was calculated as the difference in the residual forest-derived C (C<sub>3</sub>) in open pasture and the total C<sub>3</sub>-derived C beneath the tree crowns. The fraction of soil C derived from original forest and pasture trees (CC<sub>3</sub>) and from *Setaria* pasture (CC<sub>4</sub>) was calculated as follows (Nyberg & Högborg 1995):

$$C_t = CC_3 + CC_4;$$

$$CC_3 = (\delta^{13}C_t - \delta^{13}CC_4)/(\delta^{13}CC_3 - \delta^{13}CC_4); \text{ and}$$

$$CC_4 = (\delta^{13}C_t - \delta^{13}CC_3)/(\delta^{13}CC_4 - \delta^{13}CC_3)$$

where  $\delta^{13}C_t$  is the  $\delta$ -value of soil sampled in either open pasture or beneath tree canopies,  $\delta^{13}CC_4$  is the  $\delta$ -value of C<sub>4</sub> pasture litter inputs, and  $\delta^{13}CC_3$  is the  $\delta$ -value of C<sub>3</sub> tree litter inputs.

From May to December 1996, daily precipitation and throughfall were measured in open pasture, below the canopies of two *Inga*, and in nearby closed-canopy forest. Air and soil temperature was recorded monthly below *Inga* and *Psidium* crowns and in adjacent open pasture. Air temperature was recorded with mercury thermometers at 100, 50, and 0 cm above the soil surface; soil temperature was measured at 5 cm depth with stainless steel soil thermometers. Monthly temperature and light readings (selenium oxide sensor) were made during the same 2 hour period (1000 to 1200 hours). Light extinction by tree crowns was calculated by comparing the photon flux beneath tree canopies and in adjacent open pasture (1 m above ground).

## Results

### Site Conditions

*Inga* were taller and had larger stem and canopy diameters than *Psidium* (Table 1). On average, *Inga* had single stems or forked trunks, while *Psidium* grew in multi-stem clumps (up to 20 stems). The average diameter of the main *Inga* stem was 11.2 cm, 1.8 times larger than that measured in each *Psidium* clump. The canopy radius and area of the *Inga* sample trees (3.4 m and 36.8 m<sup>2</sup>) were 12% and 25% greater than those of the *Psidium* trees.

Air temperature in the shade of pasture trees was dramatically lower than that in open pasture on all dates during the 7 month sample period. The average daytime air temperature beneath *Inga* and *Psidium* canopies (100 and 50 cm above the ground) was 6°C lower than in open pasture (Fig. 1). Air temperature beneath pasture trees was 2.7°C higher than in nearby mature forest. Temperature at the soil surface did not vary between canopy or open sites. Average surface temperature was 17.1°C and ranged from 15.6 to 20.1 for all sites. Soil temperature beneath *Psidium* canopies was significantly higher ( $p < 0.0015$ ) than either *Inga* or open-pasture sites. Monthly precipitation in open-pasture sites was 295 mm (range: 41–722 mm). Throughfall under both *Inga* canopies and closed-canopy forest averaged 66% of total precipitation inputs. Light passing through *Inga* and *Psidium* canopies was 9% and 18% of the light intensity in open pasture. Closed-canopy forest extinguished all but 4% of the incident radiation.

Soil pH in both water and  $\text{CaCl}_2$  was similar beneath tree crowns and in open pasture. At the 0–5 cm depth, soil  $\text{pH}_{\text{water}}$  was 4.9 and 5.3 under *Inga* and *Psidium* crowns and 5.1 in open pasture ( $p = 0.1115$ ). Below *Inga*,  $\text{pH}_{\text{water}}$  increased to 5.0 at 5–15 cm, while it decreased to 4.8 and 5.0 below *Psidium* and in open pasture, respectively. In 0.01 M  $\text{CaCl}_2$ , pH was 0.3–0.5 units lower than the  $\text{pH}_{\text{water}}$  at both the 0–5 and 5–15 cm depths.

