LONG-TERM EFFECTS OF DEFORESTATION ON SOIL PROPERTIES AND VEGETATION IN A TROPICAL LOWLAND FOREST IN COLOMBIA.

EFECTOS DE LARGO PLAZO DE LA DEFORESTACIÓN EN LAS PROPIEDADES DE LOS SUELOS Y LA VEGETACIÓN EN UN BOSQUE DE TIERRAS BAJAS EN COLOMBIA.

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ABSTRACT

The effects of long-term deforestation on soil physical and chemical properties, grassland species composition, and seedling growth were studied in the Q. Yepes watershed in the Sierra Nevada de Santa Marta, Colombia. Deforestation since pre-Columbian times, and intensive grazing and use of fire since the arrival of the Spaniards, have caused severe soil degradation. Soil pits showed that surface erosion has removed approximately 50 cm of soil in areas currently covered by grasslands. The grassland soils have lower cation concentrations, higher levels of exchangeable Al, lower pH and lower carbon concentrations compared with soils in forest patches. Although soil particle size and extractable phosphorus (Bray II) were not significantly different between the two soil types, tree seedling growth of *Cochlospermum vitifolium* and *Ochroma pyramidale* in a pot experiment was greater in forest soils. Fires and heterogeneous soil fertility affected the biomass and diversity of grass species. Extractable phosphorus was positively related with biomass and negatively related with the number of grass species. Deforestation of tropical moist forest and the frequent use of fires have caused severe erosion, reduced fertility, and have led to the savannization of this area.

Key words: Deforestation, soil degradation, grasslands, seedling growth, grazing, Sierra Nevada de Santa Marta, Colombia

RESUMEN

Se estudiaron los efectos de la deforestación a largo plazo en las propiedades físicas y químicas del suelo, la composición de especies de los pastizales, y el crecimiento de plántulas en la cuenca de la Q. Yepes, Sierra Nevada de Santa Marta, Colombia. La deforestación desde tiempos precolombinos, el pastoreo intensivo y el uso del fuego desde la llegada de los españoles, han causado una severa degredación del suelo. Los perfiles de suelo mostraron que la erosión ha removido aproximadamente 50 cm de suelo en áreas actualmente cubiertas por pastizales. Los suelos de los pastizales tienen una concentración menor de cationes, altos niveles de Al intercambiable, bajo pH y baja concentración de carbono comparado con los suelos de los parches de bosque. Aunque el tamaño de las partículas de suelo y el fósforo extraible (Bray II) no fueron significativamente diferentes entre los dos tipos de suelo, el crecimiento de plántulas de *Cochlospermum vitifolium y Ochroma pyramidale* sembradas en bolsas fué mayor en suelo de bosque. El fuego y la fertilidad heterogénea del suelo afectaron la biomasa y la diversidad de gramíneas. El fósforo extraible fué positivamente relacionado con la biomasa y negativamente relacionado con el número de especies de gramíneas. La deforestación del bosque tropical húmedo y el uso frecuente del fuego han causado una severa erosión y reducción en la fertilidad, lo que ha conducido a la conversión de bosque húmedo a sabanas.

Palabras Clave: Desforestación, degradación de suelos, pastos, crecimiento de plántulas, pastoreo, Sierra Nevada de Santa Marta, Colombia

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INTRODUCTION

Although we know that deforestation causes the fragmentation of habitats (Harris 1984) and, in many cases, the loss of biological diversity (Wilson 1988), few studies have documented the recovery of soils and vegetation following disturbances of different intensities (Uhl et al. 1982, 1990, Uhl and Jordan 1984, Uhl 1987, 1988). In some cases, areas that have been abandoned return to forest, showing the resilience of certain forests to deforestation (Brown and Lugo 1990, Weaver 1990). Deforested areas are often converted to grasslands and show few signs of forest regeneration (Nepstad et al. 1990, Aide and Cavelier 1994). The lack of forest recovery in abandoned pastures has caused an increase in the area of grasslands even though the area under agriculture has not increased significantly (Woodwell et al. 1983).

In the Neotropics, forest are often cleared by small farmers using traditional slash-and-burn agriculture (Rudel and Horowitz 1993). After a few years, the original fertility of these nutrient poor soils decrease (Uhl 1987) and the areas are turned to pastures for cattle ranching (Myers 1989, Fearnside 1990). Secondary forests can recover in these areas (Gomez-Pompa and Vasquez-Yanes 1974) if the grasslands are not too large or if fire is not frequently used (Buschbacher 1986, Uhl 1988). Other barriers to forest regeneration include lack of seed source or vegetative propagules, seed and seedling predation, competition with herbaceous species, changes in microclimate and in the physical and chemical properties of the soils (Nepstad et al. 1990, Aide and Cavelier 1994).