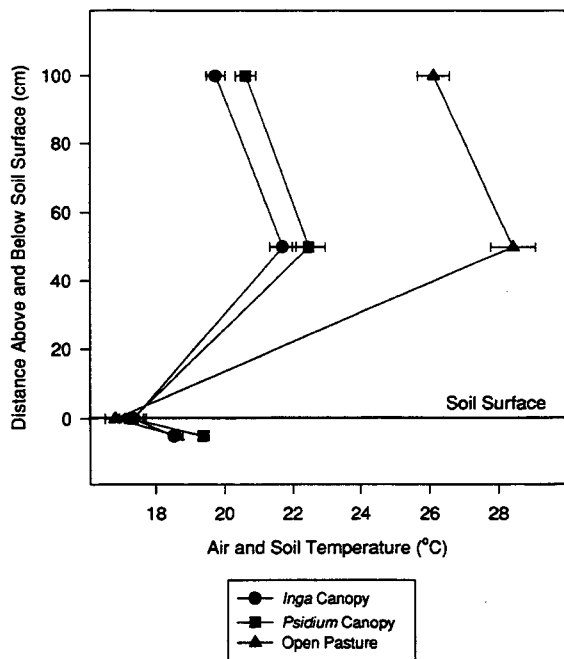


Figure 1. Air and soil temperature beneath tree canopies and in open pasture. Data are averages of monthly readings from May 1996 to January 1997 ( $\pm 1$  SE).

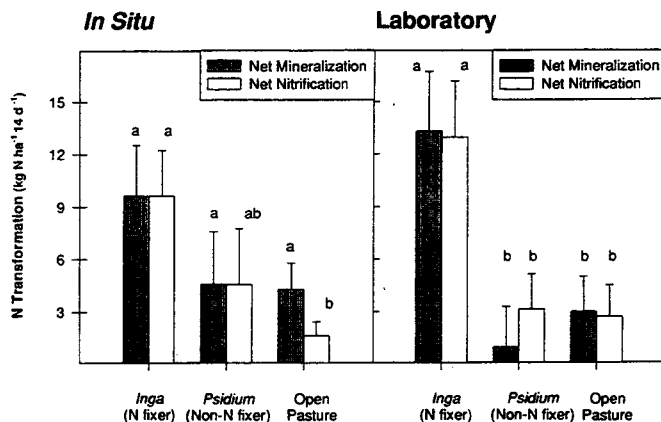


Figure 2. Net nitrogen transformation rates during 14 day *in situ* and laboratory incubations. Data show means and  $\pm 1$  SE. Bars with the same or no letter did not differ statistically according to a Tukey's means separation test (critical value = 0.05).

### Soil Nitrogen

Soil nitrogen availability was higher beneath the canopies of pasture trees than in open pasture. Extractable  $\text{NH}_4^+\text{-N}$  was 1.7 times higher in the subcanopy soil of both tree species than in adjacent *Setaria* pasture (Table 2). Under *Inga* canopies, extractable  $\text{NO}_3^-\text{-N}$  was 3.6 times higher than in open pasture (6.3 versus 1.7  $\mu\text{g N/g}$ ). *In situ* net nitrification beneath *Inga* crowns exceeded open-pasture rates more than six-fold (Fig. 2). Beneath non-nitrogen-fixing *Psidium*, neither nitrification rates nor the extractable  $\text{NO}_3^-\text{-N}$  pool were significantly greater than in open pasture. During both field and laboratory incubations, the net mineralization and nitrification rates were nearly identical, suggesting that most mineralized N was immediately nitrified. Neither soil respiration, soil moisture, nor soil temperature differed between tree canopy and open pasture soils under wet-season conditions (Table 2).

In laboratory incubations under uniform temperature and moisture conditions, the positive tree-canopy effect remained in the *Inga* soil but disappeared in the *Psidium* canopy soil. Net mineralization and nitrification rates below *Inga* were 14  $\mu\text{g N/g/14 days}$ , five times greater than in open pasture. The *Psidium* effect on *in situ* nitrification was absent during the laboratory incubation. This suggests that the effect of *Inga* on N availability is due to both improved substrate quality and ameliorated subcanopy microclimate, while any *Psidium* effect relates to improved subcanopy microsite.

Plant-tissue N concentration under both field and greenhouse conditions correlated well to net nitrification rates (Fig. 3). *In situ* and laboratory nitrification rates explained 90% to 97% of the variation in the tissue N concentration of *Sorghum* grown under greenhouse conditions and *Setaria* grown under tree canopies and

**Table 2.** Extractable soil nitrogen, soil respiration, soil moisture, and temperature (5 cm depth) beneath *Inga* and *Psidium* canopies and in open pasture (mean and SE).\*