Although it is generally accepted that the conversion of forests to pastures is associated with a decrease in soil fertility, there are few data on the long term effects of this land use. Initially, soil fertility can increase following deforestation, especially when the forest is burned rather than logged (Uhl and Jordan 1984, Uhl 1987). Studies of soils in pasture used for short periods of time have shown mixed results. For instance, some pastures have less organic matter and lower pH and cation exchange capacity than forest soils (Lal 1987) while in San Carlos de Rio Negro, Venezuela (Uhl 1987) and in La Selva, Costa Rica (Reiners et al. 1994) there were few differences in soil chemistry between undisturbed forest and sites in different stages of regeneration.

The objective of this study was to determine how deforestation and the use of fire since pre-Columbian times have affected soils, vegetation, and potential for forest recovery in the Rio Rancheria watershed of the Sierra Nevada de Santa Marta, Colombia. We compare soil physical and chemical properties of degraded anthropogenic grasslands and remnant forest patches and determine the influence of these soil characteristics on grassland biomass, species composition, and woody seedling growth.

SITE DESCRIPTION

The Sierra Nevada de Santa Marta (SNSM) is located on the Caribbean coast of Colombia and is the highest coastal mountain in the world (5800 m). Deforestation has occurred throughout the mountain and only 15% of the 2,115,873 ha is still covered with forest (FPSNSM, 1991). The study site is within the Q. Yepes Watershed (36.5 ha), a tributary of O. Valencia and Rio Rancheria at 800 m on the north-east corner of the mountain (Cavelier et al. 1998). Although the site is within a Man and the Biosphere Reserve and a National Park, approximately 78 % of the watershed is covered with grasslands (27.7 ha). The existing forest patches are restricted to steep slopes and along streams and are dominated by lowland evergreen species. The site is near the border of lowland moist and lower montane forest types sensu Holdridge (Holdridge et al. 1971).

Land use history

The SNSM has been inhabited by Amerindians (Kogi, Aruacos and Tayrona) for more than 2,000 years (Reichel-Dolmatoff 1985, Oyuela 1986). At the time of the arrival of the Spaniards, the replacement of forest by settlements and maize fields was extensive (Herrera de Turbay 1984, 1985). The arrival of the Spaniards severely reduced the population of Amerindians which stimulated forest recovery in some areas of the SNSM, but new practices including the exploitation of timber, cattle ranching, frequent fires and short rotation of the cultivated land led to further deforestation and soil degradation (Herrera de Turbay 1984, 1985, FPNSM 1991, Parsons 1992). Aerial photographs of the Rio Rancheria watershed shows that 57 % of the area below 3200 m was deforested by 1961. Some deforestation has continued during the last 30 years as a result of agriculture, cattle ranching,

the cultivation of marijuana (*Cannabis sativa*) in the 1980's, and cultivation of opium (*Papaver somniferum*) in the 1990's (Cavelier and Etter 1996). Nevertheless, an analysis of the regional history, distribution of vegetation types, and climatic conditions suggest that much of the deforestation of the Rio Rancheria watershed and savannization of what was once tropical moist forest occurred in pre-Columbian times (Cavelier *et al.* 1998).

Climate

Mean annual rainfall (1971-1976) at Hacienda Pueblito weather station (585 m, 10° 59′N, 73° 07′W) is 1486 mm. Rainfall is distributed bimodally, with peaks during May and October. During the dry seasons (January-March and July) rainfall is less than 100 mm month⁻¹ and pan-evaporation is higher than rainfall. Annual rainfall for 1992 at the study site (800 m) was 1352 mm. Mean annual temperature is 25°C with a mean monthly maximum of 27.6°C and a mean monthly minimum of 23.2°C. Although rainfall is low for tropical moist forest, frequent afternoon cloud cover should reduce evapotranspiration.

MATERIALS AND METHODS

Soil properties and plant growth.

One of the major goals of this study was to compare the differences in soils between grasslands and forest patches, but the grassland area was a mosaic of different grassland types. To include this possible source of variation in the analyses we mapped the different grassland types based on visual inspection. Nine grassland areas were identified. In each of the nine grassland sites and two forest patches, three soil surface samples (0-10 cm) were collected. The samples were dried at 60° C until constant weight and sieved using a 500 micron soil sieve. Soil characterization analyses were carried out at the Soils Laboratory, Instituto Geografico Agustin Codazzi, IGAC, Bogota, Colombia. Samples were analyzed for particle size, pH, P, carbon, cation exchange capacity (CEC), exchangeable Ca, Mg, K, Na and Al. Particle size was analyzed with the Pipette method (USDA 1967). Soil pH was measured in a slurry of soil and water (1:1 mixture). Phosphorus was determined colorimetrically after extraction in ammonium fluoride (1 M) and hydrochloric acid (0.5 M) (Olsen and Sommers 1982). Organic carbon was

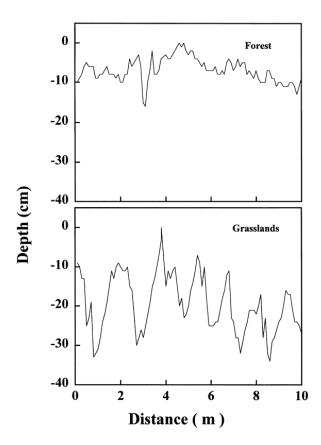


Figure 1. Soil surface microtopography along a 10 m transect in a forest and a grassland site, Sierra Nevada de Santa Marta, Colombia.

determined using acid potassium dichromate (1 M) oxidation without heating, known as the "Walkley-Black" procedure (Nelson and Sommers 1982). Cation exchange capacity was determined with ammonium acetate at pH 7.0 (Jackson 1958). Exchangeable bases were determined by the ammonium acetate method (Thomas 1982). Aluminium was determined colorimetrically after extraction in potassium chloride (1M), as described in Barnhisel and Bertsh (1982). Because of the difficulties in interpreting total soil nitrogen ion pools and rates of N mineralization and nitrification (Binkley and Vitousek 1991), nitrogen availability was indirectly estimated from leaf nitrogen concentration and plant biomass in bioassay (see below). Total leaf nitrogen of mature leaves was determined using Kjeldahl digestion (Bremner and Mulvaney 1982).

The soil surface microtopography was

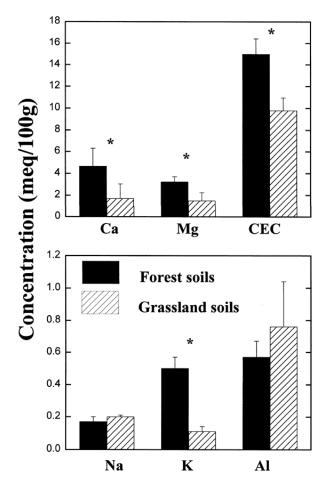


Figure 2. Mean concentration of cations and cation exchange capacity for grassland (n=27) and forest (n=6) soils. The vertical lines represent one SEM.

* represents significant differences (Mann Whitney U, p<0.05) between forest and grassland soils.

measured along a 10 m transect in one grassland and in one forest patch on similar slopes (ca. 20°) A fixed rod (accurate to the nearest centimeter) was dropped perpendicular to a measuring tape located 1 m above the soil surface. The highest point along the transect was used as a reference point (zero centimeters). Measurements were taken every 10 cm for a total of 100 measurements along each transect.

To determine the effect of forest and grassland soils on plant growth, seeds of *Cochlospermum vitifolium, Phoebe cynnamomifolia*, and *Ochroma pyramidale* were planted in 1.0 L soil bags. These species were chosen because they are common species in the forest patches and seeds were

available at the time of the experiment. For each vegetations type, soil was collected from ten sites and mixed. For each species, two seeds were planted in each of 15 soil bags for each soil type. Once the seeds had germinated only one seedling was left in each soil bag. Plants were watered daily. After three months, seedling height, number of leaves, leaf area, and root/shoot biomass ratio was determined. Leaf samples of three plants per species from the forest and grassland soil treatments were analyzed for total nitrogen (Micro-Kjeldahl).

Description of grasslands

In each of the nine grassland sites, the species composition (mainly grasses) was determined in five - 50 x 50 cm quadrats. At each site, total biomass was estimated by collecting all vegetation within two - 25 x 25 cm quadrats and drying at 70°C for 48 h. Scientific names of grass species follow Pinto (1963) and Pinto and Mora-Osejo (1966).

Comparisons between soil physical and chemical properties between forest and grassland soils, as well as comparisons between plant characteristics of seedlings grown in the two soil types, where made using the U-Mann-Whitney test.

RESULTS

Soil Properties

The grassland soils were characterized by a thin A horizon (1-10 cm) on top of saprolite derived from acidic intrusive volcanic and granitic diorite. In contrast, forest soils had an A (20 cm), B (40 cm) and C (saprolite) horizons, suggesting that surface soil erosion has removed 50 cm of the grassland soils. On most ridges covered by grasslands, erosion is so extreme that there is no A horizon and saprolite is continuously removed. On the slopes, the extreme erosion has created an irregular surface in the grasslands compared with the relatively smooth soil surface of the forest (Figure 1). In the grasslands, the depth of the depressions varied between 20 to 30 cm (Figure 1) and has created canals which accelerate water runoff and decrease rates of infiltration.

The concentration of cations, except Al and Na, and cation exchange capacity were significantly

CAVELIER, AIDE, DUPUY, EUSSE AND SANTOS

Table 1. Mean and standard error (SE) of soil particle size, pH, carbon and phosphorus in the grassland and forests soils (0-10 cm) collected in the Quebrada Yepes watershed at the Sierra Nevada de Santa Marta, Colombia. U = Mann-Whitney test, and p= probability.