Sample Location	Extractable Soil N		Soil Respiration (g CO <sub>2</sub> -C m <sup>-2</sup> /day)	Soil Moisture (%)	Soil Temperature (°C)
	NH <sub>4</sub> <sup>+</sup> -N	NO <sub>3</sub> <sup>-</sup> -N			
	(μg N/g)				
<i>Inga</i> Canopy (n = 10)	4.78 a (0.7)	6.30 a (1.2)	2.96 (0.3)	76.15 (6.1)	18.71 (0.2)
<i>Psidium</i> Canopy (n = 5)	4.93 a (0.7)	1.63 b (0.7)	2.79 (0.2)	64.32 (5.5)	19.32 (0.3)
<i>Setaria</i> Pasture (n = 15)	2.85 b (0.4)	1.74 b (0.8)	2.57 (0.2)	76.26 (7.6)	17.62 (0.3)
p =	0.0287	0.0033	0.4966	0.8018	0.1004

\*p values for one-way analysis of variance comparing tree canopy and open sites.

in open pasture. *Sorghum* grown for 60 days in soil sampled below *Inga* canopies absorbed twice as much N per unit biomass than when grown in open-pasture soil and 70% more than when grown in *Psidium* soil.

### Soil Organic Matter

Total soil N and C differed significantly in the 0–5 cm depth between *Inga* canopy and open-pasture sites (Fig. 4). Total C increased from 7.9% in the open pasture to 11.4% beneath *Inga* canopies ( $p = 0.0358$ ). *Psidium* did not increase soil C significantly above levels in open pasture. Soil C averaged 4.5% at the 5–15 cm depth and did not differ significantly among species or locations. The ratio of soil C:N averaged 12.4 and 11.9 in the 0–5 and 5–15 cm depths, respectively.

The  $\delta^{13}\text{C}$  value of the upper 15 cm of soil in undisturbed lower montane forest was  $-28.0\text{‰}$ . Forest soil is enriched by  $1.5\text{‰}$  (less negative) compared to forest litter inputs ( $-29.5\text{‰}$ ). In open *Setaria* pasture, aboveground

litter inputs have a  $\delta^{13}\text{C}$  value of  $-11.46$ , and soil C has a  $\delta^{13}\text{C}$  value of  $-22.2$  and  $-24.0\text{‰}$  in the 0–5 and 5–15 cm soil depths, respectively (Table 3). Fifteen years after the establishment of the *Setaria* pasture, residual C<sub>3</sub>-C con-

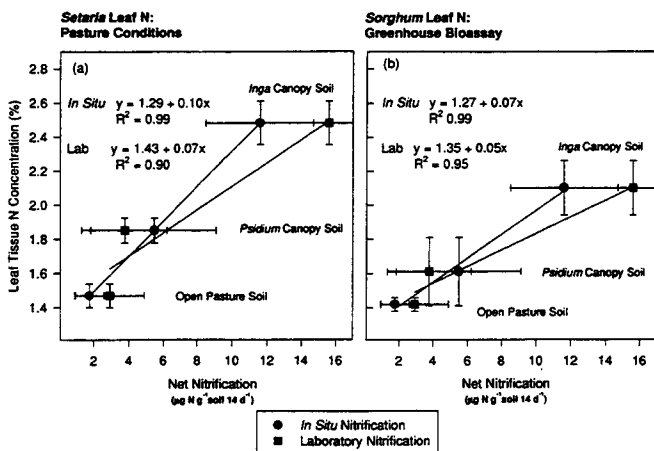


Figure 3. Correlation between net nitrogen mineralization and *Setaria* (a) and *Sorghum* leaf nitrogen concentration (b). Error bars are  $\pm 1$  SE of means.