	GRASSLAND (n=9) Mean (SE)	FOREST U p (n=6) Mean (SE)		
Soil particle size (%)				
Sand	62 (2.0)	62 (2.5)	30.0 0.72	n.s
Silt	24 (1.0)	22 (2.4)	23.5 0.67	n.s.
Clay	13 (1.0)	15 (1.5)	36.5 0.26	n.s.
pH	5.1 (0.06)	5.4 (0.11)	46.0 0.02	**
Organic carbon (%) Extractable P (ppm)	1.3 (0.08) 3.9 (0.74)	1.9 (0.19) 3.1 (0.54)	46.0 0.02 20.0 0.41	**

higher in forest than in grassland soils (Figure 2). Grassland soils were more acid and had lower organic carbon levels than forest soils (Table 1). The lower pH in the grassland soils was associated with a higher concentration of exchangeable Al. Extractable phosphorus concentrations were not significantly different between soil types, but there was greater variation within grassland sites (2.0-8.7 ppm) compared with forest sites (2.0-5.0 ppm). The two soil types had a high proportion (62 %) of sand (Table 1).

Soil effect on plant growth

There was no effect of soils on germination time for the three species. Cochlospermum vitifolium germinated after 15 d, followed by Ochroma pyramidale (25 d) and Phoebe cynnamomifolia (40 d). Seedlings of C. vitifolium and O. pyramidale grown in forest soils were taller, had greater leaf area, and more leaves compared with seedlings grown in pasture soils (Figure 3). The root/shoot biomass ratio of seedlings of C. vitifolium was higher in grassland than in forest soils while the opposite occurred for seedlings of O. pyramidale (Figure 3). Seedlings of P. cynnamomifolia showed no significant differences between forest and grassland soils for any growth characteristic. Leaf nitrogen concentration was not significantly different between forest- and grasslandsoils for any of the species.

Grassland vegetation

Although grassland soils are poor in nutrients and may have adverse effects on plant growth when compared with forest soils, these soils are variable. Levels of extractable phosphorus varied the greatest among the nine grassland sites (Table 1). The level of extractable phosphorus was negatively correlated with species richness (r= -0.86, p<0.05, Figure 4a). Site four with a extractable phosphorus concentration of 9 ppm, had only three species, while sites one and two with 2.5 ppm had 15 and 14 species, respectively. The biomass of herbaceous vegetation (mainly grasses) was positively correlated with extractable phosphorus concentration (r=0.66, p<0.05, Figure 4b). The frequency of individual species appeared to be related to extractable phosphorus concentration. In the low extractable phosphorus sites (one, two, three, five, seven, nine), all species were present and Aristida adscensionis, Schyzachyrium microstachyum and Cyperaceae sp. 4 were the most common species. In contrast, in the high extractable phosphorus sites (four, six, eight), there were only five species and Melinis minutiflora was the most common species (Table 2).

Very few saplings of tree species or shrubs were encountered in the grasslands. Some forest species were found along the forest edges (e.g. Cochlospermum vitifolium, Xylopia aromatica, Persea caerulea, Psidium caudatum, Vismia

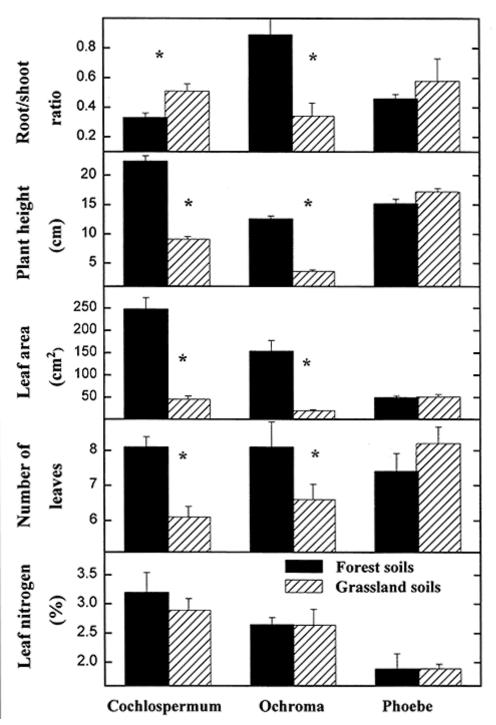


Figure 3. Mean \pm one SE of root/shoot biomass ratio, total height, leaf area, number of leaves and leaf nitrogen for seedlings of *Cochlospermum vitifolium*, *Ochroma pyramidale* and *Phoebe cynnamomifolia* grown in forest- and grassland-soils (n = 30 plants per species), Sierra Nevada de Santa Marta, Colombia. Three samples of each species from each treatment were analyzed for leaf nitrogen. * represents significant differences (Mann Whitney U, p<0.05) between forest and grassland soils.

baccifera and Clusia multiflora), but the most common species in the grasslands were those with adaptations to fire (e.g. Curatella americana, Byrsonima crassifolia, Cochlospermum vitifolium, and Miconia rubiginosa) (Sarmiento 1984, Sarmiento et al. 1985).

DISCUSSION

Grassland soils

Soil erosion was extensive in the study area and throughout the Rio Rancheria watershed. A comparison of grassland and forest soil profiles showed that 50 cm of top soil have eroded away in the grasslands. The organic matter that currently forms the A horizon in the grasslands originated from the decomposition of grass litter and roots. In contrast, the organic matter in the upper layer of the forest soils is the result of decomposition of roots and litterfall from trees, shrubs and herbs. The total carbon content in the forest soils is greater than in the grasslands due to higher carbon concentrations and thicker A and B horizons. On many steep slopes and ridges, erosion of the surface soils has exposed saprolite and created a rough microtopography that contrasts with the smooth soil surface of the forest floor. The further erosion of the saprolite is the source of the extensive quartz-sand beaches along streams and even along Rio Rancheria on alluvial terraces.

Comparisons of forest and pasture soils in Brazil (Buschbacher et al. 1988) and Costa Rica (Reiners et al. 1994) found few differences in soil chemistry. This contrasts with the present study, where soil chemistry differed between pastures and forest, and these differences affected plant growth. A major difference between these studies is the length of time that these areas have been converted and maintained as grasslands. While the Brazilian and Costa Rican sites were converted to pastures in the last 40 years, the grassland in the Q. Yepes are at least 52 years old (aerial photographs of 1942) and probably as much as 500 years old (Cavelier et al. 1998). The degradation of the grasslands soils at the study site has been so intense that the chemistry is more similar to soils of natural savannas than to the adjacent forest patches (Table 3). This is surprising given that grasslands in the Sierra Nevada de Santa Marta are the result of conversion from tropical lowland forests, while savannas are a natural ecosystem that often occur on nutrient poor

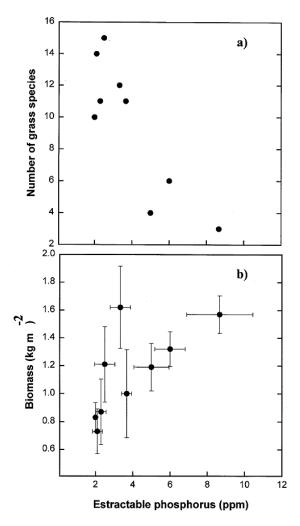


Figure 4. Relationship between extractable phosphorus in soils and a) total number of grass species in the grassland patches (site numbers are shown beside each point) and b) mean (SE) total above-ground biomass in the grassland patches.

soils that are the product of millions of year of evolution (Blydenstein 1967, Sarmiento 1984). Severe soil erosion has also been reported in the nearby Rio Fundacion watershed (Bartels 1984), suggesting that soil degradation is widespread on the southeastern flank of the Sierra Nevada de Santa Marta. Some authors relate this erosion to grazing and land use practices during the last 500 years after the arrival of the Spaniards (Parsons 1992), or even to pre-Columbian times (Cavelier *et al.* 1998).

Plant responses to grassland soils

The differences in chemistry between grassland and forest soils had significant effects on

LONG-TERM EFFECTS OF DEFORESTATION IN COLOMBIA

Table 2. Comparison of species frequency between grassland sites of high (>5 ppm; sites four, six, eight) and low (<5 ppm; sites one, two, three, five, seven, nine) soil extractable phosphorus. Frequencies were calculated as the number of times a species was present in the 15 quadrats in high P sites and 30 quadrats in low P sites and was expressed as a proportion.

Species	Frequency	
	High P	Low P
POACEAE		
Aristida adscensionis	0.06	0.34
Aristida recurvata	0.00	0.03
Arundinella hispida	0.00	0.09
Arundinella sp.	0.12	0.12
Axonopus aureus	0.00	0.09
Chloris inflata	0.06	0.03
Eragrostis ciliaris	0.00	0.06
Melinis minutiflora	0.84	0.20
Panicum olyroides	0.00	0.12
Paspalum contractum	0.00	0.09
CYPERACEAE		
Sp.1	0.00	0.06
Sp. 2	0.00	0.09
Sp. 3	0.00	0.03
Sp. 4	0.00	0.23
Sp. 5	0.12	0.17

the growth responses of the small-seeded species C. vitifolium and O. pyramidale. Individuals of these species grew taller, had more leaves and greater total leaf area in forest soils compared with individuals growing in grassland soils. The largerseeded species, P. cynnamomifolia, did not show any treatment effect. If P. cynnamomifolia was grown long enough to use the seed reserves this species would show a similar treatment effect. As expected for plants growing in rich soils (Reynolds and Pacala 1993), the root/shoot biomass ratio for C. vitifolium and P. cynnamomifolia was lower in forest-than in grassland soils. In contrast, the root/ shoot ratio for O. pyramidale was higher in forest soils. This may have occurred because O. pyramidale normally has an obligate mycorrhizal relationship, and if mycorrhizae where not present in the pasture soils there would be virtually no root growth (Janos 1980).