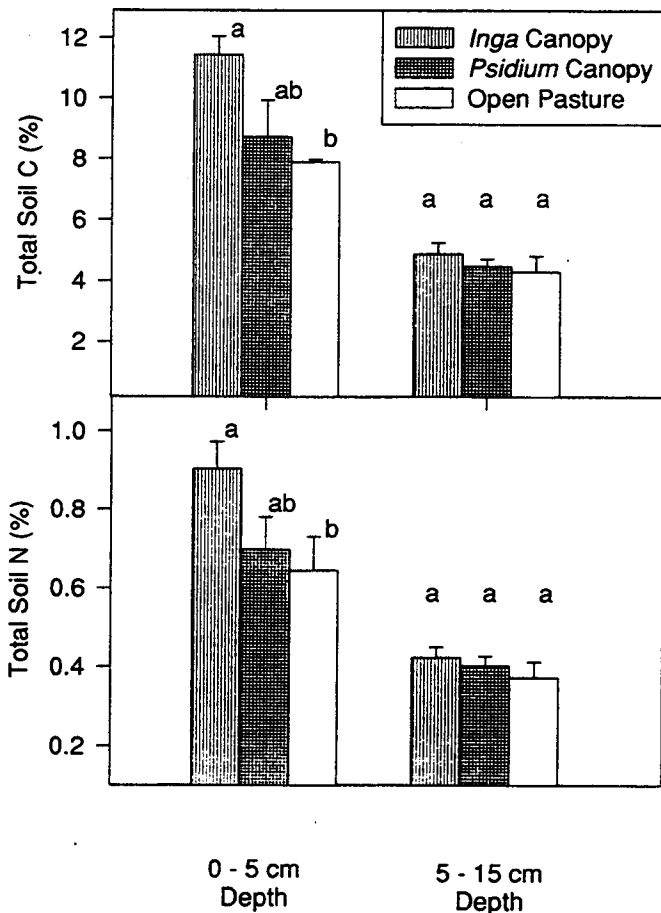


Figure 4. Total soil carbon and nitrogen beneath pasture tree and open pasture sites. Data show means and 1 SE of the mean. Bars with the same or no letter did not differ statistically according to a Tukey's means separation test (critical value = 0.05).

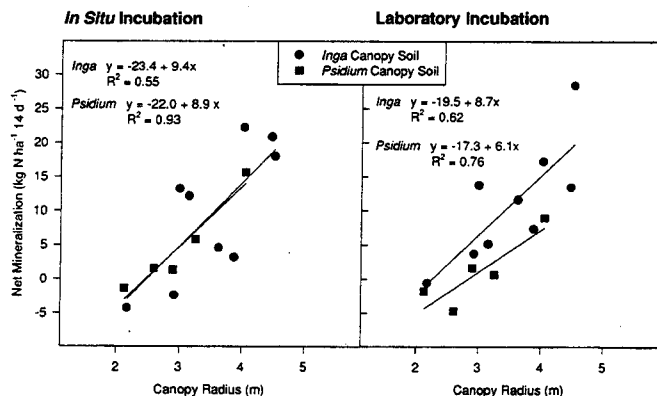


Figure 5. Net *in situ* and laboratory mineralization rates versus canopy radius.

tributes 68% and 81.5% of the total soil C in the upper 0–5 and 5–15 cm depths, respectively. Carbon inputs from pasture *Inga* increased the net proportion of  $C_3$ -C by an additional 7% in the upper 5 cm and by 1.3% in the 5–15 cm depth. This is equivalent to 16.5 Mg/ha of C added beneath *Inga* crowns over about a decade of growth. *Psidium* added an additional 2%  $C_3$ -C to the residual forest  $C_3$ -C measured in open pasture, equivalent to 4 Mg C/ha during that same period.

Average monthly leaf litter and C and N inputs were higher beneath *Inga* than under *Psidium* ( $p < 0.0030$ ). Monthly N inputs in leaf litter averaged 1.8 g/m<sup>2</sup> beneath *Inga* and 0.8 g/m<sup>2</sup> beneath *Psidium*. Respectively, *Inga* and *Psidium* recycled 21.5 and 9.5 g/m<sup>2</sup> of N and 5.6 and 4.5 t/ha of C in leaf litter annually. Leaf litter comprised 60–75% of the total litterfall beneath the pasture trees.

## Discussion

### Pasture Tree Effects

Within *Setaria* pasture, net soil nitrification rates varied from 0.1  $\mu\text{g N/g/day}$  in open pasture to 0.4 and 0.8  $\mu\text{g N/g/day}$

$\text{N/g/day}$  beneath non-nitrogen-fixing *Psidium* and nitrogen-fixing *Inga*, respectively. While *Setaria* pasture decreases soil N availability to 20% of that in intact forest soils, *Inga* return soils to pre-clearing levels. Net nitrification rates beneath *Inga* were comparable to rates measured in adjacent secondary forest (0.8  $\mu\text{g N/g/day}$ ; C. C. Rhoades, unpublished data). In a 4-year-old plantation on abandoned pastures in Costa Rica, net nitrification beneath nitrogen-fixing trees was significantly higher than beneath non-nitrogen-fixing trees and slightly higher than in open pasture (Montagnini & Sancho 1994). As in our montane site, soil N availability beneath trees established in lowland pastures was similar to levels in second-growth forest.