The difference in plant growth between the two soil treatments was related to nitrogen availability, calcium, magnesium, and potassium concentrations. Nitrogen and phosphorus are the two most nutrients needed in greatest quantities for plant growth (Chapin 1980, Medina 1984, Lambers and Poorter 1992, Werf et al. 1993). Although leaf nitrogen concentrations were not different between treatments, seedlings in forest soils were taller, had more leaves and greater leaf area, demonstrating that the total nitrogen absorbed by seedlings was higher in forest soils. Extractable phosphorus did not differ between grassland and forest types, suggesting that this nutrient alone does not explain the observed differences in plant growth. These results show that low fertility in grassland soils, along with the frequent use of fire in the region (Aide and Cavelier 1994), and a severe dry season

CAVELIER, AIDE, DUPUY, EUSSE AND SANTOS

Table 3. Comparison of soil chemical characteristics between grassland and forest sites in the Sierra Nevada de Santa Marta (mean \pm sd), and savanna and forest in Colombia and Venezuela. Data for savanna and forest sites were compiled by Sarmiento (1984). No error estimations are available for that data.

	CEC	K	Ca	Base Saturation
	(meq/100 g)			(%)
Grasslands (SNSM)	9.8 (1.2)	0.10 (0.03)	1.64 (1.35)	33.0
Savannas (n=182)	9.3	0.16	0.83	20.5
Forests (SNSM)	14.9 (1.5)	0.50 (0.07)	4.60 (1.65)	59.0
Forests (n=85)	10.5	0.29	4.10	49.0

(four to five months) have maintained the grasslands and limited the recovery of moist forest.

Grasslands in the Quebrada Yepes watershed

The vegetation at the Q. Yepes watershed is a mixture of forest and grassland patches, with different soil fertilities and species composition. There are grassland patches with few species (Melinis minutiflora) and relatively rich soils that are the result of a more recent transformation of forest to grasslands or a low frequency of anthropogenic fires. On the other hand, there are grassland patches, with a higher species richness and poorer soils, that are older or have been affected by more frequent fires than those dominated by M. minutiflora. This situation is consistent with fertilization experiments where addition nitrogen resulted in increased dominance of a few species in temperate grasslands of England (Silvertown, 1980) and North America (Tilman 1987, 1996). The dominant species are charterized by being nitrogendemanding (Tilman 1987).

With the exception of the African *M. minutiflora* (Parsons 1992), all the grass species found in this study are native to the Colombian-Venezuelan savannas (Blydenstein 1967, Sarmiento 1984). The main seed source for the grasses is the savannas of the lower Magdalena River valley or the savannas south of Lake Maracaibo in Venezuela

(Sarmiento 1984). Within the grassland matrix, there are savanna trees such as *Curatella americana* and *Byrsonima crassifolia*. Other common trees of the neotropical savanna, such as *Genipa americana*, *Xylopia aromatica* and *Cochlospermun vitifolium* (Sarmiento 1983) are also found in the Quebrada Yepes watershed, near forest edges and inside small forest patches.

The low fertility of the grassland soils and the frequent use of fire (Aide and Cavelier 1994) are the major barriers to forest regeneration. Given these conditions, the savannization of this region will continue. Although fires could be reduced by firebreaks and education, soil fertility is difficult to improve. To recover the organic matter and fertility of these eroded soils it is necessary to plant species that produce large amounts of litterfall. Trial plantings with native species were unsuccessful due to low nutrients and low soil water availability (Aide and Cavelier 1994). In these extreme conditions it may be necessary to introduce species (i.e Pinus spp. or nitrogen fixing legumes) that are capable of growing in infertile soils and that can add significant amounts of organic matter to the soil (Lugo 1992, Parrota 1992) before trying to reintroduce native trees.