There are clear species-related differences in the pasture tree effect. Nitrification rates and  $\text{NO}_3^-$ -N levels were two and four times higher beneath nitrogen-fixing *Inga* than beneath non-nitrogen-fixing *Psidium*. Scattered nitrogen-fixing trees have been shown to have a positive influence on the availability of soil N in upper montane pastures in Colombia (Carlson & Dawson 1985), in semi-arid savannas (Belsky et al. 1989) and in wooded parklands (Rhoades 1995). Non- $\text{N}_2$ -fixing trees also increase soil N availability in montane grasslands of New Zealand (Davis 1995) and semi-arid environments (Bernhard-Reversat 1982; Belsky et al. 1989; Farrell 1990). The increase in soil  $\text{NH}_4^+$ -N beneath *Psidium* probably relates to the slight increase in total soil C and N reserves (Fig. 5) resulting from leaf litter and fruit drop. Besides differences between *Inga* and *Psidium* regarding N inputs via  $\text{N}_2$ -fixation, they may also differ in terms of quality of organic matter and rates of accumulation, N inputs in wet and dryfall, nutrient scavenging by tree roots below or beyond the tree canopy, and amelioration of the subcanopy microenvironment (Breman & Kessler 1995; Rhoades 1997).

In semi-arid environments, increased soil N transformations beneath scattered trees are related to improved soil moisture and reduced air and soil temperature fluctuation.

**Table 3.** The  $\delta^{13}\text{C}$  of soil and litter inputs and the proportion of total soil carbon stock derived from  $C_3$  and  $C_4$  plants in open *Setaria* pasture, beneath *Inga* and *Psidium* canopies and in mature forest.

Sample Location	Depth cm	Soil $\delta^{13}\text{C}$	Litter $\delta^{13}\text{C}$	Proportion of Soil C from		Contribution to Soil C Stock from		
				$C_3$ -C	$C_4$ -C	$C_3$ -C	$C_4$ -C	Total
				-----%-----		-----Mg C/ha-----		
<i>Setaria</i> pasture	0–5	–22.2	–11.5	68.0	32.0	18.7	8.8	27.6
	5–15	–24.0		81.5	18.5	33.7	7.7	41.4
<i>Inga</i> canopy	0–5	–23.3	–30.0	75.0	25.0	30.0	10.0	40.0
	5–15	–24.2		82.8	17.2	39.1	8.1	47.3
<i>Psidium</i> canopy	0–5	–22.8	–30.3	71.8	28.2	21.9	8.6	30.5
	5–15	–23.8		80.2	19.8	34.6	8.6	43.1
Mature forest	0–5	–27.6	–29.2	100.0	0.0	24.1	0.0	24.1
	5–15	–27.1		100.0	0.0	54.7	0.0	54.7

tuations in subcanopy environments (Dancette & Poullain 1969; Bernhard-Reversat 1982; Farrell 1990; Belsky 1994; Rhoades 1995). In the humid montane environment in Ecuador, pasture trees had no influence on soil moisture content (Table 2) or soil surface temperature (Fig. 1). In spite of the striking difference in subcanopy air temperature (Fig. 1), similarity between field and laboratory N transformation rates (Fig. 2) suggests that the ameliorated subcanopy microenvironment does not explain the pasture tree effect on soil N availability.

Nitrogen inputs in leaf litter beneath the nitrogen-fixing *Inga* were more than twice those under *Psidium* canopies or in adjacent forest. Both leaf N concentration and leaf litter biomass inputs were greater beneath *Inga*. High concentrations of secondary chemical compounds, such as lignin and polyphenolics, slow the breakdown of *Inga* litter (Palm & Sanchez 1989; Constantinides & Fownes 1994) and may explain the greater sequestration of soil organic matter (Yamoah et al. 1986; Kachaka et al. 1993).

Larger litter inputs beneath *Inga* integrate both differences in litter characteristics as well as larger canopy volume of the trees (Table 1). The greater height and radial extent of *Inga* canopies form a canopy that is more than twice the volume of the average *Psidium* clump or tree. In active pasture, fecal deposition beneath tree canopies by either roosting birds or livestock (Belsky et al. 1989; Davis 1995) seeking cover or canopy shade concentrates nutrients in the subcanopy environment. These inputs probably increase with size of the tree canopy.

Net nitrogen mineralization is closely related to the size of pasture tree canopies (Fig. 5). Canopy radius explains 55% and 93% of the variation in the *in situ* mineralization rates for both *Inga* and *Psidium*. The relationship between soil N availability and tree size remained constant when field and laboratory N fluxes for *Inga* were compared (slope: 9.4 and 8.7;  $r^2$ : 0.55 and 0.62 for *Inga* and *Psidium*, respectively). Slope and correlation declined slightly in laboratory incubations with soil from beneath *Psidium*, suggesting that microenvironmental factors partially contribute to the tree effect for this non-nitrogen-fixer. Bernhard-Reversat (1982) found that soil N increased linearly with tree girth for leguminous *Acacia senegal* and non-nitrogen-fixing *Balanites aegyptiaca* growing in semiarid west Africa. Using stem diameter as a surrogate for tree age, Bernhard-Reversat (1982) suggested that soil organic matter (SOM) and total N increase cumulatively throughout the life of the tree.

Soil organic matter was not as closely related to tree size as were soil N transformations. Variation in canopy radius and stem diameter explained only 22% and 46% of the differences in total soil C. For nitrogen-fixing *Inga*, SOM content did not correlate to either field or laboratory soil N transformations. Net mineralization and nitrification rates beneath *Psidium*, however, had a

close positive relation to SOM ( $r^2 = 0.654$  and  $0.734$ , respectively).

*Inga* and *Psidium* lowered soil  $^{13}\text{C}$  abundance of the upper 5 cm by 1.1 and 0.6  $\delta$  units, respectively, relative to open pasture. Nyberg and Högberg (1995) measured 0.5–1.0  $\delta$  unit decreases in soil beneath a variety of tree species growing in 4- to 5-year-old plantations in Kenya. One species, *Prosopis juliflora*, increased  $^{13}\text{C}$  abundance by about 1  $\delta$  unit due to greater production of a  $\text{C}_4$  grass beneath the tree canopy. In Tanzania, 8-year-old *Prosopis* trees contributed 11% of total soil C (Jonsson et al. 1996). Under the canopy of our Ecuadorian *Inga* trees, the combination of  $\text{C}_3$  tree-litter inputs along with the shade-induced decline in  $\text{C}_4$  grass explains the 7% difference in the proportion of soil C contributed by  $\text{C}_3$  plants. Soils under *Inga* trees contained 20 Mg C/ha more total soil C in the upper 15 cm than did open-pasture soils. The added  $\text{C}_3$ -C under the *Psidium* increased the C stock in the surface 15 cm to near original forest levels, while the C stock beneath *Inga* surpassed original forest levels by nearly 10 Mg C/ha.

#### Restoration Implications

Increased structural diversity in pastures containing scattered trees extends foraging, cover, and nesting habitat beyond the forest edge and into the pasture interior. Pasture trees both extend avenues of seed dispersal and enhance tree regeneration habitats within pastures. Research at our site has indicated that bird activity and seed inputs are greatest near forest edges and in pastures containing scattered trees (Sarmiento 1996). In Amazonian pastures, da Silva et al. (1996) found that bird activity was 20 times higher in pastures containing small trees and shrubs than in treeless pasture.

Beneath tree crowns, canopy shade favors the establishment of regenerating seedlings both by ameliorating abiotic conditions and by slowing the growth and competitive ability of pasture grass. In ongoing research at our site, G. Eckert (unpublished data) has measured over 90% survival of trees transplanted beneath pasture tree canopies, compared to near 100% mortality of exposed pasture plantings. Forest seedlings were unable to tolerate the high temperature and light of the open pasture, but they adapted well to conditions beneath tree crowns. Seedling transplant success was independent of pasture tree species, indicating the importance of physical shade from tree canopies in moderating abiotic extremes of open pasture. As forest seedlings develop, increased soil fertility beneath *Inga* canopies will provide better nitrogen nutrition, similar to conditions found in intact forest.

Efforts to restore tropical montane forest should exploit the advantages of locally common land-use practice. There are a variety of native, nitrogen-fixing species

(*Alnus jorullensis* H.B.K. [alder], *Erythrina megistophylla* Diels, and other *Erythrina* and *Inga* spp.) common to secondary forest and open pasture in the lower montane region of western Ecuador. The scattered-tree system may be intensified to varying degrees. Pasture trees may be hand-planted directly into pastures, as is currently promoted by Ecuadorian agroforestry projects (Galloway 1986; Añazco-Romero 1996), or seed dispersal may be encouraged by feeding tree fruits to livestock. Beneath established pasture trees, tree seeds or seedlings may be transplanted to accelerate the arrival of forest species within pasture. In the fragmented montane landscapes of Ecuador, trees scattered within active pastures may offer a simple and effective avenue to forest restoration. Further research of pasture trees may reveal combinations that both maximize soil improvement and seed dispersal into pastures.

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