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LONG-TERM EFFECTS OF DEFORESTATION IN COLOMBIA

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LITERATURE CITED

- AIDE, T. M. y J. CAVELIER. 1994. Barriers to lowland moist tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. Restoration Ecology 2:219-229.
- BARNHISEL, R. y P. M. BERTSCH. 1982. Aluminium. pp. 275-300. In A. L. Page (ed.): Methods of soil analysis. Part 2: Chemical and microbiological properties. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.
- BARTELS, G. 1984. Los pisos morfométricos de la Sierra Nevada de Santa Marta (Colombia). Pp. 99-129. In T. van der Hammen (ed.): Studies on tropical Andean ecosystems. Vol 2. La Sierra Nevada de Santa Marta (Colombia), Transecto Buritaca- La Cumbre. J. Cramer, Berlin-Stuttgart.
- BINKLEY, D. y P. VITOUSEK. 1991. Soil nutrient availability. Pp. 75-96. In R. W. Pearcy, J. Ehleringer, H. A. Mooney and P. W. Rundel (eds.): Plant physiological ecology. Field methods and instrumentation. Chapman and Hall, London.
- BLYDENSTEIN, J. 1967. Tropical savanna vegetation of the llanos of Colombia. Ecology. 48:1-15.
- BREMNER, J. M. y C. S. MULVANEY. 1982. Nitrogentotal. pp. 595-624. In A. L. Page (ed.): Methods of soil analysis. Part 2: Chemical and microbiological properties. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.
- BROWN, S. y A. E. LUGO. 1990. Tropical secondary forests. Journal of Tropical Ecology. 6:1-32.
- BUSCHBACHER, R. J. 1986. Tropical deforestation and pasture development. Bioscience. 36:22-28.
- BUSCHBACHER, R., C. UHL y E. A. S. SERRAO. 1988. Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. Journal of Ecology. 76:682-699.
- CAVELIER, J. y A. ETTER. 1996. Deforestation of montane forests in Colombia as a result of illegal plantations of opium (*Papaver somniferum*). Pp. 541-549. In S. P.

- Churchill, H. Balslev, E. Forero and J. L. Luteyn (eds.): Biodiversity and conservation of Neotropical montane forests. The New York Botanical Garden, New York.
- CAVELIER, J., T. M. AIDE, C. SANTOS, A.M. EUSSE y J.M. DUPUY. 1998. The savannization of moist forest in the Sierra Nevada de Santa Marta, Colombia. Journal of Biogeography 25: 901-912.
- CHAPIN, F. S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics. 11:233-260.
- FEARNSIDE, P. M. 1990. Predominant land uses in Brazilian Amazonia. Pp. 233-251. In A. B. Anderson (ed.): Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest. Columbia University Press, New York, New York, USA.
- FUNDACION PROSIERRA NEVADA DE SANTA MARTA (FPSNSM). 1991. Historia y Geografía Sierra Nevada de Santa Marta. Fondo Editorial Fundación Pro-Sierra Nevada de Santa Marta, Santafé de Bogotá, D. C.
- GOMEZ-POMPA, A. y C. VASQUEZ-YANES. 1974. Studies on the secondary succession of tropical lowlands: the life cycle of secondary species. Pp. 336-342. In W. H. van Dobben y Lowe-Mcconell (eds.): Proceedings of the First International Congress of Ecology, Junk, The Hague.
- HARRIS, D. L. 1984. The fragmented forest. The Chicago University Press, London.
- HERRERA DE TURBAY, L. F. 1984. La actividad agrícola en la Sierra Nevada de Santa Marta: perspectiva histórica. Pp 501-530. In T. van der Hammen (ed.): Studies on tropical Andean ecosystems. Vol 2. La Sierra Nevada de Santa Marta (Colombia), Transecto Buritaca- La Cumbre. J. Cramer, Berlin-Stuttgart.
- HERRERA DE TURBAY, L. F. 1985. Agricultura aborígen y cambios de vegetación en la Sierra Nevada de Santa Marta. Fundación de investigaciones Arqueológicas nacionales, Banco de la República, Bogotá.
- HOLDRIDGE, L.R., W.C. GRENKE, W.H. HATHEWAY, T. LIANG y J.A. Jr. TOSI. 1971. Forest environments in tropical life zones. A pilot study. Pergamon Press, Oxford.
- JACKSON, M. L. 1958. Soil chemical analysis. Constable and Co. Ltd., London.
- JANOS, D. 1980. Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology 61:151-162.
- LAL, R. 1987. Tropical ecology and physical edaphology. John Wiley and Sons, New York.
- LAMBERS, H. y H. POORTER. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Advances in Ecological Research 23:187-261.
- LUGO, A. E. 1992. Tree plantations for rehabilitating damaged forest lands in the tropics. Pp. 247-255. In M. K. Wali (ed.): Ecosystem rehabilitation, Vol 2: Ecosystem analysis and synthesis. SPB Academic Publishing by, The Hague, The Netherlands.

- MEDINA, E. 1984. Nutrient balance and physiological processes at the leaf level. Pp. 139-154. In E. Medina, H. A. Mooney and C. Vazquez-Yanes (eds.): Physiology of plants of the wet tropics. Proc. Int. Symp. Mexico, 1983. Junk Publ, The Hague, Boston.
- MYERS, N. 1989. Deforestation rates in tropical forest and their climatic implications. Friends of the Earth, London.
- NELSON, D. W. y L. E. SOMMERS. 1982. Total carbon, organic carbon, and organic matter. Pp. 539-579. In A. L. Page (ed.): Methods of soil analysis. Part 2: Chemical and microbiological properties. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.
- NEPSTAD, D., C. UHL and E. A. S. SERRAO. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Para, Brazil. pp. 215-229. In A. B. Anderson.(ed.): Alternatives to deforestation: steps toward sustainable use of the amazon rain forest. Columbia University Press, New York.
- OLSEN, S. R. y S. R. SOMMERS. 1982. Phosphorus. Pp. 403-430. In A. L. Page (ed.): Methods of soil analysis. Part 2: Chemical and microbiological properties. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.
- OYUELA, A. 1986. De los Taironas a los Kogi una interpretación del cambio cultural. Revista del Museo del Oro (Bogotá). 17:32-43.
- PARROTA, J. 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. Agriculture, Ecosystems and Environment . 41:115-133.
- PARSONS, J. J. 1992. Las regiones tropicales americanas: misión geográfica de James J. Parsons. Fondo Fen, Bogotá, Colombia.
- PINTO, P. 1963. Catálogo de los géneros de las gramíneas de Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales. 12:95-117.
- PINTO, P. y L. E. MORA-OSEJO. 1966. Catálogo ilustrado de las plantas de Cundinamarca. Vol. 1. Gramineae, Juncaceae, Cyperaceae. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá.
- REICHEL-DOLMATOFF, G. 1985. Los Kogi; una tribu de la Sierra Nevada de Santa Marta, Colombia, Tomo I. Procultura S.A., Bogotá, Colombia.
- REINERS, W. A., A. F. BOUWMAN, W. F. J. PARSONS and M. KELLER. 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. Ecological Applications. 4:363-377.
- REYNOLDS, H. L. y S. PACALA. 1993. An analytical treatment of root to shoot ratio and plant competition for soil nutrients and light. The American Naturalist. 141:51-70.
- RUDEL, K. T. y B. HOROWITZ. 1993. Tropical deforestation. Small farmers and land use clearing in the Ecuatorian Amazon. Columbia University Press, New York.
- SARMIENTO, G. 1983. The savannas of tropical America.

- Pp. 245-288. In F. Bourliere (ed.): Tropical Savannas. Ecosystems of the World, Vol. 13. Elsevier Scientific Publishing company, Amsterdam.
- SARMIENTO, G. 1984. The ecology of neotropical savannas. Harvard University Press, Cambridge, USA.
- SARMIENTO, G., G. GOLDSTEIN y F. MEINZER. 1985. Adaptive strategies of woody species in neotropical savannas. Biological Review. 60:315-355.
- SILVERTOWN, J.W. 1980. The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass experiment. Journal of Applied Ecology. 17:491-504.
- TILMAN, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs. 57: 189-214.
- TILMAN, D. 1996. Biodiversity: populations versus ecosystem stability. Ecology. 77:350-363.
- THOMAS, G. W. 1982. Exchageable cations. Pp. 159-166.
 In A. L. Page (ed.): Methods of soil analysis. Part 2:
 Chemical and microbiological properties. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.
- UHL, C. 1987. Factors controlling succession following slashand-burn agriculture in Amazonia. Journal of Ecology. 75:377-407.
- UHL, C. 1988. Restoration of degraded lands in the Amazon Basin. pp. 326-332. In E. O. Wilson (ed.): Biodiversity. National Academy of Science, Washington, D. C.
- UHL, C., C. JORDAN, K. CLARK, H. CLARK y R. HERRERA. 1982. Ecosystem recovery in Amazon caatinga forest after cutting, cutting and burning, and bulldozer clearing treatment. Oikos. 38:313-320.
- UHL, C. y C. F. JORDAN. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology. 65:1476-1490.
- UHL, C., D. NEPSTAD, R. BUSCHBACHER, K. CLARK, B. KAUFFMAN y S. SUBLER. 1990. Studies of ecosystem response to natural and anthropogenic disturbances provide guidelines for designing sustainable land-use systems in Amazonia. Pp. 24-42. In A. B. Anderson (ed.): Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest. Columbia University Press, New York, New York, USA.
- UNITED STATES DEPARTMENT OF AGRICULTURE (USDA). 1967. Soil survey laboratory methods and procedures for collecting soil samples. Washington, DC.
- WEAVER, P. L. 1990. Succession in the elfin woodland of the Luquillo Mountains of Puerto Rico. Biotropica. 22:83-89.
- WERF, VAN DER A., VAN. M. NUENEN, A. J. VISSER y H. LAMBERS. 1993. Contribution of physiological and morphological plant traits to a species' competitive ability at high and low nitrogen availability. A hypothesis for inherently fast- and slow-growing monocotyledonous species. Oecologia. 94:434-440.
- WILSON, E. O. 1988. The current state of biological diversity. pp. 3-18. In E. O. Wilson (ed.): Biodiversity. National Academy Press, Washington, D. C.

LONG-TERM EFFECTS OF DEFORESTATION IN COLOMBIA

WOODWELL, G. M., J. E. HOBBIE, R. A. HOUGHTON, J. M. MELILLO, B. MOORE, B. J. PETERSON y G. R. SHAVER. 1983. Global deforestation: contribution to atmospheric carbon dioxide. Science 222: 1081-1086.

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